Predicting Cuvier's (*Ziphius cavirostris*) and *Mesoplodon* beaked whale population density from habitat characteristics in the eastern tropical Pacific Ocean

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ABSTRACT

Temporally dynamic environmental variables and fixed geographic variables were used to construct generalised additive models to predict Cuvier's (*Ziphius cavirostris*) and *Mesoplodon* beaked whale encounter rates (number of groups per unit survey effort) and group sizes in the eastern tropical Pacific Ocean. The beaked whale sightings and environmental data were collected simultaneously during the Southwest Fisheries Science Center's cetacean line-transect surveys conducted during the summers and autumns of 1986-90 and 1993. Predictions from the encounter rate and group size models were combined with previously published estimates of line-transect sighting parameters to describe patterns in beaked whale population density (number of individuals per unit area) throughout the study area. Results provide evidence that the previously proposed definition of beaked whale habitat may be too narrow and that beaked whales may be found from the continental slope to the abyssal plain, in waters ranging from well-mixed to highly stratified. Areas with the highest predicted population densities were the Gulf of California, the equatorial cold tongue and coastal waters, including the west coast of the Baja Peninsula and the Costa Rica Dome. Offshore waters in the northern and southern subtropical gyres had the lowest predicted *Mesoplodon* densities, but density predictions were high for Cuvier's beaked whales in the waters southeast of the Hawaiian Islands. For both encounter rate and group size models, there was no geographic pattern evident in the residuals as measured by the ratio of pooled predicted to pooled observed values within geographic strata.

KEYWORDS: OCEANOGRAPHY; PACIFIC OCEAN; MODELLING; CUVIER'S BEAKED WHALE; MESOPLODON BEAKED WHALES; HABITAT; DISTRIBUTION

INTRODUCTION

Recent scientific efforts to describe and quantify beaked and bottlenose whale (family Ziphiidae) habitats have been primarily motivated by an interest in mitigating, minimising or eliminating harmful effects of human activities on ziphiid whales for conservation or management purposes. Concerns regarding the association of beaked whale mass strandings with loud anthropogenic noise in the marine environment (e.g. Anon., 2001; Peterson, 2003; Cox *et al.*, 2006) have placed an ecological imperative on the quest for basic knowledge about these cetaceans.

Beaked whales are particularly difficult cetaceans to study because they are infrequently encountered (Houston, 1990a; Ostrom *et al.*, 1993; Weir *et al.*, 2001; Mead, 2002). Furthermore, when human observers are in close proximity, beaked whales may go unnoticed because they have long dive times, surface without a visible blow or splash (Barlow, 1999; Weir *et al.*, 2001) and are relatively silent when they are within 200m of the surface (Johnson *et al.*, 2004). As a result, most knowledge about many beaked whale species comes only from stranded specimens (Houston, 1990a; b; Palacios, 1996; Dalebout *et al.*, 2002). New species have recently been identified and described (Reyes *et al.*, 1991; Pitman *et al.*, 1999; Pitman and Lynn, 2001; Dalebout *et al.*, 2002). Dalebout *et al.* (2002) noted that, 'Of the twelve cetacean species described in the last 100 years, eight have been ziphiids, primarily of the genus *Mesoplodon*'. Nevertheless, progress is ongoing in efforts to understand the ecology of beaked whales.

It is conventionally thought that beaked and bottlenose whales prefer deep-water habitats (Jefferson *et al.*, 1993; Mead, 2002; Reeves *et al.*, 2002). Beyond this basic preference, several authors have described beaked and bottlenose whale habitat preferences for specific study areas based on qualitative or correlation studies (reviewed by Ferguson, 2005). In the Gulf of Mexico, beaked whales were found in the deepest average water depths of any cetacean species (Davis *et al.*, 1998). Most studies have reported that beaked whales are commonly seen in waters over the continental slope (in waters 200-2,000m depth) (Waring *et al.*, 2001; Hooker *et al.*, 2002; Wimmer, 2003; MacLeod *et al.*, 2004) and submarine canyons (D'Amico *et al.*, 2003; Wimmer, 2003; Wimmer and Whitehead, 2004). MacLeod *et al.* (2004) also found that Cuvier's (*Ziphius cavirostris*) and *Mesoplodon* beaked whales were most often sighted over seafloors with greater slopes than the remainder of the study area in the Bahamas. Several authors have speculated that the distribution of beaked whales (or cetaceans in general) is likely to be primarily determined by prey availability (Davis *et al.*, 1998; Cañadas *et al.*, 2002; Hooker *et al.*, 2002; MacLeod, 2005).

Various methods have been used to quantitatively model the habitat preferences of beaked whales (reviewed by Ferguson, 2005). The most commonly used method has been logistic regression or generalised linear models (GLMs) with a logistic link function to model beaked whale distribution as a function of habitat variables. Using GLM, Waring *et al.* (2001) and Hamazaki (2002) found that Cuvier's and *Mesoplodon* beaked whales off the northeastern coast of the US were associated with the outer shelf edge. Cañadas *et al.* (2002) used GLMs to examine beaked whale distributions in the Mediterranean Sea and found that functions of depth were better predictors than those of seafloor slope. Another quantitative method applied to beaked whale habitat studies is ecological niche factor

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analysis (ENFA; MacLeod, 2005), which has shown that beaked whales in the North Atlantic Frontier (from west of the Hebrides in Scotland to the west and north of Shetland) tend to occupy deeper waters in areas with higher slopes than average, and prefer southward and westward facing slopes. MacLeod and Zuur (2005) used generalised additive models (GAMs) and classification and regression trees (CART) to examine beaked whale habitat associations in the Bahamas and found that depth, seabed slope and seabed aspect were all important factors.

Few of the previous attempts to model beaked whale distribution have been based on data collected over broad geographic areas and few included substantial areas of deep-water habitat with low seafloor slope (abyssal plains). None of the previous studies included variation in beaked whale group size with habitat variables. Only the recent studies by MacLeod and Zuur (2005) allowed for nonparametric, nonlinear responses to habitat gradients. In this paper, beaked whale habitat preferences and distributions were modelled from ship line-transect surveys conducted in a vast area of the eastern tropical Pacific Ocean (ETP) that included continental shelf, slope and abyssal plain habitats. Geographic variation in the population densities (number of individuals per unit area) of two genera of beaked whales, Cuvier's beaked whales and *Mesoplodon* beaked whales (*M. densirostris, M. peruvianus,* and *Mesoplodon* spp.), were quantified by modelling variation in encounter rates (number of sightings per unit of survey effort) and group sizes using GAMs. The results suggest that some of the generalities that have been inferred from previous, more limited studies do not appear valid for these species in the ETP.

METHODS

Study area

The study area encompassed 19.6 million km² of the ETP (Fig. 1). Circulation patterns in the surface waters of the region are dominated by the zonal equatorial current system between the anticyclonic North and South Pacific subtropical gyres (Kessler, 2005). The California Current and the Peru Current form the eastern boundaries of the North and South Pacific gyres, respectively (Fig. 2). The California Current flows into the North Equatorial Current and the Peru Current flows into the South Equatorial Current. The North Equatorial Countercurrent flows towards the east in the latitudes between the North and South Equatorial Current. Three primary surface water masses exist in the ETP: the warm, low-salinity Tropical Surface Water (TSW), which includes the eastern Pacific warm pool and underlies the Intertropical Convergence Zone (ITCZ), a zonal band between 5 and 10°N where rainfall is high as a result of the north and south trade winds converging; the higher-salinity Equatorial Surface Water (ESW) (the coldest surface water mass) with the equatorial cold tongue projecting from its eastern boundary; and the cool, Subtropical Surface Waters (SSW) located towards the poleward edges of the ETP, where the highest salinities are found (Fiedler and Talley, 2005) (Fig. 2). The thermocline is strongest beneath the TSW and weakest beneath the SSW (Fiedler and Talley, 2005). Although not considered part of the ETP, but included in the analysis nonetheless, the Gulf of California is a region in which evaporation largely exceeds precipitation, resulting in highly saline surface waters. Physical and biological processes in the study area interact to yield highly productive waters in the upwelling regions of the California Current, Peru Current, equatorial cold tongue and Costa Rica Dome, in contrast to the low productivity of the oligotrophic SSWs (Ryther, 1969; Fiedler and Philbrick, 2002; Fiedler, 2002) (Fig. 2). In general, both coastal and oceanic upwelling regions are characterised by relatively weak and shallow thermoclines and high levels of chlorophyll. In comparison, the oligotrophic regions have stronger and deeper thermoclines and lower levels of chlorophyll.

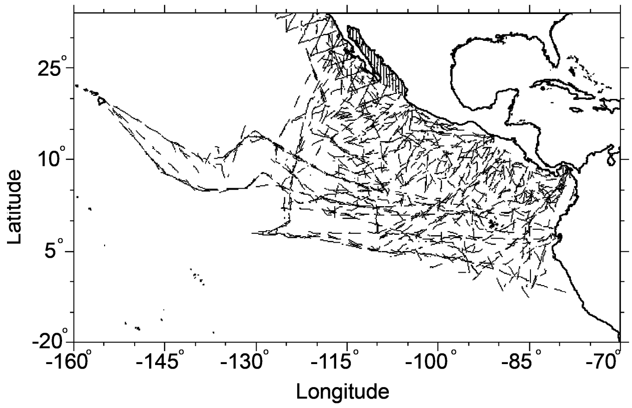


Fig. 1. Transect lines covered during the 1986-90, and 1993 shipboard cetacean line-transect surveys conducted by the SWFSC in the ETP.

Field methods

Cetacean sightings data and *in situ* oceanographic data were collected on Southwest Fisheries Science Center (SWFSC) research cruises conducted during the summer and autumn of each year 1986-90 and 1993. Two National Oceanic and Atmospheric Administration (NOAA) research vessels, *David Starr Jordan* and *McArthur*, followed standard line-transect protocols (Buckland *et al.*, 2001) to survey cetaceans in the ETP, while concurrently collecting a suite of oceanographic data over the length of the trackline.

Kinzey *et al.* (2000) provide a complete description of the SWFSC cetacean data collection procedures followed during the ship-based line-transect surveys. In brief, two teams of three visual observers rotated through three positions located on the flying bridge of the ship. Starboard and port observers used 25 × 150 'big eye' binoculars, scanning an arc of approximately 100° extending from the starboard and port beams, respectively, to 10° on the opposite side of the trackline. A third observer, the designated data recorder, searched by naked eye and occasionally 7 × 50 binoculars across the entire 180° arc in front of the ship. All cetaceans sighted were identified to the lowest taxonomic level possible. Group size estimates were recorded independently by each observer.

The *in situ* oceanographic data collected during the line-transect surveys and considered as potential predictor variables in the encounter rate and group size models were: sea surface temperature (SST); sea surface salinity; thermocline depth; thermocline strength; and the natural logarithm of surface chlorophyll concentration (hereinafter simply referred to as surface chlorophyll concentration). Details of the oceanographic data collection methods for each ship and each year 1986-90 are available in Thayer *et al.* (1988a; b; c; d), Lierheimer *et al.* (1989a; b; 1990a; b), and Philbrick *et al.* (1991a; b). Oceanographic methods and results from the 1993 cruise have not yet been published. The temperature and salinity of the sea surface were recorded continuously using a thermosalinograph and then

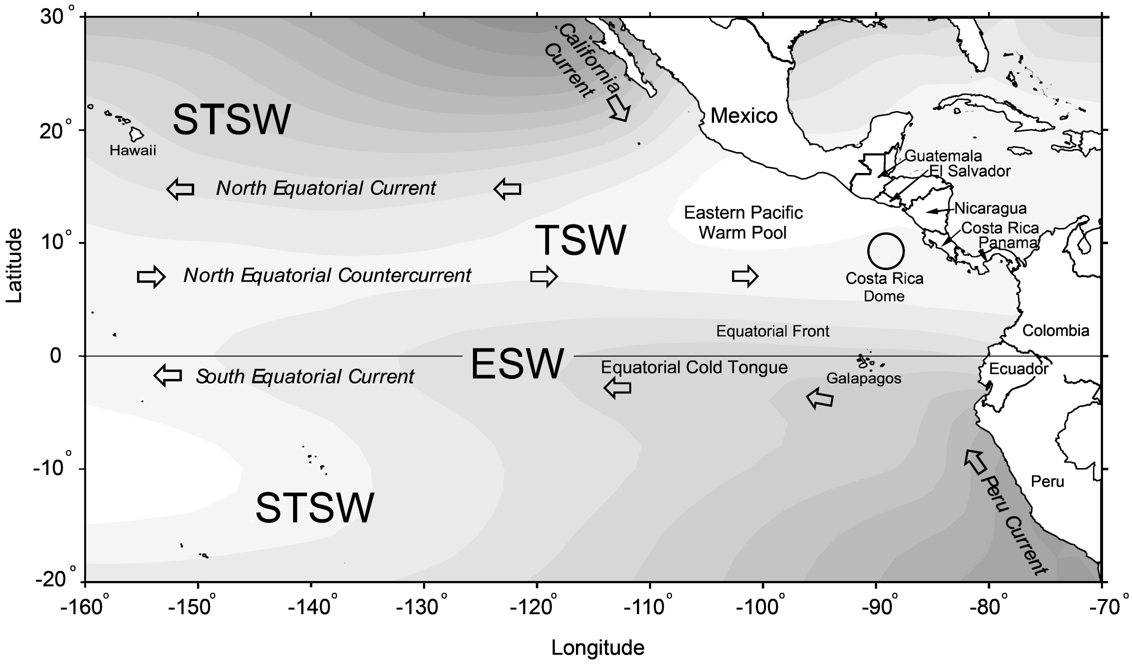


Fig. 2. Oceanography of the ETP study area. STSW: Subtropical Surface Water; TSW: Tropical Surface Water; ESW: Equatorial Surface Water.

summarised into hourly means, resulting in a spatial resolution of approximately 18.5km (Table 1). Thermocline depth and strength were derived from conductivity temperature depth (CTD) stations and expendable bathythermograph (XBT) probes, having a spatial resolution of approximately 40-110km (Table 1). Surface chlorophyll concentrations have a spatial resolution of approximately 15-130km (Table 1). Beaufort sea state was recorded while the marine mammal observers were on-effort and was updated whenever conditions changed. Beaufort sea state is a dominant factor affecting the visibility of cetaceans; therefore it was included in all models to account for potential biases due to visibility. Although it might be possible to account for the sea state visibility bias elsewhere in the density analysis, including Beaufort sea state as a predictor variable in the generalised additive model automatically accounts for correlations among other predictor variables, thereby providing a better assessment of each predictor variable's individual effects on the response variable (Hastie and Tibshirani, 1990).

Additional environmental data that were considered in the models include distance from shore, depth and slope of the ocean bottom, latitude and longitude. Offshore distance was calculated as the shortest distance between a given point on the trackline and the closest point on the North, Central or South American mainland. Depth data were obtained from the National Geophysical Data Center's TerrainBase data set, which had a spatial resolution of 5×5 minutes (approximately 9×9km). The slope was derived from the depth data in the two-step process described below.

Analytical methods

In preparation for building the models, the beaked whale sighting data and oceanographic data were summarised into 9km segments of on-effort trackline, corresponding roughly to the finest resolution of environmental data. The 9km distance for each segment was measured directly along the trackline; therefore, the start and end points of a given segment may have been less than 9km apart as measured by straight-line distance if the trackline in the segment followed bends or curves. Conversely, the straight-line distance between segment start and end points could have been greater than 9km if off-effort sections of trackline intervened between contiguous on-effort sections in a given segment. In those instances when off-effort sections separated contiguous on-effort sections, data from the discontinuous sections of on-effort trackline were summarised together if the distance between sequential sections of on-effort trackline was less than 9km. Otherwise, the on-effort section before observers went off effort was omitted and the start point for the new segment was located at the beginning of the on-effort section following the lag in effort. Due to the relatively small scale of the analysis, autocorrelation undoubtedly exists in the sighting and oceanographic data on neighbouring 9km segments. Nevertheless, the primary goal was prediction rather than explanation of ecological relationships or hypothesis testing; therefore, the problems associated with inflated sample size and autocorrelation are largely irrelevant because they do not add appreciable bias to the parameter estimates required for prediction (Neter *et al.*, 1990; Hamazaki, 2004).

Oceanographic values for each segment were calculated as weighted averages of the data from the oceanographic stations immediately before and after each segment midpoint, where the midpoint was defined as the point at which 4.5km of on-effort trackline had been covered. Inverse distance weighting (distance^{-1}) was used for thermocline depth, thermocline strength, and surface chlorophyll, whereas time^{-1} weighting was used for SST and sea surface salinity. This difference in weighting methods was necessary because the latter oceanographic data were recorded with only a time stamp. Nevertheless, the ships travelled at approximately a constant speed, so the inverse distance and inverse time weighting methods are roughly comparable. Depth values for each segment were calculated as the inverse distance weighted average depth of the four closest nodes in the TerrainBase 5×5 minute grid to the segment midpoint. Assigning slope values to each segment required two steps. First, slope values were calculated for each node on the 5×5 minute grid as the magnitude of the depth gradient:

Table 1

Temporal and spatial resolution of *in situ* oceanographic data collected during SWFSC cetacean line-transect survey cruises in 1986-90 and 1993.

Variable	Resolution
Sea surface temperature	Recorded every five minutes; summarised into hourly means (approx. 18.5km)
Sea surface salinity	Recorded every five minutes; summarised into hourly means (approx. 18.5km)
Thermocline depth*	40-110km
Thermocline strength*	40-110km
Surface chlorophyll concentration	15-130km

*These variables were derived from CTD (conductivity, temperature, and depth) and XBT (expendable bathythermographs) data.

$$\text{Slope} = \sqrt{\left(\frac{\partial z}{\partial x}\right)^2 + \left(\frac{\partial z}{\partial y}\right)^2} \qquad (1)$$

Using compass-based grid notation and representing the slope angle in degrees yields the following equation:

$$\text{Slope} = \left(\frac{180}{\pi}\right) \bullet \arctan\left\{\sqrt{\left(\frac{Z_E - Z_W}{2\Delta x}\right)^2 + \left(\frac{Z_N - Z_S}{2\Delta y}\right)^2}\right\} \qquad (2)$$

where Z_E, Z_W, Z_N, and Z_S refer to the grid nodes to the east, west, north and south of the desired node. Second, the slope for the segment midpoint was assigned the value of the slope of the node closest to the segment midpoint.

Beaked whale sightings data for each segment were summarised as the total number of groups sighted and the average group size in the segment. Prior research has shown that individual observers' estimates of group size can be biased when compared to counts made from aerial photographs and that group size estimates can be improved by applying individual-specific calibrations to correct this bias (Gerrodette *et al.*, 2002). Computing the average group size for each segment required three steps: (1) calculation of the bias-corrected group size estimate for each observer for each sighting in the segment based on individual calibration coefficients; (2) calculation of the mean group size estimate, averaged over all observers, for each sighting in the segment; and (3) calculation of the mean group size estimate, averaged over all sightings, for each segment. For (1) one of three methods was used; all methods were derived by comparing the observers' uncalibrated group size estimates with group size estimates obtained from photographs of cetacean groups taken during the surveys. Direct calibration with quasi-maximum likelihood bias correction was the preferred method and was used if the group size estimates and Beaufort sea state data necessary for the observer's calibration were available (Gerrodette *et al.*, 2002). Directly calibrated observers have two types of direct calibrations, one that is year-specific and one that is a general calibration to be used in any year (Gerrodette *et al.*, 2002). If data were not available to use the direct calibration model that was specific to a given year, the next option was to use the general direct calibration model for the observer. If neither direct calibration model could be used due to lack of data, indirect calibration with a quasi-maximum likelihood bias correction was considered (Barlow *et al.*, 1998). The indirect calibration method could be used only if an observer's best estimate of group size was available and if an indirect calibration model existed for the observer. At this stage in the selection of a calibration method, if a best estimate was not available, that observer's data was not included in the mean group size estimate for the sighting. If the indirect calibration method could not be used but a best estimate was available for the observer, then the ratio method was used (Gerrodette *et al.*, 2002):

$$\hat{s} = \frac{s_b}{\left[\sum_{i=1}^{n} m_i\right]^{-1} \left[\sum_{i=1}^{n}\sum_{j=1}^{m_i}\left(\frac{s_{b_{i,j}}}{s_{p_i}}\right)\right]} \qquad (3)$$

where,

$\hat{s}$ = observer's calibrated group size estimate,

$s_{b_{i,j}}$ = observer *j*'s best estimate of size for group *i*, and

s_{p_i} = size of group *i* estimated from photographs of group *i*.

Thus, in the ratio method, the observer's best estimate (s_b) was corrected by the ratio of observer best estimates to photographic counts, averaged over all *n* photographic calibration groups, each having *m* observer estimates. Once each observer's group size estimate was calibrated, the mean group size was calculated for each sighting as the weighted mean of the natural logarithm of the calibrated group size estimates, resulting in a weighted geometric mean group size. The calibrated group size estimates were weighted by variance^{-1}, where the value for the variance for each observer was the mean square error (MSE) reported for directly calibrated observers and observers calibrated with the ratio method (Gerrodette *et al.*, 2002) or the average square prediction error (ASPE) reported for indirectly calibrated observers (Barlow *et al.*, 1998). Finally, the mean group size estimate for each segment was calculated as the arithmetic mean of the weighted geometric mean group size estimates for all sightings in the segment.

GAMs were used to relate beaked whale sightings to the summarised fixed geographic variables and temporally dynamic *in situ* oceanographic data described above. A GAM (Hastie and Tibshirani, 1990) may be represented as:

$$g(\mu) = \alpha + \sum_{j=1}^{p} f_j\left(X_j\right) \qquad (4)$$

As in GLMs, the function $g(\mu)$ is known as the link function, and it relates the mean of the response variable given the predictor variables, $\mu = E(Y|X_1,\ldots,X_p)$, to the additive predictor $\alpha + \Sigma_j f_j(X_j)$. GAMs are nonparametric extensions of GLMs: the components $f_j(X_j)$ in the additive predictor may include nonparametric smooth functions of the predictor variables, allowing GAMs to be considerably more flexible than GLMs, which are restricted by the constraints of the linear predictor, $\alpha + \Sigma_j \beta_j X_j$. Separate GAMs were built to describe and predict beaked whale encounter rates and average group sizes. The encounter rate data were essentially clustered counts; therefore, the number of sightings in each segment were modelled using a quasi-likelihood error distribution with variance proportional to the mean and a logarithmic link function (approximating an over-dispersed Poisson distribution). Encounter rate models were built using all 9km segments, regardless of whether they contained sightings. Observed distributions of cetacean group sizes in the ETP region typically have long tails and are restricted to positive, real values. Furthermore, after correcting for bias and averaging group sizes across individuals and sightings in each segment, group size estimates are likely to be non-integer valued. Therefore, GAMs were built using the natural logarithm of group size as the response variable and a Gaussian error distribution with the identity link function. Group size models were built on only the 9km segments that contained Cuvier's or *Mesoplodon* beaked whale sightings with valid group size estimates.

The encounter rate and group size GAMs were built using *S-PLUS 6 for Windows*. Forward/backward stepwise selection of variables, with linear terms or smoothing splines having two and three degrees of freedom (df) in the scope of predictor variables, was implemented using the function *step.gam*. Models built using a maximum of four df for each variable in the scope of *step.gam* were considered, but resulting models were qualitatively similar to those limited to three df and the added complexity of the four df models appeared to have no ecological justification. Akaike's Information Criterion (AIC) was used to determine the best model at each step. Stepwise selection of variables occurred twice for each model. The first stepwise selection process started with the null model, did not contain terms for latitude or longitude and linear terms were excluded from the scope. Latitude and longitude were excluded from the first call to try to explain the observed variation in the beaked whale data using the more informative environmental data before considering fixed geographic co-ordinates. Linear functions were excluded from the first call because a few instances were found in which AIC was lower for a linear fit than for a quadratic smoothing spline, but a cubic smoothing spline was better than a linear fit. In those instances, the stepwise fitting algorithm would not go beyond the quadratic and test the AIC value resulting from splines with higher df. The second call to *step.gam* began with the best model from the first call, and included latitude, longitude and linear functions of all variables in the scope of predictor variables. It is advantageous to call *step.gam* twice because, by default, the function uses the dispersion parameter of the original gam object (Chambers and Hastie, 1993) and the estimated dispersion parameter associated with the best model from the first call to the function is likely to better represent the underlying process than that associated with the null model.

The above stepwise selection of variables finds the model that provides the best fit to the given data as judged by AIC, but it does not provide any information about the predictive power of the resulting model. To assess the predictive power of a number of models, the stepwise building procedure was performed on all combinations of the years 1986-90 with one year left out; 1993 was also included in all trials because it was a relatively small data set. This modified procedure resulted in five 'best' encounter rate models and five 'best' group size models. To evaluate which encounter rate and group size models performed best according to predictive power, cross-validation methods were applied, testing each model on the excluded year. The model with the lowest average squared prediction error (ASPE) was selected as the model with the best predictive performance. The model selected by the cross-validation process was rebuilt using the specified df and all years of data to fine-tune the smoothing splines.

The final *Mesoplodon* encounter rate model and Cuvier's group size model included latitude. To determine how the fixed geographic variable affected the predictive performance of the models, the stepwise selection and cross-validation procedures were repeated, excluding latitude and longitude from the scopes of both calls to *step.gam*. The ASPE values of the final models built without geographic variables in the scopes were compared to the final models built with geographic variables; the models with the lowest ASPE values were selected as the best overall *Mesoplodon* encounter rate and Cuvier's group size models.

To estimate beaked whale density, D, the encounter rate (n/L) and group size (S) model results were incorporated into the standard line-transect equation:

$$D = \left(\frac{n}{L}\right) S \left(\frac{1}{2 \cdot ESW \cdot g(0)}\right) \tag{5}$$

where,

n/L = encounter rate (number of sightings per unit length of trackline),
S = expected (or mean) group size,
ESW = effective strip half-width, or $1/f(0)$, where $f(0)$ is the sighting probability density at zero perpendicular distance, and
$g(0)$ = probability of detecting an animal on the trackline.

The values of $f(0)$ and $g(0)$ were those for Cuvier's and *Mesoplodon* beaked whales in the ETP and Gulf of California from Ferguson and Barlow's (2001) analysis. It was necessary to apply a bias-correction factor to the group size predictions from the GAMs because the models were built in log space and then the results were transformed back to arithmetic space, converting the group size estimate to a geometric mean in the process (Finney, 1941; Smith, 1993). The ratio estimator was used to correct for this back-transformation bias (Smith, 1993). Density estimates for each segment were smoothed to give a geographic representation of average density over the study period by using an inverse distance weighting interpolation to the first power, with the anisotropy ratio set to 1.0 in *Surfer* software (version 7.0).

To evaluate the models' fit to the observed data, the following error analysis was conducted. Encounter rate models were fitted to the observed oceanographic and geographic data for all segments in the study area and the differences between predicted and observed values for each segment (ΔER_i) were calculated:

$$\Delta ER_i = ER_{i_{predicted}} - ER_{i_{observed}} \tag{6}$$

for segment i in the study area. In addition, the ratio (R_{ER}) between pooled predicted values and pooled observed values was calculated:

$$R_{ER} = \frac{\sum_{i=1}^{n} ER_{i_{predicted}}}{\sum_{i=1}^{n} ER_{i_{observed}}} \tag{7}$$

where the summation is over the total number of segments used to build the models or the number of segments in a given geographic stratum, as described below. Group size was predicted from GAMs based on the subset of data comprised of only the segments with either Cuvier's or *Mesoplodon* beaked whale sightings, as appropriate. This subset of predictions was used to test how well the model predicted group size for each segment (ΔSS_i) and for the study area as a whole (R_{SS}) because the group size model was built on the same subset of data upon which the predictions were based. The group size predictions were corrected for the bias due to back-transforming from the log space and the computations for ΔSS_i and R_{SS} were analogous to the respective encounter rate statistics (Eqs 6 and 7). To qualitatively determine whether spatial patterns existed in the predictions for encounter rate and group size, a spatially stratified analysis was conducted in which values of R_{ER} and R_{SS} were calculated for geographic strata of approximately 5° latitude × 5° longitude.

RESULTS

In total, 90 Cuvier's beaked whale sightings and 106 *Mesoplodon* sightings were included in the models. Cuvier's and *Mesoplodon* beaked whales were sighted in groups of approximately two individuals, on average, with maximum group sizes of six and five individuals, respectively. The mean water depth where Cuvier's beaked whales were sighted in the ETP was approximately 3.4km with a maximum depth of over 5.1km; similarly, the mean depth of *Mesoplodon* beaked whale sightings was just over 3.5km and the maximum depth was approximately 5.75km (Table 2; standard deviations (SD) for all environmental variables and summary statistics for the entire study area are also presented in Table 2). Cuvier's beaked whale was found over seafloors with a mean slope of 0.732° (range: 0.003-6.425°), and *Mesoplodon spp.* were found over a mean slope of 0.673° (range: 0.006-4.935°). In addition, beaked whales in the ETP were found in waters that ranged from well-mixed to stratified, with a continuum of weak to strong thermoclines. Both species were sighted an average of 1,000km offshore, with a range of approximately 40-3,750km. The concentration of chlorophyll at the surface associated with the Cuvier's and *Mesoplodon* sightings ranged from 0.048-0.649mg m^{-3} (mean=0.203mg m^{-3}) and 0.047 to 2.26mg m^{-3} (mean=0.255mg m^{-3}), respectively.

Models for both genera predicted highest densities in the highly productive coastal and equatorial waters (Figs 3 and 4). The mean predicted Cuvier's beaked whale density resulting from the overall best encounter rate and group size models was 4.55 individuals 1,000km^{-2} (SD=1.96). The best Cuvier's beaked whale encounter rate and group size

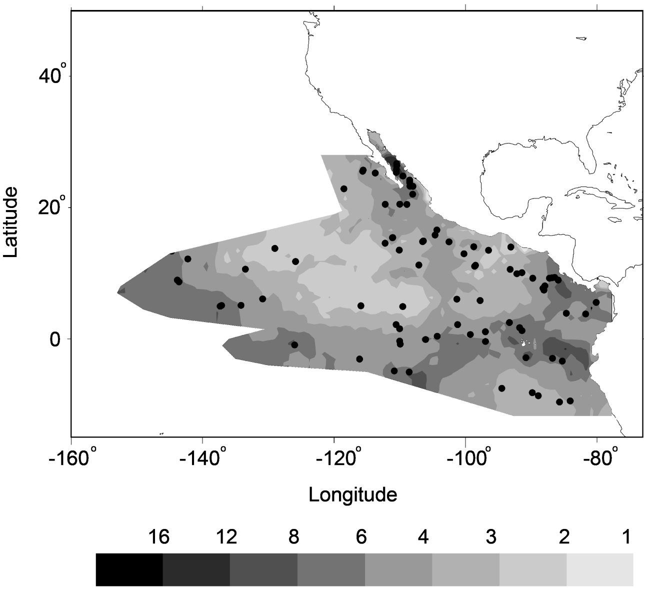
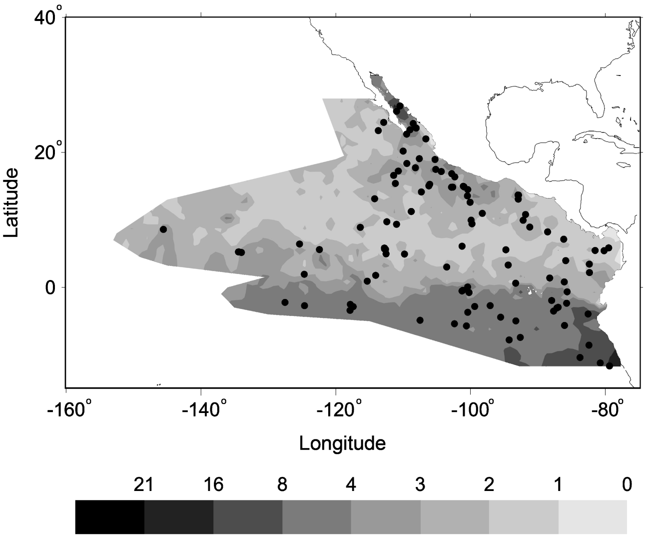


Fig. 3. Predicted Cuvier's beaked whale density (no. individuals 1,000km^{-2}) in the ETP. Predictions are for Beaufort sea state of 1. Black circles mark locations of all transect segments with on-effort Cuvier's beaked whale sightings and oceanographic data from SWFSC surveys 1986-90 and 1993.



`Fig. 4. Predicted *Mesoplodon* beaked whale density (no. individuals 1,000km^{-2}) in the ETP. Predictions are for Beaufort sea state of 1. Black circles mark locations of all on-effort *Mesoplodon* sightings and oceanographic data from SWFSC surveys 1986-90 and 1993.

Table 2

Summary statistics of environmental variables for the ETP study area and the segments in which *Ziphius* and *Mesoplodon* (*Mesop.*) beaked whale sightings occurred.

	Minimum			Mean			Maximum			Standard deviation		
	Ziphius	*Mesop.*	Study area	*Ziphius*	*Mesop.*	Study area	*Ziphius*	*Mesop.*	Study area	*Ziphius*	*Mesop.*	Study area
Beaufort*	0.8	0.2	0.2	2.9	2.9	3.7	5.0	5.0	6.0	1.3	1.3	1.1
Distance offshore (km)	42.5	36.0	3.8	1,097.8	1,052.0	1,249.7	3,670.6	3,844.6	3,851.8	1,064.5	970.0	942.2
Depth (m)	1,167.5	717.7	46.2	3,445.8	3,513.6	3,573.8	5,197.6	5,749.9	5,873.0	902.7	878.5	917.1
Slope (°)	0.003	0.006	0.000	0.732	0.673	0.504	6.425	4.935	10.487	1.145	1.097	0.935
Sea surface temperature (°C)	19.7	18.5	16.6	26.8	26.3	26.1	30.6	31.3	31.7	3.2	3.6	2.8
Sea surface salinity (psu)	30.1	30.3	16.3	33.9	34.0	33.9	35.3	35.3	35.7	0.8	1.0	1.0
Surface chlorophyll concentration (mg/m^3)	0.048	0.047	0.015	0.203	0.255	0.220	0.649	2.260	8.976	0.110	0.306	0.270
Thermocline depth (m)	15.0	15.0	11.0	53.9	56.2	61.4	151.0	126.0	211.7	24.0	23.9	28.0
Thermocline strength (°/m)	0.149	0.108	0.068	0.367	0.391	0.393	0.795	0.795	0.973	0.140	0.154	0.155

*Beaufort sea state was treated as a continuous variable in the analysis.

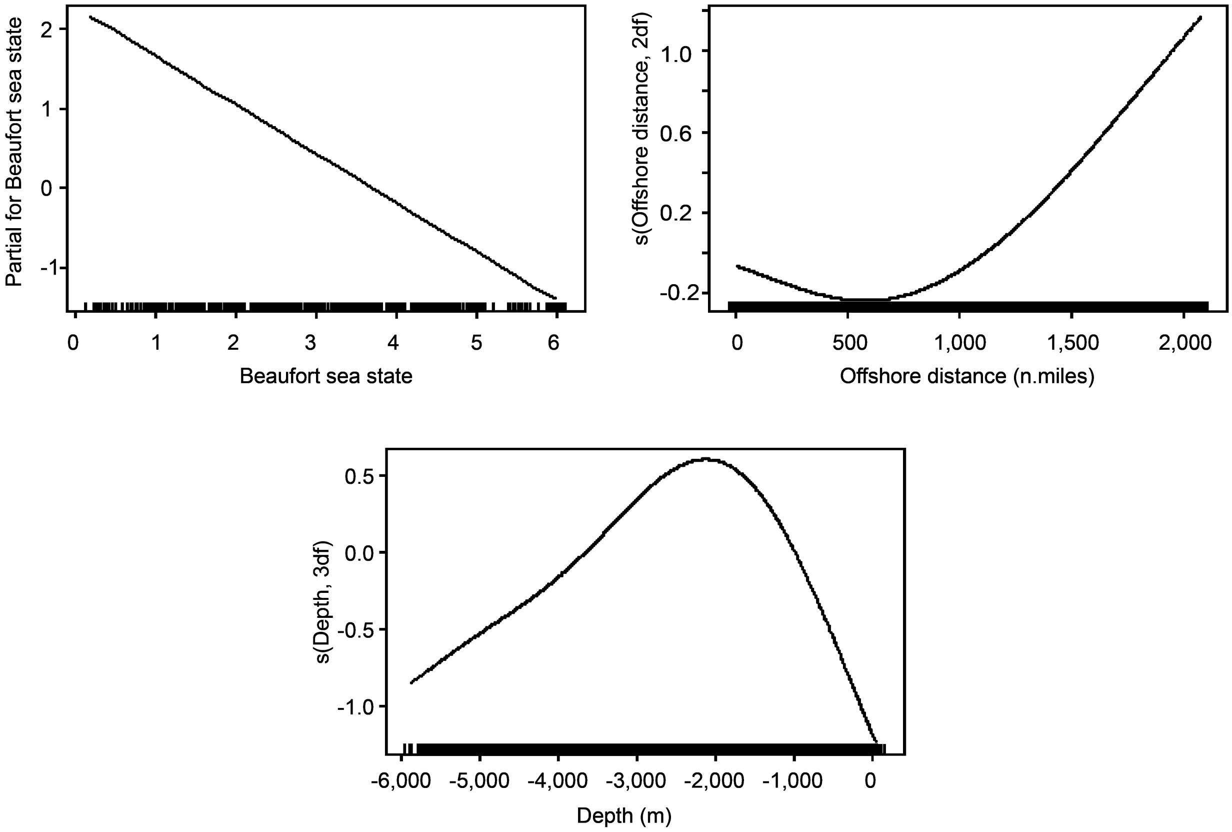


Fig. 5. Smooth spline functions of the predictor variables incorporated into the final Cuvier's beaked whale encounter rate (no. sightings/unit survey effort) GAM. Degrees of freedom for nonlinear fits are in the parentheses on the *y*-axis. Tick marks above the *x*-axis indicate the distribution of observations in all segments (with and without Cuvier's beaked whales).

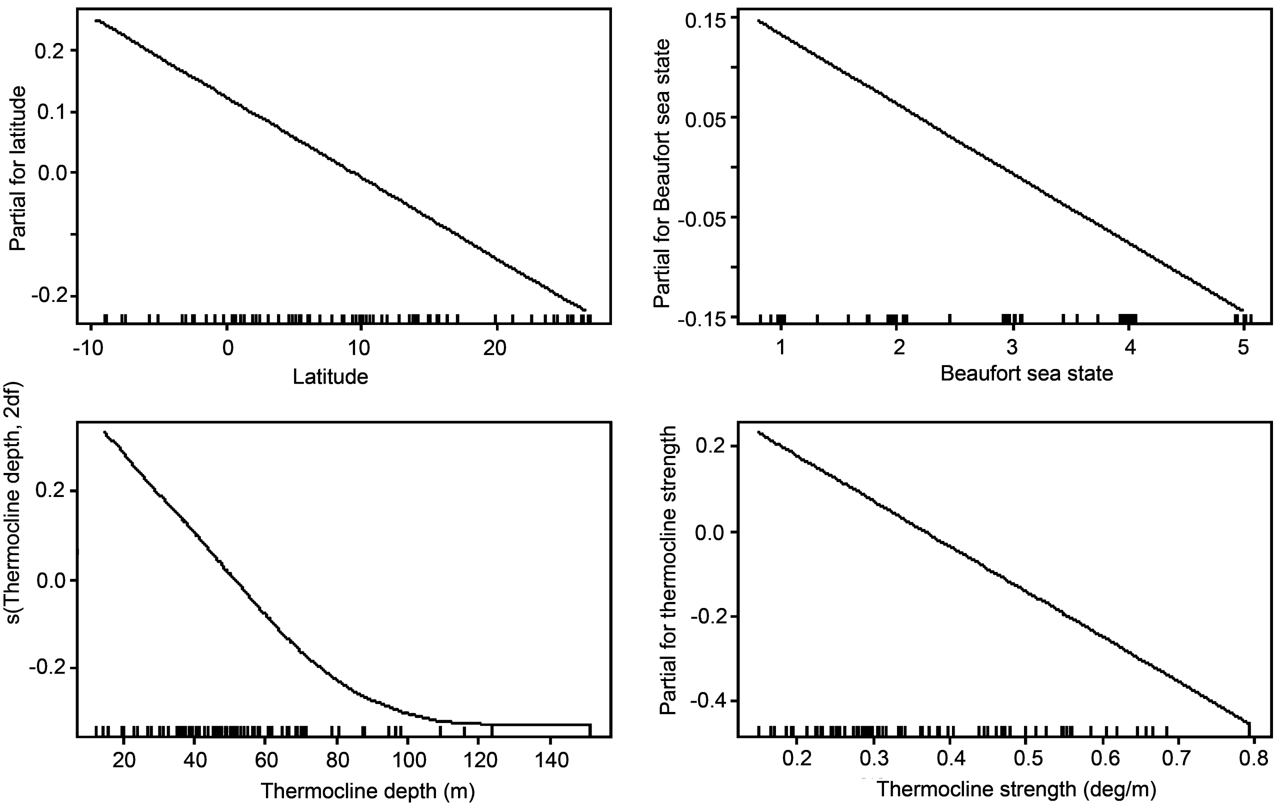


Fig. 6. Smooth functions of the predictor variables incorporated into the final Cuvier's beaked whale group size GAM. Degrees of freedom for nonlinear fits are in the parentheses on the *y*-axis. Tick marks above the *x*-axis indicate the distribution of observations in all segments with Cuvier's beaked whales.

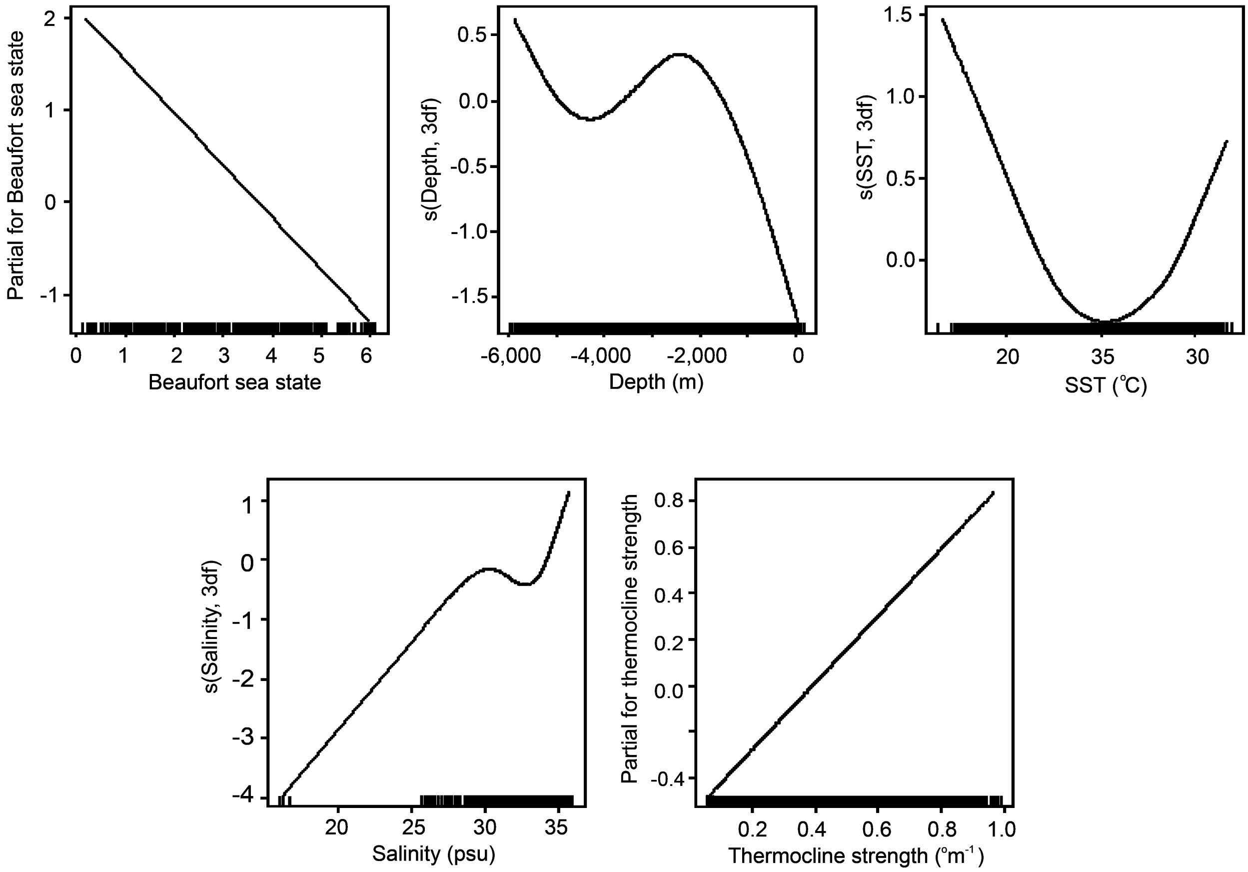


Fig. 7. Smooth functions of the predictor variables incorporated into the final *Mesoplodon* beaked whale encounter rate GAM. Degrees of freedom for nonlinear fits are in the parentheses on the *y*-axis. Tick marks above the *x*-axis indicate the distribution of observations in all segments (with and without *Mesoplodon* beaked whales).

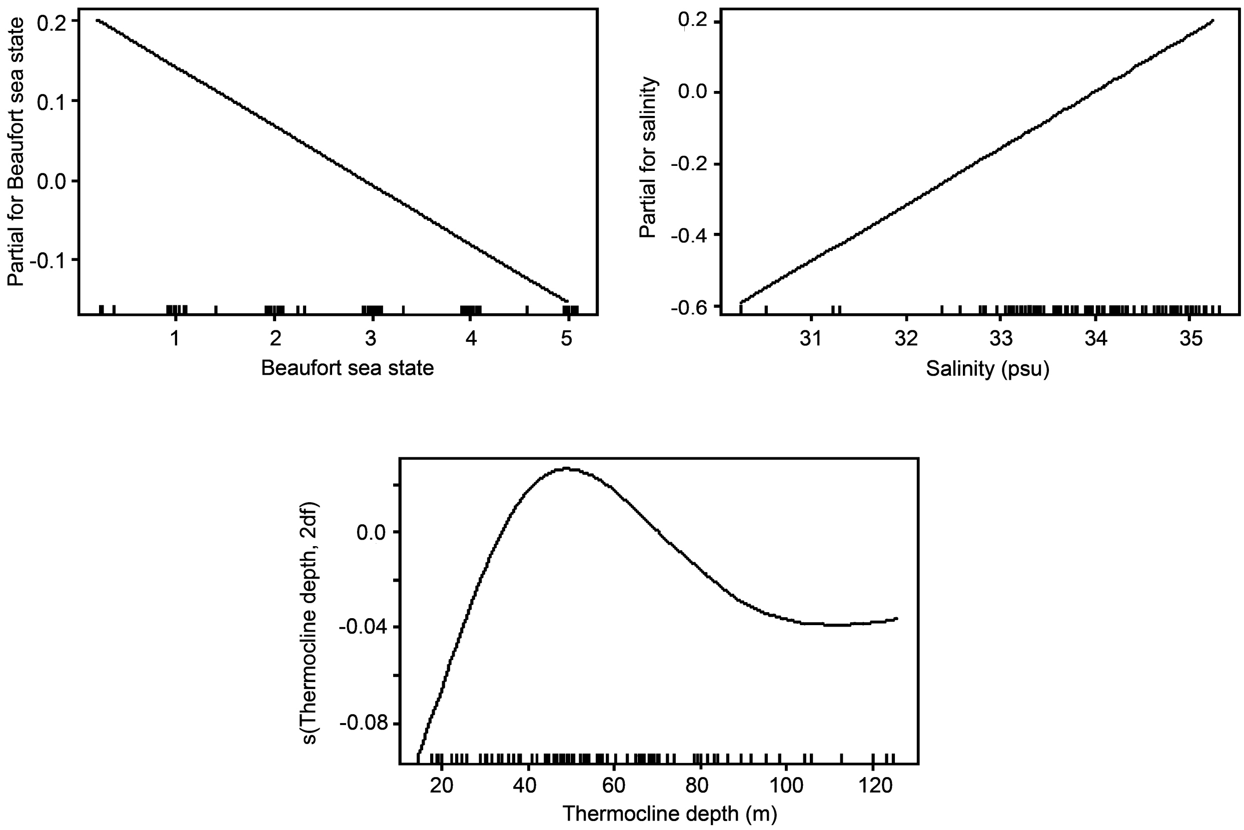


Fig. 8. Smooth functions of the predictor variables incorporated into the final *Mesoplodon* beaked whale group size GAM. Degrees of freedom for nonlinear fits are in the parentheses on the *y*-axis. Tick marks above the *x*-axis indicate the distribution of observations in all segments with *Mesoplodon* beaked whales.

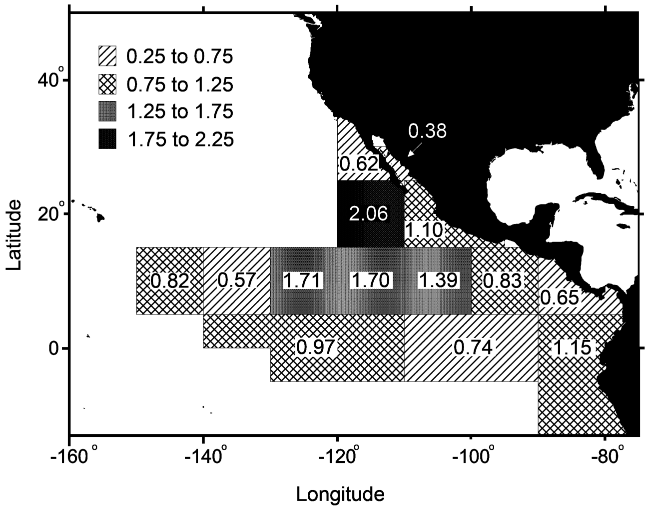


Fig. 9. Geographic distribution of residuals for Cuvier's beaked whale encounter rates measured as the ratio: R_{ER}=[Σ(predicted)/Σ(observed)]. R_{ER} values are shown in each stratum. Predictions were based on observed oceanographic data from SWFSC survey cruises in 1986-90 and 1993.

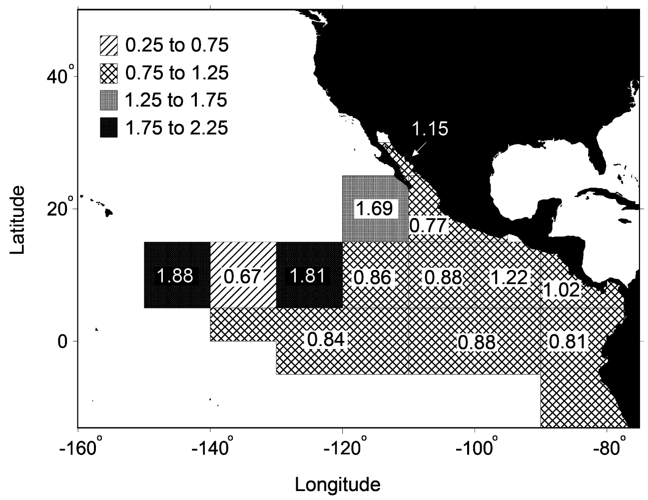


Fig. 10. Geographic distribution of residuals for *Mesoplodon* beaked whale encounter rates measured as the ratio: R_{ER}=[Σ(predicted)/Σ(observed)]. R_{ER} values are shown in each stratum. Predictions were based on observed oceanographic data from SWFSC survey cruises in 1986-90 and 1993.

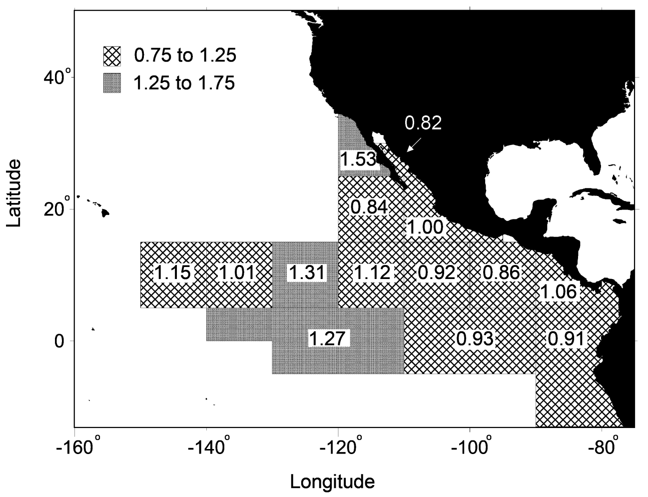


Fig. 11. Geographic distribution of residuals for Cuvier's beaked whale group sizes measured as the ratio: R_{SS}=[Σ(predicted)/Σ(observed)]. R_{SS} values are shown in each stratum. Predictions were based on observed oceanographic data from SWFSC survey cruises in 1986-90 and 1993.

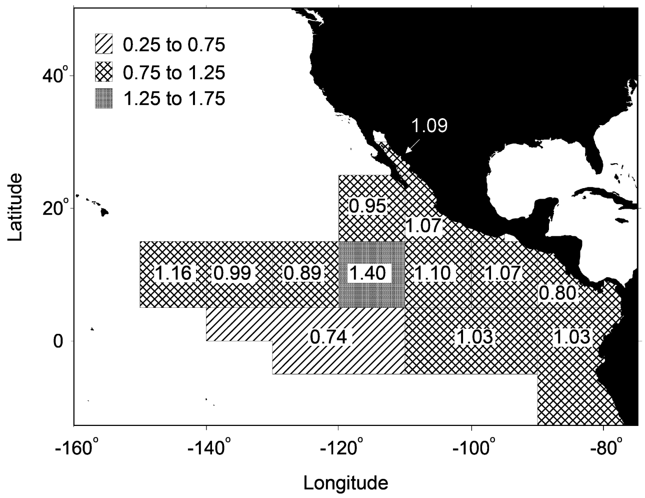


Fig. 12. Geographic distribution of residuals for *Mesoplodon* beaked whale group sizes measured as the ratio: R_{SS}=[Σ(predicted)/Σ(observed)]. R_{SS} values are shown in each stratum. Predictions were based on observed oceanography data from SWFSC survey cruises in 1986-90 and 1993.

models reduced deviance by 7.15% and 15.07% respectively, compared to the null models (Table 3). The Cuvier's beaked whale encounter rate model used only Beaufort sea state and the fixed geographic variables offshore distance and depth (Fig. 5 and Table 3), and the group size model incorporated latitude, Beaufort sea state, thermocline depth, and thermocline strength (Fig. 6 and Table 3). Beaufort sea state entered both Cuvier's models as a linear fit with negative slope, indicating smaller observed encounter rates and group sizes with increasing sea states (Figs 5 and 6). Offshore distance was included in the encounter rate model as a smoothing spline with 2df, showing a minimum around 926km (500 n.miles) and the highest rates further offshore (Fig. 5); the slight increase in encounter rate very close to shore is likely due to the cluster of sightings in the Gulf of California and along the Baja Peninsula (Fig. 3). In addition, the encounter rate model incorporated depth as a smoothing spline with 3df, and implies that Cuvier's beaked whales tended to be sighted most often in waters approximately 2km deep (Fig. 5), corresponding to the offshore edge of the continental slope. In the Cuvier's group size model, linear fits for latitude and thermocline strength suggest smaller groups at higher latitudes and in waters with stronger thermoclines (Fig. 6). Thermocline depth entered the Cuvier's group size model as a smoothing spline with 2df, with larger groups observed over shallower thermoclines, although there were few observations at deeper thermoclines and therefore, the tail of the smooth function should be interpreted with caution (Fig. 6).

Mesoplodon beaked whales were predicted to have a mean density of 2.96 individuals 1,000km^{-2} (SD=2.06). The decrease in deviance between the best *Mesoplodon* encounter rate model and the null encounter rate model was 8.39%, whereas the best group size model resulted in an 11.18% decrease in deviance (Table 4). The *Mesoplodon* encounter rate model without latitude resulted in a lower ASPE value than the model with latitude (Table 4). The *Mesoplodon* encounter rate model included Beaufort sea state, depth, SST, salinity and thermocline strength and the group size model contained Beaufort sea state, salinity and thermocline depth. The effects of Beaufort sea state were similar for both *Mesoplodon* models, suggesting that more animals were observed in calmer waters, as expected (Figs

Table 3

Summary of Cuvier's beaked whale encounter rate and group size GAMs for the ETP. Linear fits are represented by 'L1', whereas smoothing splines are represented by 'S#', where # is the associated degrees of freedom. Final selected model is indicated by **bold** font. Percent change in deviance was calculated for final selected model, rebuilt using all years' data, as: ((null deviance - residual deviance)/null deviance) x 100.

			Predictor variables										
Model	Year omitted	% change in deviance	Lat.	Long.	Beaufort	Offshore distance	Depth	Slope	SST	Salinity	Log surface chlorophyll	Thermocline depth	Thermocline strength
Cuvier's encounter rate													
	1986	-	-	L1	L1	S2	S3	-	L1	-	S2	L1	S3
	1987	-	-	-	L1	-	S3	-	-	L1	-	L1	-
	1988	**7.15**	**-**	**-**	**L1**	**S2**	**S3**	**-**	**-**	**-**	**-**	**-**	**-**
	1989	-	-	L1	L1	S2	S3	-	S3	L1	S3	L1	L1
	1990	-	-	L1	L1	S2	S3	-	S3	L1	-	L1	L1
Cuvier's group size													
	1986	**15.07**	**L1**	**-**	**L1**	**-**	**-**	**-**	**-**	**-**	**-**	**S2**	**L1**
	1987	-	-	-	-	S2	-	-	S3	-	-	-	-
	1988	-	-	L1	-	-	-	-	-	-	-	S3	-
	1989	-	-	-	-	S3	-	-	-	S2	-	L1	L1
	1990	-	-	L1	-	-	-	-	-	-	-	-	-

Table 4

Summary of *Mesoplodon* beaked whale encounter rate and group size GAMs for the ETP. Linear fits are represented by 'L1', whereas smoothing splines are represented by 'S#', where # is the associated degrees of freedom. 'NLL' designates model built without latitude or longitude. Final selected model is indicated by **bold** font. Percent change in deviance was calculated for final selected model, rebuilt using all years' data, as: ((null deviance - residual deviance)/null deviance) x 100.

			Predictor variables										
Model	Year omitted	% change in deviance	Lat.	Long.	Beaufort	Offshore distance	Depth	Slope	SST	Salinity	Log surface chlorophyll	Thermocline depth	Thermocline strength
***Mesoplodon* encounter rate**													
	1986	-	L1	-	L1	-	S3	-	S3	S2	S3	-	-
	1987	-	S3	-	L1	-	S3	-	S3	-	-	-	-
	1988	-	-	-	S3	-	S3	-	-	L1	S3	-	S2
	1989	-	L1	-	S3	-	S3	-	S3	S3	-	-	-
	1990	-	S3	-	L1	-	S3	-	S3	-	S3	-	-
	NLL	**8.39**	**-**	**-**	**L1**	**-**	**S3**	**-**	**S3**	**S3**	**-**	**-**	**L1**
***Mesoplodon* group size**													
	1986	-	-	-	L1	-	-	-	-	S2	-	-	-
	1987	**11.18**	**-**	**-**	**L1**	**-**	**-**	**-**	**-**	**L1**	**-**	**S2**	**-**
	1988	-	-	-	L1	S3	-	-	-	-	S3	-	-
	1989	-	-	-	L1	-	-	S3	-	S2	-	-	-
	1990	-	-	-	-	-	-	-	-	S2	-	-	-

7 and 8). *Mesoplodon* encounter rates and group sizes displayed positive associations with sea surface salinity (a smoothing spline with 3df in the encounter rate model and a linear term in the group size model; Figs 7 and 8, respectively), a trend that is likely due to the sightings in the Gulf of California and stretching out from the coast along 10°S (Fig. 4), both of which are regions of relatively high salinity waters (Fiedler, 1992). Similar to the Cuvier's beaked whale encounter rate model, the *Mesoplodon* encounter rate model selected depth as a smoothing spline with 3df, showing a peak at approximately 2km depth, with a secondary increase from about 4km to the maximum depth at which the genus was observed (Fig. 7). The smooth fit of SST to *Mesoplodon* encounter rate suggests a relative minimum in waters of 25°C (Fig. 7). The linear fit for thermocline strength in the *Mesoplodon* encounter rate model, showing higher encounter rates with stronger thermoclines (Fig. 7), is likely produced by the numerous sightings centred near the coast around 10°N in the TSW (Fiedler, 1992). The *Mesoplodon* group size model fits a smoothing spline with 2df to thermocline depth (Fig. 8), indicating larger groups in waters with 60m deep thermoclines, which is close to the mean value for the study area (Table 2).

The error analysis showed that the mean differences (averaged across all years and all segments used to build the models) between predicted and observed values of encounter rate and group size were zero for both Cuvier's and *Mesoplodon* beaked whales. The SDs in the differences between predicted and observed values were similar for both genera, with SD(ΔER) $\simeq$ 0.085 and SD(ΔSS) $\simeq$ 1.00. In addition, for both Cuvier's and *Mesoplodon* beaked whales, when pooling all segments used to build the models, the ratios between the pooled predicted encounter rates and the pooled observed encounter rates (R_{ER}) equalled unity out to at least two decimal places, and R_{SS} was also equal to 1.0. The geographically stratified analysis of residuals in the encounter rate for Cuvier's (Fig. 9) and *Mesoplodon* (Fig. 10) beaked whales showed that, in approximately half of the strata, the ratio of pooled predicted to observed values, R_{ER}, was close to unity (1.0 ± 0.25). Values of R_{ER} departed considerably from unity in some strata (from 0.38 to 2.06 for

Cuvier's beaked whale), but the distribution of residuals did not show much geographic pattern. Residuals in the group size estimates for pooled strata, R_{SS} , were near unity (1.0 ± 0.25) for the majority of strata for both species (Figs 11 and 12), and again there was little geographic pattern to the residuals.

DISCUSSION

The beaked whale models presented here are the first to estimate population densities. In addition, they were based upon a large study area with a substantial amount of survey effort over the abyssal plain. Although it is clear that some species of ziphiid whales are associated with continental slopes or topographic features such as seamounts, ridges and canyons in some areas, this association pattern may not hold for all species throughout their distributions. The ETP Cuvier's and *Mesoplodon* beaked whale analyses appear to expand the definition of what is considered suitable beaked whale habitat. Beaked whales in the ETP were sighted in considerably deeper waters than in any of the other studies discussed. In addition, beaked whales in the ETP were found in waters that ranged from well-mixed to stratified. High population densities of beaked whales were predicted in the southern Gulf of California, in coastal waters and in the equatorial cold tongue of the ETP study area, but beaked whales did not appear to be narrowly restricted to the highly productive waters typified by these coastal and upwelling systems and they were not limited to the continental slope and shelf waters, which is where the majority of beaked whale field studies have been conducted (Ferguson, 2005).

These analyses have shown that the extent and location of the study area can considerably affect the interpretation of results from beaked whale habitat studies. Two additional aspects of such studies with power to influence the results are the type of analytical method chosen for the analysis and the scale of the analysis. The analytical methods used in previous studies to examine beaked whale habitats ranged from hypothesis tests such as the Kruskall-Wallis one-way ANOVA (Davis *et al.*, 1998), Kolmogorov-Smirnov (Hooker *et al.*, 2002; Wimmer, 2003) and Chi-square (Cañadas *et al.*, 2002; Wimmer, 2003; MacLeod *et al.*, 2004) goodness of fit tests and the Wilcoxin signed rank test (Waring *et al.*, 2001), which determine whether a given environmental variable is related to beaked whale distribution patterns, to multivariate tools such as GLMs (Waring *et al.*, 2001; Cañadas *et al.*, 2002; Hamazaki, 2002), GAMs (MacLeod and Zuur, 2005), ENFA (MacLeod, 2005) and CART (MacLeod and Zuur, 2005), which can quantify the magnitude of the effect (i.e. how much a given environmental variable affects beaked whale distribution).

Generalised additive models were chosen for the ETP analysis because of their flexibility. One weakness of GAMs, however, is that they are data-intensive. All species of *Mesoplodon* sighted in the ETP study area were modelled together because small sample sizes of individual species (n=17 *M. peruvianus*, n=11 *M. densirostris*) prevented construction of separate models and there was a need to include a large number (n=78) of 'unidentified *Mesoplodon* beaked whales'. Grouping all *Mesoplodon* spp. together undoubtedly obscured the species-specific differences in habitat (Pitman and Lynn, 2001), thereby lowering explanatory or predictive power in the final models; this could potentially account for the low percent explained deviance in the GAMs. Other potential reasons for the relatively small reduction in deviance between the null and best GAMs exist: (1) the signal-to-noise ratio in the environment might be too high relative to the number of observations in the data set; (2) the environmental predictors used to build the models might not be strongly associated with beaked whale habitat; or (3) the error distributions specified for the encounter rate and group size models might be inappropriate. Addressing these questions and the issue of understanding and enumerating the various sources of uncertainty in the models are active areas of research. Nevertheless, as noted above, a dominant strength of GAMs is their flexibility, which manifested itself in the error analyses for Cuvier's and *Mesoplodon* encounter rates and group sizes. The error analyses found small differences between observed and predicted values, and found that the ratios of pooled predicted to pooled observed values were close to 1.0. Furthermore, in the geographically stratified residual analyses, predictions in the majority of the strata for both genera and both response variables (encounter rate and group size) were within 25% of the observed values and there was no evidence of a spatial pattern.

The spatial or temporal scale at which data are analysed in habitat studies is likely to have profound effects on the results. Ecological mechanisms affecting beaked whale distribution may be scale-specific and there may be a hierarchy of such mechanisms operating on different scales that influence where beaked whales are found. The slope of the seafloor is one variable that may be especially sensitive to the spatial scale of the analysis. For example, the steep wall of a submarine canyon is a feature that would appear in analyses conducted on scales of a few hundred meters to a few kilometres, but it would almost disappear in larger scale analyses such as that described for the ETP. Such small-scale features are likely to be important to the success of localised beaked whale foraging. Nevertheless, the animals may incorporate information from larger spatial scales, as exemplified by upwelling regions such as the Costa Rica Dome, California Current, Peru Current and equatorial cold tongue, to guide them to larger regions of enhanced foraging success. In the time domain, small scale patches with high densities of prey are likely to be temporally dynamic; therefore, instantaneous information about the present environment is most relevant for determining foraging success at a specific point and place in time. To arrive in the general vicinity of patches with high densities of prey, however, successful predators might have processed time-lagged information, averaging their foraging experiences in different regions over the past week, month, year, or decade, for example. Time lags are particularly important when proxies such as chlorophyll data are used to indicate beaked whale habitat because it is not the primary producers themselves, but the squid and mesopelageic fishes several trophic levels higher, that beaked whales eat and time lapses before energy and nutrients from the primary producers climb the food chain up to cetacean prey species (Jaquet, 1996). It is noteworthy that the ETP analysis found no associations between beaked whales and surface chlorophyll concentration, which is a biological variable commonly used as a proxy for cetacean prey. Ultimately ecologists are left with a conundrum: to determine which environmental predictors define beaked whale habitat it is important to know the scale at which to observe the ecology of the system; simultaneously, to determine the scale at which to observe the ecology of the system, it is important to know which environmental predictors define beaked whale habitat. This suggests that an iterative approach may be the best way to increase ecological understanding of these animals.

Understanding of ziphiid whale habitats may be enhanced by conducting more surveys in a greater diversity of potential habitats, thoughtfully selecting the types of environmental data collected and the scale at which they are collected, investigating the effects of scale on habitat models and explicitly accounting for detection bias (e.g. by incorporating Beaufort sea state and availability bias correction) in occurrence, density and abundance models.

RESEARCH RECOMMENDATIONS

(1) Accurate habitat models for ziphiid whales will not be possible unless surveys cover a broader range of potential habitats, including deep waters over the abyssal plains. Surveys that only cover the suspected habitat, such as slope waters, cannot be used to confirm this habitat preference.

(2) Oceanographic data should be collected in conjunction with cetacean surveys to improve the data available for habitat modelling. There is a particular need to identify the prey of ziphiid whales and to develop methods to measure their abundance.

(3) To reconcile apparent differences in results among different habitat studies, the influences of observation scale (including total survey area and the sample size used to partition that area into smaller units), detection bias (the effect of sea state on apparent density) and suite of predictor variables, must be addressed.

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REFERENCES

Anon. 2001. Joint interim report on the Bahamas marine mammal stranding event of 15-16 March 2000 (December 2001). NOAA unpublished report. 59pp. [Available at *http://www.nmfs.noaa.gov/pro_tres/overview/Interim_Bahamas_Report.pdf*].

Barlow, J. 1999. Trackline detection probability for long-diving whales. pp. 209-21. *In:* G.W. Garner, S.C. Amstrup, J.L. Laake, B.F.J. Manly, L.L. McDonald and D.G. Robertson (eds.) *Marine Mammal Survey and Assessment Methods*. Balkema Press, Rotterdam, Netherlands. 287pp.

Barlow, J., Gerrodette, T. and Perryman, W. 1998. Calibrating group size estimates for cetaceans seen on ship surveys. SWFSC Admin. Report LJ-97-11. 25pp. [Available from SWFSC, PO Box 271, La Jolla, CA].

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.

Cañadas, A., Sagarminaga, R. and García-Tiscar, S. 2002. Cetacean distribution related with depth and slope in the Mediterranean waters off southern Spain. *Deep Sea Research* 49(11):2053-73.

Chambers, J.M. and Hastie, T.J. 1993. *Statistical models in S*. Chapman and Hall, New York. 608pp.

Cox, T.M., Ragen, T.J., Read, A.J., Vos, E., Baird, R.W., Balcomb, K., Barlow, J., Caldwell, J., Cranford, T., Crum, L., D'Amico, A., D'Spain, G., Fernández, A., Finneran, J., Gentry, R., Gerth, W., Gulland, F., Hildebrand, J., Houser, D., Hullar, T., Jepson, P.D., Ketten, D., MacLeod, C.D., Miller, P., Moore, S., Mountain, D., Palka, D., Ponganis, P., Rommel, S., Rowles, T., Taylor, B., Tyack, P., Wartzok, D., Gisiner, R., Mead, J. and Benner, L. 2006. Understanding the impacts of anthropogenic sound on beaked whales. *J. Cetacean Res. Manage.* 7(3):This volume.

Dalebout, M.L., Mead, J.G., Baker, C.S., Baker, A.N. and Van Helden, A.L. 2002. A new species of beaked whale *Mesoplodon perrini* sp. N. (Cetacea: Ziphiidae) discovered through phylogenetic analyses of mitochondrial DNA sequences. *Mar. Mammal Sci.* 18(3):577-608.

D'Amico, A., Bergamasco, A., Zanasca, P., Carniel, S., Nancini, E., Portunato, N., Teloni, V., Mori, C. and Barbanti, R. 2003. Qualitative correlation of marine mammals with physical and biological parameters in the Ligurian Sea. *IEEE J. Ocean. Engr.* 28(1):29-43.

Davis, R.W., Fargion, G.S., May, N., Leming, T.D., Baumgartner, M., Evans, W.E., Hansen, L.J. and Mullin, K. 1998. Physical habitat of cetaceans along the continental slope in the north-central and western gulf of Mexico. *Mar. Mammal Sci.* 14(3):490-507.

Ferguson, M.C. 2005. Cetacean population density in the eastern Pacific Ocean: analyzing patterns with predictive spatial models. Doctoral Thesis, University of California, San Diego, Scripps Institution of Oceanography. 221pp.

Ferguson, M.C. and Barlow, J. 2001. Spatial distribution and density of cetaceans in the eastern tropical Pacific Ocean based on summer/fall research vessel surveys in 1986-96. SWFSC Admin. Rep. No. LJ-01-04. 61pp plus addendum. [Available from SWFSC, 8604 La Jolla Shores Dr., La Jolla, CA 92037, USA].

Fiedler, P.C. 1992. Seasonal climatologies and variability of eastern tropical Pacific surface waters. *NOAA Technical Report NMFS* 109:1-65.

Fiedler, P.C. 2002. The annual cycle and biological effects of the Costa Rica Dome. *Deep Sea Research* 49:321-38.

Fiedler, P.C. and Philbrick, V.A. 2002. Environmental change in the eastern tropical Pacific Ocean: observations in 1986-1990 and 1998-2000. SWFSC Admin. Rep. No. LJ-02-15.18pp. [Available from SWFSC, PO Box 271, La Jolla, CA].

Fiedler, P.C. and Talley, L.D. 2005. Hydrography of the eastern tropical Pacific: a review. *Prog. Oceanogr.* :In press.

Finney, D.J. 1941. On the distribution of a variate whose logarithm is normally distributed. *J. Roy. Statist. Soc.* Supplement 7:155-61.

Gerrodette, T., Perryman, W. and Barlow, J. 2002. Calibrating group size estimates of dolphins in the eastern tropical Pacific Ocean. SWFSC Admin. Rep. No. LJ-02-08. 25pp. [Available from SWFSC, PO Box 271, La Jolla, CA].

Hamazaki, T. 2002. Spatiotemporal prediction models of cetacean habitats in the mid-western North Atlantic Ocean (from Cape Hatteras, North Carolina, USA, to Nova Scotia, Canada). *Mar. Mammal Sci.* 18(4):920-39.

Hamazaki, T. 2004. Modelling species-habitat relationship in the marine environment: a response to Gregr (2004). *Mar. Mammal Sci.* 20(2):356-8.

Hastie, T.J. and Tibshirani, R.J. 1990. *Monographs on Statistics and Applied Probability*. 43. *Generalized Additive Models*. Chapman and Hall, London. 335pp.

Hooker, S.K., Whitehead, H., Gowans, S. and Baird, R.W. 2002. Fluctuations in distribution and patterns of individual range use of northern bottlenose whales. *Mar. Ecol. Prog. Ser.* 225:287-97.

Houston, J. 1990a. Status of Hubb's beaked whale, *Mesoplodon carlhubbsi*, in Canada. *Can. Field-Nat.* 104(1):121-4.

Houston, J. 1990b. Status of True's beaked whale, *Mesoplodon mirus*, in Canada. *Can. Field-Nat.* 104(1):135-7.

Jaquet, N. 1996. How spatial and temporal scales influence understanding of sperm whale distribution: a review. *Mammal Rev.* 26(1):51-65.

Jefferson, T.A., Leatherwood, S. and Webber, M.A. 1993. *FAO Species Identification Guide. Marine Mammals of the World*. FAO, Rome. 320pp.

Johnson, M., Madsen, P.T., Zimmer, W.M.X., Aguilar de Soto, N. and Tyack, P.L. 2004. Beaked whales echolocate on prey. *Proc. R. Soc. Lond. Ser. B.* Supplement 6(271(S6)):383-6.

Kessler, W.S. 2005. The circulation of the eastern tropical Pacific: a review. *Prog. Oceanogr.* :Accepted.

Kinzey, D., Olson, P. and Gerrodette, T. 2000. Marine mammal data collection procedures on research ship line-transect surveys by the Southwest Fisheries Science Center. SWFSC Admin. Report LJ-97-11. 25pp. [Available from SWFSC, PO Box 271, La Jolla, CA].

Lierheimer, L.J. Fielder, P.C., Reilly, S.B., Pitman, R.L., Ballance, L.T. and Behringer, D.W. 1989a. Report of ecosystem studies conducted during the 1988 eastern tropical Pacific dolphin survey on the research vessel *McArthur*. NOAA Tech. Mem. NOAA-TM-NMFS-SWFSC-132. 121pp. [Available from Southwest Fisheries Science Center, PO Box 271, La Jolla, CA 92038, USA].

Lierheimer, L.J., Fielder, P.C., Reilly, S.B., Pitman, R.L., Thomas, G.C. and Behringer, D.W. 1989b. Report of ecosystem studies conducted during the 1988 eastern tropical Pacific dolphin survey on the research vessel *David Starr Jordan*. NOAA Tech. Mem. NOAA-TM-NMFS-SWFSC-131. 125pp. [Available from Southwest Fisheries Science Center, PO Box 271, La Jolla, CA 92-38, USA].

Lierheimer, L.J., Fiedler, P.C., Reilly, S.B., Pitman, R.L., Ballance, L.T., Beavers, S.C. and Behringer, D.W. 1990a. Report of ecosystem studies conducted during the 1989 eastern tropical Pacific dolphin survey on the research vessel *McArthur*. NOAA Tech. Mem. NOAA-TM-NMFS-SWFSC-140. 123pp. [Available from Southwest Fisheries Science Center, PO Box 271, La Jolla, CA 92038, USA].

Lierheimer, L.J., Fiedler, P.C., Reilly, S.B., Pitman, R.L., Ballance, L.T., Beavers, S.C., Thomas, G.G. and Behringer, D.W. 1990b. Report of ecosystem studies conducted during the 1989 eastern tropical Pacific dolphin survey on the research vessel *David Starr Jordan*. NOAA Tech Memo NOAA-TM-NMFS-SWFSC-139. 118pp. [Available from Southwest Fisheries Science Center, PO Box 281, La Jolla, CA 92038, USA].

MacLeod, C.D. 2005. Niche partitioning, distribution and competition in North Atlantic beaked whales. Thesis, University of Aberdeen, Aberdeen, UK.

MacLeod, C.D. and Zuur, A.F. 2005. Habitat utilisation by Blainville's beaked whales off Great Abaco, Northern Bahamas, in relation to seabed topography. *Mar. Biol.* 174:1-11.

MacLeod, C.D., Hauser, N. and Peckham, H. 2004. Diversity, abundance and structure of the cetacean community on summer months east of Great Abaco, Bahamas. *J. Mar. Biol. Assoc. UK* 84:469-74.

Mead, J.G. 2002. Beaked whales, overview. pp. 81-4. *In:* W.F. Perrin, B. Wursig and G.M. Thewissen (eds.) *Encyclopedia of Marine Mammals*. Academic Press, San Diego.

Neter, J., Wasserman, W. and Kutner, M.H. 1990. *Applied Linear Statistical Models: Regression, Analysis of Variance, and Experimental Designs*. Irwin, Boston, Massachusetts, USA. i-xi+1,181pp.

Ostrom, P.H., Lien, J. and Macko, S.A. 1993. Evaluation of the diet of Sowerby's beaked whale, *Mesoplodon bidens*, based on isotopic comparisons among northwestern Atlantic cetaceans. *Can. J. Zool.* 71(4):858-61.

Palacios, D.M. 1996. On the specimen of the ginkgo-toothed beaked whale, *Mesoplodon ginkgodens*, from the Galapagos Islands. *Mar. Mammal Sci.* 12(3):444-6.

Peterson, G. 2003. Whales beach seismic research. *Geotimes* Jan 2003:8-9. [Available at *www.geotimes.org/jan03/NNwhales.html*].

Philbrick, V.A., Fiedler, P.C., Reilly, S.B., Pitman, R.L., Ballance, L.T. and Behringer, D.W. 1991a. Report of ecosystem studies conducted during the 1990 eastern tropical Pacific dolphin survey on the research vessel *McArthur*. NOAA Tech. Mem. NOAA-TM-NMFS-SWFSC-161. 132pp. [Available from Southwest Fisheries Science Center, PO Box 271, La Jolla, Ca 92038].

Philbrick, V.A., Fiedler, P.C., Reilly, S.B., Pitman, R.L., Ballance, L.T., Thomas, G.G. and Behringer, D.W. 1991b. Report of ecosystem studies conducted during the 1990 eastern tropical Pacific dolphin survey on the research vessel *David Starr Jordan*. NOAA Tech. Mem. NOAA-TM-NMFS-SWFSC-160. 117pp. [Available from Southwest Fisheries Science Center, PO Box 271, La Jolla, CA 92038].

Pitman, R.L. and Lynn, M.S. 2001. Biological observations of an unidentified mesoplodont whale in the eastern tropical Pacific and probable identity: *Mesoplodon peruvianus*. *Mar. Mammal Sci.* 17:648-57.

Pitman, R.L., Palacios, D.M., Brennan, P.L.R., Brennan, B.J., Balcomb III, K.C. and Miyashita, T. 1999. Sightings and possible identity of a bottlenose whale in the tropical Indo-Pacific: *Indopacetus pacificus*. *Mar. Mammal Sci.* 15(2):531-49.

Reeves, R.R., Stewart, B.S., Clapham, P.J. and Powell, J.A. 2002. *Guide to Marine Mammals of the World*. National Audobon Society/Alfred A. Knopf, Inc., New York. 528pp.

Reyes, J.C., Mead, J.G. and van Waerebeek, K. 1991. A new species of beaked whale *Mesoplodon peruvianus* sp. n. (Cetacea: Ziphiidae) from Peru. *Mar. Mammal Sci.* 7(1):1-24.

Ryther, J.H. 1969. Photosynthesis and fish production in the sea. *Science* 166:72-6.

Smith, R.J. 1993. Logarithmic transformation bias in allometry. *Am. J. Phys. Anthropol.* 90:215-28.

Thayer, V.G., McDonald, B.G., Ellingson, J.M., Oliver, C.W., Behringer, D.W. and Reilly, S.B. 1988a. Report of ecosystem studies conducted during the 1986 eastern tropical Pacific dolphin survey on the research vessel *McArthur*. NOAA Tech. Mem. NOAA-TM-NMFS-SWFSC-104. 112pp. [Available from Southwest Fisheries Science Center, PO Box 271, La Jolla, CA 92038].

Thayer, V.G., Pitman, R.L., Rittmaster, K.A., Thomas, G.G., Behringer, D.W. and Reilly, S.B. 1988b. Report of ecosystem studies conducted during the 1986 eastern tropical Pacific dolphin survey on the research vessel *David Starr Jordan*. NOAA Tech. Mem. NOAA-TM-NMFS-SWFSC-105. 106pp. [Available from Southwest Fisheries Science Center, PO Box 271, La Jolla, CA 92038].

Thayer, V.G., Reilly, S.B., Fiedler, P.C., Oliver, C.W. and Behringer, D.W. 1988c. Report of ecosystem studies conducted during the 1986 eastern tropical Pacific dolphin survey on the research vessel *McArthur*. NOAA Tech. Mem. NOAA-TM-NMFS-SWFSC-114. 114pp. [Available from Southwest Fisheries Science Center, PO Box 271, La Jolla, CA 92038].

Thayer, V.G., Reilly, S.B., Fiedler, P.C., Pitman, R.L., Thomas, G.G. and Behringer, D.W. 1988d. Report of ecosystem studies conducted during the 1987 eastern tropical Pacific dolphin survey on the research vessel *David Starr Jordan*. NOAA Tech. Mem. NOAA-TM-NMFS-SWFSC-115. 94pp. [Available from Southwest Fisheries Science Center, PO Box 271, La Jolla, CA 92038].

Waring, G.T., Hamazaki, T., Sheenan, D., Wood, G. and Baker, S. 2001. Characterization of beaked whale (Ziphiidae) and sperm whale (*Physeter macrocephalus*) summer habitat in shelf-edge and deeper waters off the northeast US. *Mar. Mammal Sci.* 17(4):703-17.

Weir, C.R., Pollock, C.M., Cronin, C. and Taylor, S. 2001. Cetaceans of the Atlantic Frontier, north and west of Scotland. *Cont. Shelf Res.* 21:1047-71.

Wimmer, T. 2003. Distribution of cetaceans on the continental shelf break off Nova Scotia and in adjacent waters with a focus on northern bottlenose whales, *Hyperoodon ampullatus*. Msc Thesis, Dalhousie University, Halifax, NS. 119pp.

Wimmer, T. and Whitehead, H. 2004. Movements and distribution of northern bottlenose whales, *Hyperoodon ampullatus*, on the Scotian Slope and in adjacent waters. *Can. J. Zool.* 82:1782-94.

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