



Predicting fisheries bycatch: A case study and field test for pilot whales in a pelagic longline fishery

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Abstract

Aim: Fisheries bycatch is a major threat to populations of protected species such as marine mammals, seabirds and sea turtles, and static management approaches are often unsuccessful in mitigating bycatch of these highly mobile species. Combining species distribution models (SDMs) with oceanographic data has been proposed as a means of predicting when and where bycatch is likely to occur. However, studies assessing whether SDMs can accurately predict fisheries bycatch using independent data are lacking. Assessing model performance using independent data is necessary to test whether a model is generalizable, and this is particularly important for models with management applications. Here, we use short-finned pilot whale (*Globicephala macrorhynchus*) bycatch in a pelagic longline fishery as a case study to inform efforts to mitigate fisheries bycatch.

Location: Offshore waters, north-east United States.

Methods: We integrated telemetry and oceanographic data using mixed-effects generalized additive models to predict pilot whale occurrence and assessed model performance using k-folds cross-validation. We then evaluated the model's ability to predict pilot whale bycatch using data from independent on-board observers.

Results: The model performed well, and predictions were strongly and significantly correlated with observed rates of bycatch in space and time. Temperature and proximity to mesoscale oceanographic features (thermal fronts and sea level anomalies) were important predictors of pilot whale occurrence, and as a result, spatial predictions of the risk of bycatch varied through time.

Main conclusions: Our findings demonstrate that SDMs can be used to accurately predict times and places with a high risk of bycatch, and illustrate that models using dynamic oceanographic variables can identify smaller, more specific focal management regions than static management approaches. Combining SDMs with near real-time or forecasted environmental conditions could provide a promising tool for decreasing bycatch and will be valuable in developing adaptive management strategies to mitigate fisheries bycatch of protected species.

KEYWORDS

bycatch, depredation, dynamic management, fisheries management, pilot whale, species distribution model

1 | INTRODUCTION

Marine systems are highly dynamic, and the distribution of marine organisms responds to variation in physical parameters across a range of spatial and temporal scales (Genin et al., 1994; Hunt & Schneider, 1987; McManus & Woodson, 2012; Perry, Low, Ellis, & Reynolds, 2005; Sims & Quayle, 1998). Spatial and temporal variation in the distribution of marine species leads to management challenges and erodes the efficacy of static approaches, particularly those based on spatial management (Hazen et al., 2018; Maxwell et al., 2015; O'Keefe, Cadrin, & Stokesbury, 2013). Adaptive approaches may provide more effective management of marine species, particularly for highly mobile species that forage over large spatial scales and exploit dynamic and ephemeral foraging areas (Cotté, Park, Guinet, & Bost, 2007; Dunn, Maxwell, Boustany, & Halpin, 2016; Hazen et al., 2016; Irons, 1998; Johnston, Thorne, & Read, 2005; Lewison et al., 2014; Maxwell et al., 2015; Moore & Lien, 2007; Weimerskirch, 2007). Species distribution models (SDMs) can provide valuable sources of information to inform such adaptive management approaches and can be used to predict times and places where focal species are most likely to occur (Hazen et al., 2016, 2018; Žydelis et al., 2011).

Accurately predicting species occurrence could provide a means of predicting and ultimately minimizing fisheries bycatch (Hobday & Hartmann, 2006; Howell, Kobayashi, Parker, Balazs, & Polovina, 2008), the incidental mortality of non-target species in fisheries (Lewison et al., 2014). Fisheries bycatch is an important source of mortality for many marine species and is a major threat to populations of many long-lived species of marine mammals, seabirds and sea turtles (Lewison, Crowder, Read, & Freeman, 2004; Moore et al., 2009; Read, Drinker, & Northridge, 2006; Reeves, McClellan, & Werner, 2013). Some bycaught species are released alive but are injured after becoming entangled in fishing gear, which can result in subsequent mortality (Read, 2008). Many of these species exhibit very low rates of population growth due to life history constraints (Barlow, 1995; Reilly & Barlow, 1986), making them particularly vulnerable to the effects of bycatch, especially if this results in a reduction in adult survival rates (Lewison et al., 2004). In some species, bycatch results from the intentional removal of bait or catch from fishing gear by a predator which subsequently becomes hooked and/or entangled; in such cases, these interactions also impose a direct time and economic cost to fishers. These interactions, referred to as depredation, are an increasingly frequent problem in several fisheries (Read, 2008; Read et al., 2006).

To date, most bycatch mitigation measures have focused on gear modifications, fixed marine protected areas or static time-area closures to the fishery (Carretta & Barlow, 2011; Dalton & Ralston, 2004; Lewison et al., 2014; Werner, Kraus, Read, & Zollett, 2006). Static time-area closures are unpopular with fishers (Bisack & Sutinen,

2006; Murray, Read, & SoLow, 2000; Read, 2013) and may be ineffective because the spatial distribution of bycaught species is dynamic (Hartel, Constantine, & Torres, 2015; Žydelis et al., 2011). The use of dynamic spatial approaches has been suggested as a means of improving the efficacy of management and decreasing fisheries bycatch (Dunn, Boustany, & Halpin, 2011; Dunn et al., 2016; Hazen et al., 2018). Such dynamic management approaches could reduce the extent of the managed area, providing conservation benefits while minimizing economic costs to fishery participants (Dunn et al., 2011; Hazen et al., 2016, 2018; Maxwell et al., 2015).

High-resolution satellite imagery and bathymetric grids provide continuous measurements of oceanographic variables across large spatial scales and, therefore, provide critical tools to help predict the distribution of highly mobile species. Improvements in the resolution of available cloud-free satellite imagery (e.g., the Group for High Resolution SST) have advanced our ability to resolve dynamic oceanographic variables. Similarly, bathymetric models have been improved greatly in recent years by incorporating additional depth soundings and data from a variety of sources (Beaman, O'Brien, Post, & Santis, 2011; Weatherall et al., 2015). These models have provided better characterizations of the ocean floor and have enabled the development of derived metrics such as slope maps to examine specific geological features and morphostructures associated with the ocean floor (Esteban, Tassone, Menichetti, & Lodolo, 2017). At the same time, improvements in the use of satellite-linked telemetry have facilitated the study of marine predator movements (Hart & Hyrenbach, 2009; Ropert-Coudert & Wilson, 2005). Taken together, these advances provide the foundation for quantitative studies predicting the occurrence of fisheries bycatch using bathymetric and near real-time oceanographic data (Roe et al., 2014; Žydelis et al., 2011).

Depredation poses an additional challenge for management efforts aimed at minimizing bycatch; fishing vessels and fishing gear can serve as an attractant to depredating species, and depredating animals may follow or seek out fishing vessels in order to increase the likelihood of encountering an easily accessible meal in the form of bait or catch (Gilman, Brothers, McPherson, & Dalzell, 2007; Kock, Purves, & Duhamel, 2006; Schakner, Lunsford, Straley, Eguchi, & Mesnick, 2014; Thode, Straley, Tiemann, Folkert, & O'Connell, 2007). Thus, bycatch might occur in regions outside of the predicted habitat range for depredating species. This is particularly true for species such as cetaceans since social learning plays a major role in foraging behaviour (Baird, Abrams, & Dill, 1992; Baird & Whitehead, 2000; Rendell & Whitehead, 2001; Schakner et al., 2014). It is therefore important to assess whether SDMs can be used to accurately predict the risk of bycatch before developing dynamic spatial approaches as a mitigation tool.

Here, we use short-finned pilot whale (*Globicephala macrorhynchus*) bycatch in a pelagic longline fishery as a case study to inform

efforts to model and mitigate fisheries bycatch. Short-finned pilot whales in the Northwest Atlantic depredate bait and catch in the U.S. pelagic longline fishery (Waring, Josephson, Maze-Foley, & Rosel, 2015). Some whales become entangled or hooked as a result of these interactions, resulting in mortality and serious injury (M/SI). The bycatch of marine mammals in the United States is regulated under the 1994 amendments to the Marine Mammal Protection Act (MMPA). Levels of bycatch exceeding a biological reference point (potential biological removal or PBR) are considered to be unsustainable and must be reduced to below this threshold through negotiated agreements of stakeholders on a Take Reduction Team, later translated into rulemaking by the management agency (McDonald, Lewison, & Read, 2016). The five-year average of M/SI for Northwest Atlantic short-finned pilot whales in the pelagic longline fishery recently exceeded PBR, and thus, the stock is now considered to be strategic under the MMPA (US OFR, 2016). Previous attempts to decrease pilot whale bycatch have proven to be unsuccessful. Fishing restrictions evaluated to date have included increased observer coverage for vessels fishing within the Cape Hatteras Special Research Area (CHSRA) and a reduction in mainline length to less than 20 nm for longline vessels fishing in the Mid-Atlantic Bight (US OFR, 2009). Preliminary tests of acoustic deterrents to dissuade pilot whales from approaching longlines have also proven unsuccessful in reducing depredation of catch and bait (A. Read, unpublished data). The shelf break region provides important pilot whale habitat (Thorne et al., 2017), and an examination of pilot whale-longline overlap in the Northwest Atlantic suggested that shifting longline effort into offshore waters would decrease bycatch by more than 50% (Stepanuk, Read, Baird, Webster, & Thorne, 2018). However, such a change would strongly impact fishers, requiring that a large proportion of longliners would have to alter their fishing practices. Temporal patterns in rates of pilot whale bycatch suggest that dynamic habitat variables may be important to understanding and predicting pilot whale occurrence (Stepanuk et al., 2018). Incorporating dynamic oceanographic variables into predictive habitat models to predict high-risk areas of bycatch could provide a means of decreasing pilot whale bycatch in the longline fishery, while reducing the extent of the area that longliners would need to avoid.

Until recently, knowledge of short-finned pilot whale habitat use was limited due to a lack of species-level data (Waring, Josephson, Maze-Foley, & Rosel, 2013). Short-finned pilot whales are difficult to differentiate from their congener, the long-finned pilot whale (*Globicephala melas*), at sea except under ideal conditions (Rone & Pace, 2012). The two species differ in their distribution and ecology, and only short-finned pilot whales are threatened by bycatch in the pelagic longline fishery (Gannon, Read, Craddock, Fristrup, & Nicolas, 1997; Mintzer, Gannon, Barros, & Read, 2008; Waring et al., 2013, 2015). Our analysis uses data from recent satellite telemetry studies, in which the species identity of whales at the tagging location was confirmed by genetic analysis of biopsy samples, to investigate the habitat use of short-finned pilot whales. These data allow us to examine species–environment relationships in detail and to develop predictive models for short-finned pilot whales (Figure 1).

The objectives of our study were to use pilot whale bycatch in the Atlantic pelagic longline fishery as a case study to:

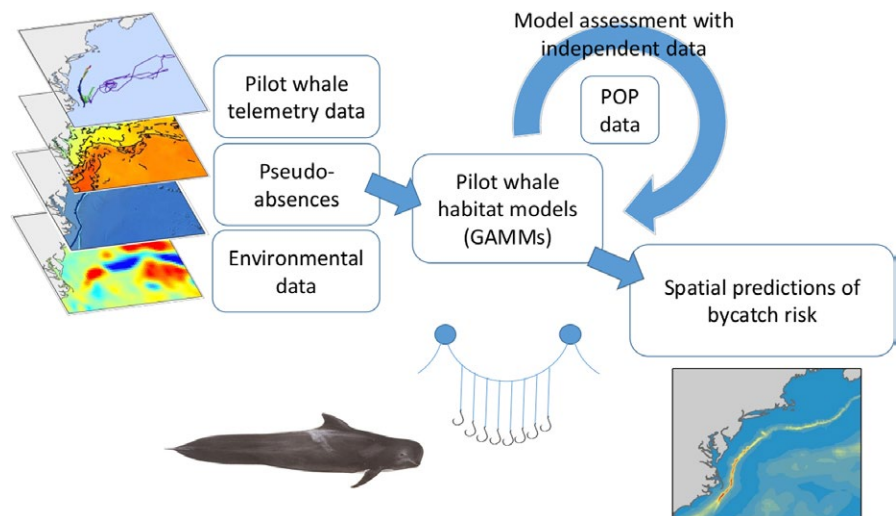
1. Develop probabilistic predictions of occurrence for bycaught species using telemetry data and spatial grids of environmental data;
2. Assess whether these predictions can be used to accurately predict fisheries bycatch using data recorded by government fisheries observers; and
3. Compare the extent of managed areas predicted using static and dynamic management approaches for mitigating bycatch.

2 | METHODS

2.1 | Study area

This research focused on the Mid-Atlantic Bight (MAB) and Northeast Coast (NEC) regions managed by the National Marine Fisheries Service (NMFS; Figure 2d; boundaries of the MAB and NEC regions defined here as 33.5°N and 43°N, respectively, extending from the coast out to 60°W), because satellite-tagged pilot

FIGURE 1 Schematic showing research methods used to develop spatial predictions of bycatch risk of short-finned pilot whales in the Northwest Atlantic. Models were assessed with k-folds cross-validation, and data from an independent on-board observer program were used to evaluate the predictive capacity for identifying locations and times with a high risk of bycatch. GAMMs: Mixed-effects generalized additive models; POP: Pelagic Observer Program



whales (described below) stayed within these regions, and because the vast majority of observed pilot whale-longline bycatch occurs within these regions (Garrison, 2007). In this region, the continental shelf drops off steeply, with depths typically increasing from less than 200 m to more than 1,000 m over a cross-shelf distance of less than 10 km. The steep bathymetry in this region is in contrast to the more gradually sloping continental shelf in the South Atlantic Bight (SAB), where depths typically increase from 200 to 1,000 m over a distance of more than 100 km (Figure 2). Temperature regimes are dominated by the effects of the warm waters of the Gulf Stream in the south and the cool Labrador slope water to the north. The position of these two water masses have dramatic effects on temperature regimes, and water temperatures can vary dramatically in space and time, both within and between years. For example, summer sea surface temperatures (SST; June through August) can vary from as high as 30°C off of Cape Hatteras (35°N) and in the Gulf Stream to as low as 8°C in the Northeast Channel south of Nova Scotia, Canada (42°N). Water temperatures within this region can show dramatic within-year variability; for example, in 2015, water temperatures in the Northeast Channel varied from approximately 1°C in April to 21°C in August.

2.2 | Pelagic longline fishery

The US Atlantic pelagic longline fishery primarily targets swordfish (*Xiphias gladius*), yellowfin tuna (*Thunnus albacares*) and bigeye tuna (*Thunnus obesus*), with secondary targets of albacore tuna (*Thunnus alalunga*) and pelagic sharks. While longline gear can be

altered to target different species, such as by varying the depth of the set, the timing of the set, the number of hooks and the spacing of hooks, multiple species are typically caught in pelagic longline sets. Swordfish feed in near-surface waters at night, and thus, sets targeting swordfish are typically deployed closer to the surface and at night, while sets targeting tunas are typically set deeper in the water column during the day (NMFS, 2006). Longline vessels primarily use Atlantic mackerel (*Scomber scombrus*) or squid (*Illex* sp.) for bait, which is typically stored frozen and then thawed prior to use (Beerkircher, Lee, Brown, & Abercrombie, 2002; Keene, Beerkircher, & Lee, 2007). Pilot whales depredate both bait and catch from longlines, and bycatch in the pelagic longline fishery is the primary source of human-caused M/SI for the Northwest Atlantic stock of short-finned pilot whales (Hayes et al., 2017). Stepanuk et al. (2018) found that seasonal variability in longline effort relative to the 1,000-m isobath influenced seasonal patterns in pilot whale-longline overlap, which was strongly and significantly correlated with rates of pilot whale bycatch. However, the role of dynamic oceanography in driving patterns of bycatch requires further attention.

2.3 | Telemetry data

We developed predictive habitat models for short-finned pilot whales using data from 35 satellite tags deployed in waters off Cape Hatteras, North Carolina, in 2014 and 2015. Satellite tags provided location data for tracked pilot whales and did not provide environmental data. Tagging efforts were conducted independent

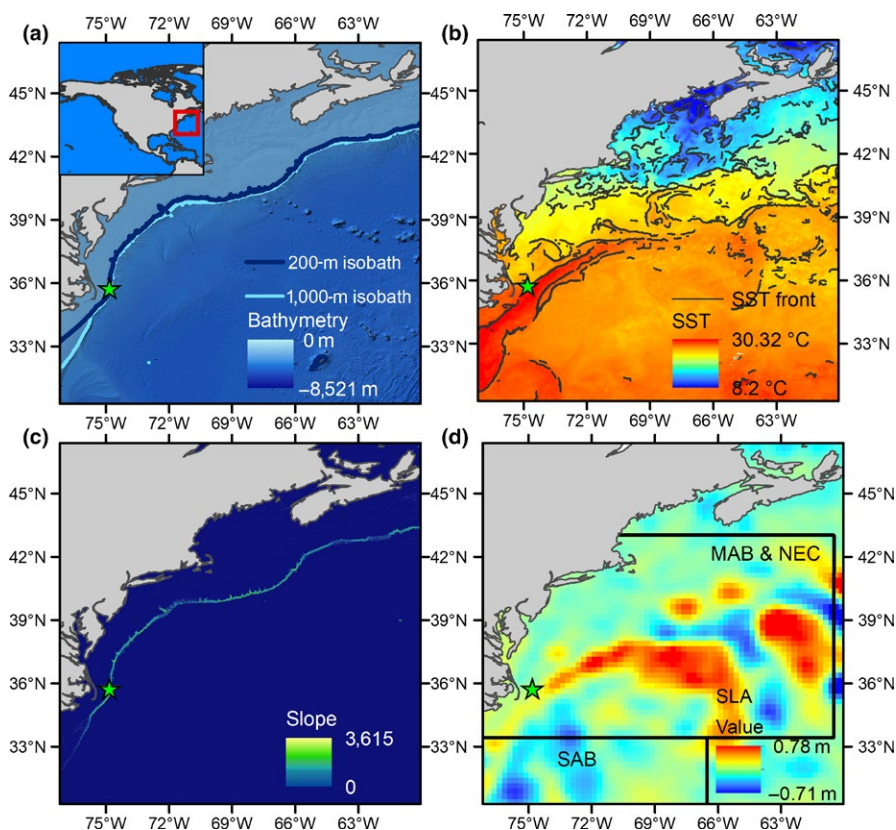


FIGURE 2 Environmental parameters in the study area used to develop the short-finned pilot whale habitat model. The Mid-Atlantic Bight and Northeast Coast (MAB and NEC) and the South Atlantic Bight (SAB) regions are shown in panel d. The green star indicates the location of tag deployments off of Cape Hatteras, North Carolina. Data are shown for 3 September 2014. SST, Sea surface temperature; SLA, Sea level anomaly

of fishing and observer effort. We used 27 SPOT5 and 8 Mk10 Wildlife Computer satellite tags, all in the Low Impact Minimally Percutaneous External-electronics Transmitter (LIMPET) configuration, attached with two titanium darts with backward facing petals. Tags were remotely deployed into the dorsal fin or base of the dorsal fin of short-finned pilot whales using a pneumatic projector (Andrews, Pitman, & Ballance, 2008; Baird et al., 2010). To provide data on habitat use over broad spatial and temporal scales, SPOT5 tags were programmed to collect data daily for the first 60 days of the deployment, every third day for the subsequent 21 days and every ninth day for the remainder of the deployment. Mk10 tags were programmed to transmit data daily for the first 20 days of the deployment, every third day for the subsequent 30 days and every ninth day for the remainder of the deployment. We used all data from tag transmissions through April 2016; resulting tag deployments ranged from 6 to 198 days (mean 68 days), and tagged whales travelled 43–1,312 km (mean 357 km) from their tagging location during these periods. Tag data were processed with the Douglas Argos-Filter to remove erroneous location estimates (Douglas et al., 2012; user-defined settings: min. rate = 15, max-redun = 3, rate-coef = 25, KeepLC = 2) and resampled to a 12-hr time frame to ensure consistent time steps between all observations. Resampling was conducted using the minimum covariance determinant (MCD) in the MASS library (version 7.3-45) of the R statistical package (version 3.3.2) to provide a robust estimate of location at each time step that is not strongly influenced by outliers occurring due to the spatial resolution of telemetry data. When fewer than four locations were available within a time window, MCD cannot be computed and the coordinate-wise median was used (Thorne et al., 2015).

2.4 | Environmental data

Our initial data exploration highlighted the importance of depth, slope and proximity to the shelf break as important factors influencing the movements of short-finned pilot whales, and previous studies suggested that water temperature, thermal fronts and Gulf Stream features are also important variables driving the habitat use of this species (Fullard et al., 2000; Thorne et al., 2017; Waring et al., 2015). We assessed bathymetric variables using GEBCO bathymetric grids (resolution 1 km; http://www.gebco.net/data_and_products/gridded_bathymetry_data/) and used the 200-m isobath as a proxy for the location of the continental shelf break. Previous studies suggested the importance of steep bathymetric gradients within the diving range of pilot whales (depths of less than 1,200 m; Quick et al., 2017), but bathymetric gradients beyond this depth range did not appear to influence pilot whale distribution (Thorne et al., 2017). We therefore assumed that slopes occurring at depths of more than 1,200 m would not influence pilot whale habitat use. We assessed the effect of bathymetric slope within the pilot whale diving range using the neighbourhood statistics tool (focal statistics) in ArcGIS to assess change in depth over a 5×5 cell grid; slopes occurring at depths of greater than 1,200 m were assigned a value of zero (Figure 2c). We used daily Level 4 Group for High Resolution Sea

Surface Temperature (GHRSSST) grids with a spatial resolution of 0.01 degrees (https://podaac.jpl.nasa.gov/dataset/JPL_OUROCEAN-L4UHfnd-GLOB-G1SST), available from June 2010 to the present, to examine water temperature and thermal fronts. We identified SST fronts using the Cayula–Cornillon edge detection tool in the Marine Geospatial Ecology Tools (MGET) for ArcGIS (front detection threshold of 0.5°C; Cayula & Cornillon, 1992; Roberts, Best, Dunn, Trembl, & Halpin, 2010). We used daily grids of AVISO mean sea level anomalies (SLA) in metres, calculated as differences in sea level from the long-term mean (<http://www.aviso.altimetry.fr/en/data/products/sea-surface-height-products.html>), downloaded via MGET.

2.5 | Fisheries observer data

We obtained data from the Pelagic Observer Program (POP) run by the NMFS, which places independent observers aboard pelagic longline vessels to record bycatch and detailed set-level data of each longline set (e.g., set and haul locations, bait type, number of hooks deployed and mainline length). The POP was initiated in 1992 and on average provides coverage of 4.8% of all longline sets each year (Keene et al., 2007). The methods used to represent longline effort in space (e.g., points, centroids, polygons) can impact results of spatial analyses, and polygons created from locations at the beginning of the set, end of the set, beginning of the haulback and end of the haulback provide the most accurate means of representing longline effort (Dunn, Kot, & Halpin, 2008). We therefore used the polygon method, creating a separate polygon for each longline set, and used mean values of environmental data from within the polygon to predict the probability of pilot whale occurrence at each set (pilot whale models described below). We then compared the predicted occurrence of pilot whales with observed rates of pilot whale bycatch, defined as bycatch per unit effort (BPUE), or the number of pilot whales caught per longline set.

2.6 | Predictive models of pilot whale occurrence

We used a binary modelling approach by comparing environmental data at locations of pilot whale presence (from satellite tracks) with locations of pseudo-absences. We generated pseudo-absences for each pilot whale track from ten temporally matched correlated random walks (CRWs) using the approach of Hazen et al. (2016; Supporting Information Figure S1). Each CRW had the same start time, start location and duration as the pilot whale tracks, and for each 12-hr time step of the pilot whale tracks, we randomly selected turning angles and step distances from the distributions observed in the telemetry data. The selection of appropriate pseudo-absences has important effects on model performance, and we constrained our CRWs using a flag value to reflect the fit of CRWs with pilot whale tracks based on overall direction and distance travelled (Hazen et al., 2016; Willis-Norton et al., 2015) as follows:

$$\text{Flag} = 2 * \left(\frac{\text{distance}_{\text{pilot whale}} - \text{distance}_{\text{CRW}}}{\text{distance}_{\text{pilot whale}}} \right) + \left(\text{angle}_{\text{pilot whale}} - \text{angle}_{\text{CRW}} \right) / 90$$

Resulting flag values ranged from 0 to 5, and we discarded CRWs with flag values in the upper quartile and those that crossed land in order to obtain pseudo-absences that represented accessible areas for pilot whales (Hazen et al., 2016). The total number of presence and pseudo-absence locations used in the model was 2,690 and 26,900, respectively.

We sampled environmental variables at each track point and pseudo-absence point, respectively. We modelled the probability of pilot whale occurrence as a function of environmental variables using mixed-effects generalized additive models (GAMMs), including a random effect for individual whales in order to account for correlation between points on an individual pilot whale track (Gillies et al., 2006; Shillinger et al., 2011; Willis-Norton et al., 2015). We ran the GAMMs using the `gamm4` package (version 0.2-5) in the `R` statistical package (version 3.3.2) using cubic spline smoothers with 4 or fewer degrees of freedom to prevent over-fitting and performed model selection by minimizing UBRE (Wood, 2004). We did not include strongly correlated environmental variables (Pearson's correlation coefficient > 0.4), such as depth and proximity to the shelf break, within the same model. The final model included the following variables: Distance to shelf break, SST, SLA, slope and distance to SST fronts.

We assessed the final model using 10-fold cross-validation and examined model performance using R^2 values, the area under the curve (AUC) of the receiver operating characteristic (ROC) plot, and model sensitivity and specificity. AUC values range between 0 and 1, with a value of 1 representing a perfect fit, values higher than 0.9 indicating an excellent fit, values of 0.80–0.90 signifying good model fit and values of 0.70–0.80 representing a fair fit (Swets, 1988). For our model, sensitivity describes the probability that a pilot whale occurrence would be correctly identified as such by the model (the true positive rate), while specificity describes the proportion of pilot whale absences that are correctly identified by the model as absences (the true negative rate). During cross-validation, data were randomly partitioned into ten data equal parts; nine were used to build and fit the models, while the last was used as the test data set to assess model performance. This process was repeated ten times so that each of the ten partitions are used once to test the model, and results from the 10-fold were averaged to examine R^2 and AUC values, model specificity and sensitivity. To examine spatial variability in predicted pilot whale habitat through time, we generated seasonal means as means of daily predictions produced from daily environmental conditions.

2.7 | Assessing predictive models using fisheries observer data

We predicted the probability of pilot whale occurrence for each longline set using environmental data as described above for monthly habitat predictions. This analysis focused on the period from June 2010 to December 2015 for which we had concurrent high-resolution SST data and POP observations of longline sets ($n = 1,474$ observed sets). Pilot whale bycatch occurs infrequently (116 pilot

whales were caught in observed longline sets, giving a mean bycatch rate of 0.079 pilot whales per longline set during the study period), and thus, bycatch is best quantified by examining rates of bycatch across multiple longline sets. We used this approach to evaluate whether the habitat model could be used to predict pilot whale bycatch in the longline fishery in four ways. First, we quantified BPUE within ten classes of predicted pilot whale occurrence probabilities generated by the model (probabilities of 0–0.1, 0.1–0.2, 0.2–0.3, 0.3–0.4, 0.4–0.5, 0.5–0.6, 0.6–0.7, 0.7–0.8, 0.8–0.9 and 0.9–1) and examined correlations between predicted probabilities and BPUE. Second, we assessed differences in predicted pilot whale occurrence probabilities for sets that caught different numbers of pilot whales (sets with no pilot whale bycatch vs. sets in which bycatch was observed; and comparisons of sets with 1 vs. 2 pilot whales caught) using Wilcoxon rank sum tests. Thirdly, we examined relationships between monthly BPUE and predicted probabilities of pilot whale occurrence for observed sets during that month. All analyses were limited to classes and time periods with at least five observed sets. Lastly, we compared spatial predictions of the model during a period of high BPUE with those from a period of low BPUE when fishing effort covered a similar spatial extent to assess whether model could be used to predict temporal periods of high bycatch, and to shed light on why bycatch was so high during these time periods. Specifically, we compared model predictions for December 2015, when pilot whale BPUE was particularly high (Stepanuk et al., 2018; 0.32 pilot whales per set), with predictions during the same month in previous years, when pilot whale BPUE occurred at more typical levels (0.077 pilot whales per set during December 2010–2014).

To examine whether predictive modelling using dynamic habitat variables could be used to identify high-risk areas for pilot whale bycatch more precisely than static management approaches, we compared the area covered by static approach discussed by Stepanuk et al. (2018) (the region 15 km inshore of the 1,000-m isobath) with the area predicted by our pilot whale habitat model seasonally within the MAB and NEC regions (Figure 2d). We examined predicted probabilities of pilot whale occurrence at the time and location of longline sets, and for illustration purposes, we considered high-risk areas for pilot whale bycatch to be those occurring at probabilities above the lower 95% confidence interval (CI) of longline sets in which pilot whale bycatch was observed. Occasionally, regions within Gulf Stream rings in distant offshore waters were identified as likely pilot whale habitat using this approach (Figure 4). As pilot whale bycatch occurs in close proximity to the shelf break and no bycatch was observed within offshore Gulf Stream waters (Garrison, 2007; Stepanuk et al., 2018), areas within Gulf Stream rings in distant offshore waters were not considered to be high-risk areas for pilot whale bycatch.

3 | RESULTS

GAMM results and k-folds cross-validation showed that the model performed well, with a mean proportion of deviance explained of

TABLE 1 Summary of mixed-effects generalized additive model of pilot whale occurrence

Estimate	Std. error	z Value	Pr(> z)	p-Value	R ²	Prop. Dev. explained	AIC	AUC	Sensitivity	Specificity
(Intercept)	-3.89	0.15	-26.44	<2E-16	0.38	42.57	9,383	0.92	0.95	0.63
Smooth terms	edf	Ref.df	Chi.sq	p-Value						
Distance to shelf break	2.99	3	684.82	<2E-16						
SST	2.73	3	66.08	1.11E-05						
Distance to SST front	2.94	3	1,813.37	<2E-16						
Slope	2.74	3	94.75	1.58E-04						
SLA	2.52	3	175.90	3.58E-03						

Note. Values represent mean values for each of the 10-folds.

42.57 for the 10-folds (Table 1). Comparisons between training and test data sets indicated a high level of agreement with model predictions, with a mean AUC of the receiver operator curve of 0.92, reflecting an excellent fit (Hosmer & Lemeshow, 2000). Model sensitivity (mean of 0.95) was higher than model specificity (mean of 0.63), indicating that the model performed well in predicting where pilot whales occurred, but occasionally predicted presences where none were observed. Given that our model was built using a limited number of tagged whales, and that there are thousands of more whales than those tracked in this study, it follows that the model would predict presences where there were no observations from telemetry data. Our model demonstrated that pilot whales occurred in regions in close proximity to thermal fronts and were associated with warm SST, intermediate bathymetric slopes and both extreme negative and extreme positive values of SLA, representing dynamic regions such as Gulf Stream meanders and rings (Figure 3). Pilot whales primarily occurred in close proximity to the shelf break, but a small number of tagged pilot whales also followed Gulf Stream waters into offshore waters for part or all of their track (Thorne et al., 2017). While in Gulf Stream waters, pilot whale tracks often paralleled the shelf break at distances of 250–350 km (Supporting Information Figure S2), leading to an increase in pilot whale occurrences relative to pseudo-absence locations at this distance.

Seasonal spatial predictions highlighted shifts in pilot whale habitat throughout the year. Most pilot whales occurred in regions of medium to high bathymetric relief at close proximity to the shelf break, but their probabilities of occurrence shifted with dynamic oceanographic variables (SST, SLA, thermal fronts). High probabilities of pilot whale occurrence were restricted to southern regions of the MAB during winter but moved north during late summer and early fall (Figure 4). The northernmost observation of a satellite-tagged short-finned pilot whale occurred in August along the shelf break in proximity to the northern flank of George's Bank (Thorne et al., 2017). This observation matched well with our spatial prediction of pilot whale habitat in the late summer/early fall, in which the northernmost location of high predicted probabilities of pilot whale occurrence was in close proximity to Georges Bank (Figure 4). At daily and weekly time-scales, Gulf Stream rings and

the intrusion of Gulf Stream waters into shelf break regions increased the probability of pilot whale occurrence in these waters (Supporting Information Figure S3).

Predicted probabilities of pilot whale occurrence were strongly and significantly correlated with BPUE for observed longline sets (Pearson's correlation coefficient = 0.84, p -value = 9.2×10^{-3}). This was also true on a monthly time-scale; months with higher observed values of BPUE had higher predicted probabilities of pilot whale occurrence (Pearson's correlation coefficient = 0.36, $p = 1.2 \times 10^{-2}$). Observed longline sets with observed pilot whale bycatch had

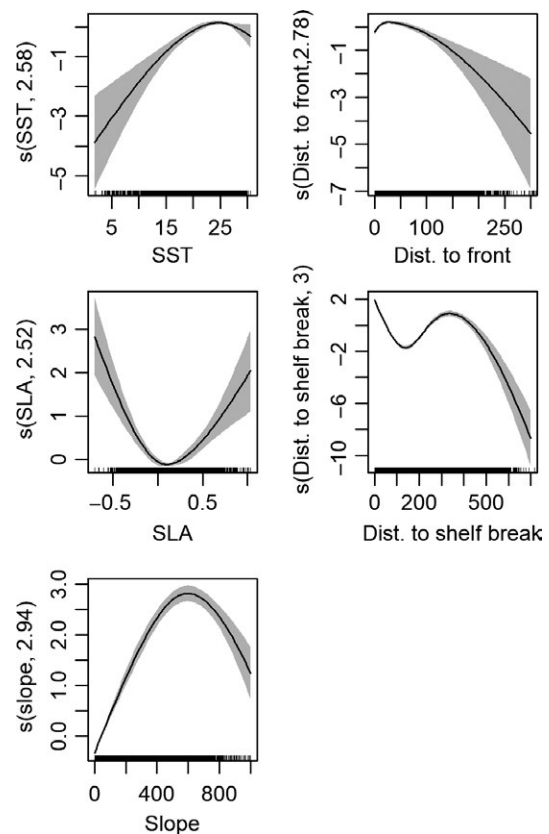


FIGURE 3 Mixed-effects generalized additive model plots of pilot whale presence/absence relative to environmental variables in the Northwest Atlantic. Shaded areas represent standard error

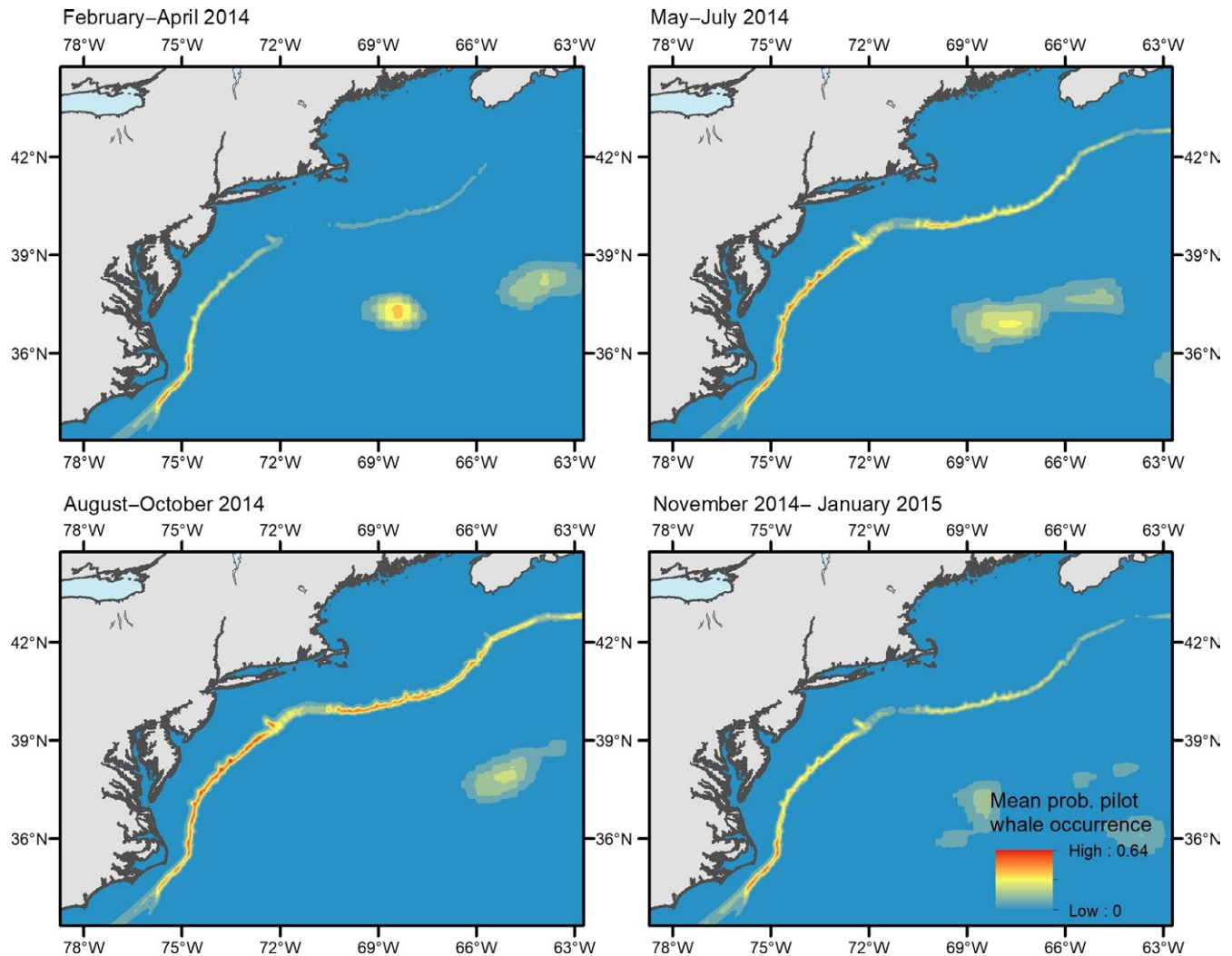


FIGURE 4 Seasonal spatial predictions of short-finned pilot whale occurrence in the Northwest Atlantic. Seasonal means were calculated as means of daily predictions produced from daily environmental conditions

significantly higher predicted probabilities of pilot whale occurrence than those in which no pilot whale bycatch was observed (Wilcoxon rank sum test, $p = 2.7 \times 10^{-9}$). Similarly, observed sets in which a single pilot whale was caught had significantly lower predicted probabilities than those in which two pilot whales were caught (Wilcoxon rank sum test, $p = 3.8 \times 10^{-2}$; Figure 5). During December 2015, when BPUE was unusually high, predicted probabilities of pilot whale occurrence for observed longline sets were significantly higher than those in December 2010–2014, when BPUE occurred at more typical rates (Wilcoxon rank sum test, $p = 1.5 \times 10^{-7}$; Figure 6). While the locations of individual longline sets could not be shown for confidentiality purposes, the spatial distribution of observed longline sets was generally similar between years, as reflected by core fishing areas represented by the 75% kernel density estimate (KDE) of observed longline sets. Higher SST values at the location of observed sets during December 2015 (Wilcoxon rank sum test, $p = 7.9 \times 10^{-10}$) were associated with higher predicted probabilities of pilot whale occurrence at the locations of observed longline sets (Figures 6 and 7).

The lower 95% CI of model probabilities for longline sets in which pilot whale bycatch was observed was 0.34. The areas in the MAB and NEC regions occurring above this threshold varied seasonally and were as follows for each of our four seasonal predictions (Figure 4): 2,673 km² for February to April (note that an additional 3,156 km² occurred within Gulf Stream cold-core rings in distant offshore waters and were not included in this estimate; Figure 4); 5,483 km² for May to July; 9,832 km² for August to October; and 2,582 km² for November to January. By comparison, the area in the MAB and NEC regions 15 km inshore of the 1,000-m isobath, which Stepanuk et al. (2018) found to have high rates of pilot whale bycatch, was 21,427 km².

4 | DISCUSSION

SDMs provide a promising tool for predicting when and where threats to protected species are likely to occur, information which is critical to effective conservation and management (Becker et al., 2012; Briscoe et al., 2018; Hazen et al., 2016, 2018; Willis-Norton

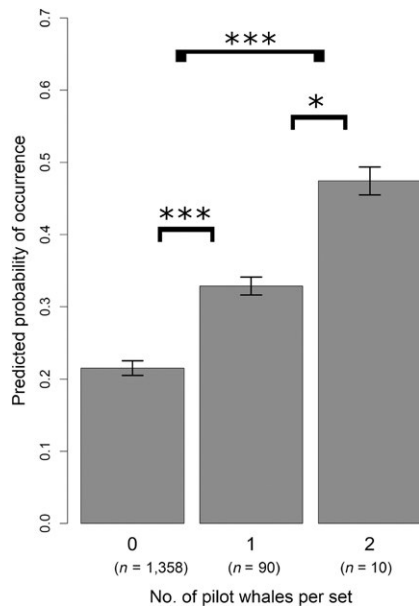


FIGURE 5 Predicted probabilities of short-finned pilot whale occurrence for longline sets observed by fisheries observers relative to the number of pilot whales caught in observed longline sets in the Mid-Atlantic Bight (MAB) and Northeast Coast (NEC). *indicates significance at the $p < 0.05$ level, ***indicates significance at the $p < 0.001$ level

et al., 2015). Assessing model performance using independent data is necessary to test whether the model is generalizable, and SDMs should be evaluated using independent data whenever possible (Chatfield, 1995; Fielding & Bell, 1997; Guisan & Zimmermann, 2000; Manel, Dias, & Ormerod, 1999; Olden, Jackson, & Peres-Neto, 2002; Pearce & Ferrier, 2000). However, in practice, model validation is frequently conducted using the same data to construct and test the model, which can bias estimates of model performance (Araújo, Pearson, Thuiller, & Erhard, 2005; Chatfield, 1995; Pearce & Ferrier, 2000; Torres et al., 2015). For models with management applications, it is particularly important that model performance be assessed rigorously using independent data to ensure that model results can be applied appropriately to a given management scenario before habitat models are integrated into decision-making. For example, marine predators can show differences in habitat preferences between regions, and extrapolating SDMs over broad spatial extents outside of the calibration area can misinform bycatch mitigation efforts (Torres et al., 2015). Further, efforts to decrease bycatch of cetaceans that depredate fishing gear should verify that model results can be applied to accurately predict where and when bycatch is likely to occur. Fishing vessels can actively attract depredating predators, and social learning can influence patterns of depredation in cetaceans; patterns of depredation might therefore differ from typical habitat use (Gilman et al., 2007; Kock et al., 2006; Schakner et al., 2014; Thode et al., 2007). Thus, studies using SDMs to indicate the risk of bycatch should also assess how model predictions relate to observed patterns of bycatch by using independent data from fisheries observers when available to validate the model. In the present study, we developed a predictive model of pilot whale

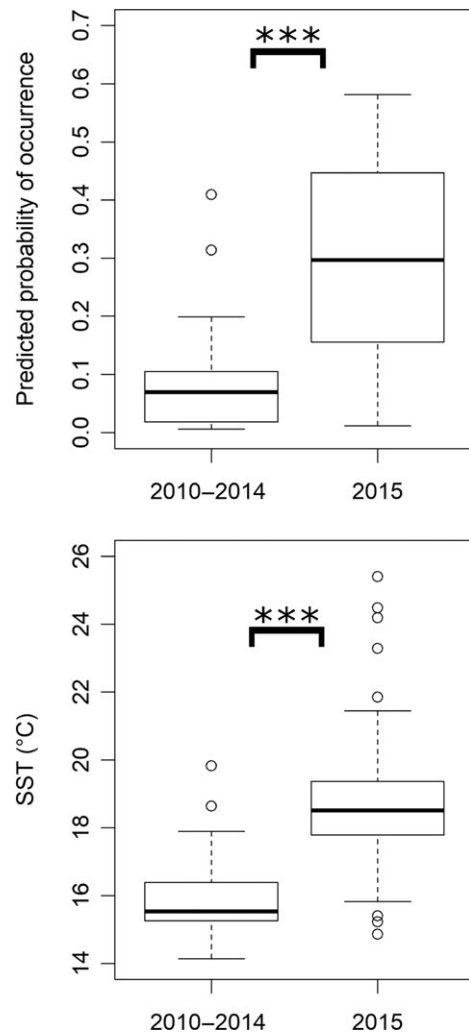


FIGURE 6 Predicted probability of short-finned pilot whale occurrence and observed SST for all longline sets observed by fisheries observers in December 2015 and in December 2010–2014, respectively. Rates of pilot whale bycatch per unit effort (BPUE) were considerably higher in December 2015 than in December 2010–2014 (0.32 pilot whales per set in December 2015 vs. 0.077 pilot whales per set during December 2010–2014). ***indicates significance at the $p < 0.001$ level.

habitat use and tested its ability to predict pilot whale occurrence using both cross-validation and independent data from government fisheries observers. Our predictive habitat model for short-finned pilot whales was not only effective in predicting their occurrence, as assessed using cross-validation, but model predictions were strongly and significantly correlated with observations of pilot whale bycatch. This indicates that pilot whale bycatch occurred in times and places identified as pilot whale habitat, and suggests that in our study area, areas in which depredation occurred did not differ from typical pilot whale habitat use.

Due to the dynamic nature of marine environments, being able to predict species distributions in both space and time is necessary to understanding and mitigating threats to marine species (Hazen et al., 2013, 2016, 2018; Howell et al., 2008; Willis-Norton et al., 2015).

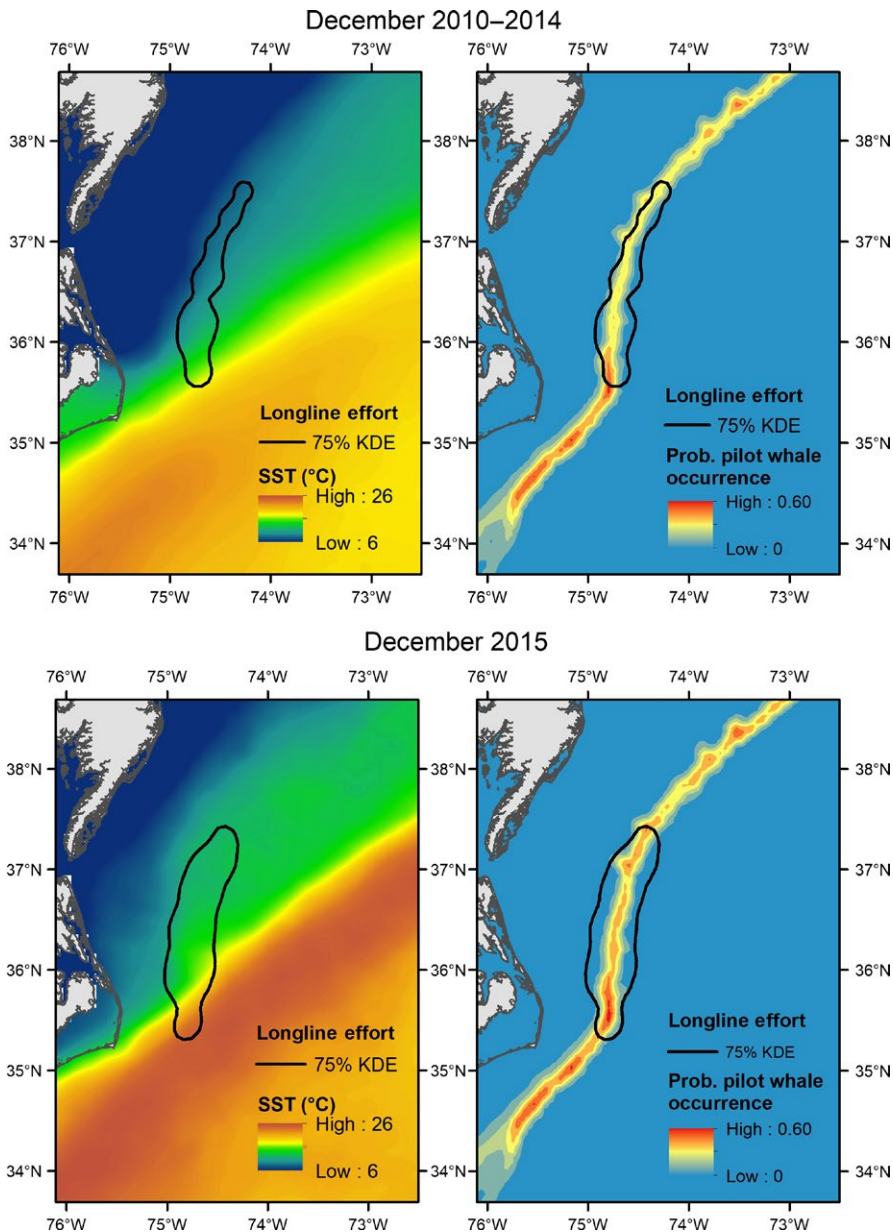


FIGURE 7 Spatial maps of SST and predicted probability of short-finned pilot whale occurrence relative to the 75% kernel density estimate (KDE) of longline sets observed by fisheries observers in December 2010–2014 in comparison with December 2015. The locations of individual longline sets could not be displayed for confidentiality purposes

We found that dynamic oceanographic variables (SST, thermal fronts, SLA) were important factors driving the habitat of short-finned pilot whales, so predicted spatial distributions of this species showed a great deal of variability through time. Dynamic variables were also useful in understanding observed temporal patterns of bycatch; for example, spatial predictions from our model and satellite SST images suggest that higher SST in the area fished played a role in the unusually high rates of BPUE observed in December 2015 (Stepanuk et al., 2018; Figures 6 and 7). Short-finned pilot whales feed primarily on mesopelagic and bathypelagic squid and fish, ectothermic prey which show distributional shifts in association with changes in temperature (Funes-Rodriguez, Hinojosa-Medina, Aceves-Medina, Jimenez-Rosenberg, & Jesus Bautista-Romero, 2006; Hsieh, Kim, Watson, Lorenzo, & Sugihara, 2009; Jensen, Perez, Johnson, Soto, & Madsen, 2011; Mintzer et al., 2008). In addition, thermal fronts and mesoscale oceanographic features such as Gulf Stream meanders

and rings may provide enhanced foraging opportunities for foraging marine predators (Dragon, Monestiez, Bar-Hen, & Guinet, 2010; Rodhouse et al., 1996; Scales et al., 2014).

This case study demonstrated that incorporating dynamic oceanographic variables into SDMs can allow times and locations with a high risk of pilot whale bycatch to be identified more precisely than approaches relying upon static habitat factors alone. The high-risk areas for pilot whale bycatch predicted by our model were considerably smaller than those identified using static variables alone, and the extent covered by the high-risk areas varied seasonally. In both February through April and November through January, predicted high-risk areas for pilot whale bycatch were constrained spatially, covering 12.5% and 12.0%, respectively, of the area identified from static habitat features (i.e. the area 15 km inshore of the 1,000-m isobath). Predicted high-risk areas occurred further north and covered a broader area from May through October due to warmer SST values in higher

latitudes during these months, reaching a maximum of 45.9% of the area identified using the static approach in August through October. However, it is important to note that particularly in winter months, the static approach examined here likely overestimates the area used by fishers; during winter months, longline fishing effort typically occurs in cooler waters than pilot whale observations, but is less likely to occur in the northernmost extent of the MAB and NEC (Stepanuk et al. 2018).

The predictive model presented here could be applied to near real-time satellite oceanographic data to produce “now-casts” of high-risk areas for pilot whale bycatch that could be used to develop management strategies to reduce pilot whale-longline bycatch (sensu Hobday & Hartmann, 2006, Howell et al., 2008, Hazen et al., 2016). In other regions, near real-time predictions of bycatch species are used to indicate regions that fishers should avoid in order to decrease bycatch, or are used by managers to regulate fisher access to spatial management zones (Hobday, Hartog, Spillman, & Alves, 2011; Howell et al., 2008). Similarly, spatial predictions of the risk of pilot whale bycatch in the MAB and SEC could be posted online and revised regularly (daily) based on the most recent environmental data to provide up-to-date information on high-risk areas that should be avoided. These predictions could be useful to fishers, allowing them to reduce costs of lost fish and bait, while providing a conservation benefit by decreasing bycatch of a protected species.

In the future, forecasts of oceanographic variables combined with cetacean habitat models could provide forecasts of cetacean occurrence and could greatly improve planning and decision-making for fishers and managers (Becker et al., 2012, 2018). The utility of this approach has been demonstrated in other applications; for example, seasonal forecasts of environmental conditions are used to predict the distribution of southern Bluefin tuna (*Thunnus maccoyii*) in the Great Australian Bight at lead times of up to 2 months. Forecasts of tuna distributions are provided online daily and are used by fishers in making operational decisions, such as when and where to fish in order to catch their quota more efficiently (Eveson, Hobday, Hartog, Spillman, & Rough, 2015; Tommasi et al., 2017). Seasonal forecasts of cetacean distributions could be used to mitigate threats, such as bycatch or ship strikes (Becker et al., 2012; Hazen et al., 2016). Seasonal forecasts of variables such as SST are currently available at lead times of up to 6–9 months, and international collaborative efforts, such as the World Climate Research Program (WCRP) S2S experiment, aim to improve forecast skill on subseasonal to seasonal time-scales. As a region strongly influenced by a western boundary current (the Gulf Stream), the model skill of seasonal SST forecasts in the north-east United States is currently low (Stock et al., 2015), but future improvements to seasonal forecasts could provide important opportunities for predicting and managing living marine resources.

Predictive models are particularly useful for informing conservation and management for species whose distributions are not well understood; by understanding how environmental conditions influence habitat use, predictions can be made in times and places where little or no data are available (Thorne et al., 2012). For highly mobile species such as cetaceans, observations often cannot be made in all habitats or time periods of interest. The telemetry data we used to

build our predictive models were collected during 2014 and 2015, and further satellite tag deployments could be used to improve the model predictions presented here. It will be important to verify that our model predictions reflect pilot whale habitat use over a broader time period. However, our model predictions showed strong agreement with observations of bycatch when applied to POP data outside the tagging period (2010–2015), suggesting that these predictions are accurate when extrapolated to other time frames. Further, our results highlight the importance of telemetry data in producing much-needed data on movement and habitat use for species such as pilot whales that are otherwise difficult to study. Due to difficulties in distinguishing the two pilot whale species, there was little species-level information on pilot whale habitat use in the North Atlantic prior to our studies, hampering our understanding of the environmental factors driving the distribution of this species that could be used to mitigate pilot whale bycatch. Telemetry data can be used to predict the detailed response of species to dynamic oceanography, facilitating the development of models that predict habitat in space and time, and are thus useful in conservation and management (Hazen et al., 2016). In the absence of telemetry data, analyses of pilot whale habitat use at the species level would be limited to observations from sightings from surveys which are very expensive and difficult to acquire; as a result, it would take a long time to obtain sufficient data to build models with a strong predictive capacity. Thus, for species that are difficult to study at sea or are sparsely distributed, telemetry studies are a powerful means of assessing the habitat use of populations facing significant anthropogenic threat and allow for informative predictive models to be developed.

While our model performed well in predicting pilot whale bycatch in the longline fishery in relation to dynamic oceanographic variables, pilot whale occurrence in distant Gulf Stream waters was not as well represented by the model. Tagged pilot whales occasionally followed Gulf Stream meanders into pelagic waters (Thorne et al., 2017), though the vast majority of telemetry locations for short-finned pilot whales (>75%) in the present study occurred within 10 km of the shelf break. Longline fishing effort is focused in proximity to the shelf break, and no pilot whale bycatch was observed within these offshore Gulf Stream waters (Garrison, 2007; Stepanuk et al., 2018). Thus, although further observations of pilot whales will be useful in understanding factors driving the use of pelagic waters, we feel that our model predictions in nearshore waters were appropriate for assessing the risk of bycatch in the pelagic longline fishery.

In addition to dynamic oceanographic variables, bathymetric variables were strong predictors of short-finned pilot whale habitat. Regions with steep bathymetric slopes in close proximity to the shelf break were positively associated with pilot whale occurrence, and rates of pilot whale bycatch are known to be higher in proximity to the shelf break (Garrison, 2007; Stepanuk et al., 2018). The shelf break region may provide enhanced foraging opportunities for pilot whales as a result of increased primary and secondary productivity at the shelf break and/or due to the presence of steep slopes which may provide a physical barrier that facilitates the capture of prey (Herman, Sameoto, & Longhurst, 1981;

Munk, Larsson, Danielssen, & Moksness, 1995; Sambrotto, Mordy, Zeeman, Stabeno, & Macklin, 2008; Thorne et al., 2017; Young et al., 2001). Tagged short-finned pilot whales did not move into waters of the South Atlantic Bight, although short-finned pilot whales are known to occur in more southerly waters of the south-eastern United States. Short-finned pilot whales occurring north of Cape Hatteras may exhibit a foraging specialization that influences their habitat use and leads to a strong association with bathymetric gradients (Thorne et al., 2017). Our model did not predict high probabilities of occurrence in these more southerly waters, where steep bathymetric gradients are restricted to deeper waters (>1,200 m depth), providing support for the importance of steep bathymetric gradients to short-finned pilot whale habitat in the MAB and NEC regions of the United States.

Our results demonstrate that short-finned pilot whale occurrence in the MAB and NEC regions of the United States can be predicted using a small number of readily available environmental parameters and that our predictive habitat model performs well in predicting bycatch of short-finned pilot whales in the pelagic longline fishery. Combining our model outputs with forecasted or near real-time oceanographic data could provide an effective means of predicting regions with a high risk of fisheries bycatch. Together with advances in satellite oceanography, telemetry data provide an important source of data for creating and testing predictive habitat models that facilitate the development of adaptive management strategies to mitigate fisheries bycatch with protected species.

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DATA ACCESSIBILITY

Short-finned pilot whale telemetry tracks are available in Movebank (www.movebank.org), under the identifier "short-finned pilot whales CRC NW Atlantic." Bathymetric and oceanographic data are available online as indicated in Section 2.

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BIOSKETCH

The shared interests of the research team focus on the use of telemetry, satellite oceanography and quantitative methods to evaluate the habitat use of pelagic marine mammals in order to inform management and conservation efforts.

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SUPPORTING INFORMATION

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

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