

Occurrence, distribution and abundance of cetaceans in Onslow Bay, North Carolina, USA

ANDREW J. READ¹, SUSAN BARCO², JOEL BELL³, DAVID L. BORCHERS⁴, M. LOUISE BURT⁴, ERIN W. CUMMINGS², JENNIFER DUNN¹, ERIN MEAGHER FOUGERES², LUCIE HAZEN¹, LYNNE E. WILLIAMS HODGE¹, ANNA-MARIE LAURA¹, RYAN J. MCALARNEY², PETER NILSSON², D. ANN PABST², CHARLES G. M. PAXTON⁴, SUZANNE Z. SCHNEIDER², KIM W. URIAN¹, DANIELLE M. WAPLES¹ AND WILLIAM A. MCLELLAN²

Contact e-mail: aread@duke.edu

ABSTRACT

In this paper the occurrence, distribution and abundance of cetaceans in offshore waters of Onslow Bay, North Carolina, USA is described. Between June 2007 and June 2010 monthly aerial and shipboard line-transect surveys were conducted along ten 74km transects placed perpendicular to the shelf break. In total 42,676km of aerial trackline (218 sightings) and 5,209km of vessel trackline (100 sightings) were observed. Seven species of cetaceans were observed, but the fauna was dominated strongly by common bottlenose and Atlantic spotted dolphins. Both species were present year-round in the study area. Using photo-identification techniques, five bottlenose dolphins and one spotted dolphin were resighted during the three-year period. In general, the abundance of cetaceans in Onslow Bay was low and too few sightings were made to estimate monthly abundances for species other than bottlenose and spotted dolphins. Maximum monthly abundances of bottlenose and spotted dolphins were 4,100 (95% CI: 1,300–9,400) in May 2010 and 6,000 (95% CI: 2,500–17,400) in March 2009, respectively. Bottlenose dolphins were found throughout the study area, although they were encountered most frequently just off the shelf break. In contrast, spotted dolphins exhibited a strong preference for waters over the continental shelf and were not encountered beyond the shelf break.

KEYWORDS: ABUNDANCE ESTIMATE; MONITORING; SURVEY-COMBINED; TRENDS; PHOTO-ID; ATLANTIC OCEAN; NORTHERN HEMISPHERE; ATLANTIC SPOTTED DOLPHIN; MODELLING; BOTTLENOSE DOLPHIN; COMMON DOLPHIN; RISSO'S DOLPHIN; ROUGH-TOOTHED DOLPHIN; FIN WHALE; SPERM WHALE; SHORT FINNED PILOT WHALE

INTRODUCTION

Understanding of the distribution and abundance of many populations of offshore cetaceans is limited because of the difficulty and expense of obtaining quantitative estimates of these parameters (Hammond, 2010). Surveys of such populations typically occur at very broad spatial scales, interspersed by long time periods (e.g. Hammond *et al.*, 2002, 2013; Gerrodette and Forcada, 2005). Thus, there is often a spatial mismatch between available data and information needed to assess the potential impact of human activities on pelagic cetaceans in specific areas. In addition, the snapshots of cetacean occurrence and density from broad-scale surveys provide no information on potential seasonal trends in these parameters.

This paper reports the results of an intensive three-year study of the occurrence, distribution and abundance of cetaceans in Onslow Bay, North Carolina, USA, within the South Atlantic Bight. In 2005, the US Navy proposed development of an Undersea Warfare Training Range (USWTR) in this area (Department of the Navy, 2009). Relatively little was known regarding the occurrence of cetaceans in the offshore waters of Onslow Bay because most previous surveys in the South Atlantic Bight had been conducted at a very coarse spatial scale (Mullin and Fulling 2003; Garrison *et al.* 2010). To address this data limitation, an intensive survey programme was begun in June 2007. In 2009, the Navy changed its preferred site for the USWTR to

an area off Jacksonville, Florida (Department of the Navy, 2009), but our surveys continued in Onslow Bay.

The proposed USWTR in Onslow Bay consisted of an area of 1,715km² that straddled the 200m isobath (Fig. 1). A variety of cetaceans were known or believed to occur in this area, including shelf-associated species such as Atlantic spotted dolphins (*Stenella frontalis*) and common bottlenose dolphins (*Tursiops truncatus*) and pelagic species, such as short-finned pilot whales (*Globicephala macrorhynchus*) (Mullin and Fulling, 2003; Garrison *et al.*, 2010). In addition, several mysticetes, such as endangered North Atlantic right whales (*Eubalaena glacialis*), likely use portions of Onslow Bay as a migratory corridor (Schick *et al.*, 2009).

A monitoring plan was developed that included monthly aerial and shipboard surveys for cetaceans and sea turtles, strip-transect surveys for seabirds and passive acoustic monitoring of cetaceans with a towed hydrophone array and a series of moored recorders. The results of three years of aerial and shipboard line-transect surveys for cetaceans, beginning in June 2007 are reported in this paper. The results of the passive acoustic monitoring programme (Hodge, 2011) and sea turtle and seabird surveys (Thorne, 2010) will be reported separately. A suite of complementary field methods (aerial surveys, vessel surveys and passive acoustics) deliberately selected to maximise the probability of detecting all cetaceans in the study area, including deep-diving and cryptic species (Barlow, 1999). To extend the time

¹ Division of Marine Science and Conservation, Nicholas School of the Environment, Duke University, Beaufort, NC 28516 USA.

² Biology and Marine Biology, University of North Carolina Wilmington, 601 South College Road, Wilmington, NC 28403 USA.

³ Naval Facilities Engineering Command Atlantic, 6506 Hampton Blvd, Norfolk, VA 23508 USA.

⁴ Research Unit for Wildlife Population Assessment, Centre for Research into Ecological and Environmental Modelling, University of St. Andrews, St Andrews, Fife KY16 9LZ Scotland.

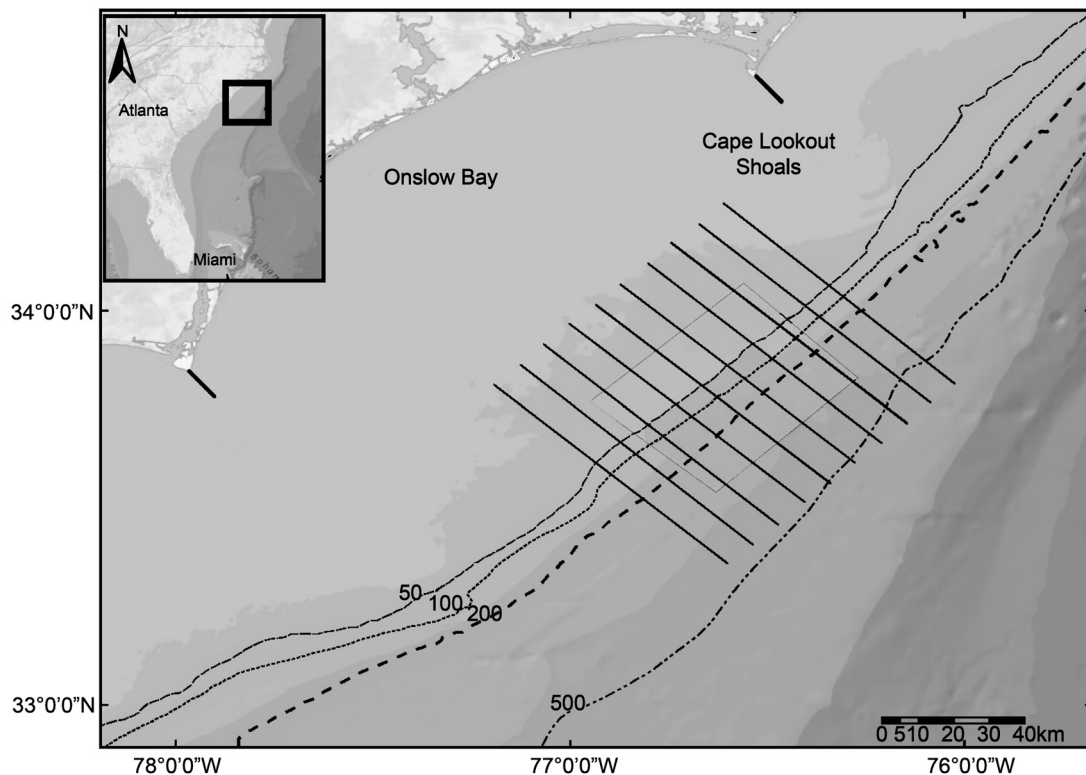


Fig. 1. The study area in Onslow Bay, North Carolina, USA, showing the tracklines used in aerial and vessel surveys. The shaded box indicates the location of the proposed Undersea Warfare Training Range (USWTR). Isobath depths are in metres. The inset shows the location of the study area within the southeastern United States. Data on the occurrence of stranded cetaceans in Onslow Bay were derived from events that occurred from Cape Lookout to Cape Fear, denoted by the two thick lines extending from shore.

series and increase the sample size of observations, an earlier series of aerial surveys conducted in this area in 1998 and 1999 was also incorporated.

The objective of the research, therefore, to provide a comprehensive description of the occurrence, distribution and abundance of cetaceans in Onslow Bay, including seasonal variation in these parameters.

METHODS

Study area

The proposed USWTR site in Onslow Bay consisted of a rectangle 46×37 km; the center of this rectangle is approximately 90 km from shore. Surveys extended beyond the proposed boundaries of the USWTR, so the total prediction area was 5,334 km². Surveys were conducted along ten transect lines that were placed perpendicular to the coast and the shelf break, each 74 km in length and spaced approximately 9 km apart, in this area (Fig. 1). Both aerial and vessel surveys used the same set of tracklines.

The dominant oceanographic feature of the study area is the Gulf Stream, which meanders back and forth over the shelf break as it flows northwards. As a result of these meanders, oceanographic conditions at any point in the study area can vary considerably in only a few days. The 200 m isobath bisects the study area (Fig. 1) which, therefore, included both the continental shelf and slope waters.

Aerial surveys

Aerial surveys were conducted from June 2007 to June 2010 inclusive in a *Cessna 337 Skymaster* at an altitude of 305 m and a speed of 185 km hr⁻¹. Surveys were conducted on days

with low sea states (Beaufort 0–3) and optimal visibility. The goal was to complete a full set of ten tracklines twice each month. The earlier set of aerial surveys was conducted over a slightly different set of tracklines in the same location from September 1998 to July 1999, also using a *Cessna 337* and a similar survey protocol, except that the plane flew at 230 m (McLellan *et al.*, 1999). Sightings data from the two sets of aerial surveys were combined. To improve precision of the detection functions of certain species, sightings from aerial surveys for right whales conducted closer to shore by the University of North Carolina Wilmington were also incorporated (all survey results reported in OBIS-SEAMAP; Halpin *et al.*, 2009).

During aerial surveys, an observer monitored each side of the plane, equipped with a GPS unit, data sheet and binoculars; each side was considered to be an independent transect. The observers recorded the start and end of transect lines, any changes in environmental variables (i.e. cloud cover, sea state, visibility and glare) and sightings of marine mammals, sea turtles and vessels. When a sighting cue was observed, the observers estimated horizontal and vertical sighting angles by eye. The aircraft then broke from the trackline and closed on the sighting location. The plane circled over the sighting to obtain photographs to confirm species identity. During each encounter, the left observer was designated as data recorder and the right observer obtained digital photographs with a Canon 40D camera and a 100–400 mm image-stabilised lens. These images were used to assist with species identification (see below), refine estimates of group size and confirm sightings of calves. A best estimate of group size was established using both field observations

and subsequent examination of digital images. Each observer independently estimated the minimum and maximum number of animals in each sighting. Once photographs and sighting data were collected, the plane returned to the initial location on the trackline and resumed survey effort. The plane did not break from the trackline for sightings of sea turtles, other marine vertebrates (e.g. sharks and rays) or vessels.

Vessel surveys

Vessel surveys were conducted from June 2007 to June 2010, inclusive, from two platforms: the F/V *Sensation*, a 16m offshore fishing vessel and the R/V *Cetus*, a modified 12m offshore fishing vessel. These two vessels were chosen for their ability to transit rapidly to and from the study area. The target of survey effort varied over the course of the study, with a maximum goal of five transects per month during the summers of 2007 and 2008. Due to seasonal variation in sea conditions, lower targets of monthly survey effort were set during winters.

Observations were made from the flying bridge (5.0m and 4.2m above waterline for the *Sensation* and *Cetus*, respectively) using naked eye and 7×50 binoculars. While on effort, two observers (one port and one starboard) scanned constantly from straight ahead to 90° abeam either side of the trackline. A third observer monitored the trackline, coordinated with the vessel skipper and acted as data recorder. The observers rotated positions (including at least one rest station) every 30 minutes. Survey speed was approximately 18km hr^{-1} . Standard line transect sampling methods for cetaceans were used, similar to those described by Barlow (2006).

The location and species identity of each cetacean group were recorded. Each observer estimated group size independently and these estimates were averaged at the end of each survey to generate a final estimate of group size. Environmental conditions (weather, sea state, depth and sea surface temperature) were recorded every 30 minutes or whenever sighting conditions changed. All sighting and environmental observations were entered into an onboard data collection system (Vis-Survey, developed by Dr. Lance Garrison, NOAA SEFSC Miami, FL) linked to a GPS unit.

During these vessel surveys a hydrophone array (Seiche Instruments, UK) was towed approximately 150m behind the vessel. The array consisted of four elements, spaced 1.2m apart, with a flat ($\pm 3\text{dB}$) frequency response between 2 and 100kHz and a sensitivity of $-165\text{dB re } 1\text{V}/\mu\text{Pa}$. High-frequency acoustic recordings at 192-kHz sampling rate were made on a laptop running *Ishmael* software (Mellinger, 2001) and a MOTU Traveler audio interface (Mark of the Unicorn, Cambridge, MA, USA). A trained acoustician monitored incoming acoustic signals aurally and visually via spectrograms in *Ishmael*, with the gain set to -96dB . Recordings were made directly to an external hard drive whenever calls were detected using *Ishmael*, at which point time and location were noted. The recording station was located in the main cabin of the survey vessel, isolated from the visual observers, so the acoustic and visual surveys functioned independently.

In addition, patterns of residency in the study area were monitored by identifying individual animals using photo-

identification techniques. Thus, whenever possible, digital photographs were obtained for photo-identification. These photographs were also used to confirm species identification and to compare identification features with those used by the aerial survey team (see below). *Canon* or *Nikon* digital SLRs equipped with 100–300mm zoom lenses were used. All photo-identification images were graded for quality and individual distinctiveness using methods described in Read *et al.* (2003).

Species identification

Digital images of each sighting were reviewed in the laboratory to confirm species identity. During the first year aerial and shipboard observers reviewed every sighting together and established a set of diagnostic features that were subsequently used to identify each cetacean species. Common bottlenose and Atlantic spotted dolphins were sometimes difficult to distinguish from the air, particularly when groups were comprised entirely of juveniles. In addition, it is difficult to differentiate short- and long-finned species of pilot whales (*G. macrorhynchus* and *G. melas*, respectively) at sea (Rone and Pace, 2012). Thus, if species identity could not be unequivocally determined, the sighting was designated to the nearest taxonomic category (e.g. ‘unidentified delphinid’).

Statistical analysis

General approach

To generate density surfaces and, where possible, identify environmental variables driving patterns of animal distribution, the probability of detection associated with each sighting was estimated and then surface density per segment of trackline within the truncation distance was estimated. Detection probabilities were estimated assuming that detection of an animal on the trackline was certain (see below for a discussion of this assumption).

The survey region is heterogeneous with substantial changes in depth and the fluctuating presence of the Gulf Stream. The adjusted density data were characterised by a high ratio of zero to non-zero segments, so density was modelled with a two-stage process: (1) the probability of presence as a logistic generalised additive model (GAM); and, (2) estimated density, given that animals were present. The product of these two prediction surfaces gave an estimated relative density surface for the study area. Abundance was then obtained by numerically integrating under these surfaces. The resulting abundances do not take into account periods when animals were submerged, and therefore unavailable for detection, or imperfect detection on the trackline. Due to limited sample sizes, only bottlenose dolphins and Atlantic spotted dolphins could be modelled.

Estimation of detection probabilities

Either a hazard-rate ($1 - \exp(-y/\sigma)^b$) or half-normal form ($\exp(-y^2/2\sigma^2)$) was used for the probability detection function (σ is the scale parameter) (Buckland *et al.*, 2001) where y is perpendicular distance. The effects of covariates, other than perpendicular distance were incorporated, into the detection function model by setting the scale parameter to be an exponential function of the covariates (Marques, 2001). Thus, the probability of detection becomes a

multivariate function, $g(y, \nu)$, representing the probability of detection at perpendicular distance y and covariates ν ($\nu = \nu_1, \dots, \nu_Q$ where Q is the number of covariates). The scale term, σ , has the form:

$$\sigma_k = \exp\left(\beta_0 \pi \sum_{q=1}^Q (B_q \nu_{kq})\right)$$

and β_0 and β_q ($q = 1, \dots, Q$) are parameters to be estimated. With this formulation, it was assumed that the covariates may affect the rate at which detection probability decreases as a function of distance, but not the shape of the detection function. In the aerial case the covariates considered were Altitude, Beaufort Sea State and Glare. In the boat case, the covariates were Species, Beaufort Sea State, Group Size and Visibility.

A backward, stepwise selection procedure (starting from the previous best model) was used to decide which covariates to include, with a minimum Akaike's Information Criterion (AIC) inclusion criterion. All initial model selection was performed in the program *Distance* (v5.0; Thomas *et al.*, 2002) and re-fitted the final selected models using a set of customised functions (mrds v.1.3.8) in *R* 2.9.2 (*R* Developmental Core Team, 2009). This facilitated estimation of variance within *R* (see below).

In general, rates of encounter rates with cetaceans were very low during the 2007–10 surveys, so detection probabilities were estimated by augmenting sightings with data gathered from the same aerial platform during surveys carried out closer to the coast and another set flown near Wallops Island, Virginia in 1998 and 1999 (McLellan *et al.*, 1999). Additional shipboard sightings were also incorporated, using the same methodology and observers, from the F/V *Sensation* obtained during a brief survey off Cape Hatteras, where cetacean densities are much higher, in 2007. All dolphin species were grouped into a single guild of delphinids to estimate detection functions and then evaluated species as a covariate when fitting the detection function. There were too few sightings to estimate density for species other than bottlenose and spotted dolphins.

Estimation of density surfaces

A modified version of the 'count model' of Hedley *et al.*, (1999) was implemented to model spatial distribution. The response variable for this model was a density based on the estimated number of individuals for a small segment i of trackline, \hat{N}_i , calculated using an estimator similar to the Horvitz-Thompson estimator (Horvitz and Thompson, 1952), as follows:

$$\hat{N}_i = \sum_{j=1}^{n_i} \frac{s_{ij}}{\int_0^w \hat{g}(y, \nu_{ij}) \pi(y) dy}, \quad i = 1, \dots, T,$$

where, for segment i , $\int_0^w \hat{g}(y, \nu_{ij}) \pi(y) dy$ is the estimated probability of detection of the j^{th} detected pod, n_i is the number of detected pods in the segment and s_{ij} is the size of the j^{th} pod. The total number of transect segments is denoted by T . By assumption, $\pi(y)$, the probability density function of actual (not necessarily observed) perpendicular distances is uniform up to the truncation distance; this is satisfied by locating transects randomly.

Having obtained the estimated number of individuals in each segment, the density in segment i , \hat{D}_i , from \hat{N}_i/a_i where a_i is the area of segment i was estimated. Segment area was calculated as the length of the segment multiplied by twice the truncation distance used to model the detection function. The survey tracklines were initially divided into distinct segments based on effort and sighting conditions. Long segments were divided and a variety of segment lengths from 5 to 13km were evaluated; 10km was chosen as an appropriate compromise between maximising the ratio of non-zero to zero segments, maintaining environmental resolution and giving some measure of spatial independence (see Results).

In most cases, the number of segments with detections was extremely low, which made fitting of models difficult, so a variety of alternative approaches were explored. Zero-inflated methods were investigated, but these proved impossible to implement successfully with the dataset. Therefore, a two-stage process was implemented: the presence or absence of animals in a particular segment was modelled using a logistic GAM and then non-zero density was modelled in each segment again with a GAM but now assuming a Gamma error structure. The predicted probability of the presence of animals in a segment was multiplied by the predicted non-zero density in that segment to obtain the predicted density of animals. This two-stage process may introduce a potential bias in that absences (zeros) are over-represented because some observed zeros were not true absences, but simply segments of low density where animals were present but not observed. Perfect correction for under detection is not possible given the absence of a $g(0)$ estimate.

The following covariates were included in the models: sea surface temperature (Temp); depth (Depth); day of year (Dayofyear); and year of survey (Year). Dayofyear was considered as a cyclic cubic spline, so the second derivative of the curve for Dayofyear met at the beginning and end of the year. Sea surface temperatures were collected during shipboard surveys, but for the aerial survey and prediction grid temperatures⁵ were obtained at 1-degree and weekly resolutions (Reynolds *et al.*, 2002). Depths were obtained from ETOPO2 at 2-minute resolution⁶. Year was trusted as a factor rather than a continuous variable because of the break in surveys between 1999 and 2007.

Temperatures and depths were associated with effort segments by finding the closest point in the temperature and bathymetry data to the midpoint of the effort segments using great circle distances (and date for temperature). Finally, Survey was incorporated as a factor to identify the survey platform (plane or boat), but only if the estimated value of the regression coefficient associated with the plane was lower than those associated with the ships, i.e. the use of Survey reflected differences in $g(0)$ between aerial and shipboard surveys.

Backwards model selection was implemented using generalised cross validation (gcv) in the *mgcv* package (v. 1.5–2) in *R* (v. 2.9.2) for covariate selection in the logistic model, augmented with diagnostic plots, using the principles described in Wood (2006). Model selection was by

⁵<http://dss.ucar.edu/datasets/ds277.0/data/oiv2/>.

⁶<http://www.ngdc.noaa.gov/mgg/image/2minrelief.html>.

generalised cross validation. All covariates were considered for inclusion in the model as 1D smooths of untransformed covariate values. A maximum of four degrees of freedom was allowed in the selection of 1D smooths for Temp, Depth and Dayofyear as the response to these variables would be unlikely to have more than two minima and maxima. The presence of unexplained spatial variation was looked for by inspection of semi-variograms of the residuals of the models. Models were fitted to all data across all years. Survey was included in all models to account for the detectability differences on the trackline between aerial and ship surveys.

Due to variation in environmental conditions along transects, it was not always split survey effort into segments of equal length (see below). Therefore, the model was weighted by segment area. The presence-only data were modelled in the same way, although sometimes simplified models were chosen for the point estimate to avoid generating spuriously high results in the bootstrap where the full range of data might not be available, leading to dubious extrapolation over the entire prediction region.

Prediction of density and variance estimation

The final models were used to predict density using a two-minute resolution prediction grid. Abundance was estimated by numerically integrating under this predicted density surface. If survey platform was included in the final model, abundance was predicted assuming the survey mode with the largest coefficient value, as this would reflect the best detection on the trackline. Predictions were made for every month of each survey year to allow comparison of seasonal trends across years.

Variance was estimated by repeating the entire abundance estimation process on a large number of samples, drawn at random from the data, to obtain a distribution of abundance estimates. Confidence intervals were derived from this distribution using the 2.5% and 97.5% percentiles to obtain the upper and lower limits. Samples were obtained by sampling transects, at random and with replacement, so that the selected effort reflected the effort in the original sample and accounted for evidence of temporal correlation in the residuals by the same sections of effort together being used. Models were refitted with the same covariates as in the original analysis but the degrees of freedom available to each smooth could be reselected, subject to the constraints mentioned above.

RESULTS

Aerial surveys

Aerial surveys of all tracklines were conducted each month from June 2007 to June 2010, with the exception of January and September 2008 and May 2010. The aerial survey covered 42,676km of trackline, with most (78%) effort occurring in Beaufort Sea States 2 and 3. An additional 12,821km of trackline were flown between September 1998 and July 1999, with effort in every month except February 1999. Taking both data sets together, 55,497km of trackline were surveyed with effort in every calendar month.

A total of 279 sightings of seven species were recorded during these aerial surveys. Atlantic spotted and common bottlenose dolphins dominated the cetacean fauna (Table 1).

Table 1

Summary of cetacean sightings in Onslow Bay, North Carolina, by platform type and period.

Species	Aerial surveys		Vessel surveys	Total
	1998–99	2007–10	2007–10	
<i>Tursiops truncatus</i>	39 (64%)	126 (58%)	51	216
<i>Stenella frontalis</i>	0	57 (26%)	36	93
<i>Delphinus delphis</i>	14 (23%)	1 (<1%)	0	15
<i>Grampus griseus</i>	3 (5%)	4 (2%)	4	11
<i>Globicephala</i> spp.	1 (2%)	7 (3%)	3	11
<i>Steno bredanensis</i>	0	3 (1%)	1	4
<i>Balaenoptera physalus</i>	0	1 (<1%)	0	1
Unidentified delphinid	3 (5%)	19 (9%)	5	27
Unidentified ziphiid	1 (2%)	0	0	1
Total	61	218	100	

The sightings included 22 unidentified delphinid schools and an observation of a single group of unidentified beaked whales in May 1999. In addition, an off-effort sighting of a single sperm whale (*Physeter macrocephalus*) was recorded while transiting to the offshore end of a trackline in October 2009. No mixed-species groups were observed. Species composition was similar in the 1998–99 and 2007–10 surveys, with two exceptions. No spotted dolphins were observed during the earlier surveys, but this species comprised more than a quarter of all sightings in the latter period. In contrast, common dolphins (*Delphinus delphis*) were observed in the earlier time period but not the more recent surveys. Based on the distribution of long- and short-finned pilot whales during summer (Waring *et al.*, 2011), it is likely that all pilot whales observed from June–August were *G. macrorhynchus*, but it was not possible to confirm species identity of pilot whales during these surveys.

Spotted and bottlenose dolphins were present throughout the year (Table 2). Sightings of bottlenose dolphins were recorded during every month, and sightings of spotted dolphins occurred in every month except July and December (Table 2), although this species was observed during vessel surveys in July (see below). There were too few sightings of other species seen to draw conclusions regarding their seasonal occurrence. Spotted dolphins were restricted to shelf waters; bottlenose dolphins were found over both shelf and deeper waters (Fig. 2a). Pilot whales, Risso's dolphins (*Grampus griseus*) and rough-toothed dolphins (*Steno bredanensis*) were exclusively found over the shelf break and in deeper waters (Fig. 2a). Mean (\pm S.E.) observed group size of bottlenose dolphins in Onslow Bay was 20.1 (\pm 2.0) in the earlier surveys and 15.1 (\pm 1.4) in the more recent period. Mean observed group size of spotted dolphins in Onslow Bay was 26.1 (\pm 3.6) in 2007–10.

Vessel surveys

A total of 5,209km of vessel survey effort was recorded from June 2007 to June 2010. Most (70%) of this survey effort was conducted in Beaufort Sea States 2 and 3. A total of 95 sightings of five cetacean species and 5 sightings of unidentified delphinids was made. Species composition (Table 1) and distribution (Fig. 2b) were similar to those observed from the aircraft, with most (87%) sightings composed of common bottlenose and spotted dolphins. Mean group sizes of bottlenose and spotted dolphins were 13.8

Table 2

Cetacean sightings by month in Onslow Bay, North Carolina, from June 2007 to June 2010. Only aerial survey effort and sightings are presented. Effort is represented by the number of tracklines, indicated in the bottom row.

Species	Month											
	J	F	M	A	M	J	J	A	S	O	N	D
<i>Tursiops truncatus</i>	12	5	17	13	14	20	2	7	4	18	13	1
<i>Stenella frontalis</i>	4	9	9	6	2	8	0	6	6	6	1	0
<i>Delphinus delphis</i>	0	0	1	0	0	0	0	0	0	0	0	0
<i>Grampus griseus</i>	0	0	0	0	1	2	0	1	0	0	0	0
<i>Globicephala</i> spp.	0	1	0	0	2	1	2	1	0	0	0	0
<i>Steno bredanensis</i>	0	0	0	1	0	2	0	0	0	0	0	0
<i>Balaenoptera physalus</i>	0	0	1	0	0	0	0	0	0	0	0	0
Tracklines	40	30	55	50	40	62	60	60	36	60	46	30

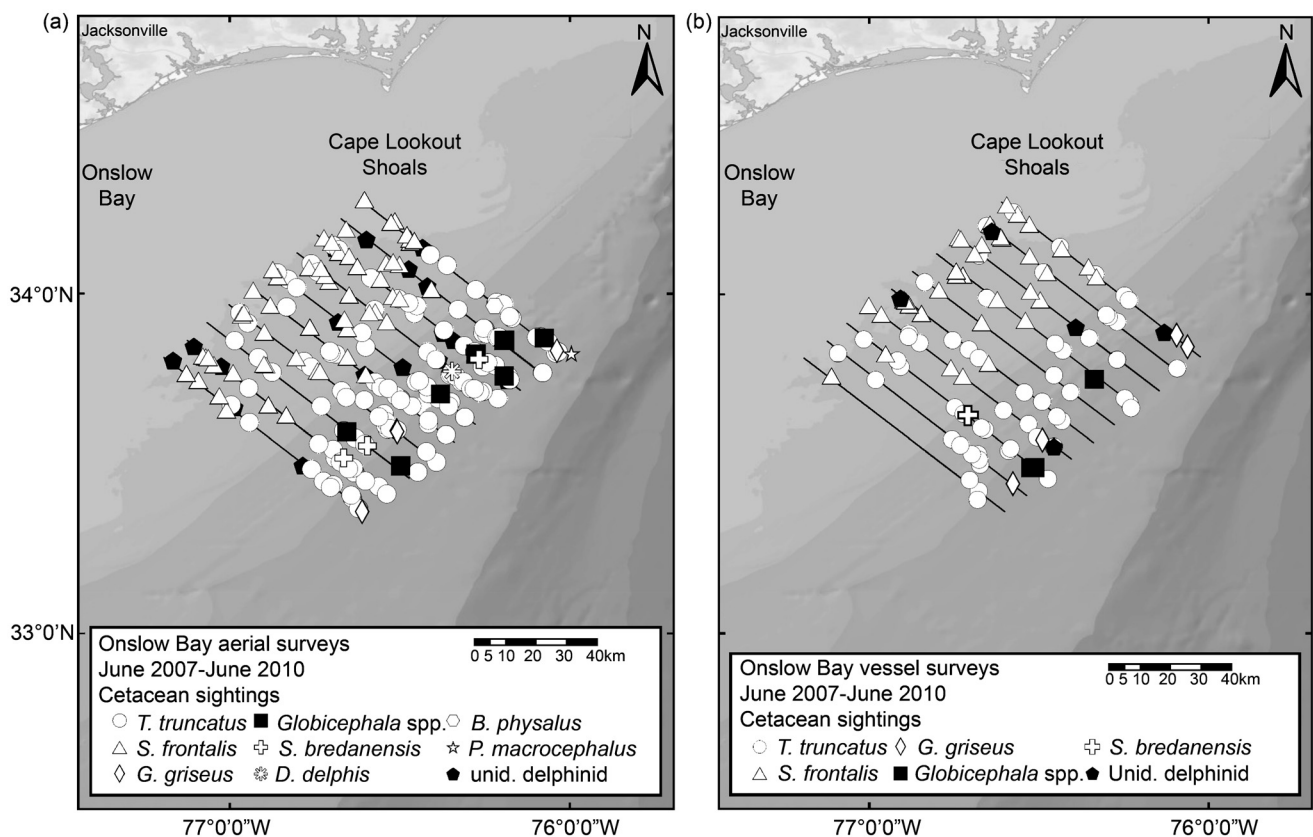


Fig. 2a. Spatial distribution of sightings of cetaceans from aerial surveys in Onslow Bay, June 2007–June 2010. The single sighting of a sperm whale was made off-effort during transit.

Fig. 2b. Spatial distribution of sightings of cetaceans from vessel surveys in Onslow Bay, June 2007–June 2010.

(± 1.5) and 22.6 (± 5.9), respectively. As was the case for aerial surveys, no mixed-species groups were observed.

The hydrophone array was towed on 41 days, for a total of 194.5 hours of combined visual and acoustic surveys. During these combined surveys a total of 109 acoustic detections of cetaceans were recorded; 68 were visually confirmed and 41 were not observed. Thus, most (62%) acoustic detections of cetaceans were also detected independently by the visual observers.

In total 3,169 digital photo-identification images of five species of cetaceans were obtained and the following animals were catalogued: 106 individual bottlenose dolphins; 49 spotted dolphins; 16 pilot whales; 12 rough-toothed dolphins; and 7 Risso's dolphins. Five bottlenose dolphins were resighted: (1) ID 9-016 on 25 July 2008 and 17 August

2009; (2) ID 4-002 on 15 September 2009 and 1 October 2009; (3) 1-004 on 1 October 2009 and 11 April 2010; (4) and (5) IDs 7-015 and 8-009, seen together on 28 April 2009, and seen together again on 20 April 2010. One spotted dolphin, ID 9-013, seen on 9 August 2009 and then again on 1 October 2009 (Fig. 3) was also matched. No individuals of other species were resighted, although the catalogue sizes for these species were small.

Statistical analysis

Sightings of all dolphins from aerial surveys were binned into 200m widths because of evidence of rounding and they were right truncated at 1.4km. The best fit dolphin aerial detection function was a hazard rate function including perpendicular distance, *Altitude* and *Beaufort Sea State* only

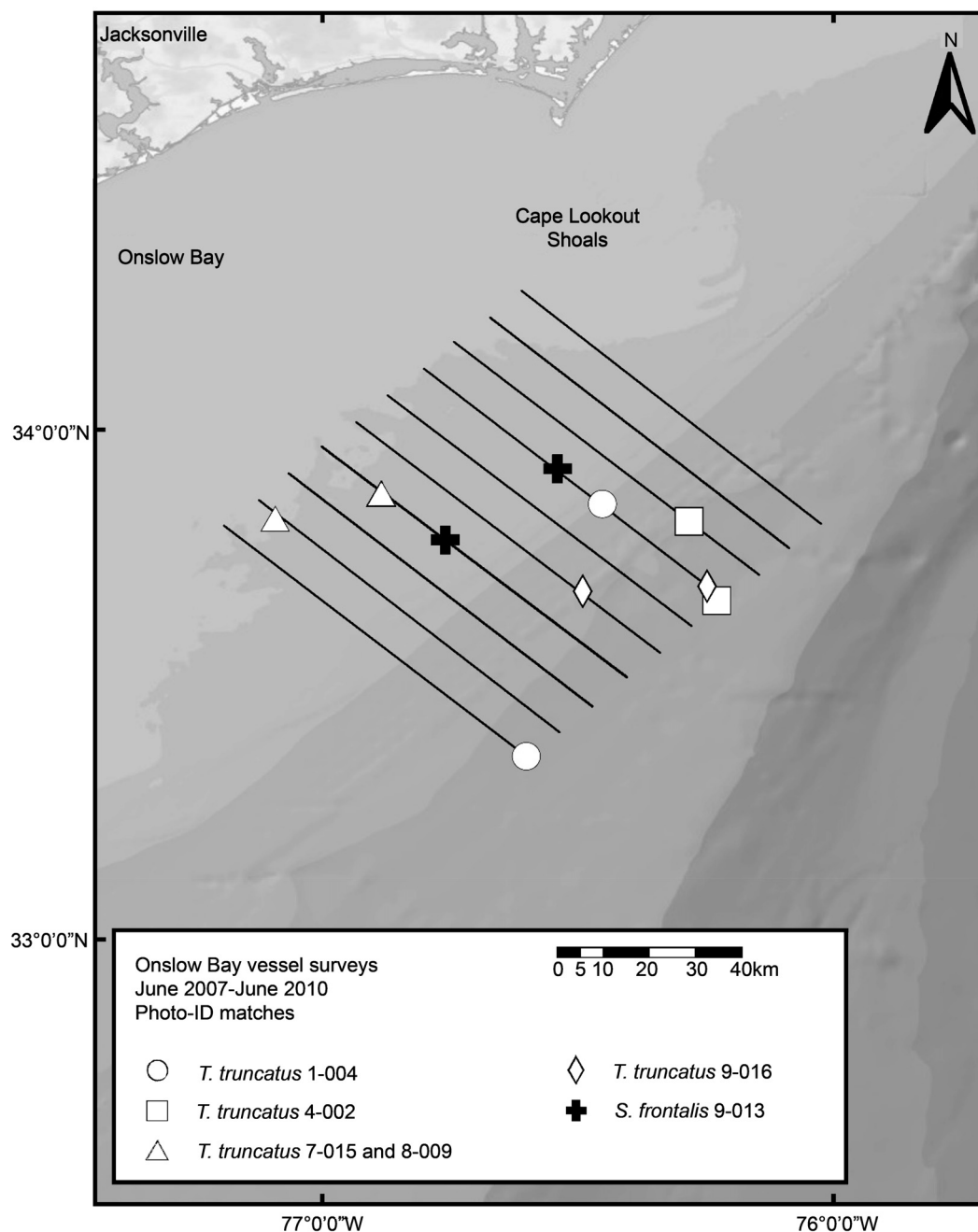


Fig. 3. Photo-identification matches of bottlenose (*Tursiops truncatus*) and Atlantic spotted dolphins (*Stenella frontalis*) in Onslow Bay, North Carolina. See text for dates of sightings.

(Fig. 4). Vessel sightings of dolphins were binned into 100-m widths and right truncated at 300m. The best fit detection function was a half-normal with Beaufort Sea State as covariate (Fig. 5). The mean aerial detection probability was 0.45 (SE = 0.02). The mean boat detection probability was 0.53 (SE = 0.05)

The tracklines for aerial and shipboard surveys were divided into 7,180 segments (5,873 aerial and 1,307 shipboard). The final fitted models for predicting density and for biological explanation are given in Table 3. Bottlenose dolphins were detected in 174 segments (2.4%). Estimated abundance of this species (rounded to the nearest hundred) varied between 600 (95% CI: 100–1,700, August 2007) and 4,100 (1,300–9,400, May 2010) (Fig. 6). These values correspond to densities of 0.117km⁻² (95% CI: 0.016–0.323) in August 2007 and 0.767km⁻² (95% CI: 0.238–1.768) in

May 2010, respectively. Bottlenose dolphins were encountered most frequently at intermediate depths, with maximal values of presence occurring just off the shelf break (Fig. 7). Abundance varied both across and within years (Fig. 6) with peak occurrence in spring and, to a slightly lesser extent, autumn (Table 2; Figs. 6 and 7). A model assuming uniformity of density in space and time (and a boat survey) produced an abundance of 1,400 (95% CI 700–2,800) equivalent to a density of 0.268km⁻² (95% CI: 0.127–0.529).

Spotted dolphins were detected in 78 segments (1%). Given the small numbers detected, estimates of abundance were, unsurprisingly, associated with wide confidence intervals (Fig. 8). Estimated spotted dolphin abundance varied from 0 in 1998–99 to 6,000 (95% CI: 2,500–17,000) in March 2009, which corresponded to a maximum density of 1.122 (95% CI: 0.475–3.182km⁻²). Spotted dolphins

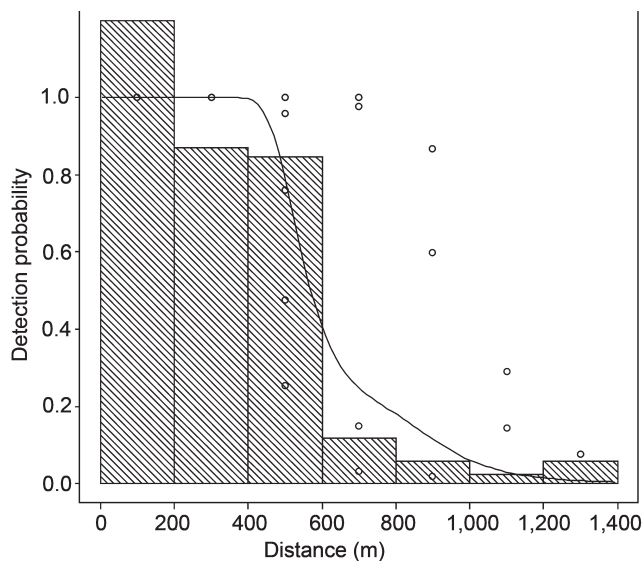


Fig. 4. Detection functions for dolphins (data binned into 200m intervals) from aerial surveys of cetaceans in Onslow Bay, North Carolina ($n = 270$) mapped over a scaled distribution of the perpendicular distances such that the area under the curve equals the area of the histogram.

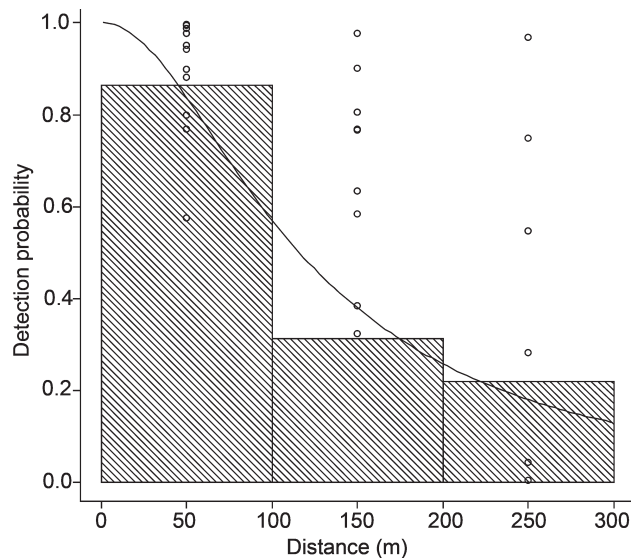


Fig. 5. Detection functions for dolphins (data binned into 100m intervals) from vessel surveys of cetaceans in Onslow Bay, North Carolina ($n = 76$) mapped over a scaled distribution of the perpendicular distances such that the area under the curve equals the area of the histogram.

exhibited a strong preference for waters over the continental shelf; their presence was not influenced strongly by either temperature or day of year, although both variables were included in the final model (Fig. 9). A model assuming uniformity of density in space and time (and a boat survey) from 2007 inclusive produced an abundance of 1,200 (95% CI 500–1,900) equivalent to a density of 0.230km^{-2} (95% CI: $0.096\text{--}0.364\text{km}^{-2}$).

DISCUSSION

Occurrence and distribution

The cetacean fauna observed in Onslow Bay included both shelf and slope-associated species, but was dominated by Atlantic spotted and common bottlenose dolphins. Spotted dolphins were restricted to the continental shelf; bottlenose dolphins were the only species to occur in both shelf and

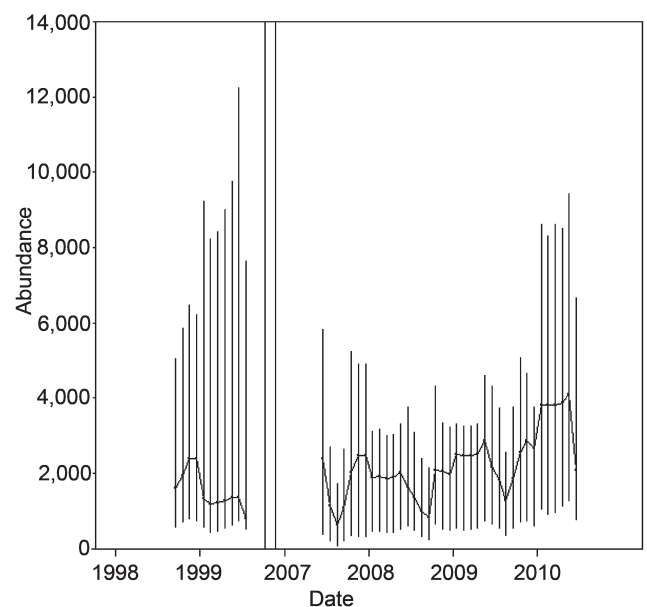


Fig. 6. Estimated monthly abundances of bottlenose dolphins (*Tursiops truncatus*), with 95% confidence intervals, in Onslow Bay, North Carolina.

slope habitats (see below). All other species occurred along the shelf break or in deeper slope waters. In total, eight species of cetaceans were observed (including the off-effort sighting of a sperm whale) and one group of unidentified beaked whales. Vessel and aerial surveys produced similar lists of species occurrence in the study area.

Fixed passive acoustic monitoring recorders in Onslow Bay also yielded detections of the calls of pygmy or dwarf sperm whales (*Kogia* spp.), minke whales (*Balaenoptera acutorostrata*) and sei whales (*B. borealis*) (Hodge 2011). Pygmy and dwarf sperm whales are noted for their cryptic behaviour, so it is perhaps not surprising that they were not observed. Despite the frequency with which these two species strand along coasts of the southeastern U.S. (see below) only a very small number of sightings have been recorded during dedicated surveys (Waring *et al.*, 2011). The calls of baleen whales can travel for long distances, so it is likely that the vocalising minke and sei whales occurred outside the area surveyed (Hodge, 2011). North Atlantic right whales were not observed in the study area, although the aerial survey team recorded three sightings of right whales close to shore in November 2007, December 2008 and November 2009 while transiting to the field site.

As had been done by Pyenson (2010), species composition from the surveys was compared with a long-term data set of stranded cetaceans from the ocean beaches of Onslow Bay (Table 4). Bottlenose dolphins dominated the stranding record in Onslow Bay. Six of the eight species observed during the surveys were also represented in the stranding record and the order of frequency was identical for these species in both data sets. A number of pelagic cetaceans were recorded as strandings in Onslow Bay but not observed during the surveys – some of these cetaceans, such as pygmy or dwarf sperm whales, are known to be cryptic (see above), but many others likely occur offshore of the study area. Others, such as humpback whales, *Megaptera novaeangliae* (Swingle *et al.*, 1993; Barco *et al.*, 2002) and harbour porpoises (*Phocoena phocoena*), are coastal species and

Table 3

Models for bottlenose and spotted dolphins in Onslow Bay, North Carolina. The term $s()$ indicates a smoothed function of the variable of interest. The number after the variable name gives the realised number of degrees of freedom. The final column gives the number of the relevant figure.

Model	Terms in model	% deviance explained	Figure
<i>Tursiops truncatus</i>			
Logistic component	$Survey + s(Depth,4) + s(Temp,3) + Year$	4.3	6,7
Non-zero density component	$Survey + s(Depth) + Year$	24.6	6
<i>Stenella frontalis</i>			
Logistic component	$Survey + s(Depth,3) + s(Temp,4) + s(Dayofyear,3) + Year$	20.2	8,9
Non-zero density component	$Survey + s(Depth,4) + Temp^*$	36.5	8

*Linear.

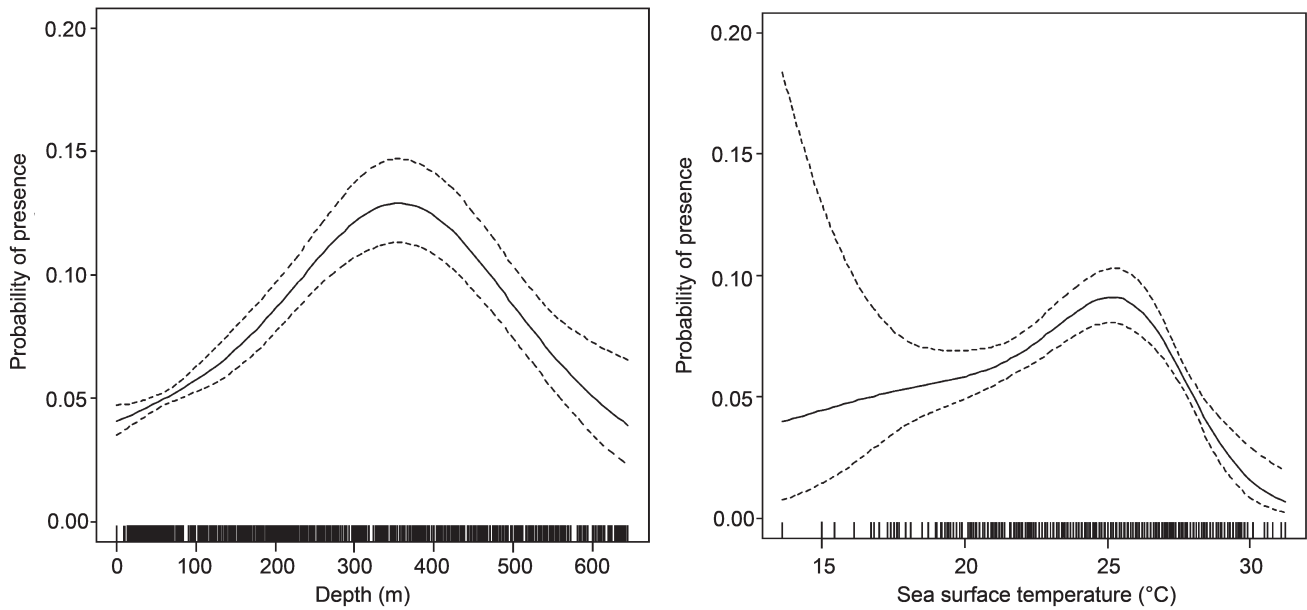


Fig. 7. Relationship between presence/absence of bottlenose dolphins and: (a) depth; and (b) sea surface temperature in Onslow Bay, North Carolina given the other terms in the model assuming a boat survey in 2010. Tick marks on the x-axis represent a datum at that covariate value. Dashed marks represent 2 standard errors lower and upper lines (approximately equal to the 95% confidence interval) associated with the uncertainty in the model only.

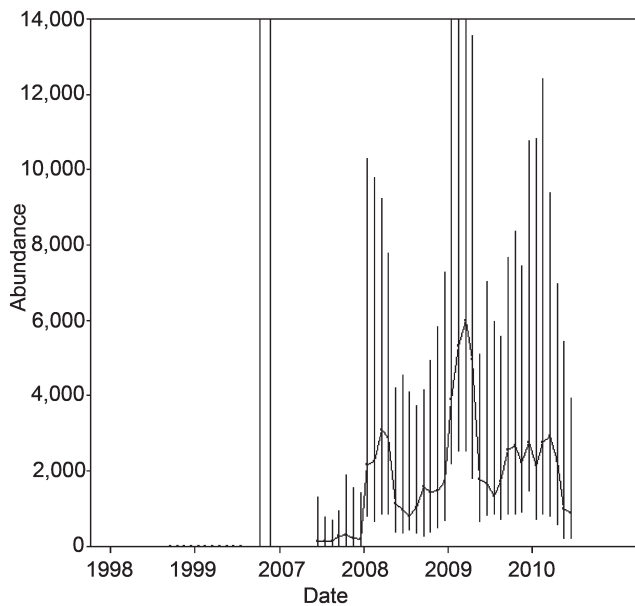


Fig. 8. Estimated monthly abundances of Atlantic spotted dolphins (*Stenella frontalis*), with 95% confidence intervals, in Onslow Bay, North Carolina.

occur well inshore of the study area. In general, there was relatively good concordance between the observations made and the stranding record.

The species composition and distribution patterns observed were similar to those recorded during previous broad-scale surveys of the South Atlantic Bight and Mid-Atlantic shelf break (Mullin and Fulling, 2003; Garrison *et al.*, 2010). Surveys did not extend far enough offshore to encounter deep-diving species, such as sperm and beaked whales, on a regular basis, although single sightings of both were recorded at the offshore limit of the study area. The moored passive acoustic monitoring system recorded sperm whale clicks throughout the year in Onslow Bay (Hodge, 2011), although like the calls of baleen whales, these sounds can travel considerable distances. On 20 November 2010 an exploratory aerial survey was conducted further offshore and encountered three groups of *Mesoplodon* spp. along the 1000m isobath. It can be concluded that most beaked and sperm whales in Onslow Bay occur offshore of the boundaries of the study area and this is supported by habitat models for beaked and sperm whales in this area (Best *et al.*, 2012).

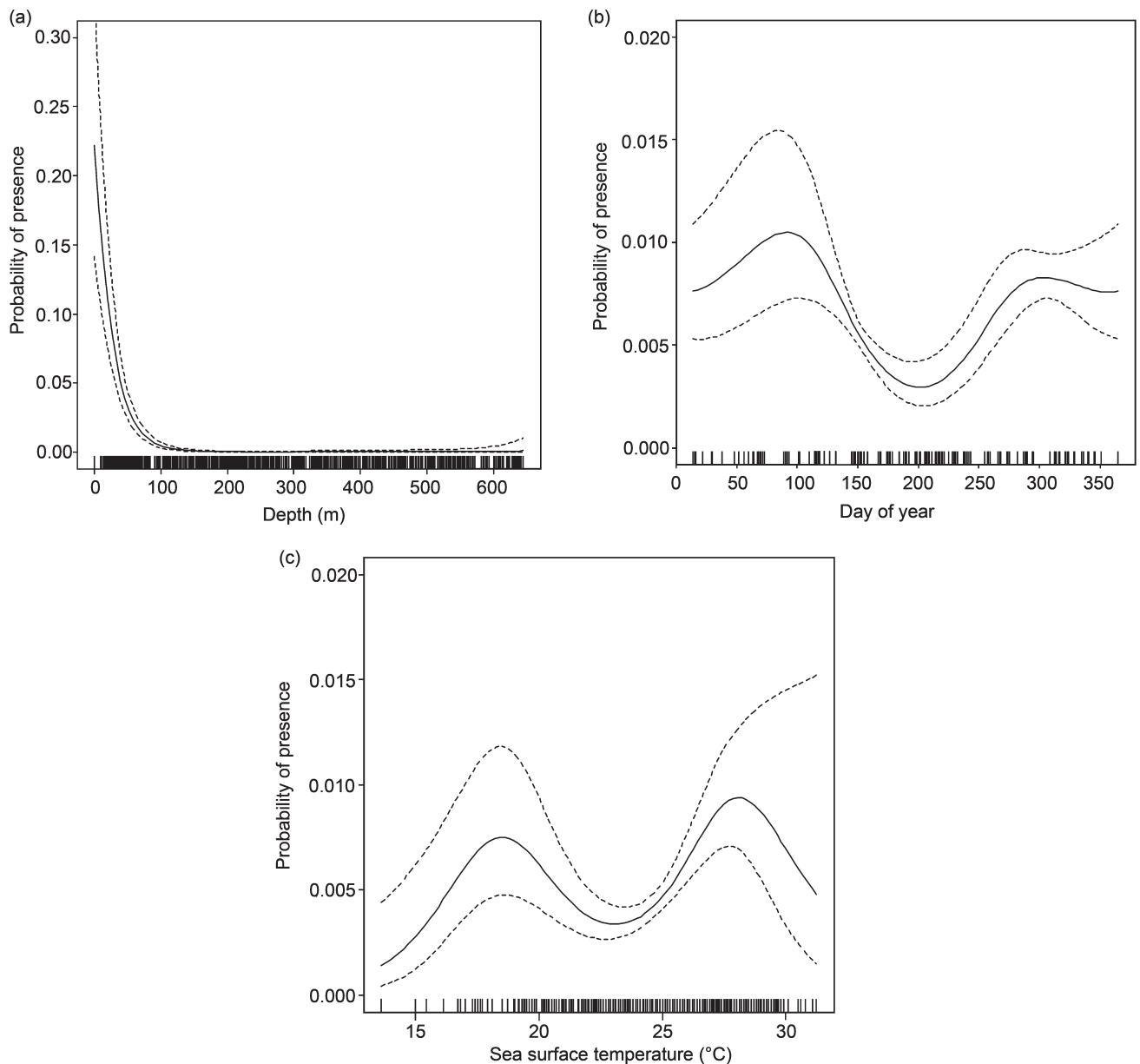


Fig. 9. Relationship between presence/absence of Atlantic spotted dolphins and: (a) depth; (b) day of year; and (c) sea surface temperature in Onslow Bay, North Carolina, given the other terms in the model assuming a boat survey in 2010. Tick marks on the x-axis represent a datum at that covariate value. Dashed marks represent 95% confidence interval associated with the uncertainty in the model only.

It is possible that the bottlenose dolphins observed over the continental shelf included both coastal and pelagic ecotypes (Mead and Potter, 1995). The two forms exhibit fixed genetic differences and probably represent distinct species (Hoelzel *et al.*, 1998); their distribution overlaps on the continental shelf south of Cape Hatteras (Torres *et al.*, 2003). The likelihood of the presence of bottlenose dolphins was greatest near the shelf break, consistent with previous observations of the offshore ecotype (Kenney, 1990). Biopsy samples and detailed photographic records of bottlenose dolphins are being collected so that the distribution of the two ecotypes in this area can be better understood.

The smaller-bodied, offshore form of Atlantic spotted dolphins (Adams and Rosel, 2006) was not observed, although these animals have been seen off Cape Hatteras, North Carolina (A.J. Read, unpublished data). Nor did we encounter several other pelagic species, such as pantropical spotted (*Stenella attenuata*) or Clymene dolphins (*Stenella*

clymene), which were recorded by Mullin and Fulling, (2003). Like the deep-diving species described above, it is likely that these pelagic species occur beyond the seaward extent of the surveys.

Both bottlenose and spotted dolphins were present year-round in Onslow Bay. Despite some evidence that the probability of their presence was affected by sea surface temperature, no clear seasonal patterns in the abundance of bottlenose dolphins were observed, even though the pelagic ecotype of this species is believed to exhibit seasonal movements along the continental slope (Kenney, 1990). There was some indication of an effect of season and/or water temperature on the probability of the presence of spotted dolphins, but this effect was small compared to the overriding effect of water depth.

Approximately 5% (5 of 106) of well-marked bottlenose dolphins and 2% (1 of 49) of spotted dolphins were resighted, despite limited photographic sampling effort.

Table 4

Summary of cetacean strandings by species on the ocean beaches of Onslow Bay, NC (see Fig. 1) from September 1998 to June 2010. Strandings are presented as the number of animals. Almost all strandings involved single individuals; there was only a single mass stranding of 12 striped dolphins in the data set, indicated by the asterisk. Cetacean sightings are ordered in decreasing frequency from Table 1 with cetacean strandings following the same order of decreasing frequency.

Species	Encountered in survey area	Number of stranded individuals
<i>Tursiops truncatus</i>	Yes	248
<i>Stenella frontalis</i>	Yes	6
<i>Grampus griseus</i>	Yes	3
<i>Globicephala macrorhynchus</i>	Yes	3
<i>Physeter macrocephalus</i>	Yes	2
<i>Delphinus delphis</i>	Yes	1
<i>Steno bredanensis</i>	Yes	0
<i>Balaenoptera physalus</i>	Yes	0
<i>Stenella coeruleoalba</i>	No	13(*)
<i>Kogia breviceps</i>	No	12
<i>Kogia sima</i>	No	6
<i>Megaptera novaeangliae</i>	No	6
<i>Phocoena phocoena</i>	No	4
<i>Balaenoptera acutorostrata</i>	No	3
<i>Feresa attenuata</i>	No	2
<i>Stenella attenuata</i>	No	2
<i>Eubalaena glacialis</i>	No	1
<i>Balaenoptera edeni</i>	No	1
<i>Peponocephala electra</i>	No	1
<i>Stenella clymene</i>	No	1
<i>Mesoplodon europaeus</i>	?	4
<i>Mesoplodon densirostris</i>	?	1
<i>Ziphius cavirostris</i>	?	2

These resightings occurred over seasons and years, suggesting some degree of structured habitat use by individual dolphins. We are not aware of any other attempts to match images of Atlantic spotted dolphins and offshore bottlenose dolphins along the US east coast, but these findings suggest that such work could provide insight into the population structure of these species.

There were two noticeable changes in species composition between 1998–99 and 2007–10. Short-beaked common dolphins were the second-most frequently observed species in 1998–99 but were almost entirely replaced by Atlantic spotted dolphins in the more recent surveys. Only one sighting of common dolphins in 2007–2010, on 9 March 2010 was made, the same day on which the only sighting of a fin whale (*Balaenoptera physalus*) was recorded. In contrast, common dolphins were observed on 14 occasions during June, July, September and October of 1998–99. Onslow Bay represents the southern limit of the range of common dolphins in the western North Atlantic (Waring *et al.*, 2011); it is possible that this limit moves latitudinally in response to environmental variables, so that common dolphins are present in the study area during some years, but not others. Common dolphins were not observed in the broad-scale surveys of the South Atlantic Bight conducted in July and August 1998 by Mullin and Fulling (2003) but were recorded north of Cape Hatteras in June–August 2004 during the survey by Garrison *et al.* (2010). The absence of spotted dolphins in the 1998–1999 surveys in Onslow Bay is puzzling. It is possible that some of the sightings of unidentified delphinids made during 1998–99 were of this species, but only three of these sightings were recorded during the more recent surveys. It is also possible that the

increase in spotted dolphin abundance (see below) over the study period represents a population incursion from more southern waters.

Abundance

The abundance of cetaceans in Onslow Bay was very low, although the data were inadequate to estimate density for species other than Atlantic spotted and bottlenose dolphins. A relatively small number of groups of these two species were encountered, resulting in wide confidence limits around the estimates (Figs. 6 and 8) and limiting the inferences that can be drawn from changes in abundance over time.

In general, the estimates of density of spotted and bottlenose dolphins are comparable with those of Mullin and Fulling (2003), who surveyed a much larger area. Atlantic spotted dolphins and bottlenose dolphins were the two most abundant species observed by these researchers, although their survey included an extensive area of pelagic habitat where coastal Atlantic spotted dolphins do not occur.

Like those of Mullin and Fulling (2003), the estimates of density presented here are negatively biased to some degree because it was not possible to meet the assumption that all groups of cetaceans on the trackline were detected (i.e. that $g(0) = 1$). Some groups of cetaceans may have been submerged as the survey vessel or aircraft transited past them (availability bias); other groups at the surface may have been missed by the observers (perception bias). The proportion of acoustic detections that were also detected visually (62%) suggests that the magnitude of this latter bias is not large, especially given that some groups of vocalising dolphins may have been out of the detection range of visual observers. The first source of bias from aerial surveys was ameliorated by forcing survey type into the models and only predicting with the factor coefficient associated with vessels (this effectively makes the $g(0)$ estimate for aircraft no more negatively biased than that for ships). It might be expected that survey platform (*Survey*) should always naturally appear in the models, as $g(0)$ should generally be higher for a ship than a plane. This was not always the case due, in part to the low power to detect this effect because of the low number of sightings. Thus, *Survey* was forced into the model for bottlenose dolphins.

Other researchers have used a variety of analytical approaches to estimate $g(0)$ directly. In vessel surveys of small delphinids (including the genera *Stenella* and *Tursiops*) Barlow and Forney (2006) estimated $g(0)$ to be 0.86 for groups of less than 20 individuals and 0.97 for groups of 20 or larger. In aerial surveys of bottlenose dolphins in California, Forney and Barlow, (1998) estimated a $g(0)$ as 0.67 for small (1–10) and 0.85 for large (>10) groups, although these values did not fully account for availability bias. Spotted and bottlenose dolphins in Onslow Bay occurred in a variety of group sizes and some groups on the trackline were not detected by our observers. Thus, the estimates of density and abundance estimates are negatively biased to an unknown degree.

Assessment of field approach

As noted above, the objective of the research was to provide a comprehensive description of the occurrence, distribution and abundance of cetaceans off Onslow Bay. A suite of complementary approaches were selected to ensure that the

presence of all cetaceans could be assessed and to maximise information collected by these different research modalities. Aerial surveys gave the advantage of relatively brief breaks in the weather, which was particularly important in winter, when survey conditions were generally poor. There have been few prior attempts to conduct regular surveys of cetaceans in the North Atlantic during winter. The surface vessels provided an independent means of assessing occurrence, distribution and abundance and, importantly, allowed investigation of patterns of residency using photo-identification methods. Merging results from the aerial and vessel surveys added a layer of complexity to the analysis, but this did not outweigh the benefit of the combined approach. Although not discussed here, the vessel surveys also allowed collection of biopsy samples that are important for studies of population structure and feeding ecology. Finally, our passive acoustic monitoring program allowed a continuous record of the presence of vocalising cetaceans in all seasons, weather conditions and during both day and night. The passive acoustic techniques also allowed determination of whether the visual surveys missed any deep-diving or cryptic species. This additional information indicated that at least some pygmy or dwarf sperm whales were present in Onslow Bay, but not detected during aerial or shipboard surveys. Despite the advantages of this complementary approach, however, the low encounter rates of cetaceans in Onslow Bay limit the statistical power with which it is possible to detect changes in density caused by anthropogenic or natural factors, given any reasonable level of survey coverage.

ACKNOWLEDGMENTS

The survey effort described here represents a considerable undertaking on the part of many individuals and several institutions; we thank all of our partners in this endeavor. Debi Palka and Bob Gisiner helped to develop the monitoring plan and Lance Garrison modified VisSurvey for our use. Dave Johnston provided considerable guidance in coordinating the vessel surveys. We also thank Ed Coffman, owner and operator of Orion Aviation, and his highly skilled pilots: John Estes, Dave Huddle, Larry Latshaw, Ron Shreck, Bob Sticle, Wayne McKendry and Stephanie Funston. A special thanks to Captains Dale Britt and Alan Scibal of the F/V *Sensation* and Matt Besch and Faith Purcell of the R/V *Cetus* for their expertise and good nature. For assistance with various aspects of field work we thank Julia Burrows, Pete Zook, Erin LaBrecque, Elliott Hazen, Stacie Koslovsky, Beth Pike, Vicky Thayer, Meagan Dunphy-Daly, Steve Thornton, Kristina Cammen, Anna McGregor, Jennifer Tennesen, Sara McDonald, Reny Tyson, Trey McDonald, Barbie Byrd, Caroline Good, Tom Ninke, Matt Bowers, John Wilson and Melissa Soldevilla. Thanks to Vicky Thayer and the NOAA Fisheries Beaufort Laboratory for stranding data from Carteret County, NC, and the Marine Mammal Stranding Program at UNC Wilmington for stranding data from Onslow, Pender and New Hanover, NC counties. All work conformed to the legal requirements of the United States; surveys were conducted under NOAA Scientific Permit 948-1692-00 held by UNCW and NOAA General Authorisation 808-1798-01 held by Duke University. Heather Foley

prepared the figures. Funding for this project was provided by Environmental Conservation – Marine Resources, Naval Facilities Engineering Command Atlantic through GeoMarine, Inc. and Parsons, Inc. We thank Jason See and Joe Campo for administering the contract.

REFERENCES

- Adams, L. and Rosel, P.E. 2006. Population differentiation of the Atlantic spotted dolphin *Stenella frontalis* in the Western North Atlantic, including the Gulf of Mexico. *Mar. Biol.* 148: 671–81.
- Barco, S.G., McLellan, W.A., Allen, J.M., Asmuth-Silvia, R.A., Mallon-Day, R., Meacher, E.M., Pabst, D.A., Robbins, J., Seton, R.E., Swingle, W.M., Weinrich, M.T. and Clapham, P.J. 2002. Population identity of humpback whales (*Megaptera novaengliae*) in the waters of the US mid-Atlantic states. *J. Cetacean Res. Manage.* 4(2): 135–41.
- Barlow, J. 1999. Trackline detection probability for long-diving whales. pp.209–21. In: Garner, G.W., Amstrup, S.C., Laake, J.L., Manly, B.F.J., McDonald, L.L. and Robertson, D.G. (eds). *Marine Mammal Survey and Assessment Methods*. Balkema Press, Rotterdam, Netherlands. 287pp.
- Barlow, J. 2006. Cetacean abundance in Hawaiian waters estimated from a summer/fall survey in 2002. *Mar. Mammal Sci.* 22(2): 446–64.
- Barlow, J. and Forney, K. 2007. Abundance and population density of cetaceans in the California Current ecosystem. *Fish. Bull.* 105: 509–26.
- Best, B.D., Halpin, P.N., Read, A.J., Fujioka, E., Good, C.P., LaBrecque, E.A., Schick, R.S., Roberts, J.J., Hazen, L.J., Qian, S.S., Palka, D.L., Garrison, L.P. and McLellan, W.A. 2012. Online marine mammal habitat modeling system for the U.S. East Coast and Gulf of Mexico. *Endang. Species Res.* 18:1–15. *Endanger. Species. Res.* 18: 1–15.
- Buckland, S.T., Anderson, D.R., Burnham, K.P., Laake, J.L., Borchers, D.L. and Thomas, L. 2001. *Introduction to Distance Sampling: Estimating Abundance of Biological Populations*. Oxford University Press, Oxford, UK. vi+ xv+432pp.
- Department of the Navy. 2009. Notice of record of decision for Undersea Warfare Training Range. *Federal Register Notice* 154: 40573.
- Forney, K.A. and Barlow, J. 1998. Seasonal patterns in the abundance and distribution of California cetaceans, 1991–1992. *Mar. Mammal Sci.* 14(3): 460–89.
- Garrison, L.P., Martinez, A. and Maze-Foley, K. 2010. Habitat and abundance of cetaceans in Atlantic Ocean continental slope waters off the eastern USA. *J. Cetacean Res. Manage.* 11(3): 267–78.
- Gerrodette, T. and Forcada, J. 2005. Non-recovery of two spotted and spinner dolphin populations in the eastern tropical Pacific Ocean. *Mar. Ecol. Prog. Ser.* 291: 1–21.
- Halpin, P.N., Read, A.J., Fujioka, E., Best, B.D., Donnelly, B., Hazen, L.J., Kot, C., Urian, K., LaBrecque, E., Dimatteo, A., Cleary, J., Good, C., Crowder, L.B. and Hyrenbach, K.D. 2009. OBIS-SEAMAP: The world data center for marine mammal, sea bird, and sea turtle distributions. *Oceanography* 22: 104–15.
- Hammond, P.S. 2010. Estimating the abundance of marine mammals. In: Boyd, I.L., Bowen, W.D. and Iverson, S.J. (eds). *Marine Mammal Ecology and Conservation: a Handbook of Techniques*. Oxford University Press, UK.
- Hammond, P.S., Berggren, P., Benke, H., Borchers, D.L., Collet, A., Heide-Jørgensen, M.P., Heimlich, S., Hiby, A.R., Leopold, M.F. and Øien, N. 2002. Abundance of harbour porpoise and other cetaceans in the North Sea and adjacent waters. *J. Appl. Ecol.* 39(2): 361–76.
- Hammond, P.S., Macleod, K., Berggren, P., Borchers, D.L., Burt, L., Cañadas, A., Desportes, G., Donovan, G.P., Gilles, A., Gillespie, D., Gordon, J., Hiby, L., Kuklik, I., Leaper, R., Lehnert, K., Leopold, M., Lovell, P., Øien, N., Paxton, C.G.M., Ridoux, V., Rogan, E., Samarra, F., Scheidat, M., Sequeira, M., Siebert, U., Skov, H., Swift, R., Tasker, M.L., Teilmann, J., Van Canneyt, O. and Vázquez, J.A. 2013. Cetacean abundance and distribution in European Atlantic shelf waters to inform conservation and management. *Biol. Conserv.* 164: 107–22.
- Hedley, S., Buckland, S.T. and Borchers, D.L. 1999. Spatial modelling from line transect data. *J. Cetacean Res. Manage.* 1(3): 255–64.
- Hodge, L.E.W. 2011. Monitoring marine mammals in Onslow Bay, North Carolina, using passive acoustics. Ph.D. thesis, Duke University, Durham, North Carolina. 196pp.
- Hoelzel, A.R., Potter, C.W. and Best, P.B. 1998. Genetic differentiation between parapatric ‘nearshore’ and ‘offshore’ populations of the bottlenose dolphin. *Proc. R. Soc. Lond. Ser. B.* 265(1402): 1,177–83.
- Horvitz, D.G. and Thompson, D.J. 1952. A generalization of sampling without replacement from a finite universe. *J. Am. Stat. Assoc.* 47(260): 663–85.
- Kenney, R.D. 1990. Bottlenose dolphins off the northeastern United States. pp.369–86. In: Leatherwood, S. and Reeves, R.R. (eds). *The Bottlenose Dolphin*. Academic Press, San Diego. 653pp.

- Marques, F.F.C. 2001. Estimating wildlife distribution and abundance from line transect surveys conducted from platforms of opportunity, Ph.D. thesis, School of Mathematics and Statistics, University of St Andrews, UK.
- McLellan, W.A., Barco, S.G., Meagher, E.M., Zvalaren, S.D. and Pabst, D.A. 1999. Offshore aerial surveys of two Mid-Atlantic sites: Wallops Island and Onslow Bay. University of North Carolina Wilmington. (unpublished). 28pp. [Available from the author].
- Mead, J.G. and Potter, C.W. 1995. Recognizing two populations of the bottlenose dolphin (*Tursiops truncatus*) off the Atlantic coast of North America: Morphological and ecological considerations. *Int. Bio. Res. Inst. Rep.* 5: 31–43.
- Mellinger, D.K. 2001. ISHMAEL 1.0 User's Guide. *NOAA Tech. Mem. OAR PMEL-120*. [Available from NOAA/PMEL, 7600 Sand Point Way NE, Seattle, WA 98115-6349].
- Mullin, K.D. and Fulling, G.L. 2003. Abundance of cetaceans in the southern US North Atlantic Ocean during summer 1998. *Fish. Bull.* 101(3): 603–13.
- Pyenson, N.D. 2010. Carcasses on the coastline: measuring the ecological fidelity of the cetacean stranding record in the eastern North Pacific Ocean. *Paleobiology* 36(3): 453–80.
- R Development Core Team. 2009. *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. ISBN: 3-900051-07-0. [Available at: <http://www.R-project.org>].

