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Original Article

Long-term climate ocean oscillations inform seabird bycatch from pelagic longline fishery

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Seabirds are facing increasing threats in both marine and terrestrial habitats, and many populations have experienced dramatic declines over past decades. Fisheries bycatch is the most pervasive at-sea threat and is of increasing concern in fisheries management and marine conservation. We predicted spatial and temporal heterogeneities of seabird bycatch probability in the US Atlantic pelagic longline fishery (PLL) through an interactive Barrier model based on observer data from the National Marine Fisheries Service Pelagic Observer Program. The Barrier model prevents bias caused by physical barriers such as coastlines by defining the spatial correlation function as a collection of paths between points and eliminating any paths across physical barriers. The integrated nested Laplace approximations methodology and stochastic partial differential equations approach were applied to fit the model, greatly reducing execution time. Seabird bycatch had a hotspot of high bycatch probability in the mid-Atlantic bight in most years, and the hotspot varied in presence and location yearly. The inter-annual variations in bycatch hotspot are correlated with Gulf Stream meanders. Special area and time fishing restrictions predicted by relationships with Gulf Stream positions might enable the US Atlantic PLL to avoid peak areas and periods of seabird bycatch and thereby support seabird conservation.

Keywords: barrier model, climate influence, seabird bycatch, spatiotemporal pattern

Introduction

Half of all seabird species are in decline, and species listed in the Agreement on the Conservation of Albatrosses and Petrels are among the most threatened (Croxall *et al.*, 2012). The most recent assessment of the global threat status of seabirds, using the International Union for Conservation of Nature red list criteria, revealed that, of the 359 seabird species, 31% (110 species) are globally threatened and a further 11% (40 species) are near threatened (BirdLife International, 2018). The major threats to seabirds include invasive alien species, bycatch in fisheries, climate change, overfishing, hunting or tapping and disturbance (Dias *et al.*, 2019). Bycatch in fisheries is recognized as the most pervasive at-sea threat faced by seabird populations (Lewison *et al.*, 2012; Phillips *et al.*, 2016; Rodríguez *et al.*, 2019), with observed impacts on up to 100 species of marine birds (Dias *et al.*, 2019). Seabirds come into conflict with fisheries when they forage behind vessels for food. Birds ingest baited hooks or become entangled with lines and then are drowned as gear sinks (Brothers, 1999; Gilman, 2001). Many seabird species, such as albatrosses and petrels, are particularly vulnerable to fisheries incidental mortality due to long natural life spans and low reproduction rates (Warham, 1990, 1996). These population characteristics cause increases in adult mortality to have more severe adverse population impacts than the loss of young birds, even leading to population collapse (Croxall and Rothery, 1991; Igual *et al.*, 2009). Understanding the factors influencing the probability of seabirds being caught as bycatch is central to both the sustainable management of longline fisheries and the conservation of seabird populations.

Multiple factors have been reported to influence seabird bycatch rate, such as geographic location, season, time of day, fishing effort, and bait type (Trebilco *et al.*, 2010; Li and Jiao, 2013). Large-scale climate indices, such as El Niño-Southern Oscillation (ENSO) in the eastern Pacific, North Atlantic Oscillation (NAO) in the North Atlantic, Atlantic Multidecadal Oscillation (AMO) in the North Atlantic and Gulf Stream meanders in the western North Atlantic, have been proposed to influence spatial–temporal patterns of bycatch and bycatch susceptibility (Durant *et al.*, 2004; Barbraud *et al.*, 2012; Gilman *et al.*, 2016). For example, changes in wind patterns and oceanographic conditions might affect the foraging efficiency and distribution of seabirds, influencing the overlap of birds and fishing distributions; unfavourable oceanographic conditions might decrease regional ocean productivity, resulting in more starving birds foraging around vessels, thus increasing bycatch risk. Knowledge of relationships of bycatch patterns or their drivers to climate cycles is useful to identify bycatch "hotspots" and to help design voluntary or mandatory changes in the deployment of effort to reduce seabird bycatch risk.

In this study, we (i) predict the temporal and spatial heterogeneity of seabird bycatch probability through an interactive Bayesian hierarchical model using the 1992–2017 pelagic longline fishery (PLL) observer data in the three contiguous US Atlantic pelagic longline fishing zones with highest seabird bycatch—the northeast coast (NEC; 60–71°W, 35–42°N), the mid-Atlantic bight (MAB; 71–82°W, 35–41°N), and the south Atlantic bight (SAB; 71–82°W, 30–35°N)—and (ii) analyse the influence of climate variability on the spatiotemporal distribution of the probability of catching a seabird. Special attention is given to the impacts of NAO, AMO, and the Gulf Stream because we hypothesized that the distributions of seabird bycatch is related to these climate indices. We selected the interactive Bayesian hierarchical modelling approach to allow us to apply multiple levels of detail to describe seabird bycatch probability in time and space.

Methods

Seabird bycatch data from Pelagic Observer Program

The Pelagic Observer Program (POP) at the National Marine Fisheries Service Southeast Fisheries Science Center has monitored the US PLL in the North Atlantic since 1992 (Beerkircher *et al.*, 2005; Diaz *et al.*, 2009). In the program, randomly selected fishing trips are accompanied by an observer, who records detailed information on fishing effort, fish species, target catch, gear specification, bycatch, and environmental conditions. The fishery operates in 11 specified fishing zones (Figure 1a) and targets tunas (*Tunnus* spp.), swordfish (*Xiphias gladius*), dolphinfish (*Coryphaena hippurus*), and sharks (Selachimorpha) (Lee and Brown, 1998). Prior to August 2004, two types of hooks (i.e. J-hook and circle hook) were used in this fishery, but J-hooks were used on ∼99% of all sets. Since August 2004, exclusive circle hook use has been legally mandated (69 Federal Register 40734). The POP attempted to cover 8% of PLL trips in each fishing zone and each calendar quarter (Diaz *et al.*, 2009) to improve the precision of bycatch estimates to a 20–30% coefficient of variation after 2004 [NMFS (National Marine Fisheries Service), 2003; Moore *et al.*, 2009]. We analysed 6469 longline sets of the POP data from 1992 to 2017 in the NEC, MAB, and SAB. Only 77 sets caught 149 seabirds; therefore, ∼99% zero observations were present in the POP data (Figure 1b). Among those identified seabirds in this program, gulls (*Larus* sp.) were the most frequently captured, followed by shearwaters (Procellariidae spp., especially great shearwaters, *Ardenna gravis*) and northern gannets (*Morus bassanus*) (Table 1). Seabird bycatch rates in the three zones showed obvious spatial and temporal patterns: 62% of seabirds were caught in the MAB, 99% of seabirds were caught in summer through winter, and a peak in catch occurred in 1997.

Covariate effects

The potential explanatory variables for model development are listed in Table 2. Year was included as a random factor in catch/bycatch analysis to explore inter-annual variation. Season

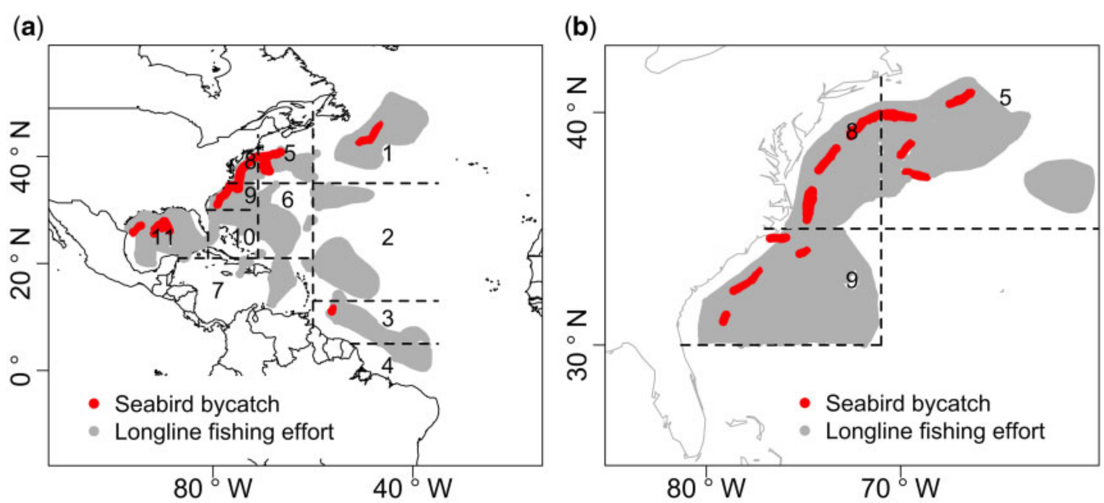

Figure 1. (a) Spatial distribution of observed longline sets (grey area) and those with seabirds caught (red strips) in all fishing zones from 1992 to 2017. (b) Spatial distribution of observed longline sets (grey area) and those with seabirds caught (red strips) in three east coast zones from 1992 to 2017. Abbreviations are as follows: 1, northeast district; 2, north central Atlantic; 3, tuna north; 4, tuna south; 5, NEC; 6, Sargasso region; 7, Caribbean region; 8, MAB; 9, SAB; 10, Florida east coast; 11, Gulf of Mexico.

Table 1. A list of seabird species caught in the POP by area.

Family	Species	NEC	MAB	SAB	Total
Laridae	Herring gull (*Larus argentatus*)	3	13	1	17
	Laughing gull (*Larus atricilla*)	0	0	1	1
	Black-backed gull (*Larus marinus*)	0	10	0	10
	Other Laridae spp.	2	21	0	23
Procellariidae	Great shearwater (*Ardenna gravis*)	7	18	0	25
	Cory's shearwater (*Calonectris diomedea*)	0	1	1	2
	Northern fulmar (*Fulmarus glacialis*)	0	1	0	1
	Other Procellariidae spp.	1	2	0	3
Sulidae	Northern gannet (*Morus bassanus*)	3	8	4	15
Pelecanidae	Brown pelican (*Pelecanus occidentalis*)	0	0	0	0
Oceanitidae	Wilson's storm petrel (*Oceanites oceanicus*)	0	1	0	1
Stercorariidae	Arctic skua (*Stercorarius parasiticus*)	0	0	0	0
Unidentified	Aves	28	11	12	51

Table 2. Potential explanatory variables included in the models.

Variables	Type	Categories/mean	Unit
Year	Categorical	1992–2017	–
Season	Categorical	Winter, spring, summer, fall	–
Target species	Categorical	Mixed species, swordfish, tuna, shark, dolphinfish	–
Longitude	Continuous	−73.86	°W
Latitude	Continuous	36.25	°N
Water temperature	Continuous	23.62	°C
Water depth	Continuous	789.60	m
Wind speed	Continuous	12.69	kn
Wind direction	Continuous	173.30	°
Wave height	Continuous	3.67	ft
Hook type	Categorical	Circle hook (13/0, 16/0, 18/0, 20/0), J-hook (7/0, 8/0, 9/0, 10/0, 11/0, 13/0, 14/0)	–
Number of hooks	Continuous	720	–
Set speed	Continuous	6.85	kn
Hook depth	Continuous	17.88	m
Additional weight	Continuous	1.10	lbs
Set duration	Continuous	3.13	hr
Haul duration	Continuous	5.71	hr
Soak duration	Continuous	8.52	hr
Bait type	Categorical	Mackerel, squid	
Set time	Categorical	Day (6:30–19:30 spring, 5:30–19:30 summer, 7:00–18:30 fall, 7:30–18:00 winter), night	
Haul time	Categorical	Day (same as set time), night	
Discard rate	Continuous	18	Inds/set

was included to explore intra-annual variation. Target species represented the different fishing practices used for each, e.g. bait type and line depth (Li *et al.*, 2012, 2016). Water temperature would affect prey availability, creating redistribution, or changed feeding behaviour of seabird populations (Durant *et al.*, 2004). Bait type was hypothesized to impact seabird bycatch (Watson *et al.*, 2005; Trebilco *et al.*, 2010). A recent study in the same region demonstrated hook type could significantly influence seabird bycatch, although its influence might be confounded by other factors, such as bait type, fishing location, season and target species (Li *et al.*, 2012). Wind and wave action might have effects on seabird flight and, therefore, on their abundance in the area (Løkkeborg, 2003; Weimerskirch *et al.*, 2012). Most seabirds are visual feeders and forage during daytime, so setting longlines at night, as when targeting swordfish, could reduce the number of birds attacking baited hooks (Løkkeborg, 2011). Deeper setting might limit bird access to baited hooks (Løkkeborg, 2011). In longline fisheries, seabirds are vulnerable to being hooked during the short period between when hooks leave the vessel and when hooks sink beyond the diving ranges of seabirds (Brothers, 1991; Løkkeborg, 2011); therefore, additional weights, by helping hooks sink more rapidly, might reduce the duration of bait availability to birds and bird vulnerability to hooking (Gladics *et al.*, 2017). Discards from vessels may attract scavenging seabirds to the area of a longline fishing operation, where they are trapped and drowned by taking bait on hooks or becoming tangled in line (Brothers, 1999). Number of hooks, set duration, haul duration, and soak duration were incorporated into analyses to determine the impacts of these variations in fishing effort on seabird bycatch. Some fishing-correlated factors including hook type, hook depth, set time, and bait type were confounded with other factors, such as year and target species (Supplementary Figure S1), which might blur the influence of these fishing-correlated factors on seabird bycatch.

Model framework

A set of Bayesian hierarchical models were developed to analyse POP bycatch presence–absence data. A binomial probability distribution governed the binary outcome of whether at least one seabird was caught. The probability model described the probability of producing a bycatch event with a logit link:

$$\text{logit}(p) = \text{intercept} + f(\text{year}) + f(\text{season}) + f(\text{target species}) + \sum s_i(x_i) + \xi_s,$$

where p is the probability of catching a seabird; f(year), f(season), and f(target species) are random effects; x_i is the ith explanatory variable; s_i is a smooth function for the ith explanatory variable, defined through a first-order random walk (RW1) process (Rue and Held, 2005; for details, see Supplementary material); and ξ_s represents the spatial effect modelled through the stochastic partial differential equation (SPDE) approach. A set of models were also extended to a spatiotemporal interaction model with time-varying spatial heterogeneity, in which ξ_s in the above equation is replaced with $\xi_{s,t}$ to represent the spatiotemporal autocorrelation.

The spatial effect was in the form of a Gaussian random field (GRF) that was defined by a mean function (assumed to be 0) and a covariance function (Banerjee *et al.*, 2014). Given the proximity of our data to the northeast US coast, we defined the covariance function as a collection of paths between two points through a simultaneous autoregressive (SAR) model, instead of a correlation function on the distance (Bakka *et al.*, 2019). The paths that crossed the physical barriers were then eliminated, so the distance between two points was not the shortest distance, but an indirect result of the new collection of available paths (Bakka *et al.*, 2019). This model, called a Barrier model, had the capability to address the effects of physical barriers but required no more computational time than the non-Barrier model (Bakka *et al.*, 2019).

Model fitting and comparison

In Bayesian statistics, traditional Markov Chain Monte Carlo (MCMC) algorithms may take a long computational time when dealing with a continuous spatial field (Rue *et al.*, 2009a; Banerjee *et al.*, 2014). As an alternative, a new statistical approach, integrated nested Laplace approximations (INLA) methodology, saves computational time by approximating the marginal posterior (Rue and Held, 2005; Lindgren *et al.*, 2011). In particular, the SPDE approach implemented in the INLA framework provides an effective solution to simulate a spatial effect by representing a continuous spatial process as a discretely indexed spatial process (Rue and Held, 2005; Lindgren *et al.*, 2011). The first step in the SPDE approach was to construct a triangular mesh to cover the spatial region (Figure 2). Compared with a regular grid, the triangular mesh set smaller size triangles in areas with more observations and larger ones in areas with fewer observations, which saved computational costs and increased the accuracy of the spatial effect where there were observations. The POP data were then projected onto the mesh. Sparse basis functions were evaluated over the adjacent mesh nodes and used to approximate the spatial effect. The mesh included some extension beyond the outer points to avoid "boundary effects", i.e. larger variance at the boundary (Lindgren and Rue, 2015).

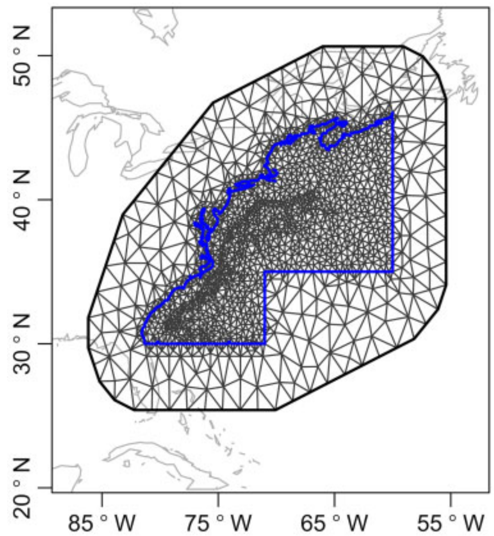

Figure 2. Mesh created in the present study. The blue line is the domain boundary. The SPDE edge effects are moved outside the domain of interest using an extension with larger triangles.

All analyses were performed using the R and R-INLA package (Rue *et al.*, 2009b). The INLA procedure estimated the marginal posterior distributions of random effects and the parameters involved in the model. There are different options offered in R-INLA with which to approximate the marginal posterior distributions, and we used the most accurate one—the Laplace (Martins *et al.*, 2013). The default and recommended settings for priors were adopted (Held *et al.*, 2010; Lindgren and Rue, 2015; Simpson *et al.*, 2017; Fuglstad *et al.*, 2019; Bakka *et al.*, 2019). These priors were non-informative priors and had little influence on the posterior distributions; hence, results mostly came from the data (for details on the priors, see the Supplementary material).

Models with different covariates and spatiotemporal effects were compared based on deviance information criterion (DIC; Spiegelhalter *et al.*, 2002) and Watanabe–Akaike information criterion (WAIC; Watanabe, 2010). The DIC is defined as

$$\text{DIC} = \bar{D} + p_D,$$

where $\bar{D}$ is the posterior mean of the deviance of the model and p_D is the effective number of parameters in the model (Spiegelhalter *et al.*, 2002).

The WAIC is defined as

$$\text{WAIC} = -2 \times (\text{LPPD} - p_D),$$

where LPPD is the log posterior predictive density (Watanabe, 2010).

The DIC has been popular recently, but it is known to have some problems. For example, DIC can produce a negative estimate of p_D. Such problems may arise partly from not being fully Bayesian in that DIC is based on a point estimate (van der Linde,

Table 3. DIC and WAIC values for models with different covariates and spatiotemporal effects.

Model	Model structure	DIC	WAIC	ΔDIC	ΔWAIC
M22	Intercept + year + season + target species + water temperature + set time + $\xi_{s,t}$	637.03	652.94	0	0
M21	Intercept + year + season + target species + water temperature + set time + ξ_s	725.99	729.79	88.96	76.85
M18	Intercept + year + season + target species + water temperature + set time	729.62	732.63	92.59	79.69
M20	Intercept + year + season + target species + water temperature + set time + discard rate	730.01	733.18	92.98	80.24
M19	Intercept + year + season + target species + water temperature + set time + haul time	731.08	734.24	94.05	81.30
M16	Intercept + year + season + target species + water temperature + soak duration	742.09	744.76	105.06	91.82
M9	Intercept + year + season + target species + water temperature + hook type	743.33	745.86	106.30	92.92
M5	Intercept + year + season + target species + water temperature + water depth	744.85	747.13	107.82	94.19
M12	Intercept + year + season + target species + water temperature + hook depth	745.81	748.33	108.78	95.39
M14	Intercept + year + season + target species + water temperature + set duration	746.29	748.42	109.26	95.48
M11	Intercept + year + season + target species + water temperature + set speed	746.30	748.47	109.27	95.53
M4	Intercept + year + season + target species + water temperature	746.13	748.48	109.10	95.54
M10	Intercept + year + season + target species + water temperature + number of hooks	746.50	748.69	109.47	95.75
M15	Intercept + year + season + target species + water temperature + haul duration	746.54	748.80	109.51	95.86
M13	Intercept + year + season + target species + water temperature + additional weight	746.68	748.83	109.65	95.89
M6	Intercept + year + season + target species + water temperature + wind speed	746.76	748.91	109.73	95.97
M7	Intercept + year + season + target species + water temperature + wind direction	746.50	748.96	109.47	96.02
M8	Intercept + year + season + target species + water temperature + wave height	746.88	749.03	109.85	96.09
M17	Intercept + year + season + target species + water temperature + bait type	747.20	749.44	110.17	96.50
M3	Intercept + year + season + target species	761.03	763.08	124.00	110.14
M2	Intercept + year + season	770.13	771.10	133.10	118.16
M1	Intercept + year	799.44	800.09	162.41	147.15

Abbreviations are as follows: ξ_s, constant spatial effect; $\xi_{s,t}$, spatial effect with a different realization every year. Models are ordered according to their ΔWAIC.

2005; Plummer, 2008). The WAIC is fully Bayesian and, therefore, uses the entire posterior distribution, so it is recommended over the DIC criterion (Gelman *et al.*, 2014). The WAIC was computed to validate the DIC in this study.

Climate indices and correlation analyses

The NAO index was obtained from NCAR (2019). The winter (i.e. December–February mean) NAO index was incorporated into our analysis because the signal:noise ratio of NAO was strongest in winter (Hurrell *et al.*, 2003). The annual AMO index based on the Kaplan sea surface temperature data set was from ESRL (2019). The annual Gulf Stream North Wall (GSNW) index was obtained from Dr Arnold H. Taylor (Plymouth Marine Laboratory, pers. comm.). The GSNW index is derived from principal component analysis of the monthly latitudinal position of the GSNW at six longitudes as the Gulf Stream leaves the northeast coast of the United States at about Cape Hatteras.

Clear spatial patterns of seabird bycatch have been observed in the POP data of the three zones, with most seabirds caught along the coastline (Figure 1b). As a first step towards diagnosing the potential drivers of the spatiotemporal distribution of seabird bycatch probability, the relationships between different climate indices and the pattern of seabird bycatch probability, shown as the year effect on bycatch probability and the geographic coordinates of the hotspot centre each year, were analysed through their cross-correlation function (CCF), a statistical approach commonly used to investigate the possible time-lagged dependence between two variables (Shumway and Stoffer, 2011). A p-value of $\leq$0.05 for the CCF test was considered significant.

Results

Model comparison and selected explanatory variables

The DIC and WAIC values of models with different covariates and spatiotemporal effects are presented in Table 3. Model performance improved by incorporating year, season, target species, water temperature, and set time; therefore, these were the selected covariates incorporated into the final model. The probability model that was fitted with a spatial effect that varied across years (M22) performed better than the model with a constant spatial effect (M21), implying that the spatial patterns of seabird bycatch in the three zones varied among years.

The year effect on logit(p) showed clear inter-annual variations and peaked around 1997 (Figure 3a). Most of the seabird bycatch was estimated to occur during summer through winter, with the highest bycatch probability in winter and the lowest probability in spring (Figure 3b). Longline sets targeting dolphinfish were estimated to produce the majority of the seabird bycatch; longline sets targeting mixed species, sharks, and tuna produced relatively intermediate values; and longline sets targeting swordfish had the lowest seabird bycatch probability (Figure 3c). There was a negative relationship between water temperature and seabird bycatch probability (Figure 3d). Daytime setting was associated with higher bycatch probability compared with night setting (Figure 3e).

Spatiotemporal effect

The mean and standard deviation of the spatial effect on logit(p) from the best model (M22) are shown in Figure 4. The mean spatial effect varied from year to year (Figure 4a). Excluding years with zero seabird observed caught (i.e. 1996, 2008, 2012 and 2013), the hotspots of high bycatch probability were in the MAB in most years, including 1992–1994, 2002–2004, 2006, 2007, 2009–2011, 2014, 2015 and 2017 (Figure 4a). The hotspots were in the NEC in 1995, 1997, 1998, 2000, and 2001 and in the SAB in 1999, 2005, and 2016 (Figure 4a). In some years, the hotspots were located near the boundaries of fishing zones (Figure 4a). The pattern of uncertainty was driven by the amount of information. Uncertainty estimates revealed

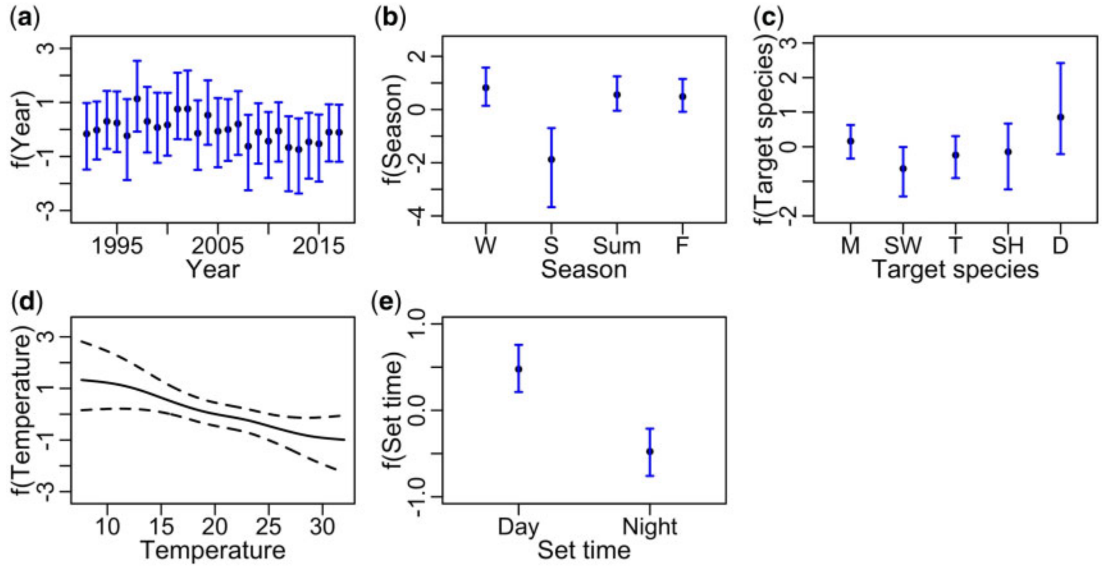

Figure 3. Effects of explanatory variables on seabird bycatch probability [logit(p)] from the interactive Barrier model. Points and solid lines represent posterior mean values; error bars and dashed lines represent 95% credible intervals. Abbreviations of seasons are as follows: W, winter; S, spring; Sum, summer; F, fall. Abbreviations of target species are as follows: M, mixed species; SW, swordfish; T, tuna; SH, shark; D, dolphinfish.

relatively low uncertainty along the coastline where most longline operations take place, and higher uncertainty farther away from the coastline (Figure 4b).

Correlations with climate indices

Time series plots of all climate indices and geographic coordinates of the centre of a hotspot are shown in Supplementary Figure S2. We performed cross-correlation analyses of the latitude and longitude of the hotspot of seabird bycatch in each year with large-scale climate indicators. Significant correlation with the latitude of hotspot centre was found only in one case: the GSNW index of 2 years past displayed a significant positive effect on the latitude of the seabird bycatch hotspot; the higher the GSNW, the more northerly the latitude of the hotspot (Table 4). There was no significant correlation between climate indices and longitude of the hotspot centre (Table 4). The year effect on logit(p) derived from the model was correlated with one climate indicator; significant positive correlation was found between the year effect and the winter NAO index of 2 years past (Table 4; cross-correlation plots in Supplementary Figure S3).

Discussion

Influence of explanatory variables

Our analyses captured the impacts of year, season, target species, water temperature, and set time on seabird bycatch probability. Although additional weight on hooks has been found to reduce seabird bycatch in other studies (e.g. Gladics *et al.*, 2017), its influence is not significant in the present study, possibly due to the limited records on added weight (i.e. 1377 longline sets without records on additional weight) and no detailed information on weight locations. Discard rate did not significantly affect seabird bycatch probability in the current study. Vessels that routinely discharge discards might attract a larger number of seabirds, increasing bycatch risk (Brothers, 1999); however, discharging on the opposite side of the vessels from the setting or hauling stations might draw seabirds' attention from baited hooks and reduce bycatch (Cherel *et al.*, 1996). The impacts of factors, such as hook depth, hook type, and bait type, were not significant, possibly because effects of these factors were confounded by their correlations with other factors, such as year and target species (Supplementary Figure S1). For example, >99% of longline sets were with J-hook before 2004, ∼61% of longline sets were with J-hook in 2004 and all longline sets were with circle hook after 2004 (Supplementary Figure S1a). The lack of comparison of both types of hook in the same fishing period limited our ability to assess their influence.

The year effect on logit(p) decreases after 2004, when the circle hook replaced the J-hook (Supplementary Figure S1a). In the present study, the commonly used sizes for circle hooks were 16/0 (1825 longline sets) and 18/0 (2059 longline sets) and for J-hooks were 8/0 (472 longline sets) and 9/0 (715 longline sets). Larger hooks might be more difficult for birds to swallow and so reduce bycatch, and, in support, a correlative study found a negative relationship between hook size and seabird bycatch rate (Moreno *et al.*, 1996). Shape may be even more important. A previous study in the same region found that use of the 8/0 J-hook led to the highest probability of catching a seabird (Li *et al.*, 2012). Another potential explanation for the declines from the 1990s to present is that the decreases in fleets of trawlers that fish for silver hake, Atlantic cod, and other groundfish in the Northwest Atlantic resulted in a reduced prey base for seabirds that scavenge for these species at trawlers off the US east coast, leading to a decrease in seabird abundance (Lear, 1998; Veit *et al.*, 2015). The seabird bycatch rate is positively related to seabird abundance (Zhou *et al.*, 2019).

Most seabird longline bycatch species, such as herring gulls (*Larus argentatus*) and great shearwaters, return to their breeding colonies in spring (Harrison, 1983; Onley and Scofield, 2013), so they are less likely to be among the spring bycatch along the US

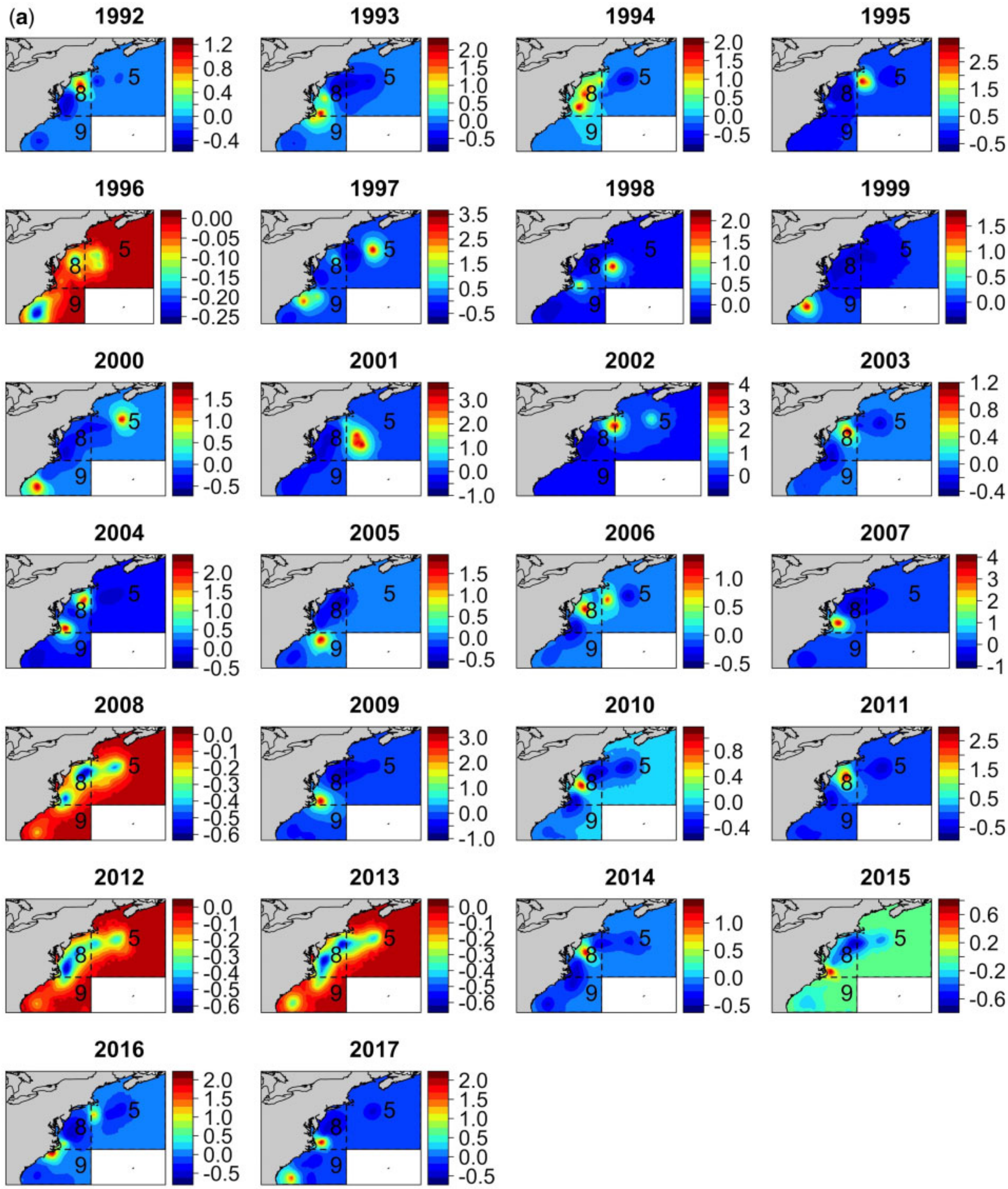

Figure 4. (a) Posterior mean and (b) standard deviation of the spatial effect of logit(p) from the interactive Barrier model (represented by $\xi_{s,t}$ in the model). Abbreviations are as follows: 5, NEC; 8, MAB; 9, SAB. Years with zero seabirds caught are 1996, 2008, 2012, and 2013.

east coast. The North Atlantic near the northeast coast of the United States is the wintering grounds of these species (Harrison, 1983), increasing their chances of being caught during winter in this area.

The influence of water temperature might have been through the food web. A negative relationship of abundance with water temperature has been reported for *Calanus finmarchicus*, a particularly valuable *Calanus* in the copepod–sand lance–seabird food chain (Grieve *et al.*, 2017). Increased prey availability under low water temperature may attract more seabirds, increasing the overlap with fisheries and thus increasing bycatch risk. Night setting produced lower probability of seabird bycatch, since most of the vulnerable seabirds are diurnal foragers (Løkkeborg, 2011).

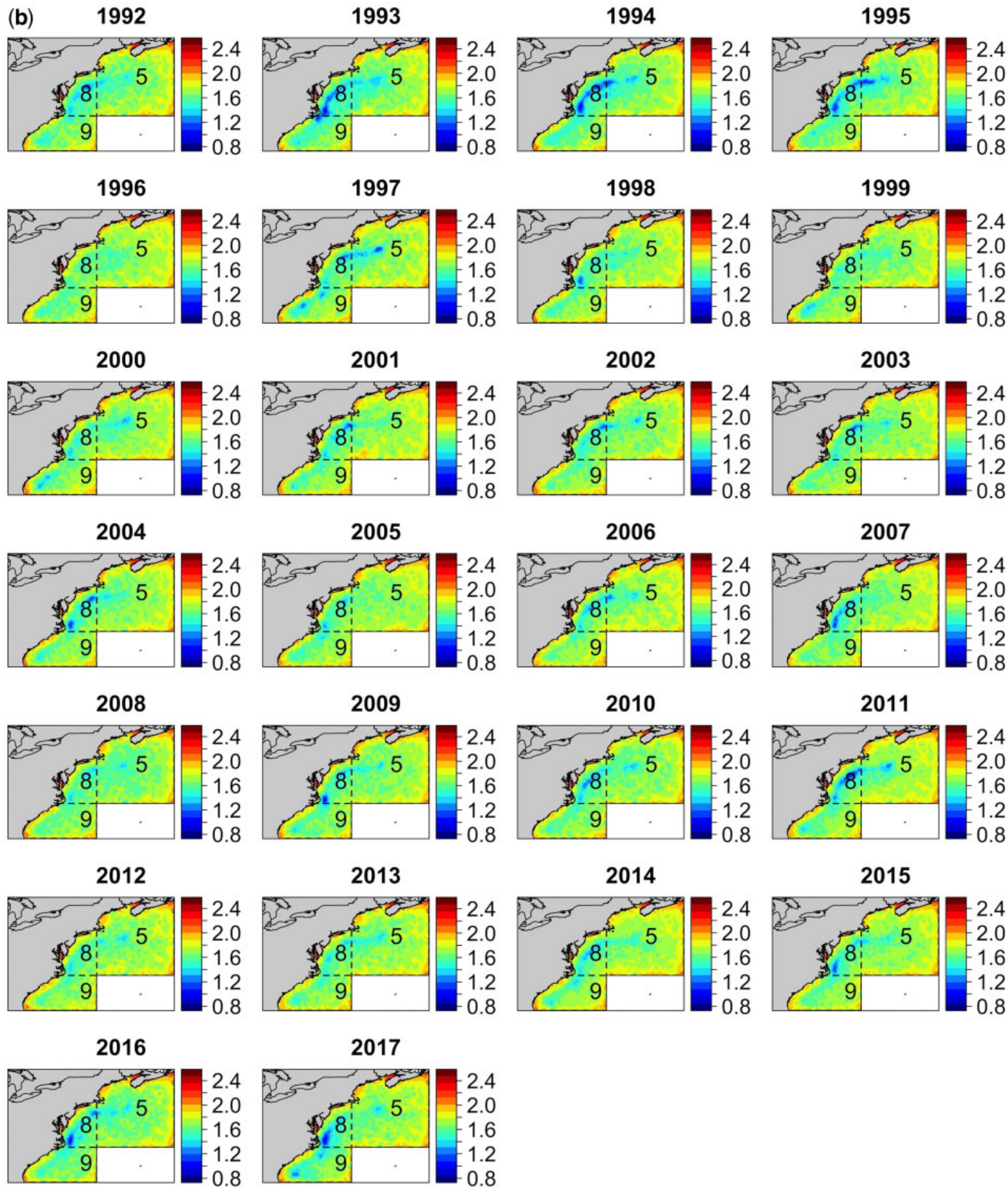

Figure 4. Continued.

The longline sets targeting dolphinfish produced the highest probability of catching a seabird, while longline sets targeting swordfish produced the lowest probability. In the POP data, longline sets targeting dolphinfish occurred in shallower waters (Supplementary Figure S1f), which increased seabird attack rates on baited hooks. More than half of longline sets targeting swordfish were set at night (Supplementary Figure S1k), when seabird bycatch is less likely.

Spatiotemporal patterns of seabird bycatch

The spatial effect introduced into this study is particularly appropriate for seabirds because of their wide distribution along the

Table 4. Cross-correlation coefficients between latitude, longitude, year effect and climate indices, and the corresponding *p*-values.

		Latitude		Longitude		Year effect	
Climate index	Lag	Coefficient	*p*-Value	Coefficient	*p*-Value	Coefficient	*p*-Value
NAO	0	−0.22	0.27	−0.22	0.25	0.046	0.81
	−1	−0.38	0.053	−0.24	0.22	−0.17	0.40
	−2	0.10	0.60	0.055	0.78	0.46	0.020*
	−3	0.37	0.057	0.37	0.058	0.14	0.49
AMO	0	−0.018	0.93	0.0040	0.98	−0.14	0.49
	−1	−0.24	0.22	−0.38	0.054	−0.24	0.22
	−2	−0.31	0.11	−0.30	0.13	−0.26	0.18
	−3	−0.13	0.49	−0.11	0.59	−0.24	0.23
GSNW	0	−0.017	0.93	−0.020	0.92	0.010	0.96
	−1	0.26	0.19	0.20	0.32	0.069	0.73
	−2	0.44	0.025*	0.38	0.052	0.33	0.089
	−3	0.18	0.35	0.28	0.16	0.18	0.36

Lag = 0 means climate index in the current year, lag = -1 means climate index of the previous year, lag = -2 means climate index of 2 years past, and lag = -3 means climate index of 3 years past.
**p*-Value <0.05.

coast. Previous studies have detected clear spatial and temporal variations of seabird bycatch in longline fisheries (Brothers *et al.*, 1999; Jiménez *et al.*, 2010; Li *et al.*, 2016). The spatial effect captures spatial autocorrelation and can improve the accuracy of estimates of seabird bycatch probability (Dormann *et al.*, 2007).

The highest seabird bycatch probability occurs in the MAB area in most years and may be associated with the high seabird activity and diversity in this region. The interaction of high freshwater inflow, expanded hard bottom, and converging ocean currents in this region (Chapman *et al.*, 1986; Steimle and Zetlin, 2000) creates frontal zones that support great biodiversity and fish productivity and then attract more seabirds and, likely, more large pelagic fishes, which attract more intensive pelagic longline fishing. The presence of at least 49 seabird species at the outer continental shelf off Cape Hatteras near the boundary of the SAB with the MAB has been documented (Lee, 1999).

Climate influence

We found that a higher GSNW index of 2 years past was associated with a more northerly position of the seabird bycatch hotspot. During a year with a higher GSNW index, the warm Gulf Stream follows a more northerly track, and the warm condition may depress the supply of *Calanus* copepods for sand lance through an effect on their food source (Grieve *et al.*, 2017), which could negatively influence seabirds, probably with a time lag. In the absence of prey in their usual foraging location, seabirds might migrate more northerly to forage. When separating from the coast at about Cape Hatteras and flowing eastward into the open ocean, the Gulf Stream meanders can result in intense long-lived mesoscale eddies, whose dynamics partly control foraging behaviour and displacement of marine top predators, including large fishes, birds, turtles and marine mammals, and then influence the distribution of pelagic longline fishing (Kai *et al.*, 2009; Scales *et al.*, 2018). Seabirds could track these mesoscale eddies to locate food patches (Kai *et al.*, 2009). The increased overlap with fisheries in the northern area would increase bycatch risk.

During a year following a winter dominated by a positive NAO, sea surface temperatures are warmer along the east coast of the United States, depressing the abundance of the natural food of seabirds. The low prey availability might increase bycatch risk since, in the absence of their natural food, starving seabirds are more likely to forage around vessels.

Model evaluation and management implication

The models presented here provide an example of how to address spatiotemporal heterogeneity in ecological phenomena. The Bayesian hierarchical spatiotemporal models were fitted through INLA and SPDE. The INLA, SPDE and their R interface allowed us to develop sophisticated models more easily. The INLA decreases the computational costs compared with MCMC simulation techniques and the SPDE directly models georeferenced data (Rue and Held, 2005; Rue *et al.*, 2009b; Held *et al.*, 2010; Lindgren *et al.*, 2011). The Barrier model, which interprets the Matérn correlation as a collection of paths between two points through an SAR model and formulates the new SAR as an SPDE, can deal with very complex barriers and reduce the computational cost compared with MCMC algorithms in the same way as the stationary model (Bakka *et al.*, 2019). Spatiotemporal heterogeneity is a common phenomenon for most species, and omitting such spatiotemporal structure may bias results (Cosandey-Godin *et al.*, 2015; Pennino *et al.*, 2014; Li *et al.*, 2016; Bi *et al.*, 2019).

Seabird bycatch estimates along the east coast of the United States through summer to winter are statistically higher than in other POP PLL statistical fishing zones and in spring. Long-term climate ocean oscillations show clear links with the spatiotemporal patterns of seabird bycatch probability. We can infer from correlations with these cyclical variables that an appropriate regional and temporal modification of fishing effort, either voluntarily by the fleet or through management actions, might significantly reduce seabird bycatch in the US Atlantic. Possible strategies to reduce seabird bycatch might include the implementation of real-time seabird bycatch hotspot avoidance in the fishing industry by means of model predictions based on long-term climate ocean oscillations (Hobday *et al.*,2011), incorporated with increased fleet communication to help vessels avoid areas or time periods when seabirds aggregate [FAO (Food and Agriculture Organization of the United Nations), 2009; Bethoney *et al.*, 2017].

In summary, seabird bycatch in the US Atlantic PLL shows clear spatial and temporal variations. The inter-annual variations in bycatch hotspot are correlated with the north–south movements of the Gulf Stream, which are likely correlated with the NAO and the Gulf Stream position in the past; high values of the NAO index, which correspond to stronger westerly and trade winds, favour more northerly paths of the Gulf Stream (Taylor and Stephens, 1998). A regulation of real-time seabird bycatch hotspot avoidance based on Gulf Stream positions could mitigate seabird bycatch.

Supplementary data

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

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