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Predictive spatial modelling of seasonal bottlenose dolphin (Tursiops truncatus) *distributions in the Mississippi Sound*

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ABSTRACT

1. Spatial distribution models (SDMs) have been useful for improving management of species of concern in many areas. This study was designed to model the spatial distribution of bottlenose dolphins among seasons of the year in the Mississippi Sound within the northern Gulf of Mexico.
2. Models were constructed by integrating presence locations of dolphins acquired from line-transect sampling from 2011–2013 with maps of environmental conditions for the region to generate a likelihood of dolphin occurrence for winter (January–March), spring (April–June), summer (July–September), and autumn (October–December) using maximum entropy.
3. Models were successfully generated using the program MaxEnt and had high predictive capacity for all seasons (AUC (area under curve) > 0.8). Distinct seasonal shifts in spatial distribution were evident including increased predicted occurrence in deepwater habitats during the winter, limited predicted occurrence in the western Mississippi Sound in winter and spring, widespread predicted occurrence over the entire region during summer, and a distinct westward shift of predicted occurrence in autumn.
4. The most important environmental predictors used in SDMs were distance to shore, salinity, and nitrates, but variable importance differed considerably among seasons.
5. Geographic shifts in predicted occurrence probably reflect both direct effects of changing environmental conditions and subsequent changes in prey availability and foraging efficiency.
6. Overall, seasonal models helped to identify preferred habitats for dolphins among seasons of the year and can be used to inform management of this protected species in the northern Gulf of Mexico.

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INTRODUCTION

Bottlenose dolphins (*Tursiops truncatus*) are a long-lived species found in coastal habitats throughout the world. They reside at the top of the marine food chain and are thus considered reliable marine sentinels (Wells *et al.,* 2004). Their presence or absence within their normal geographic range can be used to indicate spatial and temporal changes within their habitat with regard to

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environmental conditions (Hart *et al.*, 2012), the availability of prey (Hastie *et al.*, 2004), and disturbance (Carmichael *et al.*, 2012). For example, prolonged exposure to low salinity and temperature can be detrimental for the species (Carmichael *et al.*, 2012), and thus can displace animals from a given area. In contrast, hydrographic fronts, which occur at distinct transition zones from fresh water to salt water (e.g. mouths of freshwater rivers), concentrate fish and provide enhanced feeding opportunities for dolphins (Mendes *et al.*, 2002). The movement and availability of prey are among the most important factors controlling their distribution (Hastie *et al.*, 2004), but dolphin distribution is also a function of temperature, salinity, solar and lunar periodicity, and many other factors that vary over space and time (Allen *et al.*, 2001; Brager *et al.*, 2003; Hastie *et al.*, 2004). Recent developments in spatial modelling approaches (e.g. generalized linear models, maximum entropy) have allowed researchers to predict the occurrence and distribution of dolphins based on environmental variants. Such approaches are quickly becoming essential tools to enhance management and protection of the species (Edren *et al.*, 2010; Best *et al.*, 2012; Thorne *et al.*, 2012).

Spatial distribution models (SDMs) have been developed in many areas to predict the occurrence of species of special concern, including dolphins (Phillips *et al.*, 2006; Best *et al.*, 2012; Thorne *et al.*, 2012). Applications for SDMs includes development of species management plans, assessment of the influence of environmental conditions on species distributions, evaluations of the relative importance of habitats on geographic distributions, and prediction of species occurrence in unsurveyed areas (Phillips *et al.*, 2006; Thorne *et al.*, 2012). Recently, the use of presence-only SDMs have become common including those that employ Bayesian reasoning, an inductive method originally used in disease diagnosis (Aspinall, 1992) and later applied in mineral exploration (Agterberg *et al.*, 1993) and wildlife habitat modelling (Phillips *et al.*, 2006; Thorne *et al.*, 2012). Bayesian SDMs use map integration and map correlation to predict the occurrence of a resource from environmental features that affect its distribution (e.g. climate, topography) (Agterberg *et al.*, 1993; Boleneus *et al.*, 2001). The utility of these methods for predicting the spatial distribution of marine mammals has been explored in several areas using sighting records and raster-based maps of factors such as bathymetry, slope, temperature, etc. (Edren *et al.*, 2010; Best *et al.*, 2012; Thorne *et al.*, 2012). These SDMs have helped identify critically important habitat for marine mammals and thus are vital management tools in coastal areas where the potential for conflicts between humans and marine mammals is high.

A Bayesian modelling approach called maximum entropy is a general purpose, machine learning method that enables prediction of species distributions from incomplete information. Maximum entropy does this by finding the most uniform distribution of a species under a set of constraints that represent incomplete knowledge of the actual distribution (Phillips *et al.*, 2006). There are several advantages of maximum entropy over other Bayesian modelling approaches including: (1) the need for presence only data for the species of interest; (2) the ability to use continuous and categorical predictor data; (3) the use of deterministic algorithms that converge to a distribution of maximum entropy; (4) maintenance of a stable distribution with limited training data; (5) easily interpretable, continuous output scores; and (6) allowance for assessment of relative importance of predictor variables (Phillips *et al.*, 2006; Dudik *et al.*, 2007). Maximum entropy is also less stringent than traditional regression-based models as variables can possess multicollinearity and be spatially autocorrelated (Hu and Jiang, 2010; Beane *et al.*, 2013). Maximum entropy is similar to logistic regression in that each predictor variable is weighted by a constant and the estimated species distribution is divided by a scaling constant that allows all probabilities to sum to one over the extent of interest (Hernandez *et al.*, 2006). These advantages make this method especially useful for modelling species distributions with incomplete information as the maximum entropy distribution is built only from what is known about the occurrence of the species and its associated variables while avoiding making assumptions about anything unknown (Jaynes, 1989).

The Mississippi (MS) Sound within the northern Gulf of Mexico (nGoM) harbours one of the largest estuarine populations of bottlenose dolphins in the USA (Waring *et al.*, 2009). The area supports both year round residents and a large number of transient dolphins (73.5%) that inhabit the region from late spring to early autumn (Mackey, 2010). Population dynamics within the region have been studied in parts of the MS Sound (Hubard *et al.*, 2004; Miller *et al.*, 2013), but little is known about seasonal spatial distributions. This area is strongly affected by a variety of human activities including commercial and recreational fisheries, oil spills, shipping activity, and dredging. It has also been subject to some large environmental disturbances over the last several decades including hurricanes, and freshwater flood events. Dolphins have suffered as a result, as the longest running unusual mortality event (UME) on record in the nGoM began in 2010, and continues to date (NOAA, 2014). The need for models that can predict seasonal distributions of dolphins in this area is critical for helping to identify areas of importance that warrant protection. The ability to properly protect dolphins in the face of certain threats will undoubtedly be tied to the sustainability of the species within the nGoM. The purpose of this project was to construct seasonal SDMs for this region using sightings data collected from 2011–2013 along with maps of environmental factors that are important predictors of dolphin occurrence. The modelling approach included application of principles of maximum entropy to create seasonal distribution maps and assess the influence of predictor variables on the species.

METHODS

Study area

The MS Sound encompasses a 2000 km^2 area separated from the larger Gulf of Mexico by five barrier islands (i.e. Cat, Ship, Horn, Petit Bois and Dauphin) (Eleuterius, 1978) (Figure 1). Water depth ranges from 1 to 7 m and average annual water temperature ranges from 9°C in winter to 32°C in summer, and salinity ranges from 0 to 33 parts per thousand (ppt) (Christmas, 1973). National Oceanic and Atmospheric Administration (NOAA) reports estimate that the Bay Boudreau, MS Sound bottlenose dolphin stock contains more than 1400 individuals, which is among the most densely populated areas within the nGoM (Waring *et al.*, 2009).

Predictor variables

Data layers used as predictor variables in spatial distribution models were generated from the National Oceanographic Data Center (NODC) Gulf of Mexico Regional Climatology seasonal dataset (available at http://www.nodc.noaa.gov/OC5/regional_climate/GOMclimatology/). Seasonal NODC datasets used in model development represent averages from 1955–2011 at a horizontal resolution of 1° × 1° latitude/longitude grids for dissolved oxygen (DO), apparent oxygen utilization (AOU), (Garcia *et al.*, 2010a), phosphate, and nitrate (Garcia *et al.*, 2010b) and averages from 1864–2011 at a horizontal resolution of 0.1° × 0.1° latitude/longitude grids for temperature and salinity (Boyer *et al.*, 2005; Antonov *et al.*, 2010; Locarnini *et al.*, 2010). Seasons were defined as winter (January–March), spring (April–June), summer (July–September), and autumn (October–December). Seasonal point data for selected variables were interpolated using the inverse distance weighted (IDW) interpolation tool within the Spatial Analyst Extension in ESRI® ArcMap™ 10.1 to create raster data layers used in spatial distribution models. Other spatial data layers used in the model include distance to coast created using the 'Euclidean Distance' tool within the Spatial Analyst Extension to represent straight line distance to continental USA and the barrier islands. Also, a bathymetry layer was created for the region by merging 1/3 arc-second coastal digital elevation models (DEMs) obtained from NOAA National Geophysical Data Center website (Taylor *et al.*, 2008; Amante *et al.*, 2011; Love *et al.*, 2011). MaxEnt requires that all predictor layers have the same spatial extent and cell size, thus the 'Resample' tool within the spatial analyst

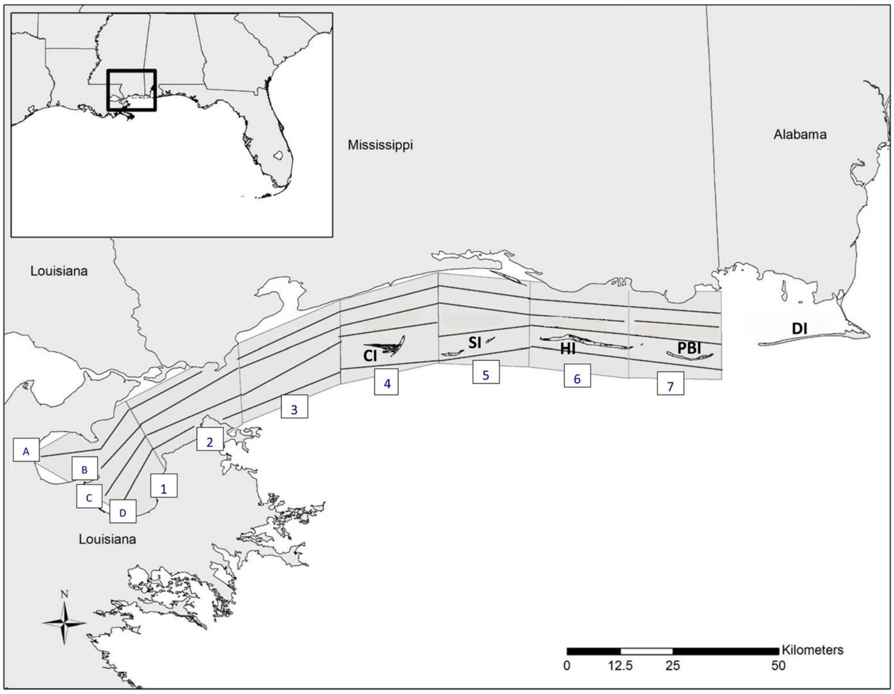

Figure 1. Study area used to develop seasonal spatial distribution models for bottlenose dolphins (*Tursiops truncatus*) within the MS Sound, USA. Survey strata are numbered 1–7 and transects are labelled A–D. Abbreviations are denoted as Cat Island (CI), Ship Island (SI), Horn Island (HI), Petit Bois Island (PBI), and Dauphin Island (DI).

toolbox was used to create cell size uniformity among predictors. All layers were then extracted to the study extent and converted to ASCII format. Statistics associated with each predictor data layer are shown in Table 1.

Dolphin sightings

Dolphin presence locations used for modelling were derived from dolphin sightings recorded from December 2011–November 2013 using a stratified random sampling design. The study area was divided into seven strata approximately 20 km × 20 km in size within which, four approximately 20 km transects, separated by a minimum distance of 2.2 km, were surveyed twice within each season (Figure 1). To maximize the probability of detecting dolphins, surveys were scheduled only when predicted wind speed was ≤ 16 km per hour and when predicted wave heights were ≤ 0.6 m. If sighting conditions deteriorated on a survey, the trip was cancelled for that survey day. Alternating transects (i.e. a and c or b and d) were surveyed from either strata one to four, or five to seven each survey day to maintain high probability of independence among sightings. The survey platform was a 9.5 m Stamas Tarpon outfitted with twin 250 horsepower, four-stroke engines carrying a boat captain and four observers at 25 km per hour. During the survey, two observers scanned the area between transects and 90° port and two observers scanned the area between transects and 90° starboard in an effort to locate dolphins. A dolphin sighting was defined as an observation of one or more dolphins by at least two observers. At the time of each sighting, the boat would travel directly to the original sighting location where a Garmin GPSmap76 global positioning system (GPS) with differential GPS accuracy of 3–5 m was used to record geographic coordinates. After coordinates were recorded, the boat travelled back to the trackline before resuming the survey. Sighting locations for each season were converted to CSV format and imported along with predictor layers into MaxEnt modelling software for model development. Each dolphin sighting was treated as one presence record regardless of group size (Bombosch *et al.*, 2014).

Table 1. Environmental variables used to create a model of seasonal dolphin distributions in the MS Sound with associated data sources and the minimum (Min), maximum (Max), and mean values for each corresponding grid dataset. Standard error of the mean is shown in parentheses for each mean value

Variable	Source	Min				Max				Mean			
		Wi	Sp	Su	Fa	Wi	Sp	Su	Fa	Wi	Sp	Su	Fa
Distance to shore (m)	Created	0	0	0	0	17,586	17,586	17,586	17,586	4,491 (39.2)	4,491 (39.2)	4,491 (39.2)	4,491 (39.2)
Salinity (ppt)	NODC[a]	6.05	4.79	7.26	9.96	28.30	32.0	33.25	33.05	17.0 (0.06)	16.0 (0.07)	22.33 (0.06)	24.85 (0.07)
Nitrates ($mg\ L^{-1}$)	NODC	2.31	5.35	0.87	1.05	4.04	8.99	1.40	1.90	3.09 (0.01)	7.06 (0.01)	1.20 (0.00)	1.56 (0.00)
Depth (m)	NGDC[b]	-18.0	-18.0	-18.0	-18.0	6.0	6.0	6.0	6.0	-4.51 (0.05)	-4.51 (0.05)	-4.51 (0.05)	-4.51 (0.05)
Phosphorus ($mg\ L^{-1}$)	NODC	0.43	0.22	0.15	0.31	0.50	0.46	0.22	0.62	0.47 (0.00)	0.34 (0.00)	0.19 (0.00)	0.47 (0.00)
Temperature (°C)	NODC	12.48	20.52	27.32	17.94	18.80	29.50	30.34	23.93	14.15 (0.02)	24.72 (0.02)	28.95 (0.01)	19.87 (0.01)
DO ($mg\ L^{-1}$)	NODC	6.51	4.99	5.35	5.74	8.45	6.50	5.92	7.39	7.58 (0.00)	5.85 (0.00)	5.59 (0.00)	6.57 (0.00)
AOU[c]	NODC	-2.14	-1.24	-1.06	-1.70	-0.80	-0.76	-0.43	-1.35	-1.56 (0.00)	-1.03 (0.00)	-0.66 (0.00)	-1.56 (0.00)

[a]National Oceanographic Data Center–data available at http://www.nodc.noaa.gov/OC5/regional_climate/GOMclimatology/
[b]National Geophysical Data Center–data available at http://www.nodc.noaa.gov/
[c]Apparent oxygen utilization

Modelling

The Program, MaxEnt (version 3.3.3, available for download at http://www.cs.princeton.edu/~schapire/Maxent/), was used to model seasonal dolphin distributions by estimating the unknown distribution (π) over the set of grid cells in the study area (X). MaxEnt assigns a probability of occurrence to each point, x, that is approximated by solving for the entropy of $\hat{\pi}$ using the equation:

$$H(\hat{\pi}) = -\sum_{x \in X} \hat{\pi}(x) \ln \hat{\pi}(x)$$

where ln is the natural logarithm, and $\hat{\pi}$ is a positive value representing the probability of occurrence for the target phenomena that sums to one over all the pixels in the study extent (Phillips *et al.*, 2006). Simply stated, this equation was used in this study to generate a distribution representing the log-LoDO (likelihood of dolphin occurrence) over the pixels within the study area that maximized entropy (i.e. was the closest to uniform) based on constraints representing our incomplete information regarding features associated with dolphin sightings.

The default regularization value of 1 was used for all models and response curves and jackknife options were selected within the program to measure individual variable importance. In addition, 30 replicate bootstrap runs were performed using 25% (n = 44, 26, 26, 35 for winter, spring, summer and autumn, respectively) of the total number of dolphin sightings (n = 174, 105, 102, 141 for winter, spring, summer and autumn, respectively). Unique test and train datasets were used for each replicate model bootstrap run. Because the total number of training sites was low, the bootstrap replication technique, which involves sampling from the original occurrence locations with replacement, helped to avoid losing valuable training data for model development. Bootstrapping worked to split the data into test and training data 30 times providing multiple estimates of model performance while allowing all occurrence data to be used with a random partition for each replicate run. Because MaxEnt is a presence only modelling method where absence data are not needed, no assumptions are made regarding where a feature does not occur. However, the MaxEnt distribution does rely on pseudo-absence data points that are randomly chosen from all background data points. This means that the MaxEnt distribution functions primarily to distinguish between occurrence and random instead of occurrence and absence. The MaxEnt default total of 10 000 random points was used to build the distribution in this modelling effort.

Model validation

Evaluation of model performance included a threshold-dependent, one-tailed binomial test on model omission and predicted area to determine if the maximum entropy distribution was better than a randomly modelled distribution. Also used to evaluate model performance was a threshold independent, area under curve (AUC) analysis, which was used to determine if a random positive instance and a random negative instance were correctly identified by the model. The AUC value ranged from 0–1 and was used to assess overall model performance where a value < 0.5 indicates that a model predicts no better than random, 0.5–0.7 indicates fair model performance, 0.7–0.9 indicates a good model, and values > 0.9 are indicative of an excellent model (Phillips *et al.*, 2006; Beane, 2010).

To evaluate environmental variable contributions to the model, logistic response curves were generated in the model output showing how each environmental variable affects the prediction using each variable in conjunction with all other variables at their mean value. Also generated were the percentage contribution and permutation importance of each variable, and jackknife analyses to assess the importance of each variable by creating a model excluding the variable of interest and a model using only the variable of interest. Jackknife analyses ultimately helped to determine how much unique information was present in each variable as it relates to the test gain, training gain, and AUC values for each spatial distribution model.

Maps were created from the ASCII logistic output for each seasonal predicted distribution that represented the average of all 30 model runs produced by MaxEnt. The ASCII file was converted to raster in ESRI® ArcMap™ 10.1. The raster layer was reclassified into five equally sized classes to represent very low, low, moderate, high, and very high LoDO for each season.

RESULTS

In total, 522 dolphin sightings were recorded from December 2011 to November 2013 with the largest number occurring during the winter (174) and the smallest number during the summer (102). Spatial distribution models were successfully generated from these data that show distinct seasonal changes in predicted habitat within the MS Sound (Figure 2). All models were good or excellent predictors of dolphin occurrence as indicated by mean AUC values, which ranged from 0.820 (SE = 0.005) in summer to 0.910 (SE = 0.007) in winter (Table 2). High model performance was also indicated by threshold dependent model evaluation for all seasons, in which the models predicted better than random for all data partitions at all selected thresholds ($P < 0.01$, one tailed).

The total area within the MS Sound associated with high LoDO ranged from 326.6 km^2 in winter to 816.5 km^2 in summer. Similarly, the total area associated with very high LoDO ranged from 50.8 km^2 in winter to 241.1 km^2 in summer (Table 2). Areas with moderate and high LoDO in winter were concentrated in the central part of the MS Sound between Bay St. Louis in the west and Pascagoula in the east. The largest area with very high LoDO was found south of Horn Island and extended for more than 20 km from east to west. All areas west of Bay St. Louis had low or very low LoDO (Figure 2(a)).

In the spring, the distribution of moderate to high LoDO was more diffuse within the region and extended well into the western MS Sound. Areas with very high likelihood in spring were found north of Horn and Petit Bois Islands extending more than 30 km and an area south of Bay St. Louis extending approximately 44 km from east to west (Figure 2(b)). In summer LoDO was high throughout the region with very high likelihood in

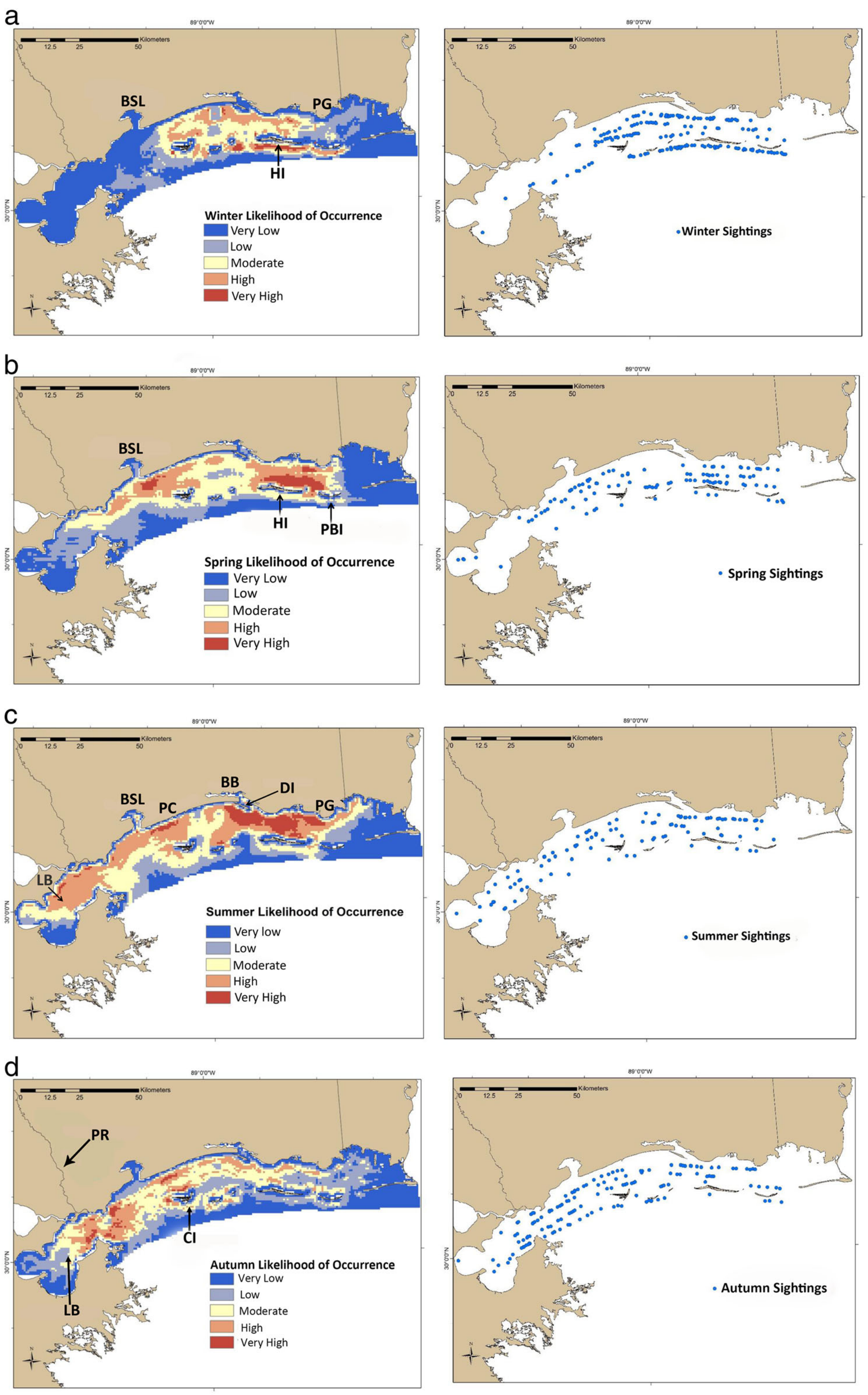

Figure 2. Likelihood of occurrence of bottlenose dolphins (*Tursiops truncatus*) within the MS Sound, USA for (a) winter (January–March), (b) spring (April–June), (c) summer (July–September), and (d) autumn (October–December). Abbreviations are denoted as Bay Saint Louis (BSL), Pascagoula (PG), Horn Island (HI), Petit Bois Island (PBI), Lake Borgne (LB), Pass Christian (PC), Biloxi Bay (BB), Deer Island (DI), and Pearl River (PR). Predicted distributions were generated using maximum entropy spatial modelling software, MaxEnt.

Table 2. Bottlenose dolphin (*Tursiops truncatus*) sightings from 2011–2013 during the winter (January–March), spring (April–June), summer (July–September), and autumn (October–December) season within the MS Sound, USA. Also shown are area under curve (AUC) values, which indicate overall model performance

Season	Total sightings	AUC values[a]	H LoDO[b] (km^2)	VH LoDO[c] (km^2)
Winter	174	0.910 (0.005)	326.6	50.8
Spring	105	0.844 (0.006)	463.0	133.4
Summer	102	0.820 (0.007)	816.5	241.1
Autumn	141	0.903 (0.006)	464.8	61.6
Total	522	-	-	-

[a]Standard error of the mean is shown in parentheses.
[b]High likelihood of dolphin occurrence (H LoDO) – total area associated with a high LoDO.
[c]Very high likelihood of dolphin occurrence (VH LoDO)–total area associated with a very high LoDO.

nearshore areas of the western MS Sound and Lake Borgne (Figure 2(c)). A large nearshore area extending from Biloxi in the west to Pascagoula in the east was also predicted to have very high LoDO. This included a large area south-west of Deer Island. Overall, the model predicted that a vast majority of the region was potential habitat including parts of Bay St. Louis and Biloxi Bay that were not sampled in this study. Similar to summer, the autumn also had a wide distribution of moderate and high likelihood areas, but a distinct westward shift in very high likelihood areas was predicted for the region (Figure 2(d)). The largest concentration of habitat with very high LoDO was near the mouth of the Pearl River in Lake Borgne.

The influence of predictor variables on spatial distributions differed between all seasons (Table 3). Consistently among the most important predictors in all seasons was distance to shore, which was the most important predictor variable in winter and autumn models, and was second most important in spring and summer models. Salinity was the most important predictor in summer and was the second most important predictor in autumn. Response curves for all seasons showed that the highest probability of dolphin occurrence was found to be in a narrow range of distance to shore (i.e. 2200–2800 m) followed by a steady decline with increasing distance from shore (Figure 3). However, logistic probability of occurrence beyond 17 000 m from shore was highest in autumn (0.31) followed by summer (0.26), spring (0.18), and winter (0.07).

Salinity had varied effects on predicted spatial distributions among seasons (Figure 4). In winter, the highest probability was associated with salinity >13 ppt. Spring probability had a distinct peak at 23 ppt followed by a sharp decline. Logistic probability of dolphin occurrence during summer remained at 0.7 when salinity was between 15 and 19 ppt, but declined sharply when salinity was >19 ppt. The relation between logistic probability and salinity in autumn was complex with several inflection points along the range of salinity values from 7–35 ppt; however, logistic probability never fell below 0.3 for any salinity value. Although the range of nitrate values varied considerably among seasons of the year, the relation between nitrates and logistic probability of occurrence was

Table 3. Percentage contribution and permutation importance for all variables used to predict seasonal spatial distributions of bottlenose dolphins (*Tursiops truncatus*) in the MS Sound, USA. Seasons are defined as winter (January–March), spring (April–June), summer (July–September), and autumn (October–December)

Variable	Percent contribution (%)				Permutation importance [a] (%)			
	Winter	Spring	Summer	Autumn	Winter	Spring	Summer	Autumn
Distance to shore	20.3	21.1	32.4	25.9	23.6	16.5	22.7	19.8
Salinity	9.6	12.0	43.0	19.9	8.4	18.9	45.2	16.2
Nitrates	16.6	3.0	3.3	9.5	9.3	5.2	9.8	10.2
Depth	9.4	2.3	3.7	12.2	15.2	2.0	4.8	12.2
Phosphorus	10.2	3.2	7.3	9.3	11.1	3.2	3.4	6.5
Temperature	11.9	23.1	2.3	5.2	15.7	18.4	2.3	4.9
DO	12.9	19.9	2.3	12.8	9.3	8.6	3.4	8.0
AOU[b]	9.3	15.3	5.8	10.4	7.3	23.0	8.4	22.4

[a]Permutation importance values for each variable are determined by randomly permuting the variable values among the training points and quantifying the ensuing decrease in training AUC.
[b]Apparent oxygen utilization

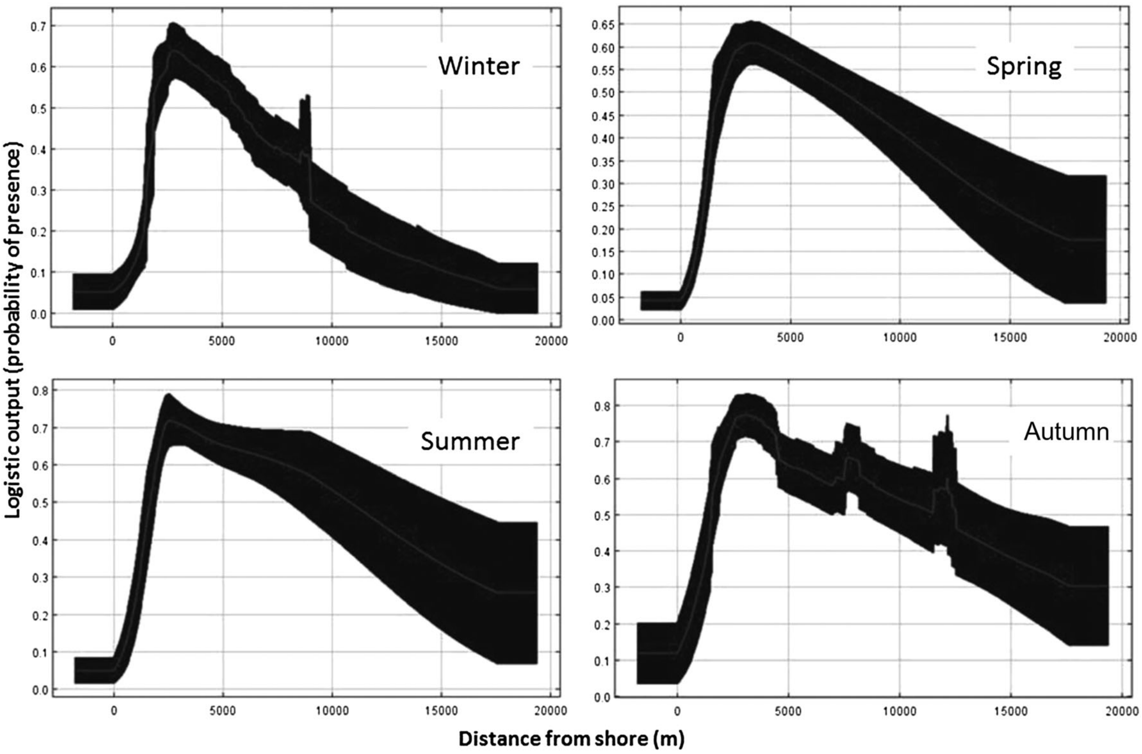

Figure 3. Logistic probability of bottlenose dolphin (*Tursiops truncatus*) presence in the MS Sound, USA as a function of distance from shore (m) for the winter (January–March), spring (April–June), summer (July–September), and autumn (October–December) season.

consistent among all seasons, where higher probabilities were associated with higher nitrate values (Figure 5).

The effect of elevation (i.e. depth) on probability of dolphin occurrence also varied among seasons (Figure 6). Probability was highest (0.83) in winter at depths of 15–20 m followed by a steady decline to a probability of 0.5 in shallow areas less than 5 m deep. This relation was unique from other seasons as probability of presence in spring and autumn was highest near 5 m and summer probability was highest at depths of 5–10 m. Temperature varied considerably among seasons as did the relation between occurrence and temperature (Figure 7). Logistic probability of occurrence increased with increasing temperature in spring, summer, and autumn, but decreased with increasing temperature in winter. The relation between occurrence and temperature in winter and autumn was complex with numerous inflection points in each curve. Distinct peaks in occurrence at 13°C and 21°C were associated with the highest probability in winter and autumn, respectively.

DISCUSSION

Maximum entropy models generated in this study clearly show varied spatial distributions of bottlenose dolphins among seasons in the MS Sound. Seasonal changes in distribution are not surprising and have been described in several areas where factors such as distance to shore, temperature, salinity, and depth were important predictors of cetacean occurrence (Edren *et al.*, 2010; Best *et al.*, 2012). The results presented here provide a measure of the relative importance of these variables for dolphins in a temperate nGOM estuary and demonstrate the shifting importance of such factors among seasons of the year. Factors such as temperature and salinity fluctuate considerably across seasons and can directly influence habitat suitability for bottlenose dolphins (Edren *et al.*, 2010; Best *et al.*, 2012; Carmichael *et al.*, 2012). This study showed that predictors such as distance to shore and depth, which do not fluctuate across season, had varied effects on predicted distributions within each season. This

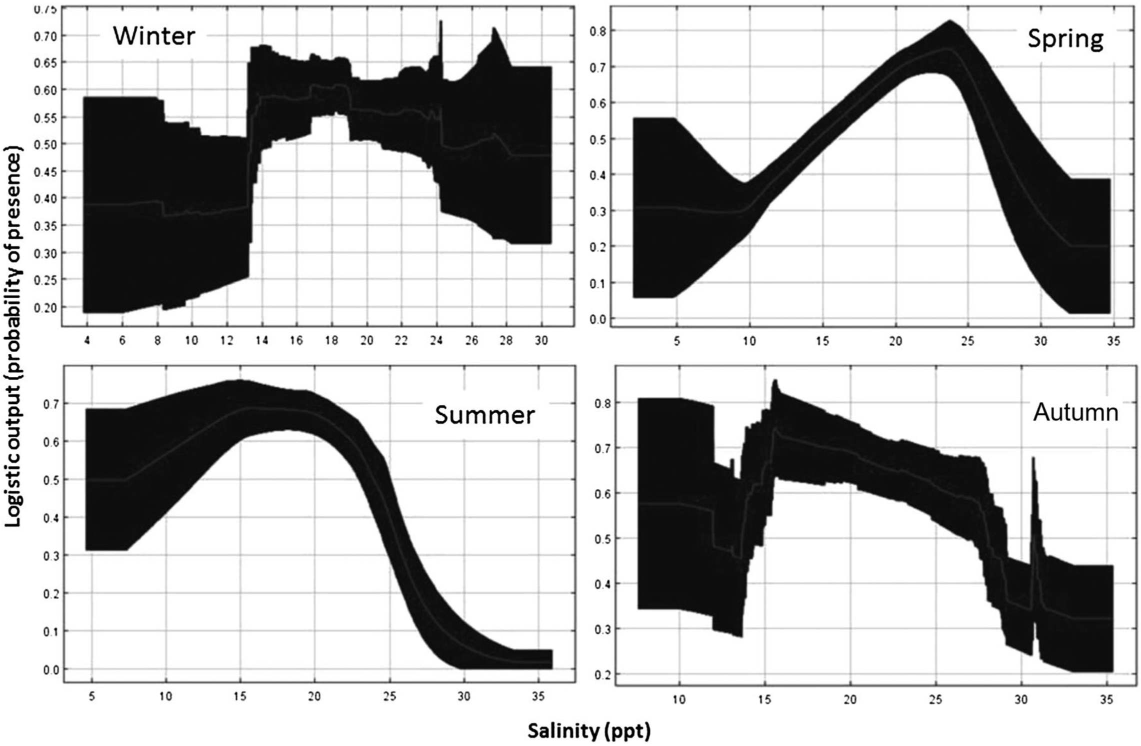

Figure 4. Logistic probability of bottlenose dolphin (*Tursiops truncatus*) presence in the MS Sound, USA as a function of salinity (ppt) for the winter (January–March), spring (April–June), summer (July–September), and autumn (October–December) season.

was demonstrated in the winter model as depth was an important predictor relative to spring and summer, and the relation between depth and dolphin occurrence indicated a preference for deep water in winter.

A variety of species reside within the MS Sound that have been shown to be important dolphin prey in the Gulf of Mexico including soniferous species such as pinfish (*Lagodon rhombiodes*), pigfish (*Orthopristis chrysoptera*), gulf toadfish (*Opsanus beta*), and sheepshead (*Archosargus probatocephalus*) and schooling species such as striped mullet (*Mugil cephalus*) and gulf menhaden (*Brevoortia patronus*) (Barros and Wells, 1998; Hoese and Moore, 1998). These species have unique life histories and tolerance ranges for physical conditions that influence their spatial distribution within the nGOM. Some will migrate offshore in late autumn, and will not return until water temperature increases in the spring (Pattillo *et al.*, 1997). For example, gulf menhaden typically reside in nearshore areas from April–November, before moving offshore in December to spawn (Lewis and Roithmayr, 1981; Vaughan *et al.*, 1996). Similarly, striped mullet spawn at the edge of the continental shelf during the colder months of the year (Ditty and Shaw, 1996). The models presented here do not account for changes in prey availability; however, the distribution of prey has been linked with seasonal habitat use of dolphins in other areas (Wilson *et al.*, 1997; Hastie *et al.*, 2004). Thus, both direct and indirect effects associated with changing physical conditions must be considered when interpreting these models.

Winter distribution

Although the number of sightings was highest in winter, the predicted area with very high and high LoDO was smaller compared with other seasons. Model evaluation indicated that the winter model had the highest predictive capacity, which probably resulted from a tighter distribution of sightings during this time of year. During winter, population size in the MS Sound has been estimated at 1413 individuals, much lower than an

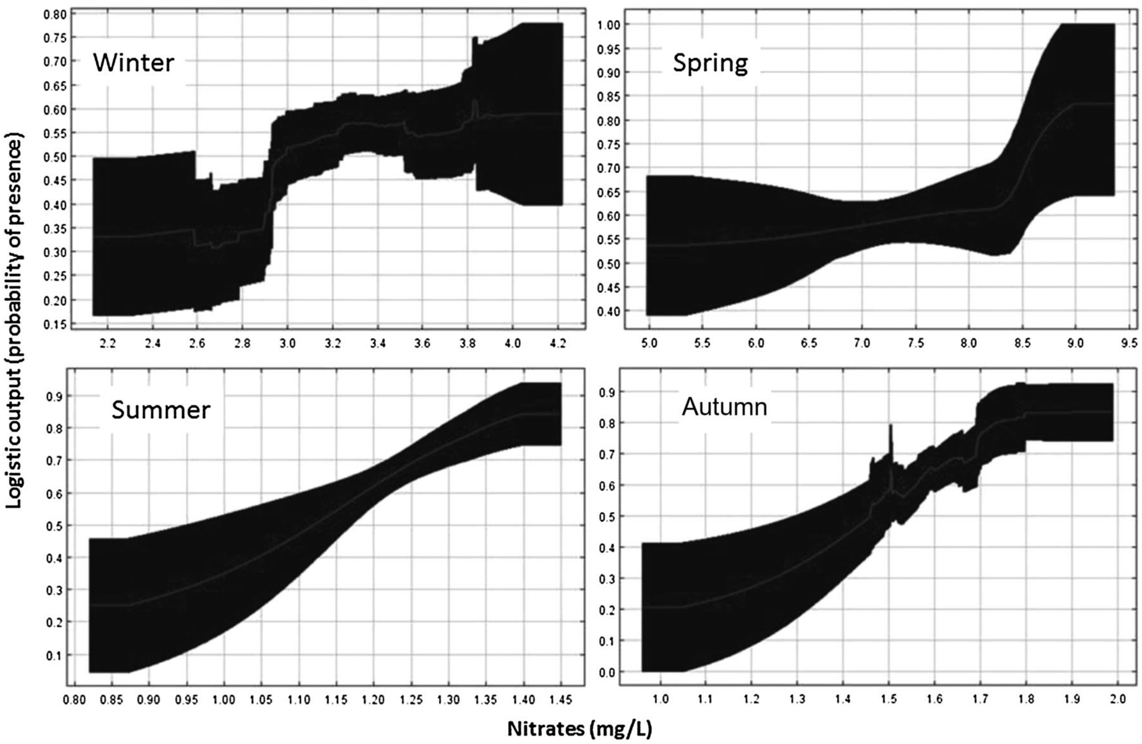

Figure 5. Logistic probability of bottlenose dolphin (*Tursiops truncatus*) presence in the MS Sound, USA as a function of nitrate concentration (mg L^{-1}) for the winter (January–March), spring (April–June), summer (July–September), and autumn (October–December) season.

estimated summer population size of 2255 (Miller *et al.*, 2013). A reduction of nearly 40% in the population in winter indicates that a large number of transient animals emigrate during the winter months, suggesting that dolphins that remain in the area in winter are year-round residents (Hubard *et al.*, 2004; Mackey, 2010). Predicted distributions in winter suggest that habitat use of these residents is restricted primarily to an area south of Horn Island. Response curves showed the highest probability of occurrence was at depths of 15–20 m, which is deeper than the vast majority of the MS Sound. This suggests that dolphins may avoid shallow areas with lower water temperature (Yeates and Houser, 2008) and show preference for deeper habitats further offshore. Also greater prey availability in offshore areas (Lewis and Roithmayr, 1981; Ditty and Shaw, 1996; Vaughan *et al.*, 1996), could influence winter habitat selection (Hastie *et al.*, 2004).

Response curves indicated that higher salinity is preferred by dolphins in winter as probability of occurrence increased sharply at salinities above 13 ppt. An influx of fresh water is common throughout this time of year as several river systems that drain large upland areas with colder climates see increased flow rates from late winter to spring. The Mississippi River watershed drains approximately 3 107 986 km^2 of land that extends northward into Canada (National Park Service, 2014), and consequently carries large volumes of cold water from these areas during the late winter and early spring seasons. While the system does not drain directly into the region, the Bonnet Carre´ spillway, near Montz, Louisiana releases water during high flow periods into Lake Pontchartrain, Lake Borgne, and the MS Sound. The spillway has not been opened since 2011 but leaks during the flood season occur at a rate of 283 $m^3 s^{-1}$ (US Army Corps of Engineers, 2014). Fresh water originating from the spillway has been implicated as a source of stress for many organisms (GEC, 2009; LeBlanc *et al.*, 2012). Dolphins are no exception as the effects of cold fresh water can have a variety of sub-lethal effects including a reduction in

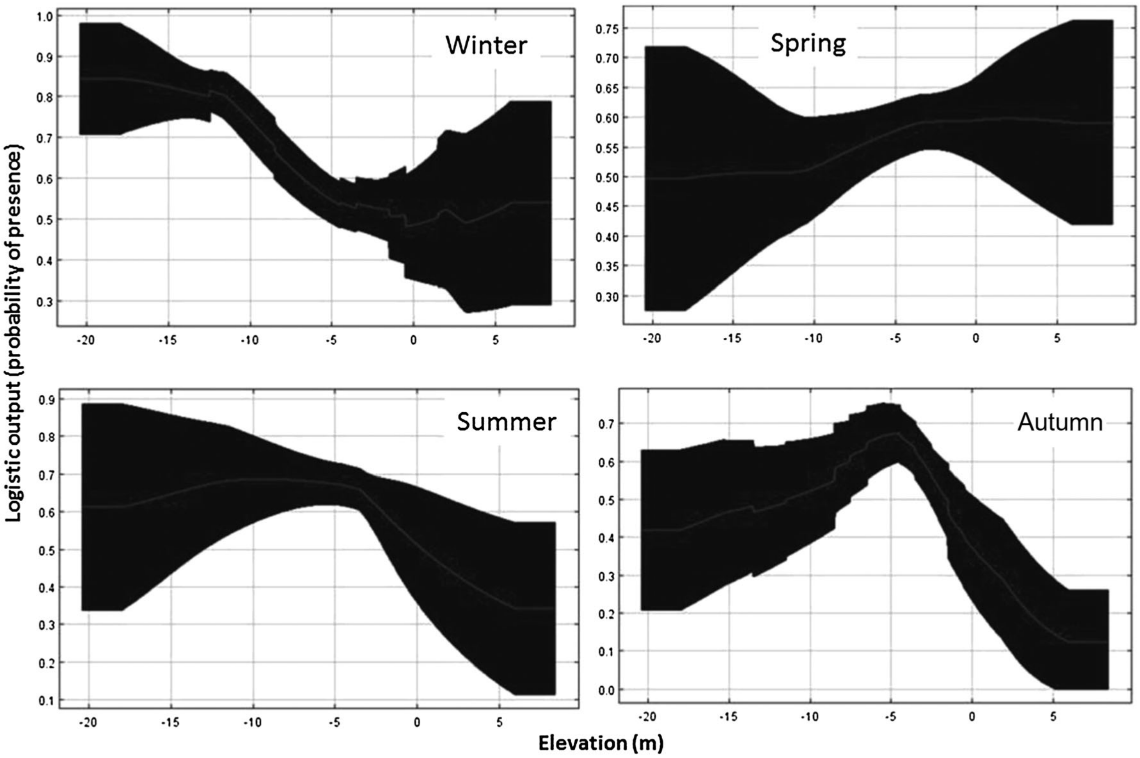

Figure 6. Logistic probability of bottlenose dolphin (*Tursiops truncatus*) presence in the MS Sound, USA as a function of elevation (m) for the winter (January–March), spring (April–June), summer (July–September), and autumn (October–December) season. Negative elevation values represent areas below sea level.

immunocompetence and production of freshwater lesions (Carmichael *et al.*, 2012; Hart *et al.*, 2012). Thus, a preference for higher salinity waters is not surprising and appears to be evident from the compact geographic distribution in winter and the low LoDO near the mouths of major rivers.

Spring distribution

Predicted distributions in the spring show a more diffuse spatial pattern with very high LoDO in a small area near Bay St. Louis in the western MS Sound and a larger area spanning 30 km from east to west north of Horn and Petit Bois Islands. The importance of temperature in the spring and predicted distributions inside the islands indicates a preference for higher temperatures and for the interior of the MS Sound relative to winter. This suggests that higher temperatures increase habitat suitability for dolphins directly or indirectly from increased prey availability within the MS Sound as temperature increases from winter to spring (Lewis and Roithmayr, 1981; Ditty and Shaw, 1996; Vaughan *et al.*, 1996; Pattillo *et al.*, 1997). Similarly, elevated salinity in spring within the embayment probably resulted in an expansion of suitable habitat for dolphins and prey. The availability of prey species was probably strongly influenced by salinity as it is among the most important factors controlling fish assemblage structure in estuarine systems (Barletta *et al.,* 2005).

Nitrate levels in spring were higher throughout the region compared with all other seasons, particularly near the mouth of the Pascagoula River in the eastern MS Sound. This area was also associated with high and very high LoDO. The Pascagoula River watershed drains 24 864 km^2 of land in MS and Alabama and transports high nutrient loads to the MS Sound (MS Department of Environmental Quality, 2007). While elevated nitrate levels can become toxic (Camargo *et al.*, 2005), it also stimulates primary (Mallin *et al.*, 1993) and secondary production in estuarine

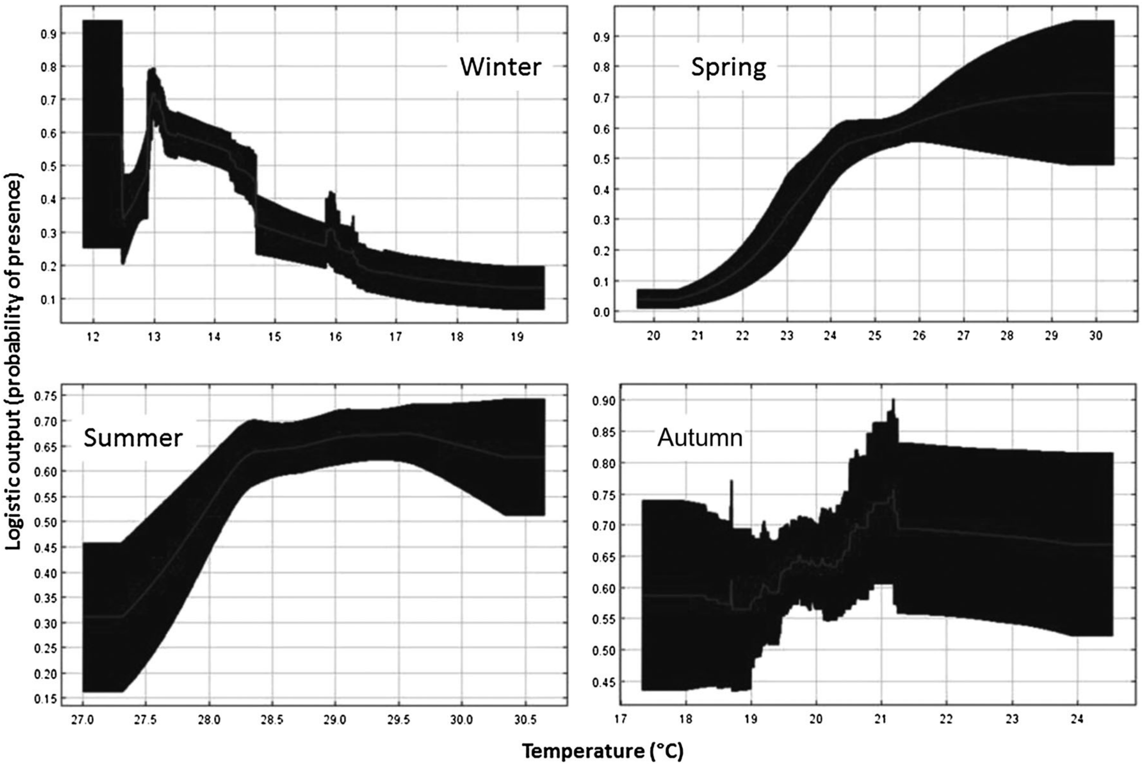

Figure 7. Logistic probability of bottlenose dolphin (*Tursiops truncatus*) presence in the MS Sound, USA as a function of temperature (°C) for the winter (January–March), spring (April–June), summer (July–September), and autumn (October–December) season.

systems (Nixon and Buckley, 2002). An increase in dolphin probability of occurrence with increasing levels of nitrates in all seasons suggests that dolphins may select areas with high nitrates within the MS Sound. An association between dolphin occurrence and high nitrates has not been demonstrated in the MS Sound, or in other regions; however, given that nitrates stimulate local primary and secondary production, this hypothesis warrants further investigation.

Also associated with freshwater influx in estuaries are hydrographic fronts. Fronts readily form in transition zones from fresh water to salt water, and have the propensity to concentrate fish (Franks, 1992). Dolphins have been seen exploiting hydrographic fronts in other areas where prey density is high and foraging efficiency is increased (Mendes *et al.*, 2002). No direct evidence of this type of feeding was noted during this study, but given the potential importance of this feeding strategy in estuarine systems, this phenomena should be investigated in the MS Sound.

In addition to potentially being important foraging areas for dolphins, locations with a very high LoDO could also be an important area for mating and calving. Spring is the dominant calving season in the MS Sound (Hubard *et al.*, 2004; Pitchford *et al.*, 2013) and is the time of year when the greatest amount of social activity occurs among dolphins in the region (Miller *et al.*, 2010). More work should be done to more clearly delineate hotspots for calving as protecting these areas is very important for ensuring sustainability of dolphins in this region.

Summer distribution

A unique characteristic of the summer model was that LoDO was moderate to high in unsampled areas such as Bay St. Louis and Biloxi Bay. These areas had low LoDO in the other seasonal models, which suggests environmental conditions in autumn, winter, and spring are generally not conducive to use by dolphins. Population size within the MS Sound has been estimated to be highest in summer (Hubard *et al.*, 2004; Miller *et al.*, 2013) as both resident and transient dolphins are found throughout the region (Mackey, 2010). Greater abundance of dolphins during summer and exploitation of the entire area including inland bays and bayous probably reflects greater suitability of environmental conditions and subsequent increases in the availability of prey, which are widespread throughout the region in summer (Pattillo *et al.*, 1997). Similarly, areas nearshore had very high LoDO in summer relative to other seasons, which again suggests that environmental conditions and prey availability in these areas played a large role in habitat suitability. Other embayments within the nGoM have reported similar habitat use and have hypothesized shifting prey distributions as a major cause (Irvine *et al.*, 1981; Maze and Wursig, 1999).

Autumn distribution

As with spring and summer, LoDO for the autumn is higher for areas within the MS Sound relative to areas outside the barrier islands. The autumn model also showed an expansive distribution of moderate and a westward distribution of high and very high LoDO including a large area near the mouth of the Pearl River. Little is known about dolphin habitat use within the western MS Sound; however, these results signify the importance of this habitat for dolphins in autumn. As mentioned previously, dolphins often exploit habitats near fresh water and salt water boundaries because these areas readily concentrate prey and as a result increase foraging efficiency (Mendes *et al.*, 2002). A distinct area of high and very high LoDO near the mouth of the Pearl River suggests that dolphins may be feeding on hydrographic fronts in this area. Dolphins have been shown to feed more often during the autumn in the MS Sound, potentially to build up fat stores for the coming winter months when prey is scarce (Miller *et al.*, 2010). While little is known about prey availability in this area, the anomalous spatial distribution of dolphins relative to winter, spring, and summer suggests that environmental conditions and potentially prey availability favours habitation of the western MS Sound during this time.

Most cetacean research in the MS Sound has previously been focused in areas to the east of Ship Island (Hubard *et al.,* 2004; Miller *et al.,* 2013) where the estimated population size of bottlenose dolphins has been estimated to be at its lowest (268 dolphins) in autumn relative to other seasons (Hubard *et al.*, 2004). Similarly, the autumn model presented here shows a relative decrease in the use of the central MS Sound (i.e. a part of the MS Sound between Horn and Petit Bois Islands) during autumn. However, high and very high LoDO in the western MS Sound suggests that the density of dolphins within the region is not uniform in autumn as LoDO was much higher west of Cat Island relative to other parts of the MS Sound. These findings indicate that this area should be studied more in the future especially with regard to its importance for dolphins in autumn.

Model limitations

A potential source of error in these models relates to low spatial and temporal resolution of predictor data. The model was created from seasonal mean values over long time periods with low spatial resolution (Boyer *et al.,* 2009; Antonov *et al.*, 2010; Garcia *et al.*, 2010a, b; Locarnini *et al.*, 2010). Environmental conditions vary widely in the region over geographic space and on very short timescales (Rakocinski *et al.,* 1996). Interpolation and averaging are necessary to create predictor layers for the model, but mask a great deal of the actual spatial and temporal variation in environmental conditions. As such, model predictions must also be interpreted as the likelihood of occurrence given average environmental conditions.

Another limitation relates to constraints associated with transect sampling. Because of the large size of the MS Sound, sampling was limited to four transects. Thus, dolphin sightings were only in areas close to these transects and did not extend into Alabama waters. The eastern part of the embayment within Alabama waters was included in the models to provide predicted distributions in this area. However, no actual presence locations and slightly different physical conditions relative to the larger MS Sound may have resulted in underestimation of the true LoDO in this area. For example, temperature was a very important predictor in the spring season, and mean temperatures in Alabama waters were 3–5°C cooler than the majority of the MS Sound based on interpolated temperature data. The predicted distribution for spring shows very low LoDO in Alabama waters during spring, which may underestimate the importance of this habitat for dolphins. Further, sea surface temperature was also used to create predictor layers for each season. Temperature variation within the water column relative to the surface should be considered in future models to refine the relation between temperature and dolphin occurrence.

It is also important to note that these models were developed using a limited set of predictor variables that certainly do not encapsulate all potential factors that could influence spatial distributions. As previously noted, inclusion of factors such as prey density would probably increase the performance of the model as we hypothesize that this may be a major factor driving seasonal variation in spatial distributions. Future studies could seek to generate this information by compiling available data and establishing a sampling regime to generate maps of prey distributions among seasons. A host of other variables that may influence dolphin occurrence (e.g. seabed slope, bottom type, and seagrass density) could also be created for use in future models. However, the MS Sound is relatively uniform with respect to these factors. Seagrass coverage is limited to a very small spatial extent along the northern shore of the barrier islands (Carter *et al.,* 2011) and the majority of the bottom is considered unstructured, mudflat with the exception of oyster reef habitats in the western MS Sound (MS Department of Marine Resources, 2013). The variables used in our models are those that probably affect dolphin occurrence and exhibit a greater degree spatiotemporal variation.

Model application

The MS Sound is a highly productive region of the nGoM and is thus home to a large recreational and commercial fishery. Widespread use of the MS Sound by dolphins from summer to autumn results in high potential for interactions with fisheries as commercial shrimping, crabbing, and recreational fishing are common throughout this time of the year (MS Department of Marine Resources, 2014). It is impossible to eradicate interactions between dolphins and fisheries because of the substantial overlap in prey species targeted by dolphins and humans; however, use of these predictive tools could have benefits for both.

Seasonal models presented here delineate several hotspots where the potential for dolphin–fishery interactions is high. Use of these models as a mitigation tool to inform commercial fishing operations could minimize these interactions, thus reducing by-catch of dolphins and the potential for fishery-related injury and mortality. For example, spring is the dominant mating and calving season for dolphins in the MS Sound (Pitchford *et al.*, 2013) and the spring model identified an area of very high LoDO spanning 30 km from east to west, north of Horn and Petit Bois Islands. This suggests that this area may deserve protection during spring to sustain or enhance reproductive rates and limit calf mortality. In addition to protecting dolphins, predictive models could also help fisherman avoid interactions with nuisance dolphins. Dolphins have been responsible for reductions in catch per unit effort in many areas (Noke and Odell, 2002; Read, 2008). Access to predictive maps could reduce the potential for these interactions, which could ultimately enhance the economic vitality of fisheries.

Another major application for these models is to provide assistance to state and federal agencies involved in planning and regulating resource extraction. Oil and natural gas extraction is currently not permitted within the majority of the interior MS Sound; however, there are several areas that have been deemed leasable for seismic surveys and drilling by the Mississippi Development Authority (MS Development Authority, 2013). Seismic surveys, placement of rigs, and ensuing noise can affect dolphin sensory capabilities (Tyack, 2008) and alter their ecology by affecting prey species (Popper *et al.,* 2003). Predictive models presented here could be used to mitigate or prevent conflicts between these activities and dolphins by delineating critical habitats that should be avoided.

Finally, it is important to note that these models serve as an important baseline regarding the current seasonal distributions of dolphins in this region. With an increasing number of natural and human threats, periodic delineation of critical habitat and assessment of changes in habitat over time is needed to effectively protect dolphins in the MS Sound. Before development of these models, limited data have been available regarding the spatial distribution of dolphins throughout the nGoM. Future research that examines spatial distributions will benefit from having a baseline to assess change over time and change in response to environmental perturbations.

CONCLUSIONS

In spite of some limitations, these models provide valuable information for seasonal distributions of dolphins in the MS Sound that can improve management of this protected species. Overall, model outputs provide an estimate of broad-scale spatial distributions, but also have the capacity to predict occurrence at a fine scale. These results could be used to enhance research and monitoring of dolphin populations. Given a large number of human threats to dolphins within the northern Gulf of Mexico region, greater understanding of geographic preferences is pivotal for the sustainability and protection of these populations.

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