

# Habitat use of toothed whales in a marine protected area based on point process models

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**ABSTRACT:** Toothed whales (Odontocetes) are highly mobile animals that play key trophic roles in ecosystems and whose habitats often overlap with areas of human activity. To mitigate detrimental effects of this overlap, it is critical to understand their habitat use patterns. The Stellwagen Bank National Marine Sanctuary in the western Gulf of Maine is a hypothesized foraging area for toothed whale species and an area of high human use, but odontocete habitat use there is poorly understood. While a large whale watch community provides a robust, long-term, opportunistic sighting data set, those data are not standardized. To overcome this limitation, we used point process models to analyze 10 yr of opportunistic sighting data. We identified spatial distribution patterns and environmental predictors for the 2 most common odontocete species in the sanctuary, Atlantic white-sided dolphins *Lagenorhynchus acutus* and harbor porpoise *Phocoena phocoena*. Habitat use differed among months, and depth, slope, substrate, and salinity were the most important and consistent predictors for both species. Models identified both persistent and shifting hotspots within the sanctuary. While presence was strongly associated with several covariates, environmental predictors did not fully explain shifting hotspots. This work highlights the importance of long-term opportunistic data collection and provides new knowledge on habitat use to inform assessment and management of potential human impacts on odontocetes in a federal marine protected area.

**KEY WORDS:** Presence-only · Species distribution models · Stellwagen Bank · Odontocetes · Atlantic white-sided dolphins · Harbor porpoise

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## 1. INTRODUCTION

The Stellwagen Bank National Marine Sanctuary (SBNMS) is a 2181 km<sup>2</sup> federally protected area located in Massachusetts Bay in the southwestern Gulf of Maine, USA. The sanctuary encompasses Stell-

wagen Bank, a shallow underwater plateau and prominent bathymetric feature that drives much of the region's oceanography, leading to high productivity and providing essential habitat for several protected baleen whale species (Overholtz & Nicolas 1979, Jiang et al. 2007). Stellwagen Bank is also a

hypothesized foraging area for protected toothed whales, and several species are known to use the sanctuary year-round (Waring et al. 2015); however, toothed whale (odontocete) habitat use, ecology, and overlap with human activity remain poorly understood.

Toothed whales can play key roles in structuring and maintaining healthy ecosystems through direct and indirect impacts on trophic dynamics (Bowen 1997, Kiszka et al. 2015, Estes et al. 2016). They can exert strong top-down predation effects through consumption of diverse species of fish and invertebrates (Bowen 1997, Estes et al. 1998, Overholtz & Link 2007, Craddock et al. 2009). Foraging strategies of toothed whales may mediate interactions between other species (e.g. forage fish and birds), and the wide-ranging movements of many toothed whale species could facilitate transportation of biomass and nutrients over large scales (Roman & McCarthy 2010, Kiszka et al. 2015, Estes et al. 2016). The overall abundance and highly mobile nature of many toothed whale species intensifies trophic impacts. Understanding effects of toothed whales on specific ecosystems requires knowledge of toothed whale occurrence, distribution, and abundance within that region.

Toothed whales are also vulnerable to human activities, which are especially abundant in SBNMS throughout the year. Fishing occurs year-round and includes both mobile and fixed gear (Wiley et al. 2003). Interaction with fishing gear is a global concern for many toothed whale species (Read et al. 2006) and at least one species, the harbor porpoise, is known to face excessive bycatch in Gulf of Maine fisheries (Read 2013). In addition, large commercial shipping vessels transit Massachusetts Bay in and out of the port of Boston, creating considerable noise and potentially degrading habitat (Hatch et al. 2008, 2012, Parks et al. 2009). The presence of boats and associated noise are known to influence toothed whale behavior (Nowacek et al. 2001, Buckstaff 2004, Jensen et al. 2009, Pirota et al. 2015), potentially negatively impacting both individuals and the sanctuary ecosystem. While there is potential for frequent and widespread overlap between these species and human activity in the sanctuary, information on toothed whale habitat use in relation to areas or times of human activity is necessary for evaluating and/or mitigating potentially negative human impacts.

Species distribution models (habitat models) typically aim to describe the distribution of a species as a function of environmental variables (Redfern et al. 2006, Elith & Leathwick 2009, Palacios et al. 2013). Presence/absence data and environmental covari-

ates may be modeled using conventional statistical methods (generalized linear models [GLMs] or generalized additive models [GAMs]) with the goals of predicting species' distributions, estimating abundance or probability of presence, or identifying important environmental predictors of species' distributions (Guisan et al. 2002). For species that are understudied, rare, or difficult to observe, designing standardized surveys to collect presence/absence data can be impractical and expensive. For many species, the only data available are opportunistic in nature. Opportunistic data, also known as presence-only data, contain sighting locations of the species of interest with no associated absence information. Fitting species distribution models using presence-only data requires specialized statistical methods, such as BIOCLIM, DOMAIN, Genetic Algorithm for Rule-Set Prediction (GARP), Environmental-Niche Factor Analysis (ENFA), pseudo-absence regression, and Maximum Entropy (MaxEnt) (Phillips et al. 2006, Tsoar et al. 2007, Fithian & Hastie 2013). Recently, point process models have emerged as a natural framework for presence-only modeling of species distributions and offer several advantages over other presence-only methods (Renner et al. 2015).

Presence-only data often arise as a point process, a set of point events in which the number of points and their locations are known. Point process models describe the number of points and their locations by intensity,  $\lambda(s)$ , the limiting expected number of point events (sighting records) per unit area. Point process models are closely related to other regression methods (GLM, MaxEnt, pseudo-absence regression; Warton & Shepherd 2010, Renner & Warton 2013, Renner et al. 2015); the intensity is typically modeled as a function of some environmental covariates. One type of point process model for studying species distributions is the inhomogeneous Poisson model, which assumes that (1) point events are independent of each other and (2) intensity,  $\lambda(s)$ , varies spatially and according to environmental covariates (Renner et al. 2015). The first advantage of point process models is the ability to test the assumption of point independence with existing tools. If points violate the independence assumption, which is often the case with presence-only data, point process models offer alternative methods that account for dependence between points.

The second major advantage to point process models relates to a clear interpretation of the modeled quantity. Intensity represents an abundance estimate of the expected number of presence records per unit area; it is not a probability. A presence record may

comprise one or more individuals, or one or more clusters of individuals; hereafter, we refer to a presence record as a sighting. Whether presence-only methods can produce absolute estimates of probability of occurrence is still debated (Royle et al. 2012, Hastie & Fithian 2013). With intensity, we can study and compare patterns in abundance of species sightings (Fithian & Hastie 2013, Hastie & Fithian 2013, Renner et al. 2015). Furthermore, we take advantage of all available information by jointly modeling the number of points and their locations, whereas other presence-only methods reduce the number of sightings to presence or absence within grid cells, resulting in loss of information.

Here, we used point process models and 10 yr of opportunistic sighting data to examine monthly distributions of Atlantic white-sided dolphins *Lagenorhynchus acutus* (hereafter referred to as white-sided dolphins) and harbor porpoise *Phocoena phocoena*, the 2 most common toothed whale species in the SBNMS. Our primary motivation was to increase understanding of the sanctuary ecosystem with a preliminary exploration of toothed whale habitat use. Our main goals were to identify important environmental influences on toothed whale habitat use, changes in species distributions during the year, and differences between species.

## 2. METHODS

### 2.1. Sighting data

Opportunistic sightings of white-sided dolphins and harbor porpoise in and around SBNMS (Fig. 1) were made available by the Center for Coastal Studies (Provincetown, MA), the Whale Center of New England (Gloucester, MA), the Dolphin Fleet (Provincetown, MA), NOAA Fisheries Northeast Fisheries Science Center (Woods Hole, MA), and the New England Coastal Wildlife Alliance (Middleboro, MA). We chose a recent 10 yr period (2004–2013) for which environmental covariate data were available. Sightings were recorded from whale watch vessels, research vessels, and aerial surveys. Most data were collected aboard commercial whale watching vessels. These companies run trips on as many days as possible from mid-April through mid-October. Effort is maximal from June–August with near-daily trips, but can diminish to as few as 2 to 5 d wk<sup>-1</sup> in April–May and September–October, depending on the operation. Vessels often target the sanctuary region and transit through the same general areas when de-

parting and returning. Our data set contains sightings from vessels departing from Plymouth, Provincetown, Boston, and Gloucester, providing relatively widespread spatial coverage and reducing spatial bias linked to areas close to any one port (Fig. 1). While data collection for odontocetes was opportunistic, effort information was available for some trips, potentially enabling traditional analysis of presence/absence data. However, we treated sightings as presence-only data for several reasons: (1) effort information was not readily accessible for all available data, (2) all platforms targeted baleen whales; surveys were not designed to study toothed whale species, (3) to integrate data from multiple organizations with different data collection protocols and formats, and (4) to use as much data as possible.

Based on the authors' experience, it was common for multiple vessels to view and record the same animals, sometimes several times per day and at the same time, likely leading to unintended duplicates in the data. To eliminate duplicate sightings, we ran-

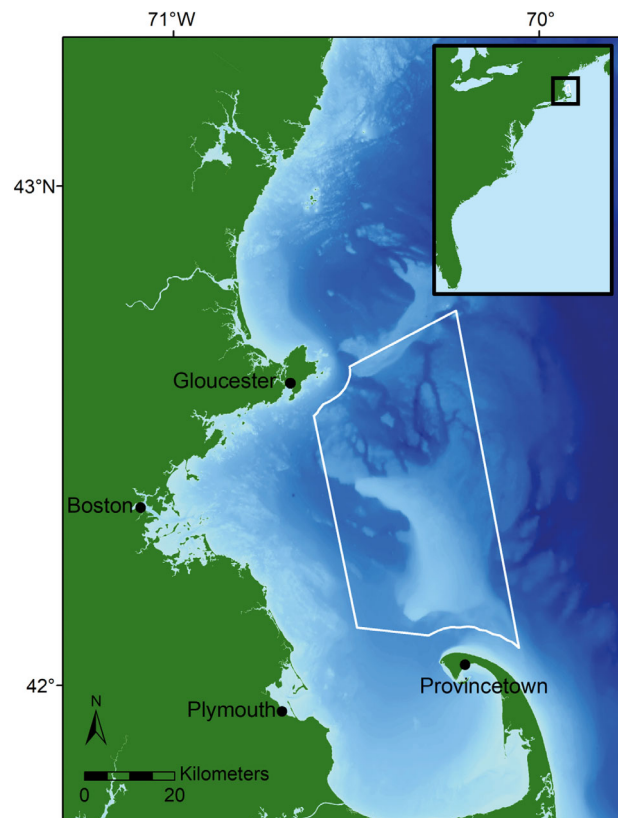


Fig. 1. Stellwagen Bank National Marine Sanctuary located in Massachusetts Bay. Sanctuary boundaries are shown in white and encompass the shallow area of Stellwagen Bank. Darker and lighter blue shading represents deeper and shallower water, respectively. Most toothed whale sighting data were recorded from vessels leaving the ports of Provincetown, Gloucester, Boston or Plymouth

domly selected 1 sighting  $d^{-1}$  from those within the sanctuary boundaries for each species, which resulted in a 31–63 % reduction in the number of sightings for each month (see Table 1). While thinning the data this way could reduce the amount of information about true spatial distributions and artificially introduce spatial independence between sighting locations, we chose a conservative approach to avoid an artificial inflation in sightings that could confound potential biological effects. Further, diagnostics of spatial dependence between points (see 'Point process models' section below) were similar between thinned point patterns and point patterns using all available sightings, suggesting little reduction in spatial information. We arbitrarily chose 20 sighting records  $mo^{-1}$  as a minimum requirement for analysis. This resulted in 7 models of white-sided dolphin distribution (April–October) and 2 models of harbor porpoise distribution (April and May). Sighting data were transformed to a point pattern object in UTM projection using the 'spatstat' package (Baddeley et al. 2015) in R v.3.3.3 (R Core Team 2017).

## 2.2. Environmental variables

Environmental variables were selected based on important physical features of the study area and previous work modeling the distributions of these species (Selzer & Payne 1988, Palka 1995). Depth, sea floor slope, backscatter intensity (as a proxy for substrate type), sea surface temperature (SST), chlorophyll *a* (chl *a*) concentration, and sea surface salinity were included in models. Bathymetric data were downloaded from the US Geological Survey, Coastal and Marine Geology Program's multi-beam bathymetric survey, resulting in a 10 m horizontal resolution and <1 m vertical depth resolution raster grid (Butman et al. 2007). Sea floor slope was calculated using the resulting bathymetric raster and the terrain function in the 'raster' package (Hijmans 2016). Multi-beam backscatter intensity data at a 10 m resolution were downloaded from the US Geological Survey, Coastal and Marine Geology Program (Butman et al. 2007). Backscatter intensity is a measure of the hardness and roughness of the seabed as determined by the strength of reflected sound waves using multi-beam sonar. Generally, higher backscatter values represent harder, coarser substrates and lower values represent softer, finer substrates. Backscatter values were used to classify sediment into 1 of 3 categories: mud (1–75), sand (76–165) or gravel (166–255) (Valentine et al. 2003).

Satellite-derived variables included SST and chl *a* data for the months of April through October from 2004–2013. Daily blended Multi-scale Ultra-high (~1 km) Resolution (MUR) Level 4 SST data from the Group for High Resolution Sea Surface Temperature (GHRSSST) were obtained from the Physical Oceanography Distributed Active Archive Center (<http://podaac.jpl.nasa.gov/dataset/JPL-L4UHFnd-GLOB-MUR>). Daily Level 1 ocean color files were acquired from the NASA Ocean Biology Processing Group (<https://oceandata.sci.gsfc.nasa.gov>) for Moderate Resolution Imaging Spectroradiometer (MODIS-Aqua) ([https://oceancolor.gsfc.nasa.gov/data/10.5067/AQUA/MODIS\\_OC.2014.0/](https://oceancolor.gsfc.nasa.gov/data/10.5067/AQUA/MODIS_OC.2014.0/)) and Sea-viewing Wide Field of View (SeaWiFS) (<https://oceancolor.gsfc.nasa.gov/data/10.5067/ORBVIEW-2/SEAWIFS/L1/DATA/1/>) sensors. Level 1 (~1 km resolution) ocean color data were processed to Level 2 using SeaDAS (v.7.3.1), and the chl *a* data (O'Reilly et al. 1998, Hu et al. 2012) were binned into ~2 km bins prior to merging the data from both sensors to reduce data gaps. For both SST and chl *a*, monthly variability was greater than inter-annual variability. Files for each variable were averaged to produce monthly rasters for April through October in each year, and then monthly files for all years were combined to produce a single mean raster for each month using the 'raster' package (Hijmans 2016). Long-term multi-year averages of environmental variables are typically sufficient when seasonal variability exceeds inter-annual variability and the selected time steps reflect this intra-annual variability (Mannocci et al. 2017). For all individual years, most chl *a* and SST values in a given month were within 1 standard deviation of the 10 yr mean and all values were within 2 standard deviations.

Salinity data were downloaded from the Northeast Coastal Ocean Forecast System (NECOFS; <http://fvcom.smast.umassd.edu/necofs/>), which is based on the Finite Volume Community Ocean Model (FVCOM) (Chen et al. 2006, Beardsley et al. 2013). Surface salinity values in NECOFS were estimated hourly on an unstructured triangular grid (horizontal resolution ranged from <1 to ~5 km inside the sanctuary). These values were averaged and linearly interpolated to create a raster of ~1 km resolution for each month for each year. Monthly rasters for all years were averaged to produce a single mean salinity raster for each month using the 'raster' package (Hijmans 2016). For all individual years, most salinity values for a given month were within 1 standard deviation of the 10 yr mean and all values were within 2 standard deviations.



Opportunistic data often exhibit spatial bias in survey effort (Reddy & Dávalos 2003). Species are more likely to be recorded in areas where observers are more likely to encounter them, raising the concern that presence-only models may represent observer or sampling bias versus the true distribution of a species (Phillips et al. 2009, Warton et al. 2013). Several methods exist for accounting for observer bias (Phillips et al. 2009, Renner et al. 2015). Warton et al. (2013) suggest modeling survey bias directly by including covariates in the model that represent sampling bias and then correcting for this bias when making model predictions. Our data set was collected from platforms focused on baleen whales and could be biased by whale location. To account for survey bias, we included baleen whale density as an observer variable. We used baleen whale sightings data from some of the same platforms as toothed whale sightings during a portion of our study period (2004–2007). Monthly, kriged density plots of whale sightings were created in ArcGIS v.10.5 (ESRI) using a 5000 m search radius. Kriging is an interpolation method used to create an estimated surface from point values. We standardized baleen whale density for each month so that values ranged from 0 to 1. Whale density and all environmental data rasters were cropped to sanctuary boundaries, transformed to UTM projection, and resampled to the same resolution (~1 km). Fig. 2 shows an example of environmental covariates for the month of April. Prior to

analysis, pair-correlation plots of all environmental variables were created for each month, and values greater than 0.7 resulted in removal of 1 correlated variable. SST was highly correlated with salinity in May, June, July, and October and was therefore removed in those models.

### 2.3. Point process models

One simple model, the Poisson point process model, assumes that sightings (points) are independent of one another (conditional on environmental covariates) and exhibit no correlation. Prior to analysis, we used the  $K$ -function,  $K_{\text{inhom}}(r)$ , and pair-correlation function,  $g_{\text{inhom}}(r)$  for inhomogeneous point processes to assess correlation in monthly point patterns (Ripley 1977, Baddeley et al. 2000, 2015). Ripley's  $K$ -function is the cumulative average number of data points falling within a distance,  $r$ , of a typical data point. The generalization of Ripley's  $K$ -function for inhomogeneous processes,  $K_{\text{inhom}}$ , accounts for spatially varying intensity as a function of environmental covariates. For a given point pattern, values of  $K_{\text{inhom}}(r)$  greater than the theoretical value ( $\pi r^2$ ) suggest clustering of points, while values of  $K_{\text{inhom}}(r)$  less than the theoretical value suggest inhibition of points.

The pair-correlation function is essentially the probability that 2 points are separated by a distance equal to  $r$ , divided by the corresponding probability

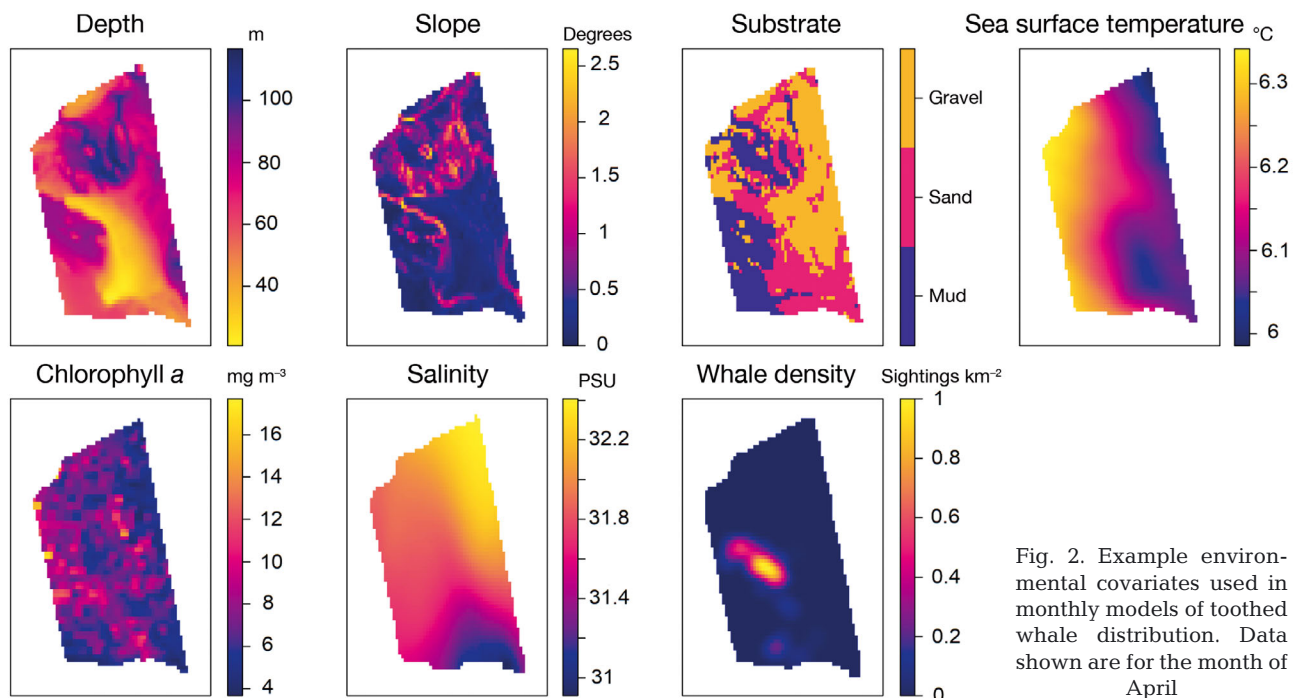


Fig. 2. Example environmental covariates used in monthly models of toothed whale distribution. Data shown are for the month of April

for a Poisson process. Values  $>1$  indicate that distances between points are more likely than if a pattern were random (Poisson) and are suggestive of clustering. Alternatively, values  $<1$  indicate that distances between points are less common than would be expected were the pattern random and are suggestive of inhibition between points, which results in more regular spacing between points.

Estimates of the  $K$ -function and pair-correlation function require an estimate of the intensity of the point process. In 'spatstat', the intensity is estimated using kernel smoothing, which requires the selection of sigma, the standard deviation of the kernel that controls the amount of smoothing (Baddeley et al. 2015). We chose values for sigma that produced the best match between the theoretical and observed  $K$ -functions (Taylor et al. 2013) and used those same values for calculating the pair-correlation function. Sigma values were as follows: 9, 9, 10, 9, 9, 7.5, and 7.5 for white-sided dolphins from April through October, and 7.5 and 20 for harbor porpoise in April and May, respectively. For the pair-correlation function, we included Monte Carlo pointwise envelopes resulting from 99 simulations as a measure of deviation from Poisson behavior.

Based on our data exploration, we chose to fit log-Gaussian Cox process (LGCP) models for each month for both species. In an LGCP, intensity is a spatially varying, random function ( $\lambda_s$ ) that depends on both observed environmental covariates, and a stochastic Gaussian process,  $\xi(s)$ , that represents unobservable or unmeasured factors associated with the distribution of the species, as follows:

$$\ln \lambda(s) = \mathbf{x}(s)' \boldsymbol{\beta} + \xi(s) \quad (1)$$

where  $\boldsymbol{\beta} = \{\beta_1, \dots, \beta_p\}$  is a vector containing parameters corresponding to  $p$  environmental covariates  $\mathbf{x}(s)$ . The random field,  $\xi(s)$ , is a spatial process with zero mean and a covariance function that depends on the distance between points, so intensity at locations that are closer together in space are assumed to be more positively correlated than those further apart. We assumed that  $\xi(s)$  captures all spatial dependence in the data that cannot be explained by measured covariates included in the model. The random intensity function causes points to appear to be more or less abundant in areas, producing a clustered appearance, or 'hotspots'. LGCPs are useful models for dealing with effects of clustering between points or the effects of unmeasured covariates (Møller et al. 1998, Baddeley et al. 2015). We fit LGCP models with an exponential spatial covariance function and the Palm likelihood method (Tanaka et al. 2008, Proke-

šová et al. 2013) using the 'spatstat' package in R (Baddeley et al. 2015). A set of quadrature (background) points placed throughout the study area were required to estimate the likelihood (Renner et al. 2015). We examined changes in the likelihood with different resolutions of quadrature points and chose regularly spaced quadrature points approximately 1 km apart (Warton & Shepard 2010, Renner et al. 2015).

All covariates were retained in models to compare covariate effects across months. We evaluated the predictive power of models using the area under the receiver operating characteristic curve (AUC). AUC is the probability that a randomly selected data point has a higher predicted intensity than a randomly selected spatial location, and measures the ability of the fitted model to separate the spatial domain into areas of high and low density of points. AUC values range from 0 to 1, with 0.5 indicating a complete lack of discriminatory power (Baddeley et al. 2015). We further examined the importance of individual covariates by running models including each covariate alone and calculating AUC (Friedlaender et al. 2011).

Predicted intensities (sightings  $\text{km}^{-2}$ ) for all models were calculated using a common level of observer bias (whale density = 1), which we propose represents the highest level of observer coverage over the study area. We note here that due to our sampling method (1 sighting  $\text{d}^{-1}$ ), the units of the predicted response variable are likely more complex than sightings  $\text{km}^{-2}$ ; however, we presented model predictions as intensity for simplicity (sightings  $\text{km}^{-2}$ ). Goodness-of-fit for all models was evaluated by computing pointwise Monte Carlo envelopes of the pair-correlation function for 99 simulations of the fitted model using the envelope function in 'spatstat'. All analyses were conducted using R v.3.3.1 (R Core Team 2017).

### 3. RESULTS

#### 3.1. Atlantic white-sided dolphins

The number of white-sided dolphin sightings and their spatial distribution differed between months (Table 1, Fig. 3). After selecting 1 random sighting  $\text{d}^{-1}$  (essentially the number of sighting days  $\text{mo}^{-1}$ ), the most sightings occurred in August, followed by May. October and June had the fewest sightings.

In April and May, the highest concentrations were observed in the southwestern portion of the sanctuary, which corresponds to the southwest corner of Stellwa-

Table 1. Opportunistic sightings of toothed whale species by month from 2004–2013. Total sanctuary sightings are all toothed whale sightings within Stellwagen Bank National Marine Sanctuary. Randomly selected sanctuary sightings are the number of sightings after selecting 1 random sighting  $d^{-1}$ , and are those used in models

Month	Sanctuary sightings	
	Total	Randomly selected
<b>White-sided dolphins</b>		
April	145	62
May	231	86
June	88	44
July	146	69
August	340	127
September	86	60
October	44	25
<b>Harbor porpoise</b>		
April	100	34
May	146	56

gen Bank (Fig. 3). In May, sightings increased in the southeast corner and the southwestern concentration drastically decreased in June. The southeastern concentration of sightings persisted through October. Sightings became more widely dispersed from north to south from June through August. A secondary hotspot occurred on the northwest corner of Stellwagen Bank in April, August, September, and October, but was less prominent in other months (Fig. 3).

$K_{inhom}$  plots showed near-Poisson to slight clustering of points from ~0 to ~6 km and regularity of points from ~6 to 11 km (Fig. 3B). Assessment of pair-correlation functions and histograms of pairwise distances provided additional support for clustering of points in most months (Fig. 3C,D). The pair-correlation function for April showed a peak at distances less than 1 km (Fig. 3C). The curve stayed above the theoretical Poisson line until about 2 km, but never exceeded highest and lowest simulation values indicated by pointwise Monte Carlo envelopes. This suggested slight, but not significant, clustering of points at spatial scales less than 2 km. A histogram of pairwise distances revealed 2 peaks; there were many pairs of points separated by 2–8 and 30–36 km (Fig. 3D), which further supports the existence of 2 loose clusters on the northwest and southwest corners of Stellwagen Bank (Fig. 3A). Point patterns can exhibit different behavior at different spatial scales; dependence of points at 1 spatial scale can lead to correlation between points at a different spatial scale. Pairs of points within clusters produce many small pairwise distances, while pairs of points be-

tween clusters produce many large pairwise distances (Fig. 3D). Based on all 3 diagnostics, our interpretation is that clustering of points at small spatial scales drives apparent regularity of points at larger spatial scales.

September and October exhibited similar patterns, though peaks in the pair-correlation function appeared at different values and exceeded pointwise Monte Carlo envelopes, suggesting that clustering may be stronger for these months. The pairwise correlation function clearly exceeded pointwise Monte Carlo envelopes in all months except April, suggesting stronger clustering.

The importance of individual environmental covariates and relationships with intensity differed between months (Table 2, Fig. 4). Generally, depth, slope, substrate, and salinity were the most common significant predictors of white-sided dolphin intensity. Shallower depths and higher slope values were consistently associated with higher intensity of sightings in all months. Sandy substrates and lower salinity values were associated with higher intensity in most months (Table 2).

In April, white-sided dolphin intensity peaked along the southern edge of the sanctuary south of Stellwagen Bank (Figs. 3 & 4), with a smaller area of elevated intensity on the northwest corner of Stellwagen Bank. These areas reflect significant contributions from SST, salinity, and slope. In May, intensity was highest along the southwest corner of Stellwagen Bank, southeast corner of the sanctuary, and the steep slopes of northern Stellwagen Bank, reflecting the apparent importance of depth, substrate, slope, and salinity (Fig. 2). In June, a spatial shift occurred; sightings increased in the northern part of the sanctuary and sightings on the southwest corner drastically decreased. The predicted distribution for June highlights shallow Stellwagen Bank, reflecting the significant contribution from sandy substrate (Table 2, Fig. 4). Substrate was the only categorical variable used in the models. Coefficient values for sand and gravel were expressed as the difference relative to mud, which is included in the intercept term. Predicted intensity for July was highest on Stellwagen Bank in shallow areas and near steep slopes. The predicted distribution for August was similar to June, highlighting shallow areas with sandy substrates that extend further to the southeast. October had a similar predicted distribution to July, though no covariates were identified as significant predictors for October (Table 2, Fig. 4). The predicted distribution for September was similar to other months in that it highlighted the southern part of the

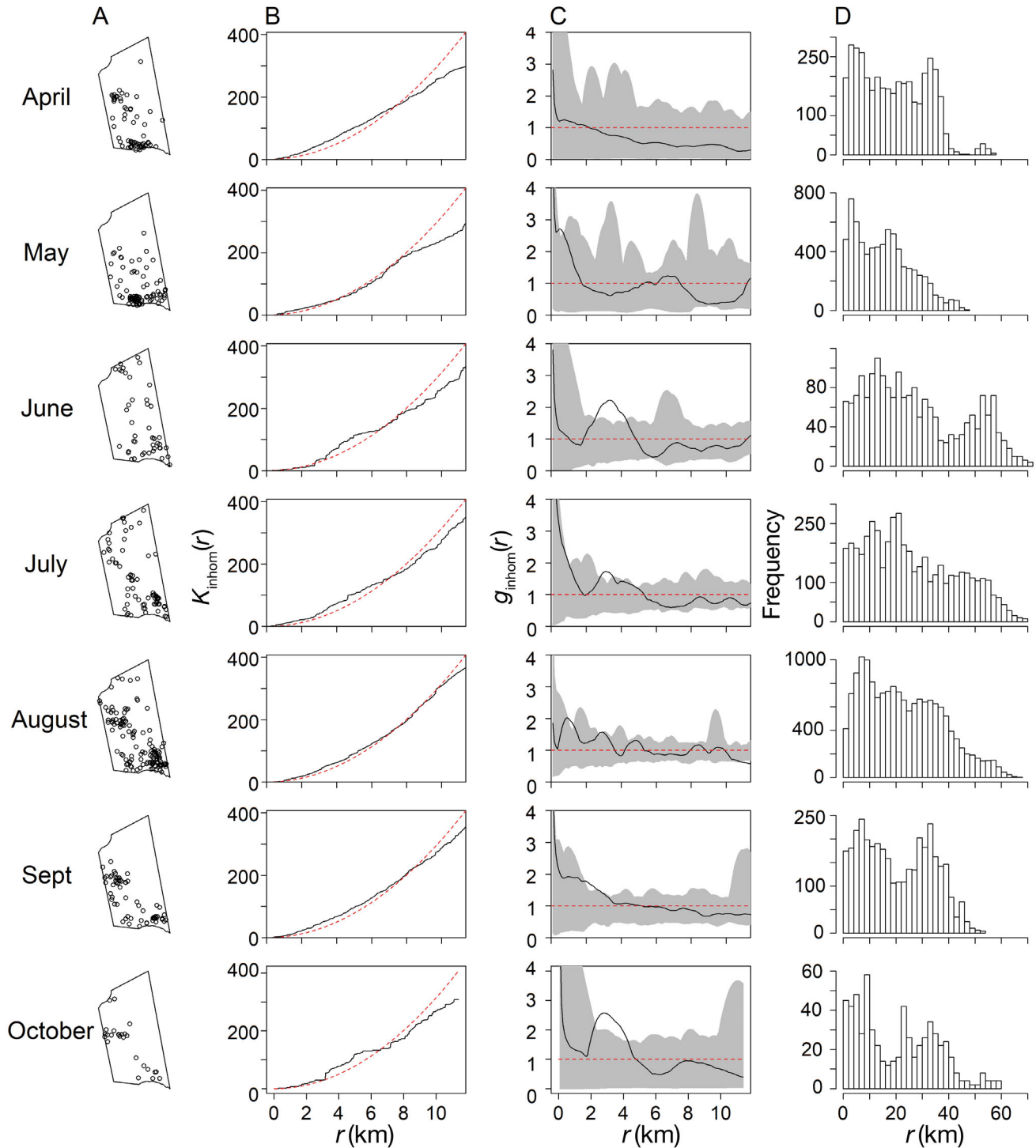


Fig. 3. Diagnostics for point independence for white-sided dolphins. (A) Distribution of white-sided dolphin sightings in the Stellwagen Bank National Marine Sanctuary plotted by month. (B) Inhomogeneous  $K$ -function,  $K_{\text{inhom}}(r)$ , for each point pattern. Red dashed line: theoretical values for an inhomogeneous Poisson point pattern; black solid lines: observed inhomogeneous  $K$ -function of the data. Plots suggest clustering if the black line exceeds the red line or regularity if the black line falls below the red line. The x-axis,  $r$ , is the range or distance between pairs of points in kilometers (km). (C) Pair correlation functions,  $g_{\text{inhom}}(r)$ , for each point pattern. Red dashed line: theoretical values for an inhomogeneous Poisson point pattern; black solid lines: observed pair-correlation function of the data; gray envelopes: high and low values of pointwise envelopes from 99 Monte Carlo simulations of the original point pattern in (A). Plots suggest clustering if the black line falls above Monte Carlo envelopes or regularity if the black line falls below Monte Carlo envelopes. (D) Pairwise distances between all pairs of points for each monthly point pattern



Table 2. Parameter estimates and 95 % confidence intervals for each monthly model for Atlantic white-sided dolphins and harbor porpoise. Log-Gaussian Cox process (LGCP) models were fit using Palm likelihood. SST values are missing from those months where SST was highly correlated with salinity and was omitted from models. \*p < 0.05; \*\*p < 0.01; \*\*\*p < 0.0001

Parameter	Harbor porpoise			White-sided dolphin					
	April	May	April	May	June	July	August	September	October
Intercept	43.36 -21.67, 108.39	113.15 62.98, 163.32***	90.55 29.91, 151.18**	191.1 92.69, 289.51**	23.01 -45.90, 91.91	20.08 -90.21, 130.38	-94.85 -210.41, 20.72	-54.58 -214.64, 105.48	46.76 -229.11, 322.62
Depth	-0.07, 0*	0 -0.02, 0.01	-0.04, 0.02	-0.02 -0.05, 0.01	-0.04, 0.01	-0.04 -0.07, -0.01**	-0.04 -0.06, -0.02***	0 -0.02, 0.03	-0.03 -0.06, 0
Slope	0.21 -0.70, 1.13	0.5 -0.17, 1.17	0.69 0.03, 1.35*	1.29 0.43, 2.16**	0.24 -0.63, 1.11	0.84 0.12, 1.66*	0.45 -0.08, 0.9	-0.19 -1.02, 0.64	0.86 -0.12, 1.83
Substrate sand	0.75 -0.42, 1.93	0 -0.78, 0.79	0.04 -0.83, 0.92	-0.68 -1.59, 0.23	1.21 0.02, 2.39*	0.59 -0.42, 1.60	0.08 -2.07, -0.26*	-0.27 -1.26, 0.71	0.06 -1.25, 1.38
Substrate gravel	-0.36 -1.93, 1.22	1 0.16, 1.85*	-0.45 -1.62, 0.72	-0.3 -1.49, 0.88	0.37 -0.99, 1.74	-0.47 -1.67, 0.73	-1.16 -2.07, -0.26*	-1.13 -2.47, 0.21	-1.1 -2.89, 0.68
Sea surface temperature	16.41 7.94, 24.89***		10.95 4.37, 17.54**				1.07 -2.18, 4.33	5.4 -0.22, 11.01	
Salinity	-4.71 -7.47, -1.95***	-3.76 -5.39, -2.13***	-5.13 -7.46, -2.81***	-6.21 -9.40, -3.02***	-0.84 -3.08, 1.40	-0.69 -4.23, 2.85	2.31 -0.55, 5.18	-1.37 -5.01, 2.28	-1.58 -10.22, 7.07
Chlorophyll <i>a</i>	0.16 -0.05, 0.36	-0.03 -0.27, 0.22	0.08 -0.1, 0.26	0.06 -0.27, 0.39	-0.55 -1.74, 0.64	-0.09 -0.38, 0.55	0.24 -0.11, 0.59	-0.23 -1.16, 0.69	0.09 -0.21, 0.39
Whale density	3.57 1.26, 5.87**	1.03 0.37, 2.42	3.23 1.21, 5.26**	-1.17 -3.93, 1.58	-1.82 -5.44, 1.79	-2.27 -5.06, 0.52	0.6 -1.29, 2.49	4.38 2.26, 6.50***	1.59 -0.75, 3.92

sanctuary, but differed in that it reflected negative associations with both sand and gravel (Table 2, Fig. 4)

SST was only included in April, August, and September models. While a consistent positive relationship with intensity was observed in all months, SST was significant only in April and based on predicted intensity maps, seemed to play little role in influencing white-sided dolphin intensity. Chl *a* was never a significant predictor of intensity. Interestingly, intensity distributions were not always associated with increased baleen whale density. Baleen whale density was negatively associated with intensity in May, June, and July.

Individual covariate models showed that substrate had the most predictive power of all variables for all months except May (Fig. 5). AUC values for substrate alone were greater than full model AUC values for all months except May and September (Fig. 5). AUC values for depth and salinity were greater than 0.6 for all months, revealing some discriminatory power (Fig. 5). Interestingly, slope showed little to no predictive power despite significant contribution in some full models. Baleen whale density also showed high predictive power in single-variable models, but was only significantly associated with intensity in April and September (Table 2, Fig. 5).

We evaluated model goodness-of-fit using Monte Carlo pointwise envelopes of 99 model simulations from the fitted model and comparing the pair-correlation function of model simulations to that of the data. Model fits appeared adequate except for the months of June and October, where observed values slightly exceeded Monte Carlo envelopes (Fig. S1 in the Supplement at [www.int-res.com/articles/suppl/m609p239\\_supp.pdf](http://www.int-res.com/articles/suppl/m609p239_supp.pdf)).

### 3.2. Harbor porpoise

The number of harbor porpoise sightings and their distributions differed between months and from those of white-sided dolphins (Table 1, Fig. 6). Harbor porpoise sightings were more frequent in

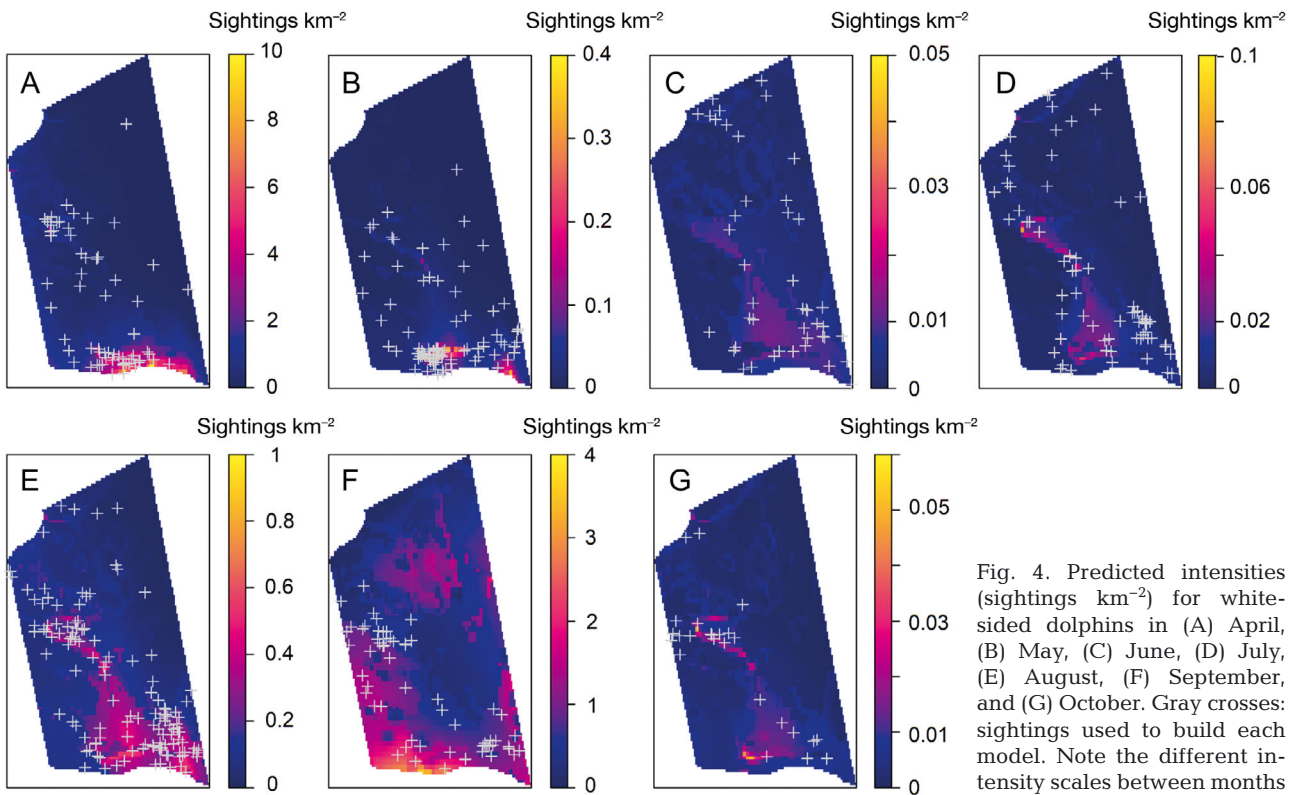


Fig. 4. Predicted intensities (sightings km<sup>-2</sup>) for white-sided dolphins in (A) April, (B) May, (C) June, (D) July, (E) August, (F) September, and (G) October. Gray crosses: sightings used to build each model. Note the different intensity scales between months

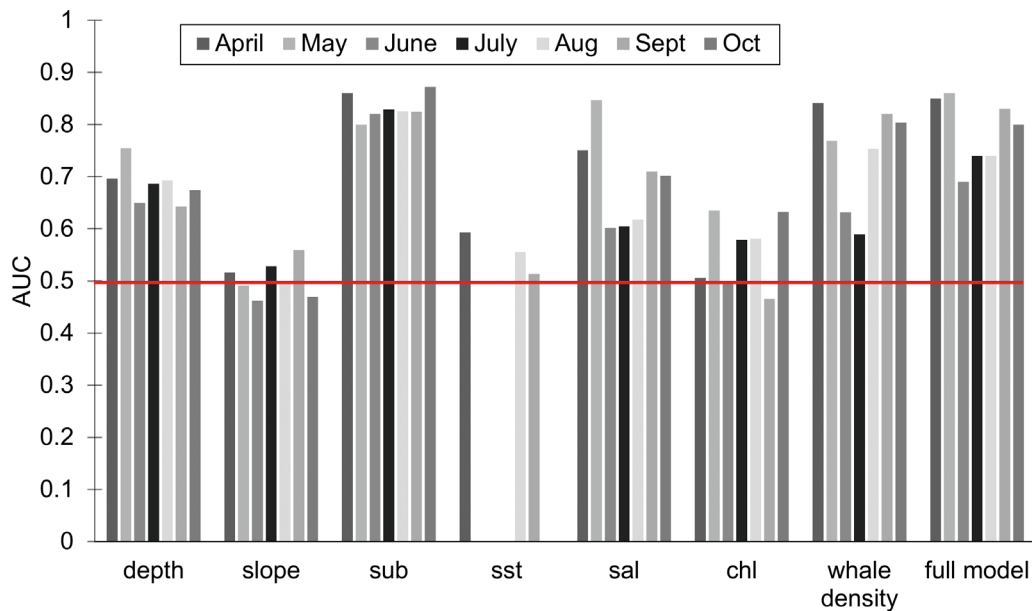


Fig. 5. Area under the receiver operating characteristic curve (AUC) values for single-variable model runs for white-sided dolphins. AUC is the probability that a randomly selected data point has a higher predicted intensity than a randomly selected spatial location and measures the ability of the fitted model to separate the spatial domain into areas of high and low density of points. AUC values range from 0 to 1, with 0.5 indicating a complete lack of discriminatory power. Sea surface temperature was often highly correlated with salinity and was removed from analysis in those months. Depth: depth; slope: sea floor slope; sub: substrate; sst: sea surface temperature; sal: salinity; chl: chlorophyll *a*; whale density: baleen whale density

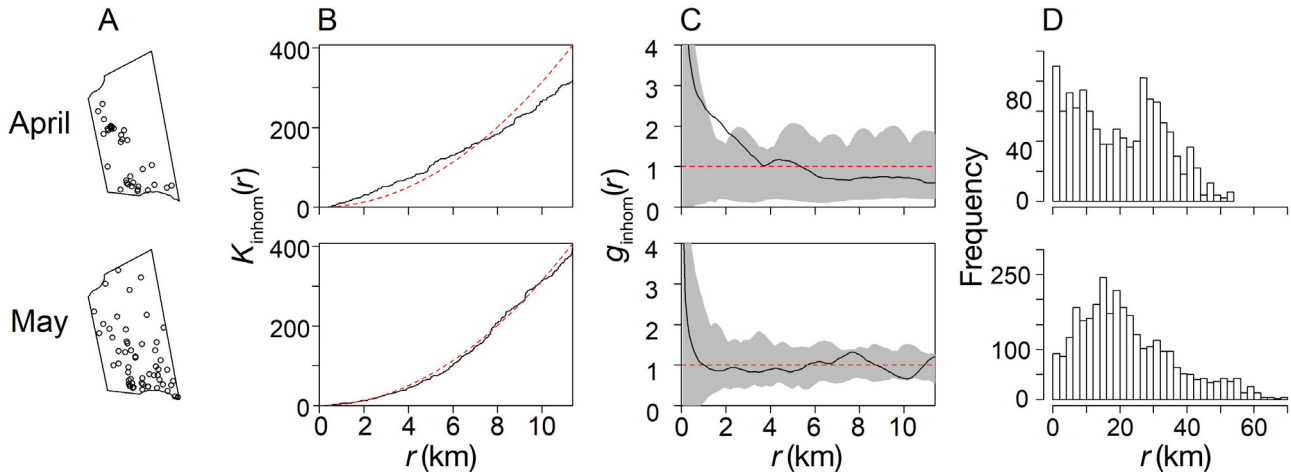


Fig. 6. Diagnostics for point independence for harbor porpoise. (A) Distribution of harbor porpoise sightings in the Stellwagen Bank National Marine Sanctuary plotted by month. (B) Inhomogeneous  $K$ -function,  $K_{inhom}(r)$ , for each point pattern. Red dashed line: theoretical values for an inhomogeneous Poisson point pattern; black solid lines: observed inhomogeneous  $K$ -function of the data. Plots suggest clustering if the black line exceeds the red line or regularity if the black line falls below the red line. The  $x$ -axis,  $r$ , is the range or distance between pairs of points in kilometers (km). (C) Pair correlation functions,  $g_{inhom}(r)$ , for each point pattern. Red dashed line: theoretical values for an inhomogeneous Poisson point pattern; black solid lines represent the observed pair-correlation function of the data; gray envelopes represent high and low values of pointwise envelopes from 99 Monte Carlo simulations of the original point pattern in (A). Plots suggest clustering if the black line falls above Monte Carlo envelopes or regularity if the black line falls below Monte Carlo envelopes. (D) Pairwise distances between all pairs of points for each monthly point pattern

May, but were less common than white-sided dolphin sightings in April and May (Table 1).

The distribution of harbor porpoise sightings in April was similar to that of white-sided dolphins. A concentration existed on the northwest and southwest corners of Stellwagen Bank (Fig. 6A). The pairwise correlation function showed slight, small-scale clustering, and pairwise distances exhibited 2 peaks, as with white-sided dolphins (Fig. 6B–D). May distributions differed between the 2 species (Figs. 3 & 6). May sightings of harbor porpoise exhibited less clustering than sightings of white-sided dolphins.  $K_{inhom}$  and  $g(r)$  for harbor porpoise were near the Poisson theoretical curve for all distances, and pairwise distances revealed many intermediate distances.

The importance of environmental covariates and relationships with intensity also differed between months for harbor porpoise. Similar to white-sided dolphins, SST and salinity were significant predictors for harbor porpoise distribution in April (Table 2). Depth was also a significant predictor of harbor porpoise intensity. Spatial distribution of predicted intensities for both species were similar in the southern part of the sanctuary, though greater intensity was predicted for harbor porpoise on the northwest corner of Stellwagen Bank and overall predicted intensity values were greater for white-sided dolphins (Figs. 4 & 7). Contrary to white-sided dolphins, gravel showed a significant positive relationship with intensity for har-

bor porpoise in May and this was the only significant predictor (Table 2). The distribution of predicted intensities for both species in May was also similar, with highest intensities of harbor porpoise predicted along the southern edge of Stellwagen Bank and in the middle of the sanctuary in gravel areas (Figs. 4 & 7).

As with white-sided dolphins, slope always exhibited a positive association with intensity (Table 2). Slope and SST all exhibited the same relationships for harbor porpoise as for white-sided dolphins (Table 2). For harbor porpoise, AUC values for full models were 0.89 and 0.76 for April and May, respectively.

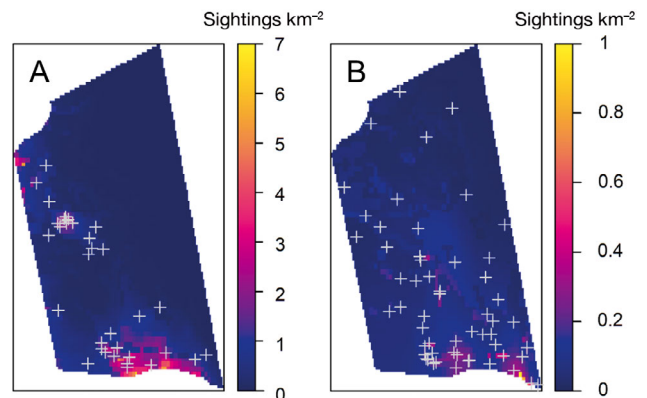


Fig. 7. Predicted intensities (sightings km<sup>-2</sup>) for harbor porpoise in (A) April and (B) May. Gray crosses: sightings used to build each model. Note the different intensity scales between months

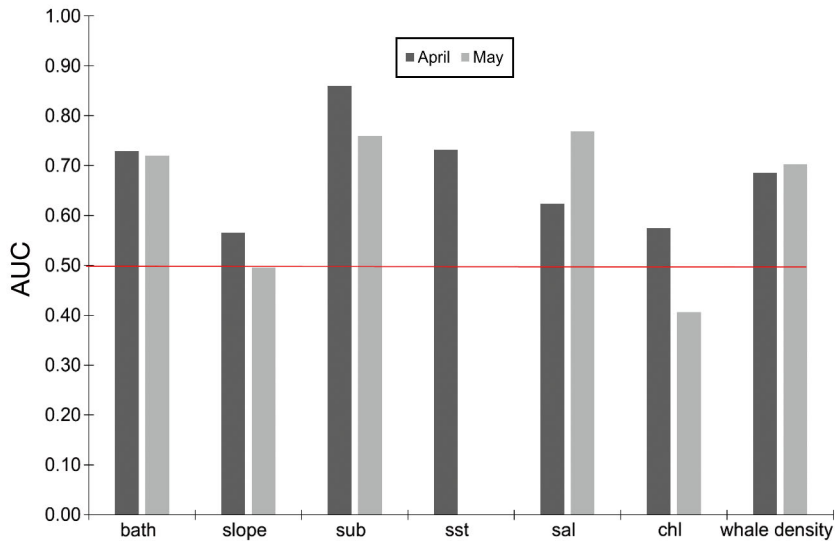


Fig. 8. Area under the receiver operating characteristic curve (AUC) values for single-variable model runs for harbor porpoise. See Fig. 5 for AUC details. Depth: depth; slope: sea floor slope; sub: substrate; sst: sea surface temperature; sal: salinity; chl: chlorophyll *a*; whale density: baleen whale density

Substrate, depth, whale density, and salinity showed high discriminatory power in single-variable model runs, while slope and chl *a* showed little to no discriminatory power (Fig. 8). Monte Carlo simulations of the pair-correlation function from fitted models indicated adequate model fits for both harbor porpoise models (Fig. S2).

#### 4. DISCUSSION

The aim of this work was to provide the first analysis of toothed whale habitat use in SBNMS, filling a major knowledge gap in a well-studied, critically important area for marine mammals and human use. To our knowledge, this study is one of the first to explicitly use point process models to examine marine mammal distributions (Skaug et al. 2004, Y. Yuan et al. preprint <https://arXiv.org/abs/1604.06013>). Our data set included a large volume of sightings collected from whale watching vessels, and the high intensity effort of these vessels provided a level of consistency not always present in opportunistic data sets. This allowed us to make cautious inferences about the frequency of toothed whale sightings in the sanctuary. Annual fluctuations in the number of sightings and their temporal and spatial distributions likely exist; however, at minimum, our long-term data set highlights areas of persistent importance to toothed whales, and at best, represents the true distribution of toothed whales in the sanctuary. Model predictions

were presented as intensity (sightings  $\text{km}^{-2}$ ) for simplicity, but predicted response values could be interpreted differently based on sampling methodology (1 random sighting  $\text{d}^{-1}$ ). However, we focused on identifying relative spatial distributions of species, not necessarily relative abundance estimates. We believe spatial distributions are reliable predictions despite the sampling method because diagnostics of spatial dependence between points was similar between thinned and full point patterns.

##### 4.1. Frequency of sightings

The number of white-sided dolphin sightings differed between months (Table 1). Based on total numbers of sightings, April, May, July, and August may represent important times for white-sided dolphins in the sanctuary. Conversely, June had the second fewest number of sanctuary sightings despite maximal whale watching effort at that time of year. This likely reflects decreased use of Massachusetts Bay by white-sided dolphins during June. Weinrich et al. (2001) examined the frequency of opportunistic white-sided dolphin sightings from 1984–1997 on Stellwagen Bank and Jeffrey’s Ledge. Sightings were common in April, relatively uncommon in May and June, and then common again from July through October. Our observations are generally consistent with those findings except for the month of May. Differences may reflect variation in the study period, the degree of spatial effort bias between studies, or both.

Sample sizes of harbor porpoise sightings were large enough to model distributions only in April and May. Here, presence-only data was consistent with knowledge of harbor porpoise movements throughout the Gulf of Maine, showing increased presence in the southwestern Gulf of Maine in spring (Hayes et al. 2016).

##### 4.2. Distribution patterns and environmental predictors

Odontocete distributions and important environmental predictors differed between months, supporting the use of a monthly modeling time scale. Identification of hotspots or shifts in hotspots may have

been difficult or impossible using seasonal or annual time scales. While aggregating data over a 10 yr period could strip away environmental or sighting variation, monthly spatial variation in environmental conditions was relatively similar between years, and sighting locations did not show significant pattern changes between years (Figs. S3 & S4).

Full models and single-predictor models did not always identify the same covariates as being important. White-sided dolphin full models identified depth, slope, substrate, and salinity as the most common significant predictors. Single-predictor models showed that substrate, whale density, salinity, and depth can be important discriminatory variables. In single-predictor models for each month, substrate had the most influence, while slope had little to no influence. Harbor porpoise models exhibited similar patterns. Apparent discrepancies in the identification of the most important predictors between full and single-predictor models are likely the result of multiple covariates containing either similar information, or information at different scales. For example, shallower areas on Stellwagen Bank are typically associated with sandy bottoms (Fig. 2). In single-variable models, both depth and substrate correlate well with white-sided dolphin and harbor porpoise sightings (Figs. 5 & 8); however, when combined in full models, these variables are not always significantly associated with intensity because they likely are accounting for the same information. The same is true for whale density, with the highest densities occurring in shallow, sandy areas. While slope showed little to no discriminatory power in single-variable models, the inclusion of slope in full models added information to help explain toothed whale sightings, and therefore slope is sometimes a significant predictor. Consideration of full and single-predictor model results is crucial in interpreting which environmental covariates are most influential.

The consistent relationship of topographic variables with intensity in most full models and their high discriminatory power in single-predictor models emphasizes the importance of these variables in influencing toothed whale distributions; higher intensities of white-sided dolphins and harbor porpoise were typically associated with shallow depths, higher slopes, and sandy substrates (Fig. 2). Variable and poor predictive performance of dynamic covariates in single-variable models suggests that these factors are not as important in determining toothed whale distribution in the sanctuary. Alternatively, the temporal or spatial scales of analysis may be too coarse in this case to capture responses of animals to these

variables in the environment. Chl *a* was not a significant predictor of white-sided dolphin or harbor porpoise distribution in any month and showed little to no discriminatory power based on AUC (Table 2, Figs. 5 & 8). This was not surprising, given the temporal and spatial lags expected between primary production and consumption by top predators (Grémillet et al. 2008, Palacios et al. 2013). The relatively small spatial scale of Stellwagen Bank and the overall high productivity of the entire area (Cahoon et al. 1993) may also decrease the importance of local variability in chl *a*.

Comparisons with studies at other sites can be challenging due to vastly different study environments. Previous habitat-use studies on white-sided dolphins and harbor porpoise that encompass the Gulf of Maine involved much larger spatial scales. Selzer & Payne (1988) examined distributions over the Northwest Atlantic continental shelf, while Pittman et al. (2006) modeled distributions for the entire southeastern Gulf of Maine from Massachusetts Bay to Georges Basin. Spatial scale differences may explain the increased importance of temperature in previous work not seen in our study. Salinity was a significant predictor in 2 months for white-sided dolphins and 1 month for harbor porpoise and also showed consistent relationships with intensity for all but one month, but showed more variability in predictive power in single-variable models (Fig. 5). Temperature and salinity ranges in our study did not exceed  $\sim 2^{\circ}\text{C}$  or  $\sim 2$  PSU in a given month, providing little environmental variability. These small differences are probably not biologically meaningful relative to the large-scale variation in environmental conditions experienced by either species over the extent of their range.

Nevertheless, our work corroborates previous studies of these species in the broader Gulf of Maine, providing support for depth, slope, substrate, and salinity as important environmental predictors. Higher intensities on southern Stellwagen Bank in April and May and preferences for shallower depths and higher slopes are consistent with previous work. Selzer & Payne (1988) reported preferences of white-sided dolphins for areas of high sea floor relief, and Pittman et al. (2006) showed associations with shallower depths. Pittman et al. (2006) also predicted higher abundance of white-sided dolphins along the southern edge of Stellwagen Bank in spring. Additional important predictors of white-sided dolphin distribution were colder temperatures, lower salinities (Selzer & Payne 1988), and the combined abundance of sand lance, herring, mackerel, and hake



(US Department of Commerce 2010). Previous work investigating white-sided dolphin distributions over the US continental shelf and the Scotian shelf identified depth, SST, and distance to the 200 m depth contour to be important factors affecting white-sided dolphins (Cetacean and Turtle Assessment Program 1982, Gowans & Whitehead 1995).

Harbor porpoise preferences for shallower depths confirms work by Palka (1995), who found that temperature, depth, and fish density were highly correlated with harbor porpoise distribution in the Gulf of Maine/Bay of Fundy. Harbor porpoise preferred water temperatures from 10–13.5°C and depths from 30–70 fathoms (55–129 m) (Palka 1995). The temperature preference reported by Palka (1995) may explain the higher numbers of harbor porpoises observed in May in the sanctuary, where SSTs ranged from 9.6–10.4°C.

Clustering of sightings can occur when habitat is favorable for a species, but it is impossible to determine if sightings exhibit true clustering (positive interaction) or strong inhomogeneity (Baddeley et al. 2015). True clustering or positive correlation between sightings refers to clustering that cannot be explained by the environment, while inhomogeneity refers to clustering that is due to animals responding to a heterogeneous environment. Clusters of white-sided dolphin and harbor porpoise sightings were composed of points from multiple years (Figs. S1 & S2), suggesting that these areas are persistently attractive to white-sided dolphins and harbor porpoise. Points from multiple years cannot truly 'interact' with each other; therefore, it is likely that point patterns for toothed whales are actually inhomogeneous and appear clustered due to favorable environmental conditions that are stable over time. While AUC values indicate generally good model performance for each individual month, the combination of significant environmental variables for each month and the relative performance of individual covariates models in each month does not account for clusters or distribution shifts over time for white-sided dolphins or harbor porpoise. These results imply that important spatial covariate(s) are missing from our models. Our choice of an LGCP was highly appropriate given the model's underlying theory: intensity is random and spatial variation in intensity is due to both observed and unobserved environmental covariates.

We hypothesize that an important missing covariate is prey distribution. The importance of topographic variables and the significance of prey distribution in previous work (US Department of Commerce 2010) supports this hypothesis. Sandy areas less than 50 m

deep, like the northwest and southwest corners of Stellwagen Bank, are preferable habitats for sand lance *Ammodytes* spp., the primary forage fish on Stellwagen Bank (Robards et al. 2000, US Department of Commerce 2010). Sand lance are a known prey item for white-sided dolphins in the Gulf of Maine (Craddock et al. 2009) and for harbor porpoise in the northeast Atlantic and Salish Sea (Santos & Pierce 2003, Nichol et al. 2013), but there is mixed evidence supporting the importance of sand lance as prey in the Gulf of Maine. Visual observations of either species feeding on sand lance are sparse (Weinrich et al. 2001) (although such observations are likely difficult to make) and studies of stomach contents documented sand lance in the stomach of just one white-sided dolphin (Recchia & Read 1989, Gannon et al. 1998, Craddock et al. 2009). The southwest-to-southeast shift in white-sided dolphin distribution from spring to summer could reflect an annual shift in prey density, availability, or type. Herring can be found in the southeast corner of the sanctuary (US Department of Commerce 2010) and are important prey for white-sided dolphins and harbor porpoise (Recchia & Read 1989, Gannon et al. 1998, Craddock et al. 2009).

Trawl survey data for fish species were not available for the entire sanctuary region at spatial or temporal resolutions suitable for our study. In addition, trawl survey gear is not designed for small species like sand lance. Toothed whale habitat models may be greatly improved with inclusion of individual fish species or families as covariates, but availability of fish distribution data limits capabilities. This emphasizes the need for better data on fish distributions to characterize linkages between marine mammal distributions and their prey.

### 4.3. Model fit and improvements

Model fits appear to be adequate, except for the white-sided dolphin models for June and October, in which the data exhibits clustering not accounted for by the model (Fig. 6). This implies that missing covariates may influence white-sided dolphin distribution more in these months. Our models were constructed for the purpose of data exploration and are a good first step in understanding toothed whale distribution in the sanctuary. However, model interpretation may benefit from greater quantification of uncertainty and regularization of model parameters (Renner et al. 2015). This work may inform development of more complex models using Bayesian, R-INLA, or marginal maximum likelihood approaches

(Baddeley et al. 2015, Renner et al. 2015, Thorson et al. 2015).

We used simple linear relationships in these models to increase interpretability. While toothed whale distributions often assume more complex relationships with environmental covariates (Hastie et al. 2005), linear relationships seem reasonable given the relatively small ranges of environmental covariates within our study area. Inclusion of additional non-spatial covariates, however, may improve our models. Two potentially important covariates not accounted for here were year and behavior. Combining sighting and environmental data over years was necessary due to small sample sizes, but this aggregation may have resulted in missed annual or cyclical trends. Furthermore, while we chose the smallest time scale possible with our data, temporal scales of days to weeks may be necessary to describe relationships between highly mobile toothed whales that adapt to and exploit dynamic environments and resources, particularly on small spatial scales (Redfern et al. 2006, Scales et al. 2017). Spatial-temporal LGCP models do exist; however, accounting for temporally varying covariates is a recent development (Ahn et al. 2014, Thorson et al. 2015). More easily implementable methods for space-time point process models would enhance studies of species distributions.

Models could also benefit from the inclusion of toothed whale behavior. We did not include behavior because there was no standard ethogram across these opportunistic data sets. The occurrence of clustered sightings in the sanctuary supports the hypothesis that Stellwagen Bank is a foraging ground for toothed whales. Weinrich et al. (2001) reported that boat interaction and traveling were the 2 most common behaviors exhibited by white-sided dolphins. If traveling were the predominant behavior of toothed whales in the sanctuary, it is possible that animals could show no or little association with particular environmental covariates. Including behavior in models or only modeling sightings where animals were observed or inferred to be feeding could produce stronger relationships with environmental covariates (Hastie et al. 2004).

We attempted to account for sampling bias by including baleen whale density as an observer bias covariate. While many factors influence effort and, therefore, observer bias on whale watching vessels, baleen whale density is likely the best available measure of observer bias. In the authors' experience, whale watch operators will often travel further from their home port, passing smaller concentrations of whales, to see higher densities of baleen whales. If

baleen whale density accurately reflects observer bias and observer bias exists, we would expect positive relationships between baleen whale density and predicted toothed whale intensity. Baleen whale density was significantly and positively associated with white-sided dolphin or harbor porpoise intensity only in April and September, and was negatively associated with intensity in May–July (Table 2). However, baleen whale density alone showed considerable discriminatory power for most months (Figs. 5 & 8). Interpretation of relationships between toothed whale intensity and whale density is unclear, but several explanations are possible. Toothed whales could use different habitat than baleen whales, and observer bias may not be an issue in this case. Overlapping prey preferences between baleen and toothed whales and positive relationships between baleen whale density and toothed whale intensity in single-variable models suggests this explanation is unlikely. Secondly, it is likely that baleen whale density alone contains valuable environmental information about toothed whale sightings, but full models contain covariates that correlate better with toothed whale distributions, making baleen whale density not as useful when these other covariates are included in models. Lastly, the available estimates of baleen whale density included sightings collected during the first 3 yr of our study period. Incorporating baleen whale sightings from the entire study period may produce a better match between baleen whale density and toothed whale intensity.

We caution here that while baleen whale density is likely the best representative variable of observer bias, it could also be used as an environmental variable. There is likely overlap between baleen whale and odontocete habitat, suggesting that whale density could reflect the 'best' habitat. Without an actual measure of effort, it is impossible to untangle effects of habitat versus effort, which could produce biased predictions if whale density only reflects best habitat. Whale density may also operate as a proxy for some environmental information that was not directly included in our models, such as prey density. In this case, it would not be directly possible to disentangle this additional habitat factor even with whale watching effort. We believe that baleen whale density likely represents both observer bias and best habitat here, but general agreement between our results and those of previous studies lends confidence to our predicted distributions. Future work should explore new variables to account for observer bias.

This work provides the first systematic analysis of toothed whale occurrence and habitat use in the

SBNMS. Based on the existence of persistent concentrations of toothed whales, we provide evidence that Stellwagen Bank is an important area for toothed whales in the spring, summer, and fall. Winter models were not possible due to little observation effort and poor weather. Future work focusing on addressing winter habitat use could use passive acoustic monitoring, which can occur year-round and has proved highly successful in monitoring marine mammal occurrence in Massachusetts Bay (Mussoline et al. 2012, Risch et al. 2013). Given that toothed whales could play key roles in trophic dynamics and energy flow throughout the sanctuary, further work should be conducted to allow them to be incorporated into food web models and management plans.

Our work provides baseline information about toothed whale habitat use to inform studies evaluating overlap with, and potential impacts of, human activities. We showed that white-sided dolphins and harbor porpoise partially overlap in spatial distribution, and potentially, ecological niche, suggesting that these species could be vulnerable to similar human activities. Bycatch and potential ocean noise exposure are the biggest concerns for marine mammals on Stellwagen Bank (Hatch et al. 2012, Read 2013). Finally, our work was only possible because of continued support for the collection and maintenance of opportunistic data in the sanctuary region. Massachusetts Bay has one of the richest opportunistic marine mammal data sets in the world, and our work underscores the value of such long-term opportunistic data collection.

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