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Tight spatial coupling of a marine predator with soniferous fishes: Using joint modelling to aid in ecosystem approaches to management

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Abstract

Aim: Understanding the distribution of marine organisms is essential for effective management of highly mobile marine predators that face a variety of anthropogenic threats. Recent work has largely focused on modelling the distribution and abundance of marine mammals in relation to a suite of environmental variables. However, biotic interactions can largely drive distributions of these predators. We aim to identify how biotic and abiotic variables influence the distribution and abundance of a particular marine predator, the bottlenose dolphin (*Tursiops truncatus*), using multiple modelling approaches and conducting an extensive literature review.

Location: Western North Atlantic continental shelf.

Methods: We combined widespread marine mammal and fish and invertebrate surveys in an ensemble modelling approach to assess the relative importance and capacity of the environment and other marine species to predict the distribution of both coastal and offshore bottlenose dolphin ecotypes. We corroborate the modelled results with a systematic literature review on the prey of dolphins throughout the region to help explain patterns driven by prey availability, as well as reveal new ones that may not necessarily be a predator–prey relationship.

Results: We find that coastal bottlenose dolphin distributions are associated with one family of fishes, the Sciaenidae, or drum family, and predictions slightly improve when using only fish versus only environmental variables. The literature review suggests that this tight coupling is likely a predator–prey relationship. Comparatively, offshore dolphin distributions are more strongly related to environmental variables, and predictions are better for environmental-only models. As revealed by the literature review, this may be due to a mismatch between the animals caught in the fish and invertebrate surveys and the predominant prey of offshore dolphins, notably squid.

Main Conclusions: Incorporating prey species into distribution models, especially for coastal bottlenose dolphins, can help inform ecological relationships and predict marine predator distributions.

KEYWORDS
bottlenose dolphins, ecological modeling, joint modeling, marine ecology, marine mammals, predator + prey, Sciaenidae, species interactions, *Tursiops truncatus*

1 | INTRODUCTION

Species distributions within an environment are mediated by both abiotic and biotic factors. The spatial distribution of predators in marine systems is driven by environmental conditions, such as temperature (Barbieri, 2005; Mintzer & Fazioli, 2021; Yeates & Houser, 2008), and intra and interspecific species interactions, such as competition and predation (Hanson & Defran, 1993; Ratcliffe et al., 2014; Shane et al., 1986). Marine predators maintain community function and structure through top-down control and promoting ecosystem health (Baum & Worm, 2009; Duffy, 2003; Estes et al., 2011; Heithaus et al., 2008; Wells et al., 2004). However, they face a variety of anthropogenic threats which, left unmanaged, can have detrimental cascading effects on ecosystems (Davidson et al., 2012; Dulvy et al., 2014; Estes et al., 2011; Richards et al., 2021). Direct threats to marine predators include mortality through overfishing and bycatch. Indirect threats include habitat alteration, reduced prey from fishing and climate change (Davidson et al., 2012; Dulvy et al., 2014; Myers & Worm, 2005; Richards et al., 2021). Understanding which abiotic and biotic factors influence the distribution of predator populations is, therefore, essential for effective management, and in some cases, population recovery (Duffy, 2003; Estes et al., 2011; Harvey et al., 2017; Hazen et al., 2019).

Most research on the distribution of marine predators, including sharks (Osgood et al., 2021), seabirds (Orgeret et al., 2022) and toothed whales (Roberts et al., 2016), has focused on relating their distributions to physical aspects of their environment in the form of species distribution models (Palacios et al., 2013 for review). These models do not fully capture ecological processes, such as trophic interactions, that can directly influence the distribution of marine predators (Barros & Wells, 1998). This historical reliance on correlative environmental models that ignore biotic relationships is likely due to the difficulty of collecting such data and the mismatch in available data sets—with information on species within a system often collected at different spatial and temporal scales or extents (Fauchald et al., 2000; Torres et al., 2008). However, in the western North Atlantic continental shelf, the existence of data sets collected by long-term fish and invertebrate and marine mammal surveys provides an excellent opportunity to understand the influence of both the environment and trophic interactions on the distribution of an ecologically important marine predator: the common bottlenose dolphin (*Tursiops truncatus*—hereafter referred to as bottlenose dolphins).

Two bottlenose dolphin ecotypes, coastal and offshore, inhabit the western North Atlantic and differ in their genotypes (Costa et al., 2022), phenotypes (e.g. morphology see (Mead & Potter, 1995), haematological profiles (Duffield et al., 1983; Hersh & Duffield, 1990) and parasite load (Mead & Potter, 1990)). The coastal ecotype occurs in estuarine and coastal waters from Florida north to the New York Bight (Hayes et al., 2021), and the offshore ecotype occurs from Florida to New England and occasionally as far north as the Scotian Shelf (Hayes et al., 2020, 2021). There is overlap between the distributions of coastal and offshore bottlenose dolphins from Florida to Cape Hatteras, North Carolina, but north of Cape Hatteras, the two ecotypes do not co-occur (Garrison et al., 2002; Kenney, 1990; Torres et al., 2003). Offshore bottlenose dolphins are distributed along the continental shelf and shelf break region and are exclusively found in 40 m or deeper water (Garrison et al., 2002), while coastal bottlenose dolphins are found inside the 25-m isobath (Kenney, 1990).

The range of bottlenose dolphins fluctuates on a seasonal basis north of North Carolina (Hayes et al., 2020, 2021). Environmental conditions, especially temperature (Hare et al., 2016), and species composition of the ichthyofauna vary seasonally in these temperate regions (Nye et al., 2011; Sullivan et al., 2005). Some coastal bottlenose dolphins move north to New England in the warm water months and return south to Virginia and North Carolina in winter (Hayes et al., 2021). Offshore dolphins also extend northwards seasonally in the warm water months (Baird et al., 1993; Gowans & Whitehead, 1995; Winn, 1982), but do not seem to exhibit such a drastic seasonal change in their distribution (Baird et al., 1993; Kenney, 1990), although we know less of the movements of these animals. These seasonal changes in distribution are believed to be driven by temperature (Kenney, 1990) and movements of prey (Barco et al., 1999; Barros, 1993; Friedlaender et al., 2001). In this region, bottlenose dolphins have been observed in sea surface temperatures of 1–31°C with an average of 19.7°C (Kenney, 1990). They feed on a variety of prey, predominantly fish and squid (Barros & Odell, 1990; Gannon & Waples, 2004; Hart, 1997; Mead & Potter, 1995; Shane et al., 1986). To quantify and understand drivers of bottlenose dolphin distribution along the US east coast, previous studies have employed a variety of approaches, from localized studies (Barco et al., 1999) to distribution models that span the entire continental shelf (Roberts et al., 2016; Torres et al., 2003). However, these approaches have struggled to directly connect the predators with other species (like prey), while accounting for the influence of environmental factors.

Understanding the relationship between marine predators and their prey has significant implications for their management and for marine spatial planning. Bottlenose dolphins in US waters are managed under the federal Marine Mammal Protection Act. Several stocks of bottlenose dolphins along the US east coast, especially those that utilize Mid-Atlantic waters, are considered to be strategic or depleted, meaning that human-caused mortalities are above sustainable levels or their population levels are below optimum sustainability respectively (H.R.2760, 1994; Hayes et al., 2021). It is, therefore, necessary to understand their distributions as human–wildlife interactions and human-induced changes to the environment continue to occur and new ones will likely arise in the future. For example, as increasing ocean temperatures cause fish distributions to shift (Kleisner et al., 2017), predators may follow, potentially leading to new and unexpected socio-ecological relationships (Record et al., 2019). Furthermore, models assessing the potential effects of offshore wind development on predator distributions must also consider the impacts on other populations of species. For example, if wind farms act to aggregate prey (Methratta & Dardick, 2019), predators, such as the bottlenose dolphin, may aggregate around wind turbines.

The health of marine predator populations also has implications for their ecosystems (Moore, 2008). Depending on the system, bottlenose dolphins are either meso- or apex predators and therefore can directly or indirectly affect the dynamics of populations of other species through predation or competition (Kiszka et al., 2015; Moore, 2008; Roman & Estes, 2017; Wells et al., 2004). Impacts on bottlenose dolphins may in turn have serious implications for entire communities within an ecosystem.

Here, we incorporate potential prey into distribution models to better understand the drivers of the occurrence and movements of bottlenose dolphins along the US east coast. Specifically, we assess the influence of both environmental covariates and fish and invertebrate species and families on the distribution and abundance of bottlenose dolphins using a multifaceted approach. First, we infer which fish and invertebrate species, families and environmental variables influence bottlenose dolphin density through modelling, then we evaluate the strength of these relationships through prediction. Finally, we corroborate the ecological significance of these modelled relationships with a systematic literature review of diet studies.

2 | METHODS

2.1 | Modelling data sets

The study area for this analysis includes the Mid-Atlantic Bight and Northeast from Cape Hatteras, North Carolina to Cape Cod, Massachusetts extending to the edge of the continental shelf break. This ecosystem is characterized by a productive and shallow continental shelf that supports a diversity of marine species including commercially important marine fish (Love & Chase, 2007), marine mammals (LaBrecque et al., 2015) and sea turtles (Hodge et al., 2022). The shallow continental shelf and adjacent metropolitan areas make the Mid-Atlantic bight and Northeast an economically robust region which supports a diversity of ocean uses including fishing, shipping, recreation, tourism and emerging wind farm development (Lathrop et al., 2017).

Our research approach combined fish and invertebrate biomass (kg/20-min tow) from the National Oceanic and Atmospheric Administration (NOAA) Northeast Fisheries Science Center (NEFSC) bottom trawl surveys with detection-corrected bottlenose dolphin density (abundance/km^2) from line-transect surveys (Figure 1a) by matching monthly overlap within 0.25°×0.25° grid cells (Figure 1b). We selected this spatial grain as it captured enough overlap between the two data sets to conduct analyses (1535 total overlapping points). For example, at a coarser grain of 0.5°×0.5° grid cells, there were only 1160 overlapping points, and at a finer grain (0.025°×0.025°), there were only 1230. Environmental data (sea surface temperature (SST), sea surface salinity (SSAL) and depth) were measured in situ during the fish and invertebrate surveys and averaged across grid cells and months as well.

Fish and invertebrate data were acquired from the NEFSC bottom trawl survey, which has been conducted since 1963 in the spring, fall and winter, and collects biomass and distribution data for over 250 fish and invertebrate species. Trawl surveys are conducted within predefined strata based on depth (Figure 1a). The survey employs a stratified random sampling design, with stations allocated proportionally to stratum area (number of trawls=42,702). The trawls utilize a 12-mm mesh codend liner to retain smaller bodied and juvenile fishes and invertebrates. All fish and invertebrates were weighed and counted and identified to the species level (Azarovitz, 1981). We measured biomass density as species-specific biomass (kg/tow) per month within each grid cell (average monthly kg per 20-min tow/grid cell). We also summarized the data to the family level as family-specific biomass per month within each grid cell to run separate family-based models (see below).

Bottlenose dolphin density data (abundance/km^2) were collected from directed line-transect surveys as effective abundance per segment (Figure 1a). The original surveys were conducted by the NEFSC, New Jersey Department of Environmental Protection (NJDEP), Southeast Fisheries Science Center (SEFSC), University of North Carolina Wilmington (UNCW) and Virginia Aquarium and Marine Science Center (VAMSC), spanning the years 1992–2016. For more information on the original dolphin surveys, see Table S1. The original surveys were processed to account for detectability (plane vs. boat detectability differences accounted for by applying a detection function) and availability (animals that were submerged and unavailable for detection) and/or perception bias (animals that are hard to detect despite being at the surface). These detection-corrected abundance estimates have been utilized for habitat-based cetacean density models for the entire U.S. Atlantic coast by NOAA and the U.S. Navy (Roberts et al., 2016). To minimize the influence of outlier values, we used the square root of both the dolphin density and fish and invertebrate biomass values for modelling.
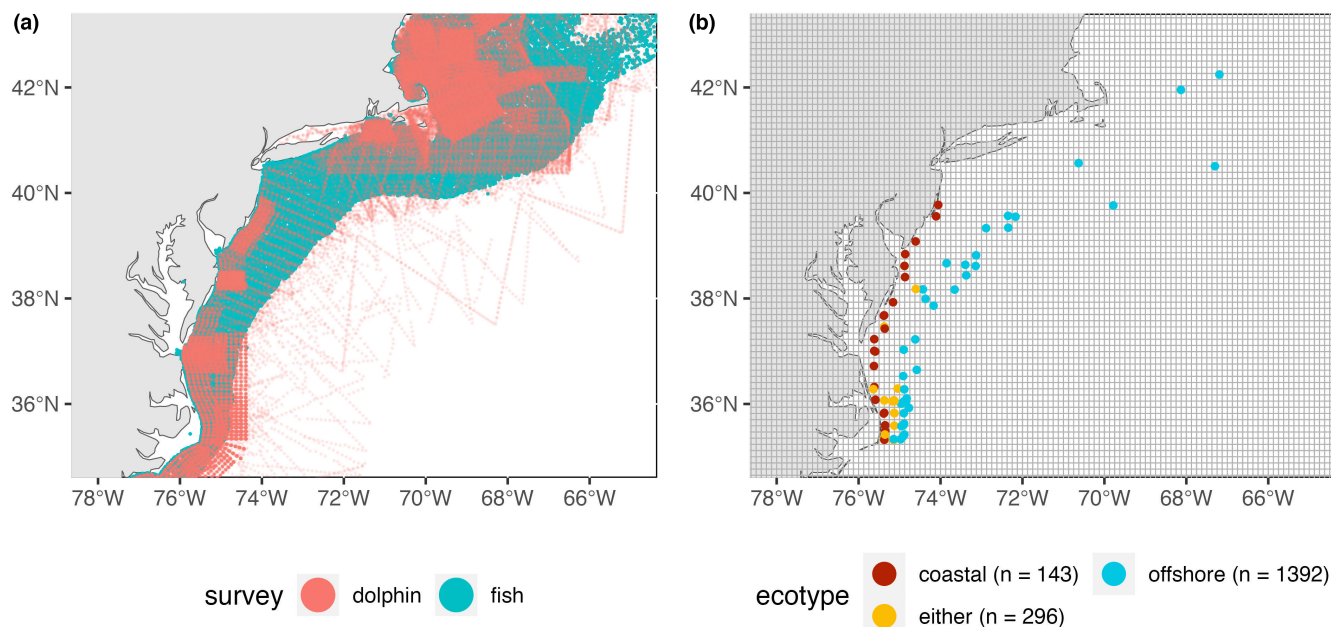
FIGURE 1 (a) Dolphin (red) and fish and invertebrate (blue) survey extents in the Mid-Atlantic Bight and Northeast. Note the dolphin surveys are continuous from the shore out over the shelf break and are overlapped by the fish and invertebrate survey. (b) Overlapping dolphin and fish and invertebrate data north of Cape Hatteras, NC separated into coastal and offshore ecotypes (n = total number of overlapping monthly data points).

After combining the dolphin and fish and invertebrate data, we separated the overlapping grid points according to bottlenose dolphin ecotype. North of Cape Hatteras, the two ecotypes are separated by depth and specifically the 25-m isobath (Kenney, 1990). All dolphins sampled in waters of 40m depth or greater belong to the offshore ecotype (Garrison et al., 2002), so we used this criteria for our analysis <25 m depth = coastal (n overlapping points = 143, 21 positive dolphin abundance), >40 m depth = offshore (n overlapping points = 1392, 38 positive dolphin abundance, Figure 1b). We excluded overlapping points that occurred in depths between 25 and 40 m (n excluded = 296, Figure 1b). There is more overlap of the two ecotypes south of Cape Hatteras (Torres et al., 2003), so we focused on the region north of Cape Hatteras. More of the fish and invertebrate trawls overlap with offshore dolphin points compared with the coastal dolphin points, which is likely due to the timing and location of the trawls—the fish and invertebrate trawls occur in the spring and fall months and cover more of the northeast portion of our study region, and coastal dolphins are likely present in the Mid-Atlantic, which is the northern extent of coastal dolphin ranges (Garrison et al., 2002; Hayes et al., 2021; Kenney, 1990) in the summer months.

2.2 | Modelling

We had two main goals in our modelling approach (1) to infer which fish and invertebrate species, families and environmental variables are important drivers of bottlenose dolphin abundances and distributions and (2) to assess whether environment-only or fish-only

models are better suited for predicting bottlenose dolphin distributions. We applied each approach to the fish and invertebrate data summarized at the family level as well as species level (Figure 2).

2.3 | Inference: assessing the importance of fish and environment on dolphin distributions independently

For the first goal, we utilized both single-species (family) models and joint species (family) models to assess the influence of environmental variables and fish and invertebrates on the distributions of bottlenose dolphins. We separated the data by ecotype and inferred the relative importance of species (families) as well as environmental variables using generalized linear models (GLMs), random forests, Pearson's correlation and a joint modelling approach. Research has shown that there is variability among different modelling methods in terms of predicting species distributions, and, in some cases, ensemble approaches, that combine multiple models, are preferred (Grenouillet et al., 2011). In order to not bias results to one modelling method, we chose to examine four types of modelling approaches that differ in their underlying structures, to assess if results are similar across models. While generalized additive models (GAMs) have gained popularity in species distribution modelling, we chose not to run GAMs due to the small sample size of our study that would lead to overfitting when using GAMs (Karatekin et al., 2019). We ran GLMs with coastal or offshore bottlenose dolphin density as the response variable and iterated through each environmental variable (SST, SSAL, depth) and each fish and invertebrate species (family) separately (starting with
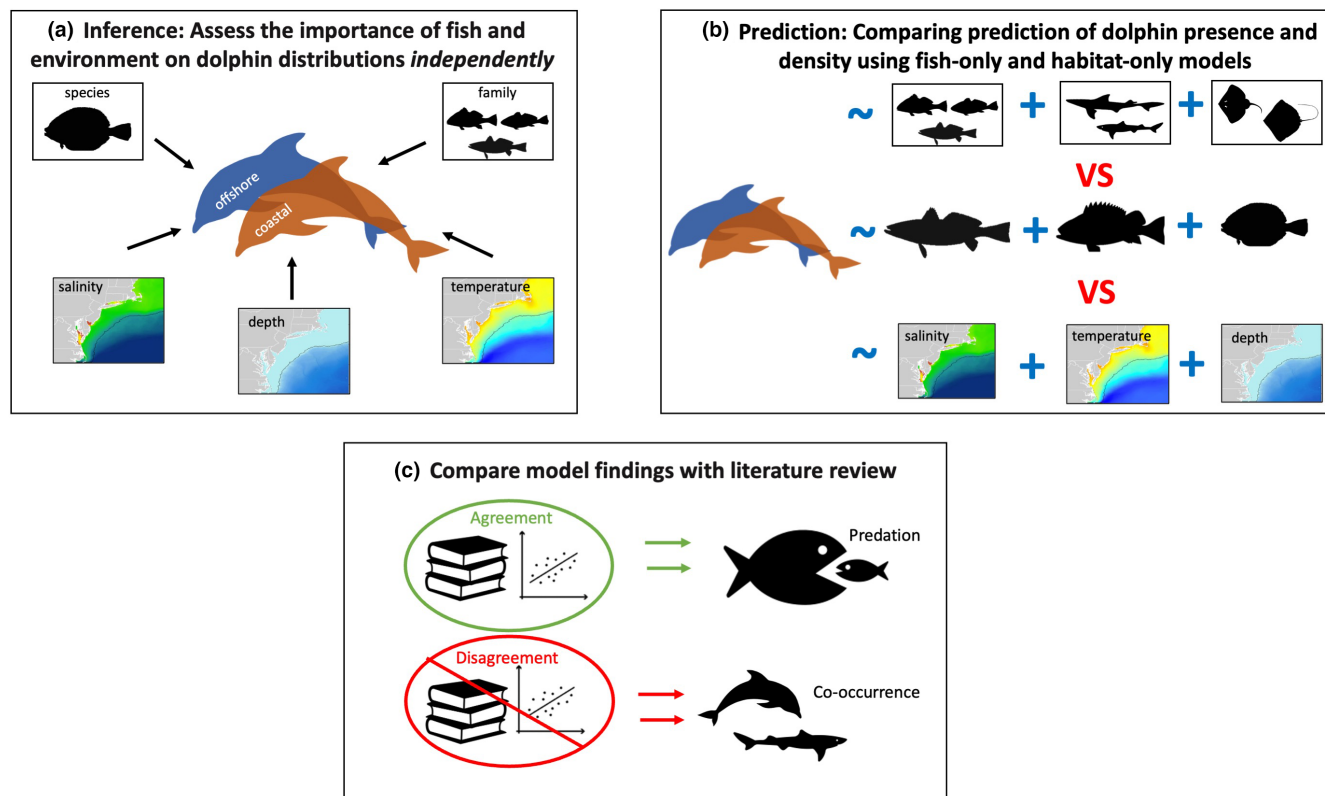
FIGURE 2 Study workflow. (a) We start by iteratively assessing the importance of fish and invertebrate families and species and the environment on coastal and offshore dolphin densities. (b) Then, using the fish families and species identified as important for modelling in (a), we predict dolphin densities and presences using fish family-only, fish species-only and environment-only models to compare predictive capabilities of these three differing approaches. (c) Finally, we compare findings from the modelling portion of the study to results from an extensive literature review. When model findings agree with the literature, especially stomach content studies, we suggest the modelled relationships are predator–prey, when findings disagree, we suggest co-occurrence and further research is needed.

all 214 fish and invertebrate species (75 families) that co-occur with at least one dolphin data point—see Tables S2 and S3 for species and families selected and model results). We calculated the difference between the deviance explained of each model from the null model. Because of the phenological importance of seasonality for dolphin migrations (Hayes et al., 2020, 2021), we incorporated month as a variable for all GLM models. We also ran random forest models for the coastal and offshore bottlenose dolphin ecotypes using the party package (Strobl et al., 2009) in R (version 4.3) and calculated the conditional permutation importance of each variable (number of trees = 500, number of preselected variables per tree = 5). Random forests, a machine-learning algorithm similar to classification and regression trees (Brieman, 1984), has been extensively utilized by ecologists because of their high accuracy, ability to depict interactions between categorical and continuous variables and greater interpretability compared to methods such as neural networks (Cutler et al., 2007). The conditional permutation importance is a measure of a variable's importance given the other variables in the model—thus accounting for the correlation between variables that tend to inflate variable importance estimates in the traditional permutation or Gini importance measures (Strobl et al., 2009). Finally, we calculated the Spearman correlation between coastal or offshore bottlenose dolphins (monthly density (abundance/km^2) per grid cell) and

each environmental variable as well as fish and invertebrate species (families; monthly density (kg/tow) per grid cell).

Single-species models capture the individual effects of a single fish or invertebrate species (family) on bottlenose dolphin densities, but joint models allow for environmental effects as well as dependence between species (families). We utilized the generalized joint attribute model (GJAM) developed by Clark et al. (2017). GJAM is a multivariate Bayesian model which allows us to jointly model the marine fish, invertebrate and dolphin community and account for direct and indirect responses to the environment. Inference is assessed using Gibbs sampling, which is based on a Markov chain Monte Carlo (MCMC) algorithm that works by conditioning on the observed value of different variables in each iteration. GJAM returns all parameters on the observation scale, in this case, kg/tow (per grid/month) and abundance/km^2 (per grid/month). Products of model fitting include a species-by-species covariance matrix (Σ), species responses to predictor variables (**B**) and predicted responses. The species-by-species covariance matrix Σ captures residual co-dependence between species after removing the main structure explained by the model (also referred to as the residual correlation matrix). We ran separate GJAM models for the coastal and offshore bottlenose dolphins including commonly co-occurring species (families) as well as SST, SSAL, month and depth. The coastal and offshore models were each

run for 60,000 iterations and a burn-in of 10,000 (see Figures S1 and S2 for MCMC chains depicting convergence). Rare species can cause hierarchical Bayesian models to not converge, so we only modelled species that co-occurred with coastal or offshore dolphins in at least 17 or 30 grid points respectively (coastal = 27 species, offshore = 21 species, see supplemental GJAM figures for species (Figures S3 and S4)). This number of co-occurring species was the maximum number of rare species that allowed the models to converge. The model background and structure has been described previously (Clark et al., 2017; Roberts et al., 2022). We assessed potential spatial and temporal autocorrelation on the coastal GJAM model, and detected limited evidence of either (Figure S5).

2.4 | Prediction: comparing prediction of dolphin presence and density using fish-only and habitat-only models

From the inference-based models, we developed an understanding of the fish species, families and environmental variables that are strongly related to coastal and offshore bottlenose dolphin distributions. We utilize those species and families and predict in- and out-of-sample dolphin density using a model that considers only the environment and a model that randomly considers the top three associated species (families) from each modelling result plus month (to stay consistent with the inference-based approach above). Using a bootstrapping procedure ($n = 100$), we randomly selected three species (families) out of the top 20 with the highest explanatory power (Table 1; deviance explained vs. the null model for GLMs, conditional permutation importance for random forests and residual correlation and environmental covariance for GJAM for species-specific models, family-specific models can be found in Table S4). We then compare predictive performance for the environment-only models (four covariates) and the fish-only models (four covariates). Because a species' distribution is driven by processes that govern occurrence (range limitations) as well as processes that govern abundance (population productivity), modellers have used two-step (e.g. delta, hurdle) approaches to estimate species distributions (Grüss et al., 2014). We are interested in how environmental variables and co-occurring fish and invertebrate species and families influence both processes, so we separate out our predictive modelling into presence–absence models (occurrence) and density models (abundance).

For out-of-sample prediction, we used the same bootstrapping procedure as above, and iteratively ($n = 100$) trained each model on a random 70% of the data set (coastal $n = 100$ and offshore $n = 974$) and tested prediction on 30% (coastal $n = 43$ and offshore $n = 418$), to minimize the influence of outlying data. In-sample and out-of-sample predictions were evaluated using R^2 and root mean squared error (RMSE). R^2 is a measure of the average squared difference between the observed and predicted values and is unitless. R^2 is calculated as $(1 - \text{sum}((\text{predicted} - \text{observed})^2)/\text{sum}((\text{observed} - \text{mean}(\text{observed}))^2))$. RMSE is a measure of the average squared difference between the observed and predicted values,

measured in the same units as the input data; thus, an RMSE of 0.41 bottlenose dolphin suggests that average predicted dolphin density differed from observed dolphin density by 0.41 dolphins per km^2. For the presence–absence version of each model, we calculated the area under the receiver operator curve (ROC) for in-sample and out-of-sample observed versus predicted values. The ROC curve is a measure of model performance which plots true-positive rate versus false-positive rate, and the area under the ROC curve (AUC) provides a single measure of accuracy. The value of the AUC is between 0.5 and 1.0. A value of 0.8 for the AUC means that for 80% of the time, a random selection from the positive group will have a score greater than a random selection from the negative group (Fielding & Bell 1997). In general, a model with an AUC value above 0.7 is considered a good model.

The predictive performance for each modelling approach (GLMs, random forests and GJAM), ecotype (offshore and coastal) and response variable type (density and presence/absence) are presented for both in- and out-of-sample prediction (Table 1 for species-specific, Table S4 for family-specific). Out-of-sample prediction is a good measure of how well a model predicts on data it has not seen, but given the small sample size for coastal bottlenose dolphins, we exercise caution when interpreting out-of-sample results. Finally, the environment-only versus fish-only modelling approach above is not suitable for a joint modelling approach (where the fish and dolphins are on the left side of the equation and the environment is on the right); thus, we trained and tested the GJAM model using conditional prediction—whereby the predicted bottlenose dolphin density and presence is conditioned on the associated species (families) as well as the environmental variables. We present results for unconditional prediction that defines the mean values of bottlenose dolphin density or probability of presence from the environmental covariate values and fitted coefficients (similar to the environment-only models above) as well as conditional prediction which adds information from the residual covariance of the associated fish and invertebrate species (families).

2.5 | Literature review

To validate the fish and invertebrate species and families that were identified as important by modelling and determine the existence of predator–prey relationships, we completed a systematic literature review of bottlenose dolphin feeding and diet studies in the western North Atlantic. Coastal and offshore bottlenose dolphins within the modelling area are known to use waters from Florida to the Scotian Shelf (Hayes et al., 2020). We therefore conducted a systematic Google Scholar search for each known bottlenose dolphin study site and inhabited geographic feature from Florida to the Scotian Shelf (56 search strings in total, see Table S5 and the Supplemental Materials for details on the literature review methods described throughout this section).

In total, 1182 unique references from scientific and grey literature were produced (the top 50 references were selected per each

TABLE 1 Models used and results.

Model	Advantages	Disadvantages	Top 3 variables (coastal, offshore)	Prediction			
				Environment		Fish	
				In-sample (coastal, offshore)	Out-of-sample mean±sd	In-sample	Out-of-sample
GLM	Aimed at inference, models linear associations well, computationally simple and easy to interpret. Can compare environment vs. species importance through inference as well as prediction	Does not model nonlinear relationships explicitly	(Added deviance vs. Null) Silver perch, red drum, weakfish weakfish, pinfish, SST	R^2 =.16 RMSE=.41 AUC=0.88, R^2 =.11 RMSE=.36 AUC=0.94	R^2 =−.07±.56 RMSE=.43±.11 AUC=0.83±0.08, R^2 =−.02±.24 RMSE=.37±.12 AUC=0.89±0.06	R^2 =.26±.11 RMSE=.38±.03 AUC=0.86±0.03, R^2 =.15±.03 RMSE=.35±.01 AUC=0.88±0.01	R^2 =−.16±.65 RMSE=.44±.11 AUC=0.82±0.1, R^2 =−.88±.37 RMSE=.45±.23 AUC=0.80±0.09
RF	Aimed at prediction, can model nonlinear associations. Conditional importance accounts for the correlation among predictor variables. Can compare environment vs. species importance through inference as well as prediction	Conditional importance is computationally expensive.	(Conditional importance) spot, weakfish, banded drum SST, smooth dogfish, spotted hake	R^2 =.30 RMSE=.38 AUC=0.94, R^2 =.24 RMSE=.33 AUC=0.98	R^2 =.04±.16 RMSE=.42±.09 AUC=0.84±0.1, R^2 =−.03±.34 RMSE=.38±.12 AUC=0.89±0.05	R^2 =.29±.06 RMSE=.37±.02 AUC=0.91±0.03, R^2 =.16±.04 RMSE=.35±.01 AUC=0.94±0.003	R^2 =.09±.18 RMSE=.41±.09 AUC=0.84±0.09, R^2 =−.001±.22 RMSE=.38±.12 AUC=0.85±0.07
Joint model (GJAM)	Incorporates the correlation among dependent variables (species), relying on residual correlation to account for other underlying processes (species interactions, missing environmental variables). GJAM avoids nonlinear link functions (unlike GLMs) and integrates both discrete and continuous data using censoring. Allows for conditional prediction. Can only compare environment vs. species importance through conditional vs. unconditional prediction	Difficult to tease out confounding environmental vs. species effects in residual correlations. Computationally expensive and can be difficult to implement. Noisy, zero-inflated species data can sometimes inhibit conditional prediction performance	(Residual covariance) spot, weakfish, spiny dogfish smooth dogfish, clearnose skate, Atlantic mackerel (Environmental covariance) spot, Atlantic croaker, clearnose skate spotted hake, rosette skate, smooth dogfish	R^2 =.19±.003 RMSE=.33±.007 AUC=0.87±0.004, R^2 =.13±.00 RMSE=.36±.00 AUC=0.94±0.004	R^2 =.09±.13 RMSE=.34±.05 AUC=0.83±0.09, R^2 =.05±.21 RMSE=.35±.13 AUC=0.94±0.026	R^2 =.27±.05 RMSE=.31±.01 AUC=0.91±0.01, R^2 =.53±.01 RMSE=.36±.00 AUC=0.94±0.006	R^2 =.09±.19 RMSE=.34±.05 AUC=0.85±0.08, R^2 =−.01±.36 RMSE=.36±.12 AUC=0.34±0.03
Spearman	Understand the direction and strength of a relationship.	No evidence of causal relationships, cannot control for other variables, no predictive capacity	spot, banded drum, weakfish rosette skate, spotted hake, southern kingfish				

Note: Advantages and disadvantages of each modelling technique, top three variables for inferring coastal and offshore (blue) dolphin distributions and how they were assessed, in- and out-of-sample prediction metrics (R^2, RMSE, AUC) for models just using the environmental variables and models just using top associated fish species (family information in Table S4).

search string). Articles were screened by two reviewers using the Colandr software package (Cheng et al., 2018), which is an online, multiuser platform to systematically synthesize text-based evidence. References that did not focus on the western North Atlantic and did not contain information on bottlenose dolphins and prey were excluded. After screening, 59 primary references were coded for prey by two reviewers using a preestablished protocol, and 49 were used in analysis (Table S9 and Figure S6). We removed references where prey were identified, but the dolphin ecotype was unknown, the data source was not attributable or the prey were at the classification of phylum or higher.

Within a reference, we determined the dolphin ecotype (coastal or offshore), region (Southeast, Mid-Atlantic, Northeast or East) and source of data (e.g. stomach content, isotope, direct observation) for each reported unique prey item (e.g. species, genus, family). We considered a data point to be a unique prey item per unique combination of ecotype, region and data source within a reference (see Table S6 for details on coding criteria and Table S7 for all prey values). There was often more than one data point per reference, because multiple independent sources of prey data were often reported for different ecotypes and/or locations within a reference.

Overall, far fewer references contained prey items for offshore dolphins than coastal dolphins ($n=10$ vs. $n=44$), and more references had prey for the Southeast ($n=30$) than the Mid-Atlantic to Northeast ($n=21$). The majority of studies were either descriptions of stomach contents ($n=16$) or observational ($n=15$) and identified prey to the species level ($n=41$). Most references were from scientific journals ($n=26$) and North Carolina had the highest representation among states ($n=16$; Figure S6).

We assessed trends in prey species and families by calculating the prevalence of each unique prey species and family across studies for coastal and offshore dolphins in the Southeast (i.e. Florida to South Carolina) and Mid-Atlantic to Northeast (i.e. North Carolina to the Scotian Shelf) regions. Given the small number of references with prey items for the Northeast (3 of 49 and exclusively offshore bottlenose dolphins), we assessed Mid-Atlantic and Northeast data together as one region. If the region for a prey item was coded as 'East', then the prey item counted for both the Southeast and Mid-Atlantic to Northeast regions. For species prevalence, we tallied the total number of each unique prey species (one per ecotype–region–data source combination within a reference). When calculating the family prevalence, we derived prey family values from the species or genera of reported prey when necessary. We reported each unique prey family once per ecotype–region–data source combination within a reference to avoid overcounting and inflating prevalence results for family data. When reporting prevalence, prey items given higher than the species or family level were still included as category NA.

Across references, there were 93 prey data points at the family level for coastal Mid-Atlantic to Northeast dolphins, 163 for coastal Southeast dolphins, 18 for offshore Mid-Atlantic to Northeast dolphins and 23 for offshore Southeast dolphins. There were 82 prey data points at the species level for coastal Mid-Atlantic to Northeast

dolphins, 198 for coastal Southeast dolphins, 10 for offshore Mid-Atlantic to Northeast dolphins and 14 for offshore Southeast dolphins. We also calculated the proportion of references that each unique prey species and family was reported in for coastal dolphins in the Mid-Atlantic to Northeast ($n=17$) and Southeast ($n=28$), as well as offshore dolphins in the Mid-Atlantic to Northeast ($n=7$) and Southeast ($n=5$). Again, more prey data points and references existed for the Southeast region and for coastal dolphins.

Stomach content data provide insight into the relative importance of prey species, genera and families; thus, we further extracted information from references reporting stomach content composition, specifically % frequency and % number of prey species (7 references, see Tables S8 and S9). Percent frequency (also referred to as % occurrence) is the number of stomachs in which a unique prey item is documented divided by the total number of stomachs. Percent number is the total count of specimens of a unique prey divided by the total number of all prey specimens documented in stomachs. We calculated the average % frequency and average % number for each unique prey species across studies for coastal dolphins in the Mid-Atlantic (three studies, the Northeast is not represented because coastal dolphins do not inhabit the Northeast region, see Table S6) and coastal dolphins in the Southeast (four studies). Only one study had % frequency and % number data at the species level for offshore dolphins, and it was in the Southeast.

3 | RESULTS

3.1 | Inference

From our modelling approach, we can infer that the distribution of coastal bottlenose dolphins is more driven by drum fish (family Sciaenidae) than environmental conditions (Figure 3a–e, Figure S7). Although our models differed in their underlying structure (Table 1), there was strong agreement among models in terms of the importance of explanatory families and species, especially for coastal bottlenose dolphins. In both the family-based models and species-based models, Sciaenids had the strongest relationship with coastal bottlenose dolphin abundance. For example, when examining at the species level, spot (*Leiostomus xanthurus*) or silver perch (*Bairdiella chrysoura*) had the strongest associations with coastal dolphins measured as conditional importance (Figure 3a), deviance explained (Figure 3b) and Spearman correlation (Figure 3c), as well as in the joint model. In the joint model, environmental covariance measures how species covary with environmental conditions—with coastal bottlenose dolphins strongly covarying with spot and Atlantic croaker (*Micropogonias undulatus*; Figure 3d). Finally, the residual covariance captures residual co-dependence between species after removing the main structure explained by the model. Thus, spot and weakfish (*Cynoscion regalis*) have a strong positive residual covariance with coastal bottlenose dolphins (Figure 3e), which could suggest an unmeasured environmental variable or dependence between these species and coastal bottlenose dolphin abundance (see Figures S3 and S4 for the complete GJAM results).
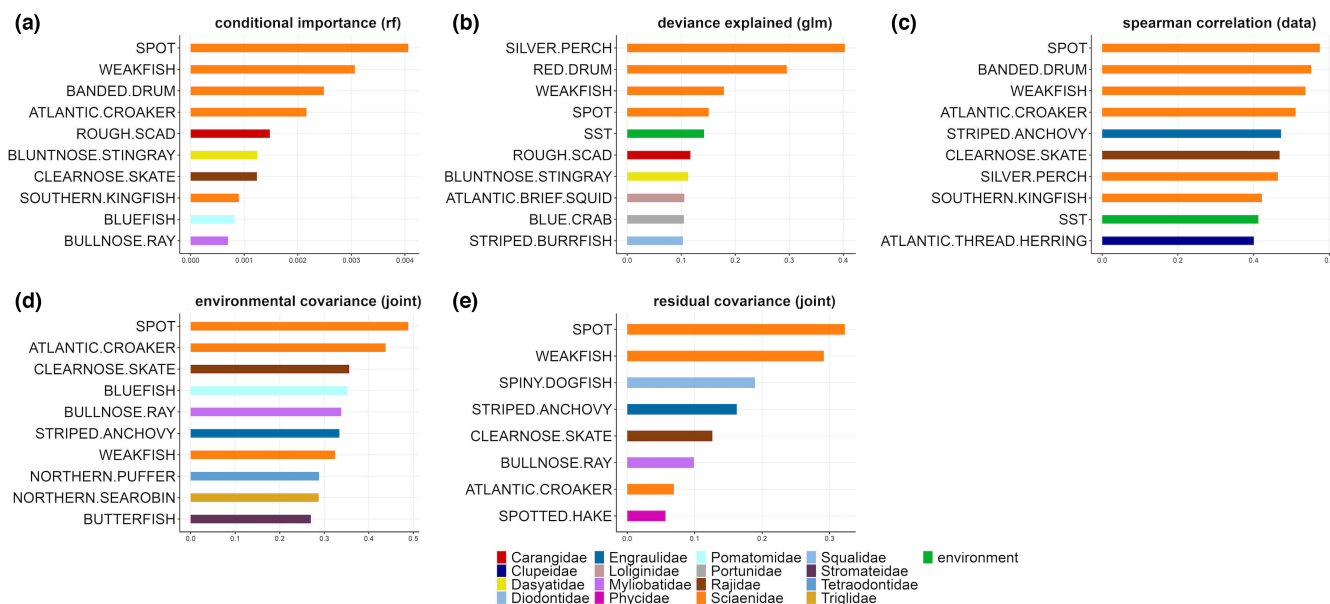
FIGURE 3 Importance of environmental covariates and other overlapping species for coastal dolphin distributions. Conditional importance from random forest models (a), deviance explained compared to the null model for GLMs (b), Spearman correlation in the data set (c), environmental covariance from joint modelling (d) and residual covariance from joint modelling (e). Species colour coded based on family with environmental variables noted in green.

The offshore bottlenose dolphin ecotype was largely associated with SST, Phycidae and Triakidae (top family for conditional importance, Spearman correlation, environmental covariance and residual covariance; Figure S8), but when explored at the species levels, no species clearly stands out, and relationships depend on the model considered. However, spotted hake, smooth dogfish and rosette skate were consistently strongly associated with offshore bottlenose dolphin abundance in the random forest model (Figure 4a), Spearman correlation (Figure 4c) and the environmental covariance from the joint model (Figure 4d). SST was strongly associated with offshore bottlenose dolphin density in the random forest and GLM models (Figures 4a and 3b).

3.2 | Prediction

Predictions from the family-based models performed worse than the species-based models for both coastal and offshore bottlenose dolphins in- and out-of-sample, except for the fish-only in-sample random forest model (both coastal and offshore)—thus, we present species-specific models in the main text (Table 1) and family-specific results can be found in Table S4. Overall, random forests performed best in terms of in- and out-of-sample prediction out of all of the modelling techniques.

Coastal in-sample predictive performance improved slightly in GLM models that only include fish species ($R^2 = .26$, RMSE $= .38$) versus models that only incorporate the environment ($R^2 = .16$, RMSE $= .41$; Table 1), but not for presence–absence versions of the model (GLM AUC $= .86$ vs. 0.88, RF AUC $= .91$ vs. 0.94). GLM out-of-sample predictive performance is worse for models that only consider fish species versus models that just consider the environment, but random forest out-of-sample performance is better for the fish-only models.

Conditional prediction was better in-sample, while both conditional and unconditional were virtually identical out-of-sample for density, and conditional prediction was slightly better for presence–absence.

Predictive performance was weaker in the in-sample and out-of-sample predictions for the density of the offshore bottlenose dolphins compared to the coastal bottlenose dolphin models, but better for presence–absence offshore models. GLM predictions are slightly better in the fish species only in-sample abundance models versus the environment-only models (Table 1), and predictions are better for the environment-only models out-of-sample. In-sample presence–absence models performed better than the models for coastal bottlenose dolphins and performed best for models that just consider the environment (AUC $= 0.94$ vs. 0.88). Predictions from the random forest and GJAM models demonstrated similar results (Table 1).

3.3 | Literature review

From the literature review, we identified the top 10 prey (family and species), separated by region and ecotype (prevalence and percentage of references; Figure 5). The Sciaenidae family (drums) ranked first in prevalence and percentage of references for the Mid-Atlantic coastal dolphins with spot, Atlantic croaker and weakfish ranking highest among species (prevalence and percentage of studies) for this region and ecotype. The Triglidae family (sea robins) ranked first in prevalence and percentage of studies for the Mid-Atlantic to Northeast offshore dolphins and northern shortfin squid (*Illex illecebrosus*) was the only prey identified at the species level for these studies. The Mugilidae family (mullet) ranked first in prevalence and percentage of studies for the Southeast coastal dolphins and flathead
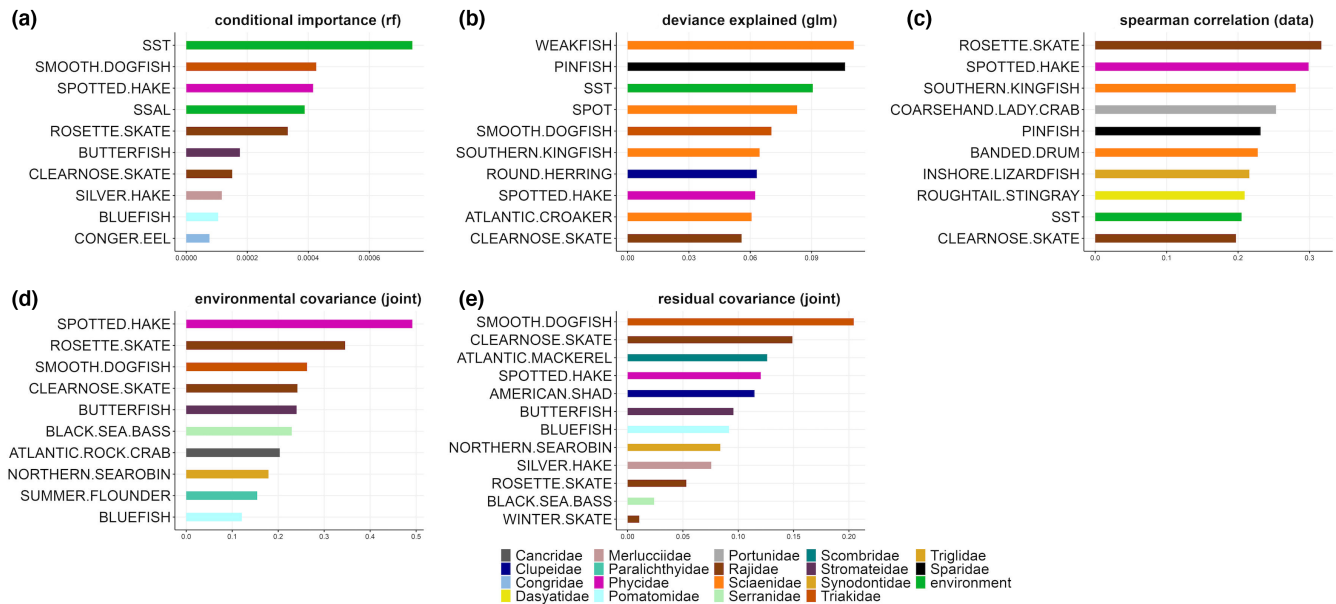
FIGURE 4 Importance of environmental covariates and other overlapping species for offshore dolphin distributions. Conditional importance from random forest models (a), deviance explained compared to the null model for GLMs (b), Spearman correlation in the data set (c), environmental covariance from joint modelling (d) and residual covariance from joint modelling (e). Species colour coded based on family.

grey mullet (*Mugil cephalus),* spot and spotted seatrout (*Cynoscin nebulosus*) ranked highest among species (prevalence and percentage of studies) for this region and ecotype. The Ommastrephidae family (squid) ranked first in prevalence and percentage of studies for the Southeast offshore dolphins and Atlantic bird squid **(***Ornithoteuthis antillarum***)**, pinfish and ladyfish (*Elops saurus*) ranked highest among species (prevalence and percentage of studies) for this region and ecotype.

We further examined the literature on stomach content to assess relative prevalence of each of the prey species for Mid-Atlantic to Northeast (Figure 6a) and Southeast (Figure 6b) stomach content studies. Again, weakfish, Atlantic croaker and spot ranked highest in terms of average percent frequency and average percent number within Mid-Atlantic to Northeast coastal dolphin stomachs (Figure 6a). All three of these species belong to the Sciaenidae family. American stardrum (*Stellifer lanceolatus*), spot and Atlantic brief squid ranked highest for average percent frequency, and American stardrum, Atlantic croaker and American silver perch ranked highest for average percent number within Southeast coastal dolphin stomachs (Figure 6b). There were more stomachs (136±68.4) in Mid-Atlantic to Northeast coastal studies versus Southeast coastal studies (40.2±36.0). Only one prey was reported at the species level for offshore dolphins (Atlantic bird squid – Figure 6b) from one stomach in one study.

4 | DISCUSSION

Our model-based approach had two main goals: (1) to determine whether we could infer relationships between the density of

bottlenose dolphins and environmental variables or co-occurring fish species and families and (2) to use this information to test predictive performance of models that consider only fish versus models that consider only the environment. Using various modelling techniques, we were able to infer a strong relationship between coastal bottlenose dolphins and Sciaenid fishes (drums), and in-sample predictions of their density improve slightly when considering these fish instead of just the environmental variables. This tight relationship between coastal bottlenose dolphins and drums aligns with our findings from the literature review on diet. Specifically, four of the top six species that helped explain coastal dolphin distributions are known prey of dolphins (silver perch, weakfish, spot, banded drum), suggesting that the strong relationship found in modelling is a predator–prey interaction. This result corroborates other research indicating that bottlenose dolphins hunt by listening for soniferous prey, referred to as the 'passive listening hypothesis' (Gannon et al., 2005) and suggests that noise pollution from coastal development, shipping activity and other human uses could be detrimental to dolphin foraging.

The strong relationship between coastal bottlenose dolphin distributions and their soniferous prey may inform how coastal bottlenose dolphins will react to future anthropogenic factors. For example, anthropogenic climate change is influencing the distribution and abundance of several of the fish species that we found to be strongly associated with coastal bottlenose dolphins. For instance, warming ocean temperatures have led to a northward expansion of the range of Atlantic croaker along the east coast of the United States (Hare & Able, 2007). Warmer winters allow croaker and other cold-sensitive juveniles to overwinter and persist north of their historical ranges, so their predators may also shift their distributions.
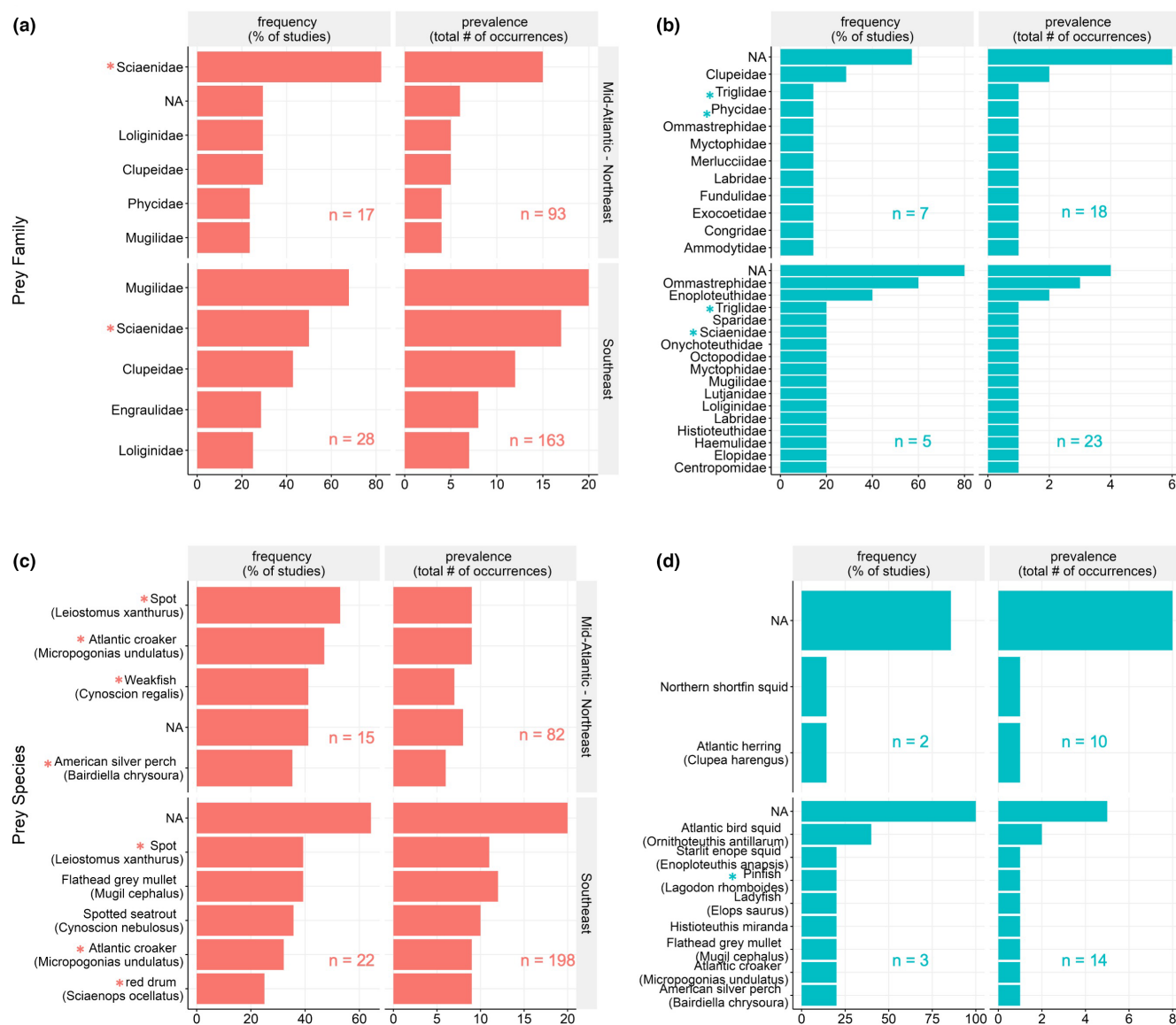
FIGURE 5 Literature review results. Frequency (percentage of studies documenting each prey family) and prevalence (total number of unique occurrences of each prey family) for the Mid-Atlantic to Northeast and Southeast for coastal (a) and offshore (b) ecotypes. Species-level frequency and prevalence of prey for coastal (c) and offshore (d) ecotypes. We show the top 10 prey (species and family) from the literature review for each ecotype across the regions. *N* represents the total number of studies (frequency) and the number of total prey identified for each ecotype within each region (prevalence). NA indicates prey were not identified to the family (a, b) or species (c, d) level. Asterisk (*) represents species that were top inferential species or families in the modelling portion of this study (top three for any modelling type, see Table 1).

Consequently, shifts in bottlenose dolphins would likely have cascading effects throughout the ecosystem if their prey shifted at different rates, given their estimated rate of consumption (Smith et al., 2015). Research has begun to examine shifts in marine mammal distributions with climate change. Thorne and Nye (2021) found that pilot whale populations are shifting faster than their prey, and Thorne et al. (2022) and Chavez-Rosales et al. (2022) found evidence of poleward shifts in their distributions. A closer examination of the potential shifts of bottlenose dolphins driven by changes in the distribution of their prey species is warranted, and accurate estimates of the distribution of these prey species under ocean warming will further help elucidate potential future changes in dolphin distributions.

The development of offshore wind farms in the northwest Atlantic may change the distribution of key prey species, either through disrupting their migration routes or acting as fish aggregating devices, as has been documented in Europe (Methratta & Dardick, 2019). Wirth and Warren (2019) found that artificial reefs off of the New York Bight increased the abundance of weakfish and oyster toadfish, which resulted in bottlenose dolphins aggregating in the area (Wirth & Warren, 2019). Along the Block Island Wind Farm, the first wind farm constructed in North America,
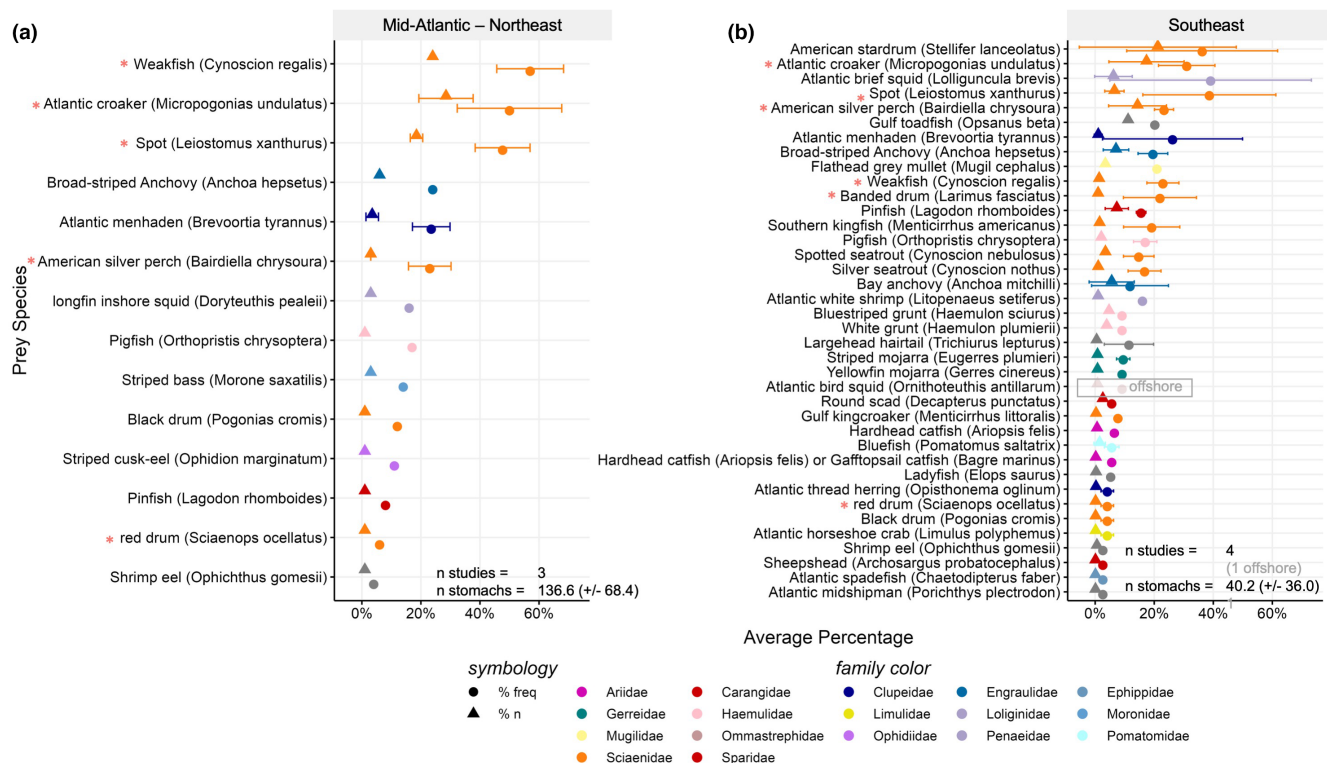
FIGURE 6 Stomach content studies. Mean percent frequency (circle) and number (triangle) of prey for Mid-Atlantic to Northeast (a) and southeast (b) stomach content studies that identify at the species level. Data represents prey for coastal dolphins, with the one offshore prey species boxed. The number of studies and average number of stomachs for studies in each region (±1 standard deviation) is displayed above the x-axis of each graph. Asterisk (*) represents species that were top inferential species in the modelling portion of this study (top three for any modelling type, see Table 1).

recreational fishers are drawn to the area due to increased fish biomass (ten Brink & Dalton, 2018). In general, when evaluating the impacts of wind infrastructure on bottlenose dolphin distributions, our results suggest that management must consider the potential indirect effects of wind farms on dolphins and other marine mammals and protected species that result from changes to prey distributions in addition to the more commonly studied effects of acoustic disturbance.

The tight coupling of coastal bottlenose dolphins and several commercially important fish species has implications for bycatch potential and fisheries interactions. Many of the prey identified as important in the literature review and strongly associated with coastal dolphins in the modelling portion of this study support important commercial and recreational fisheries (e.g. Atlantic croaker and weakfish), some of which utilize gear (gillnets) that result in by-catches of coastal bottlenose dolphins (Friedlaender et al., 2001; Mercer, 1989). We have shown that models incorporating fish can predict the presence of coastal dolphins better than those relying only on environmental factors, so management approaches could use the presence of these species to minimize harmful human–wildlife interactions; however, the cost of collecting prey data may hinder this approach. This may be particularly relevant for the stocks of bottlenose dolphins in the Mid-Atlantic that are experiencing human-caused mortality at unsustainable rates (i.e. strategic, Hayes et al., 2021).

Our modelling results also identified several important fish species that we did not identify as important prey species from our literature review. For example, coastal bottlenose dolphins were strongly associated with spiny dogfish, another commercially important species on the east coast of the United States (Dell'Apa et al., 2015). Spiny dogfish are also harvested with gillnets known to take bottlenose dolphins as bycatch (Friedlaender et al., 2001). We postulate that this close relationship is a result of co-occurrence (targeting similar prey in similar environmental conditions) rather than a predator–prey interaction. Similarly, our models also highlighted the importance of the Dasyatidae (rays) and Squalidae (dogfish) families as predictors of dolphin distributions.

Overall, our findings agree with several empirical studies that link the distribution of bottlenose dolphins to their prey (Hanson & Defran, 1993; Hart, 1997; Shane et al., 1986) and stomach-content studies which provide strong evidence of diet specificity at the family and species level (Gannon & Waples, 2004; Volker, 2020). Few previous models have been able to account for prey when modelling dolphin distributions with some previous research finding no strong statistical association between the presence of bottlenose dolphins and their prey (Browning et al., 2014; Torres et al., 2008). This work was, however, conducted at small spatial scales on dolphins with limited ranges. In comparison, we examined relationships between dolphins and prey at a regional scale encompassing entire populations. At this broader scale (both spatial and ecological), we were able to

identify strong ties between the distributions of predators and prey. Indeed, research suggests that at a local scale (on the individual-animal level), prey move away from predators, and thus, their densities are negatively correlated (Lambert et al., 2019; Walker & Macko, 1999), but at larger scales (such as the regional focus of our study), prey and predator densities are more likely to be correlated (Fauchald et al., 2000; Pascual & Levin, 1999; Rose & Leggett, 1990). By encompassing the entire Mid-Atlantic to Northeast region, we were able to make broad conclusions about the associations between bottlenose dolphins and fish.

Unlike coastal bottlenose dolphins, the distribution of the offshore ecotype of bottlenose dolphins was more strongly related to the environment. We suggest that the offshore ecotype is tightly linked to specific features of their environment, such as the warm water of the Gulf Stream and the productive shelf break. Importantly, trawl surveys may not capture pelagic or mid-water prey consumed by offshore bottlenose dolphins. For example, trawl studies mostly target bottom-dwelling species, and offshore bottlenose dolphins feed higher in the water column (Williams et al., 1999), on epipelagic fish and cephalopods (Walker & Macko, 1999). Indeed, our literature review confirmed that offshore dolphins are more associated with squid (northern shortfin squid and Atlantic bird squid). In general, abundance predictions were weak for offshore bottlenose dolphins both when considering the environment or co-occurring fish and invertebrates. This weak model performance reflects how little we know about these offshore dolphins, which is also evident in the literature review. In general, the stronger model performance when using presence–absence models suggests that we may be able to accurately predict where offshore bottlenose dolphins occur, but not necessarily their density.

Finally, although our study is a good first step at examining the underlying mechanisms driving the distributions of large marine predators, we were limited by the overlap of the data sets. Both the fish and invertebrate and marine mammal surveys included thousands of data points, but their spatial and temporal overlap was comparatively small. Still, we were able to use an ensemble modelling approach to identify ties between certain fish species and families and the distribution of coastal dolphins. Our out-of-sample prediction was limited by sample size, but we showed that models using prey species can sometimes outperform environment-only models. We demonstrate this using models that are better suited for inference (GLMs) as well as prediction (random forests).

5 | CONCLUSION

Models that incorporate the combined effects of environmental variables and species associations on predator distributions offer insights that cannot be obtained from species–environment models alone. These predator–prey biotic dependencies as well as co-occurrences with other non-prey species should be considered when drafting ecosystem-based management plans and marine spatial

planning efforts. A focus solely on environmental models may miss important dependencies that may be impacted by other activities. For example, species distribution models considering the impacts of wind infrastructure development should consider both direct and indirect effects on ecosystems through joint modelling frameworks. In addition, future forecasts of climatic impacts on marine species distributions should also consider joint modelling approaches to better account for potential differences in predator and prey species responses. In general, we have shown here that the distribution of a common marine mammal predator is closely tied to fish in addition to environmental variables. Our work could be extended to further examine predator–prey interactions including other marine mammals, seabirds and sharks. The continental shelf off of the east coast of the United States is a biologically rich and interconnected ecosystem, and ecological models should reflect this reality.

CONFLICT OF INTEREST STATEMENT
The authors declare no conflict of interest.

PEER REVIEW
The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ddi.13746.

DATA AVAILABILITY STATEMENT
The fish and invertebrate data used in the analysis are publicly available and can be downloaded here: https://oceanadapt.rutgers.edu/. Raw sightings of bottlenose dolphins and associated survey effort are available from the Ocean Biodiversity Information System–Spatial Ecological Analysis of Megavertebrate Populations (OBIS-SEAMAP) repository, which includes contact information and data sharing permissions for data used in this study: https://seamap.env.duke.edu. Derived estimated abundance and detection functions were fitted according to the methods detailed in Roberts et al. (2016). Additional information is available at https://seamap.env.duke.edu/models/Duke/EC. Data from the literature review are available in the supplemental materials. The code needed to run the analysis can be found here https://doi.org/10.5061/dryad.cc2fqz69g.

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Author contributions: SMR and AMJ conceived and designed the study; SMR analysed the data with inputs from AMJ, JN, JR, AR and PH; AMJ conducted the literature review with major contributions from JL and KP. SMR and AMJ wrote the article and JN, JR, AR, and PH provided insightful comments on the text. SB, LG, WM and DB supported the data collection. All authors read and approved the final version of the manuscript.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.