



Spatial models of delphinid (family Delphinidae) encounter rate and group size in the eastern tropical Pacific Ocean

Megan C. Ferguson^{a,b,*}, Jay Barlow^a, Paul Fiedler^a,
Stephen B. Reilly^a, Tim Gerrodette^a

^a NOAA Southwest Fisheries Science Center, 8604 La Jolla Shores Dr., La Jolla, CA 92037, USA

^b Scripps Institution of Oceanography, La Jolla, CA 92093-0208, USA

Received 13 August 2004; received in revised form 28 September 2005; accepted 17 October 2005

Available online 6 December 2005

Abstract

We use temporally dynamic environmental variables and fixed geographic variables to construct generalized additive models to predict delphinid (family Delphinidae) encounter rates (number of groups per unit survey effort) and group sizes in the eastern tropical Pacific Ocean. The delphinid sighting data and environmental data were collected simultaneously during the Southwest Fisheries Science Center's cetacean line-transect surveys conducted during the summer and fall of 1986–1990 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 the density (number of individuals per unit area) of delphinids throughout the study area. Areas with the highest predicted 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 densities. 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. © 2005 Elsevier B.V. All rights reserved.

Keywords: Oceanography; Pacific Ocean; Modeling; Dolphins; Delphinidae; Habitat; Occurrence; Density; Encounter rate; Group size; Generalized additive models (GAM); Line-transect

1. Introduction

Since the mid-1900s, the number and type of human activities that can adversely affect marine ecosystems

has increased along with public awareness thereof. Policymakers have responded by requiring that those who wish to engage in activities that may be detrimental to the marine environment formally assess the potential impact of their activities. A large proportion of the high risk activities occur on a relatively small spatial scale. Ideally, the scale of analyses used in a risk assessment would match the scale of the proposed activity

* Corresponding author. Tel.: +1 858 546 7118; fax: +1 858 546 7003.

E-mail address: Megan.Ferguson@noaa.gov (M.C. Ferguson).

and affected area. Research into dolphin populations in the eastern tropical Pacific Ocean (ETP) provides a case study of how science has been stimulated by, and responded to, the changing anthropogenic demands on marine ecosystems.

ETP dolphin populations gained the international attention of scientists, public policymakers, and conservationists in the late 1960s when it became evident that large numbers of dolphins were being killed incidental to purse seine fishing operations for tuna (Perrin, 1969). In the mid-1970s, the National Marine Fisheries Service (NMFS) initiated research to determine the status of the affected ETP dolphin populations, and NMFS has continued this effort to the present. A key component of the NMFS strategy has been to conduct large-scale shipboard surveys to further understanding of the dynamics and abundance of ETP dolphin populations and the animals' relationships to the ecosystem in which they are embedded. Since 1979, the NMFS, Southwest Fisheries Science Center (SWFSC) surveys have followed line-transect protocols to estimate the abundance of cetaceans in the region; beginning in 1986, SWFSC research surveys expanded to study the ETP ecosystem, collecting physical and biological oceanographic data to provide a con-

text in which to interpret the results from the cetacean studies.

The ETP study area (Fig. 1) spans approximately 20 million km² of the Pacific Ocean; therefore, the scale of the SWFSC research vessel surveys is relatively large compared to areas affected by high risk activities such as seismic surveys and military exercises. Nevertheless, this ETP study area does not encompass the entire range of any cetacean species (other than the vaquita, *Phocoena sinus*, which is not considered here) and interannual variability in abundance estimates for many species has been attributed to movement of animals in and out of the survey region (e.g., Gerrodette and Forcada, 2002a). Understanding how these movements can affect abundance estimates, which ultimately depends upon how population density relates to the environment, is a multi-scale problem. The large-scale question is, What is overall range of the species? The small-scale questions relate to habitat: What is the population density in a given area and what environmental factors affect the distribution and variability in abundance of the species? Our research aims to better understand the small-scale habitat questions. Traditional methods of density estimation (e.g., line-transect) do not provide the needed level of geographic

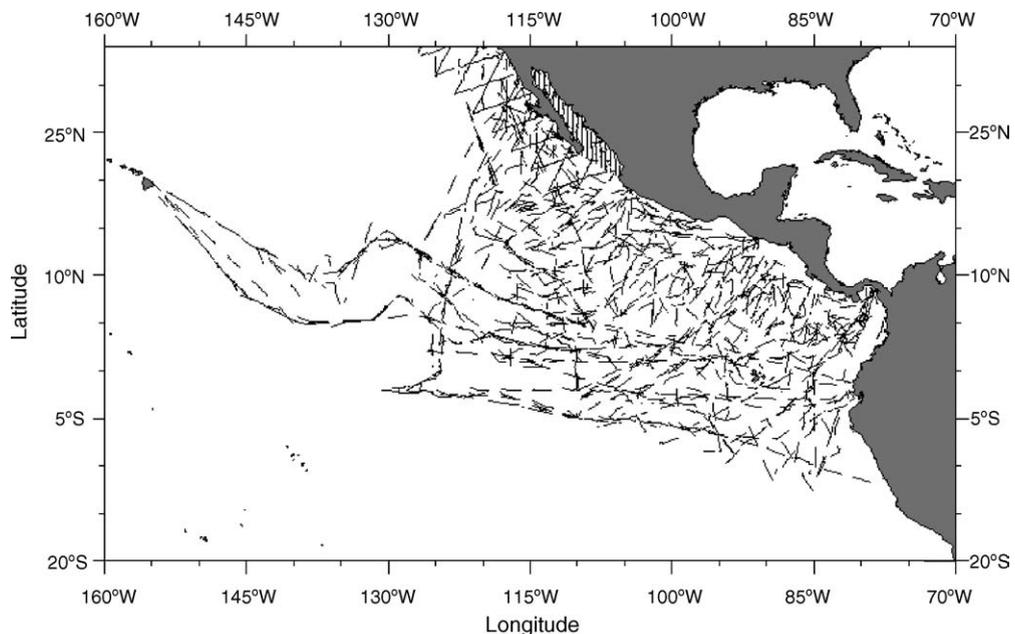


Fig. 1. Transect lines covered during the 1986–1990 and 1993 line-transect surveys conducted by the Southwest Fisheries Science Center.

resolution and do not provide any deeper understanding of the factors that might be causing changes in distribution. Cetacean sighting data from past line-transect surveys conducted by SWFSC contain information on the small-scale distribution of individuals. These data, in association with information about the marine environment from relevant oceanographic studies, may be used to (1) estimate dolphin densities on smaller spatial scales and to (2) understand how environmental variability affects variability in cetacean distribution and abundance.

Considerable work has been done to investigate the distribution and, more specifically, the habitat of ETP dolphins in relation to encounter rate (number of groups of animals observed per unit survey effort). Au and Perryman (1985) defined habitat characteristics of common (*Delphinus delphis*), striped (*Stenella coeruleoalba*), spotted (*Stenella attenuata*) and spinner (*Stenella longirostris*) dolphins in the ETP. They qualitatively identified two contrasting patterns in the distribution of dolphin sightings and postulated that the patterns were linked to the physical oceanography in the region. In particular, Au and Perryman (1985) noted that common and striped dolphins tended to occur in upwelling-modified conditions typical of waters along the equator and in the eastern boundary currents, whereas spotted and spinner dolphins were found in warm, low salinity surface waters over a strong, shallow thermocline in tropical waters off Mexico. The results from Reilly's (1990) statistical analyses on ETP dolphin data supported Au and Perryman's (1985) hypotheses about spinner, spotted, and common dolphin habitat, but suggested that striped dolphin habitat could not be distinguished from the upwelling-modified or tropical habitats based on the variables used in the analysis, which included thermocline depth and σ_t (a measure of seawater density). Furthermore, Reilly (1990) found that spotted, spinner, and striped dolphin distributions move offshore in the summer, when the countercurrent thermocline ridge at 10°N shoals. Reilly and Fiedler (1994) used canonical correspondence analysis (CCA) to study how encounter rates of ETP dolphins related to the physical oceanography of the region during the period from 1986 to 1990. Their results were in agreement with Reilly's (1990), identifying cool upwelling areas as common dolphin habitat, warm tropical areas as spotted and spinner dolphin habitat, and finding that the amount of vari-

ance explained by the environmental data was the least for striped dolphins. Reilly and Fiedler (1994) noted that the interannual variability in the species data was largely accounted for by the interannual variation in the environment. They suggested that dolphin abundance estimates might be improved by using the results of the CCA either to (1) post-stratify the sighting data before using standard line-transect methods to estimate abundance or (2) quantify the amount of good habitat, and extrapolate to the proportion of each population in the study area at the time of the survey. Reilly et al. (2002) investigated dolphin encounter rate data from 1998 to 2000 with CCA and found that, in comparison to Reilly and Fiedler (1994), there was no substantial change in patterns of dolphin habitat use between the late 1980s and the late 1990s.

We use generalized additive models (GAMs) to mathematically model the relationships between cetacean sighting data from 6 years of SWFSC line-transect surveys and in situ oceanographic data that were collected simultaneously. We chose to use a GAM framework for several reasons. First, GAMs are data driven statistical models, so they can be used to quantitatively explore species-habitat relationships when little is known about the underlying mechanisms responsible for generating the observations (Guisan et al., 2002; Olivier and Wotherspoon, 2005). In a comparison of modeling techniques, Moisen and Frescino (2002) found that GAMs built on real (as opposed to simulated) data performed marginally better than other techniques (classification and regression trees, artificial neural networks, and linear models) when predicting data from test samples. Another advantage is that GAMs may be used to produce spatial predictions that are functions of the environment, unlike geostatistical methods (e.g., kriging) which produce spatial predictions based upon location only (Lehmann et al., 2003). Finally, GAMs are well-suited to model continuous relationships; this characteristic is in contrast with techniques such as classification and regression trees, which are based on a series of binary decisions derived by dichotomizing the data (Olivier and Wotherspoon, 2005).

Hedley et al. (1999) and Forney (1999, 2000) used GAMs to relate cetacean encounter rates to environmental and geographic variables, but the extrapolation from expected number of groups to the expected number of individuals is not straightforward if group size

varies spatially. Spatial variation in group size is indeed evident in the delphinid populations in the ETP. Hedley and Buckland (2004) described, but did not implement, analytical methods for creating spatial models of cetacean group size. We build on these previous studies to produce the first geo-spatial line-transect population density estimates for cetaceans from separate encounter rate and group size GAMs for delphinids (species in the family Delphinidae) in the ETP.

The following delphinid species were included in our analysis: spotted dolphin (*S. attenuata* and *S. attenuata graffmani*), eastern spinner dolphin (*Stenella longirostris orientalis*), whitebelly spinner dolphin (*S. longirostris*), long-beaked common dolphin (*Delphinus capensis*), short-beaked common dolphin (*D. delphis*), striped dolphin (*S. coeruleoalba*), rough-toothed dolphin (*Steno bredanensis*), bottlenose dolphin (*Tursiops truncatus*), Risso's dolphin (*Grampus griseus*), Pacific white-sided dolphin (*Lagenorhynchus obliquidens*), Fraser's dolphin (*Lagenodelphis hosei*), northern right whale dolphin (*Lissodelphis borealis*), melon-headed whale (*Peponocephala electra*), pygmy killer whale (*Feresa attenuata*), false killer whale (*Pseudorca crassidens*), killer whale (*Orcinus orca*), long-finned pilot whale (*Globicephala melas*), short-finned pilot whale (*Globicephala macrorhynchus*), and "dolphin, unidentified to species." We pooled all species of dolphins

in the ETP for two reasons. First, dolphins, oceanic sharks, tunas, sperm whales, pilot whales, and ziphiid (beaked) whales comprise a guild of apex predators that prey upon fish and squid in the pelagic marine environment, and obtaining more information about the guild is valuable to ecologists and public policy-makers (Smith and Casey, 1992). Second, this analysis can provide a baseline with which to compare dolphin species-specific habitat analyses.

2. Methods

2.1. Study area

The study area encompasses 19.6 million km² of the eastern tropical Pacific Ocean (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, 2006). 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

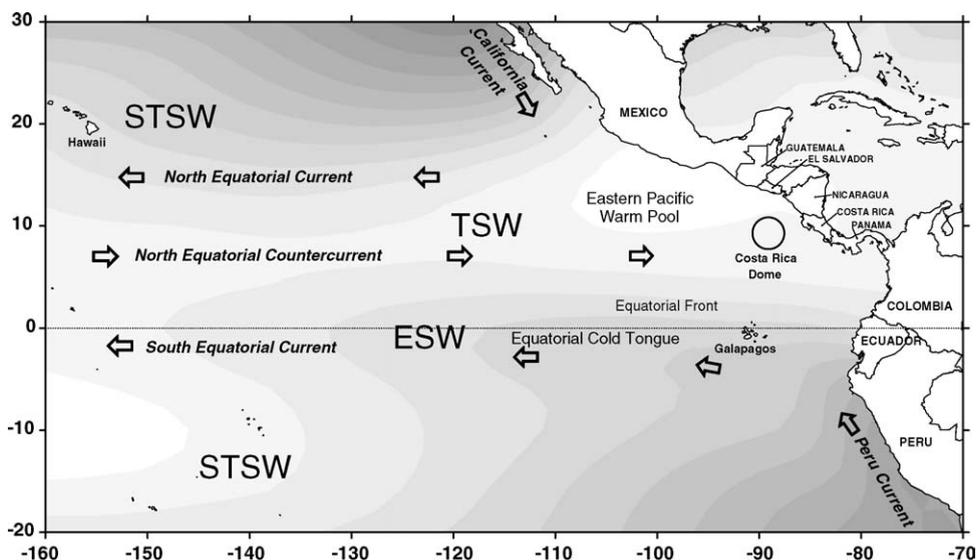


Fig. 2. Oceanography of the eastern tropical Pacific study area. STSW: Subtropical Surface Water; TSW: Tropical Surface Water; ESW: Equatorial Surface Water. Shading indicates relative sea surface temperatures.

and South Equatorial Current. Three primary surface water masses exist in the ETP: the warm, low-salinity Tropical Surface Water, 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 (the coldest surface water mass) with the equatorial cold tongue projecting from its eastern boundary; and the cool, Subtropical Surface Water located towards the poleward edges of the ETP, where the highest salinities are found (Fiedler and Talley, 2006) (Fig. 2). The thermocline is strongest beneath the Tropical Surface Water and weakest beneath the Subtropical Surface Water (Fiedler and Talley, 2006). 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. The physical and biological oceanography in the study area interact to produce 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 Subtropical Surface Water (Ryther, 1969; Fiedler and Philbrick, 2002; Fiedler, 2002) (Fig. 2). In general, both coastal and oceanic upwelling regions are characterized 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.

2.2. Field methods

Cetacean sighting data and in situ oceanographic data were collected on SWFSC research cruises conducted during the summer and fall of each year from 1986 to 1990, and in 1993 (Fig. 1). Two National Oceanic and Atmospheric Administration (NOAA) research vessels, the David Starr Jordan and the McArthur, followed standard line-transect protocols (Buckland et al., 2001) to survey cetaceans in the eastern tropical Pacific Ocean, 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 “bigeye” 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 with 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 between 1986 and 1990 are available in Thayer et al. (1988a, 1988b, 1988c, 1988d), Lierheimer et al. (1989a, 1989b, 1990a, 1990b), and Philbrick et al. (1991a, 1991b). 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 summarized as hourly means, resulting in a spatial resolution of approximately 18.5 km (Table 1). Thermocline depth and strength were derived from CTD

Table 1

Temporal and spatial resolution of in situ oceanographic data collected during SWFSC cetacean line-transect survey cruises in 1986–1990 and 1993

Variable name	Resolution
Sea surface temperature	Recorded every 5 min; summarized into hourly means (approximately 18.5 km)
Sea surface salinity	Recorded every 5 min; summarized into hourly means (approximately 18.5 km)
Thermocline depth ^a	40–110 km
Thermocline strength ^a	40–110 km
Surface chlorophyll concentration	15–130 km

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

(conductivity temperature depth) stations and XBT (expendable bathythermograph) probes, having a spatial resolution of approximately 40–110 km (Table 1). Surface chlorophyll concentrations have a spatial resolution of approximately 15–130 km (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, Beaufort 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 as a predictor variable in the generalized 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, 1999). In addition, Beaufort sea state can be thought of as an environmental predictor because it reflects the strength of the winds, which varies geographically.

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 9×9 km). Slope was derived from the depth data in the two-step process described below.

2.3. Analytical methods

In preparation for building the models, the delphinid sighting data and oceanographic data were extracted for each 9 km segment of on-effort trackline, corresponding roughly to the finest resolution of environmental data. The 9 km distance for each segment was measured directly along the trackline; therefore, the start and end points of a given segment may be less than 9 km 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 be greater than 9 km 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 summarized together if the distance between sequential sections of on-effort trackline was less than 9 km; 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 neighboring 9 km segments. Nevertheless, our primary goal was prediction rather than explaining 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 4.5 km 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 sea surface temperature 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 traveled at approximately a constant speed during surveys, 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 min 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 min grid as the magnitude of the gradient in depth:

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

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

equation:

$$\text{slope} = \left(\frac{360.0}{2\pi} \right) \arctan \left[\sqrt{\left(\frac{Z_E - Z_W}{2 \Delta x} \right)^2 + \left(\frac{Z_N - Z_S}{2 \Delta y} \right)^2} \right] \quad (2)$$

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.

Delphinid sighting data for each segment were summarized 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 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) calculate the bias-corrected group size estimate for each observer for each sighting in the segment based on individual calibration coefficients; (2) calculate the mean group size estimate, averaged over all observers, for each sighting in the segment; (3) calculate the mean group size estimate, averaged over all sightings, for each segment. For the first step, calculating individual observers' calibrated group size estimates, 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 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:

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

where \hat{s} is the observer's calibrated group size estimate, $s_{b_{i,j}}$ the observer j 's best estimate of size for group i , and s_{p_i} the size of group i estimated from photographs of group i (Gerrodette et al., 2002). 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, a 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 MSE (mean square error) reported for directly calibrated observers and observers calibrated with the ratio method (Gerrodette et al., 2002) or the ASPE (average square prediction error) 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.

Generalized additive models were used to relate delphinid sightings to the summarized fixed geographic variables and temporally dynamic in situ oceanographic data described above. A GAM may be

represented as (Hastie and Tibshirani, 1999)

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

As in generalized linear models (GLMs), the function $g(\mu)$ is known as the link function, and it relates the mean of the response variable given the predictor variables, $\mu = E(Y|X_1, \dots, X_p)$, to the additive predictor $\alpha + \sum_j f_j(X_j)$. 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, $\alpha + \sum_j \beta_j X_j$. Separate GAMs were built using smoothing spline functions to describe and predict delphinid encounter rates and average group sizes. The encounter rate data were essentially clustered counts; therefore, the number of sightings in each segment was modeled using a quasi-likelihood error distribution with variance proportional to the mean and using a logarithmic link function (approximating an over-dispersed Poisson distribution). Encounter rate models were built using all 9 km segments, regardless of whether they contained sightings. Observed distributions of dolphin group sizes in the ETP region typically have long tails and are restricted to the 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 noninteger 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 9 km segments that contained delphinid 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 (d.f.) in the scope of predictor variables, was implemented using the function *step.gam*. Models built using a maximum of four d.f. for each variable in the scope of *step.gam* were considered, but resulting models were qualitatively similar to those limited to three d.f., and the added complexity of the four d.f. 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 delphinid data using the more informative environmental data before considering fixed geographic coordinates. 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 degrees of freedom. 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, 1991), 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 1986–1990 with 1 year left out; 1993 was 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 re-built using the specified degrees of freedom and all years of data to fine-tune the smoothing splines.

The final delphinid encounter rate model included longitude, and the group size model included both latitude and longitude. To determine the effect that fixed geographic variables had on the predictive performance of the model, 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 encounter rate and group size models.

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

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

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

The values of $f(0)$ and $g(0)$ were the arithmetic average of those given for the delphinids in the ETP by Ferguson and Barlow (2001). 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 anisotropy ratio set to 1.0 in Surfer software (Version 7.0).

To evaluate the models' fit to the observed data (the data used to build the models), the following error analysis was conducted. Encounter rate models were fit 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:

$$\Delta ER_i = ER_{i_{\text{predicted}}} - ER_{i_{\text{observed}}} \quad (6)$$

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

$$R_{ER} = \frac{\sum_{i=1}^n ER_{i_{\text{predicted}}}}{\sum_{i=1}^n ER_{i_{\text{observed}}}} \quad (7)$$

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 delphinid sightings. This subset of predictions was appropriate for testing 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 \times 5° longitude.

3. Results

The data extracted from the SWFSC cruises for this analysis contained 2548 delphinid sightings in 11,802 on-effort segments, covering 106,218 km of on-effort trackline. The three most frequently encountered species were striped, offshore spotted, and bottlenose dolphins; Fraser's dolphins and common dolphins had the largest bias-corrected group sizes averaged across all sightings and segments (Table 2). The observed line-transect data showed some spatial structure in delphinid group sizes, with larger groups in the waters around the Baja Peninsula, the Costa Rica Dome, and the equator (Fig. 3).

The best delphinid encounter rate model contained eight terms: longitude, Beaufort sea state, offshore distance, depth, SST, sea surface salinity, surface chlorophyll concentration, and thermocline depth (Table 3; Fig. 4). Surface chlorophyll concentration

Table 2

Number of samples (n) used to build the encounter rate and group size GAMs, and mean bias-corrected group size (averaged across all sightings and all segments) for each delphinid species in the analysis

Common names	Scientific names	Encounter rate (n)	Group size (n)	Mean group size
Dolphin, unidentified to species		735	398	26.11
Striped dolphin	<i>S. coeruleoalba</i>	493	471	55.48
Offshore pantropical spotted dolphin	<i>S. attenuata</i>	302	293	131.03
Bottlenose dolphin	<i>T. truncatus</i>	296	274	24.12
Risso's dolphin	<i>G. griseus</i>	206	189	18.64
Eastern spinner dolphin	<i>S. longirostris orientalis</i>	144	138	108.82
Short-beaked common dolphin	<i>D. delphis</i>	131	129	230.38
Rough-toothed dolphin	<i>S. bredanensis</i>	123	120	15.46
Short-finned pilot whale	<i>G. macrorhynchus</i>	122	117	18.29
Pilot whale, unidentified to species	<i>Globicephala</i> sp.	68	62	17.18
Whitebelly spinner dolphin	<i>S. longirostris</i>	56	56	82.54
Killer whale	<i>O. orca</i>	42	41	5.45
Long-beaked common dolphin	<i>D. capensis</i>	25	23	411.69
False killer whale	<i>P. crassidens</i>	25	19	11.00
Pygmy killer whale	<i>F. attenuata</i>	23	23	30.12
Pantropical spotted dolphin, unidentified subsp.	<i>S. attenuata</i>	19	18	186.20
Spinner dolphin, unidentified subsp.	<i>S. longirostris</i>	15	13	147.74
Coastal spotted dolphin	<i>S. attenuata graffmani</i>	15	15	124.00
Common dolphin, unidentified subsp.	<i>Delphinus</i> sp.	12	10	311.14
Fraser's dolphin	<i>L. hosei</i>	11	11	440.05
Melon-headed whale	<i>P. electra</i>	6	5	257.70
Pacific white-sided dolphin	<i>L. obliquidens</i>	3	3	127.38

Group size models used only sightings for which complete group size data were available, as discussed in the text.

was incorporated into the model as a smoothing spline with two d.f., whereas the remaining variables were selected as smoothing splines with three d.f. The decrease in deviance from the null model to the best

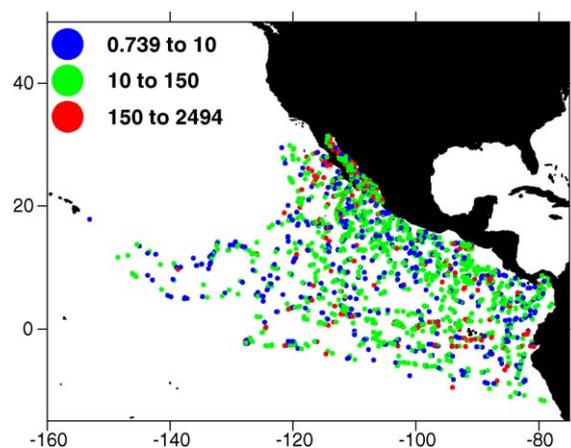


Fig. 3. Average size of delphinid groups in 9km segments used to build group size GAMs. Data were collected during 1986–1990 and 1993 shipboard cetacean line-transect surveys conducted by the Southwest Fisheries Science Center.

encounter rate model was 12.12% (Table 3). The overall best group size GAM contained six terms: latitude, longitude, offshore distance, depth, slope, and SST (Table 3, Fig. 5). The best group size model built without latitude and longitude resulted in a higher ASPE value in the cross-validation process. The variables latitude, offshore distance, depth, and SST were accepted into the model as linear terms; longitude appears as a smoothing spline with two d.f. (although it shows little departure from linearity; Fig. 5); and seafloor slope was included as a smoothing spline with three d.f. The decrease in deviance from the null model to the overall best group size model was 4.95% (Table 3).

When the selected encounter rate and group size models were applied to in situ data from the cruises on which they were built, the resulting density predictions ranged from 26 to 5205 individuals/1000 km² (mean = 387, S.D. = 405). Regions with the highest predicted 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 (Fig. 6). Offshore waters in the northern and

Table 3
Summary of delphinid encounter rate and group size GAMs for the eastern tropical Pacific

Model	Year omitted	Predictor variables										
		Lat	Long	Beaufort	Offshore distance	Depth	Slope	SST	Salinity	ln(surface chlorophyll)	Thermocline depth	Thermocline strength
Encounter rate	1986		S3	S3	S3	S3		S3	S3		S3	S3
	1987		S3	S3	S3	S3		S2	S3		S3	S3
	1988		S3	S3	S3	S3		L1	S3		S3	S3
	1989	S3		S3	S3	S3		S2	S3	S2	S3	S3
	1990		S3	S3	S3	S3		S3	S3	S2	S3	
Group size	1986	S3	S2		L1			L1				
	1987	L1	S2		L1	L1	S3	L1				
	1988	S3						L1	S2	S2	L1	
	1989	S3				L1		L1		L1	S2	
	1990	L1						L1	S3	L1	S2	

Linear fits are represented by “L1”, whereas smoothing splines are represented by “S#”, where # is the associated degrees of freedom. Final selected model indicated by bold font. Percent change in deviance was calculated for final selected model, rebuilt using all years’ data, as: $((\text{null deviance} - \text{residual deviance})/\text{null deviance}) \times 100\%$. Percent change in deviance was 12.12% for the encounter rate model and 4.95% for the group size model.

southern subtropical gyres had the lowest predicted densities.

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. The standard deviation of the differences in predicted and observed encounter rates was 0.5 and the range was -9.0 to 1.15 groups. For the group size model, the standard deviation of the differences was 134.6 and range was -2412.5 to 288.9 individuals. When pooling all segments used to build the models, the ratio of pooled predicted to pooled observed was 1.0 for both models. The geographically stratified analysis of R_{ER} showed that, in over half of the strata, the ratio of pooled predicted to pooled observed encounter rates is close to 1.0 (± 0.25), and there was no apparent geographic pattern in the ratio values (Fig. 7). The range of R_{ER} values was from 0.5 to 3.4 (50% underestimate to 340% overestimate by the model). The geographically stratified R_{SS} values spanned a broader range (0.4 – 12.6), although, in approximately half of the strata, predicted values were within 25% of observed, and geographic pattern was not evident in the ratio values (Fig. 8) with the possible exception of a contiguous block of cells south of the equator between 90° and 110° W, which all have higher predicted than observed values.

4. Discussion

GAMs are commonly used to model the relationships between habitat predictors and species presence/absence (e.g., Moisen and Frescino, 2002; Seoane et al., 2004; Olivier and Wotherspoon, 2005) or relative population abundance measures such as the number of seabird nests in a colony (Olivier and Wotherspoon, 2005). Our use of generalized additive models in this analysis is unique because we are able to predict the density of individuals throughout the study area. Previous analyses of cetacean habitat associations in the ETP (Reilly, 1990; Reilly and Fiedler, 1994; Reilly et al., 2002) and elsewhere (Forney, 1999, 2000; Hedley et al., 1999; Hedley and Buckland, 2004) examined the relationship of group encounter rate (another relative measure of population abundance) to environmental predictors, but did not include variation in group size. Understanding the variability in population density requires using information on both encounter rate and group size. Although there was some qualitative evidence of increased delphinid group sizes in the waters around the Baja Peninsula, the Costa Rica Dome, and the equator, our models explained relatively little of the variability in the observed data as judged by percent decrease in deviance. This inability to detect patterns could be due to an inappropriate choice for the group size sampling distribution. The gamma distribution was

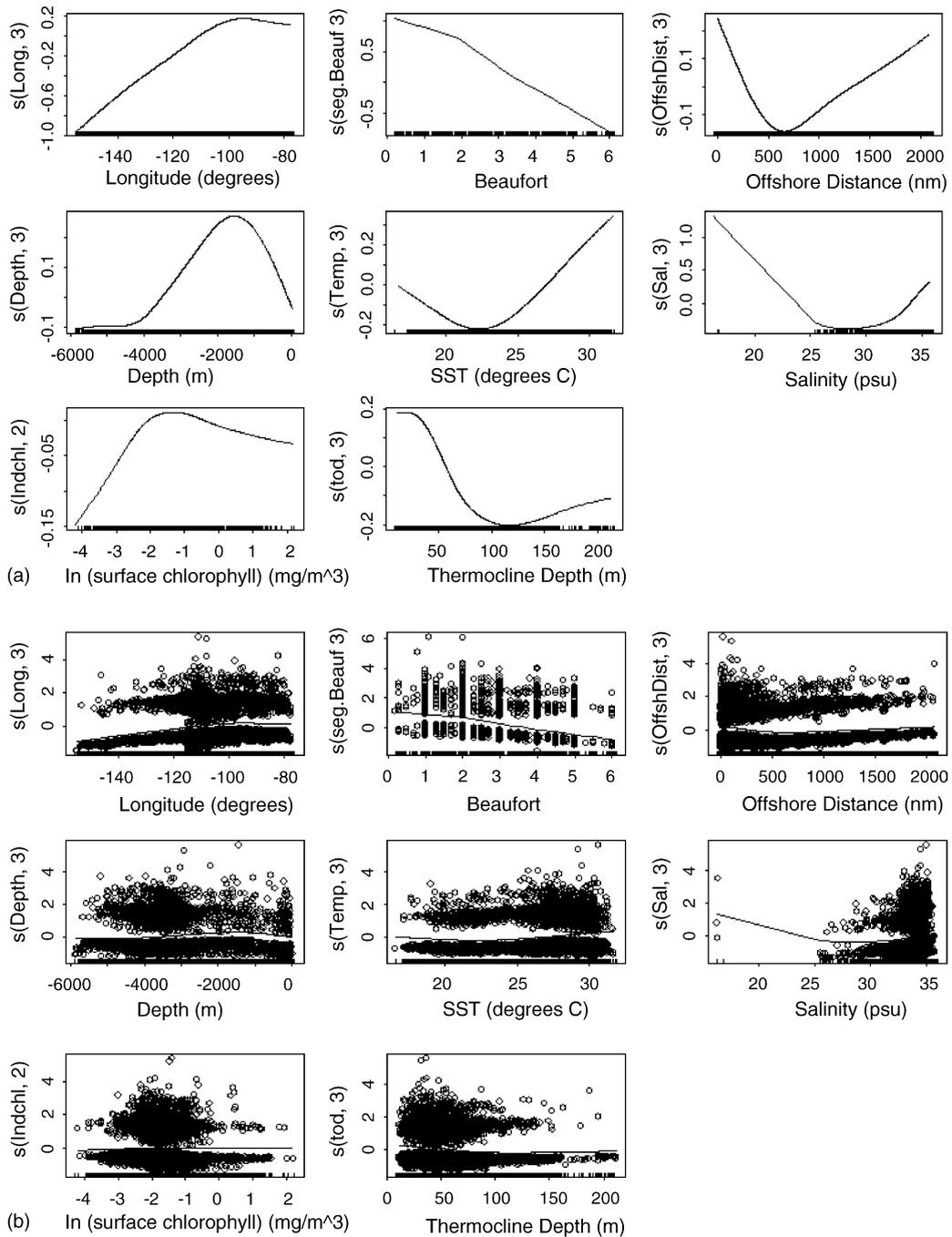


Fig. 4. Smooth spline functions of the predictor variables incorporated in the final delphinid encounter rate (no. of sightings/unit survey effort) GAM. Degrees of freedom for nonlinear fits are in the parentheses on the y-axis. Tick marks above the x-axis indicate the distribution of observations in all segments (with and without delphinids). (a) Scaling of y-axis varies among predictor variables to emphasize model fit. (b) Partial deviance residuals shown as open circles. Scaling of y-axis is constant among predictor variables.

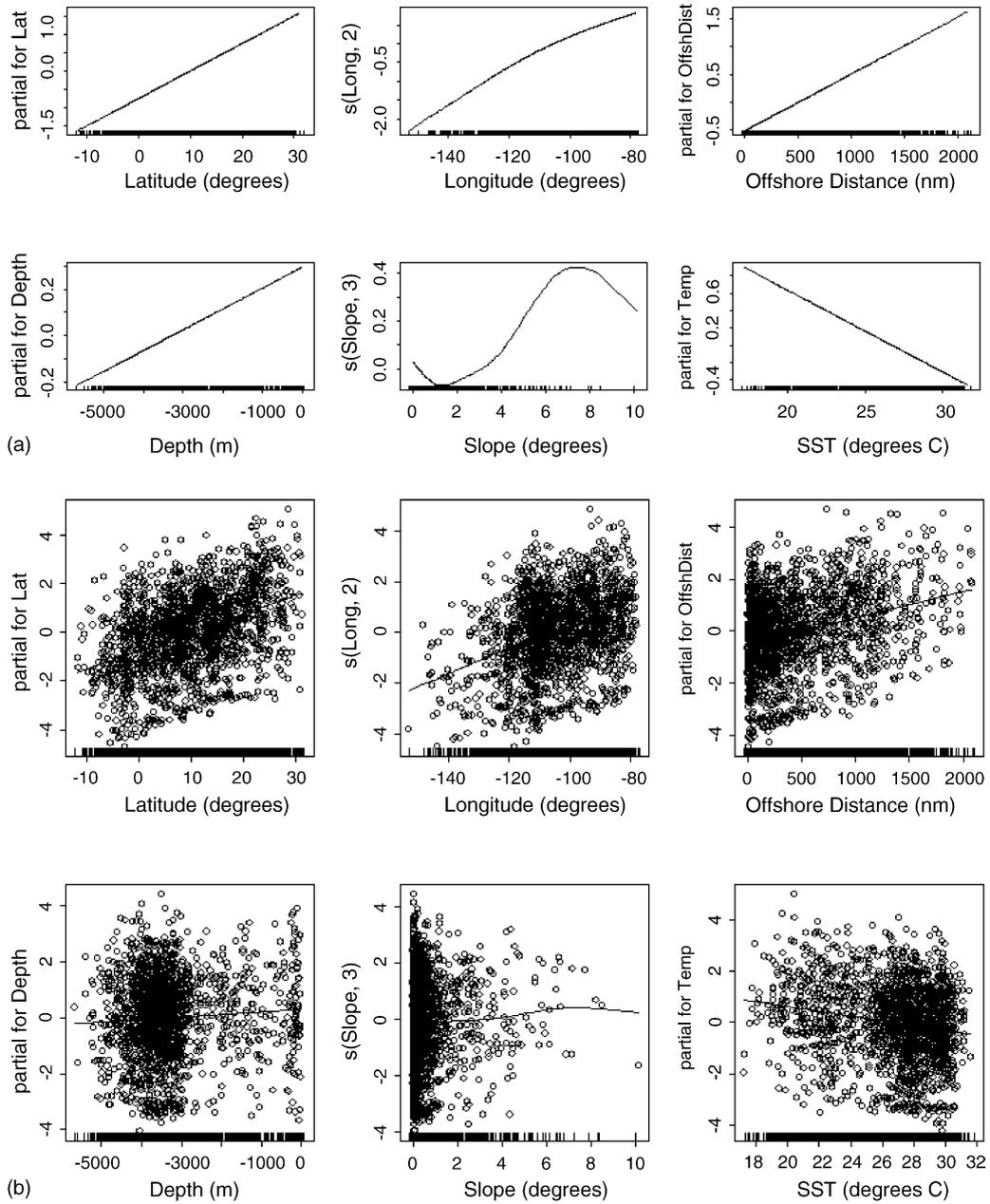


Fig. 5. Smooth spline functions of the predictor variables incorporated in the final delphinid group size GAM. Degrees of freedom for nonlinear fits are in the parentheses on the y-axis. Tick marks above the x-axis indicate the distribution of observations in all segments with delphinid sightings. (a) Scaling of y-axis varies among predictor variables to emphasize model fit. (b) Partial deviance residuals shown as open circles. Scaling of y-axis is constant among predictor variables.

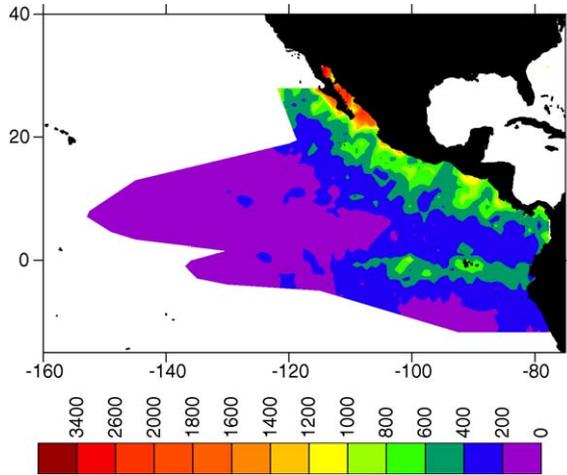


Fig. 6. Predicted delphinid density (no. of individuals/1000 km²) in the eastern tropical Pacific Ocean. Predictions are based on oceanographic data collected during the 1986–1990 and 1993 cetacean line-transect surveys conducted by the Southwest Fisheries Science center. Predicted values were smoothed in geographic space using inverse distance weighting.

also tested on the group size data and found to perform poorly relative to the lognormal distribution we used. It is also possible that we did not measure the appropriate elements of the ecosystem, such as abundance or density of prey species, in order to identify the existing patterns. This lack of success in modeling group size may be due to a mismatch in our predictor variables, and it may vary by species, location, or time, so it would be prudent to examine each case separately.

Generalized additive models were chosen for the ETP analysis because of their flexibility. In our analysis, the flexibility of the GAM was manifest in the plots of the smooth functions for the predictor variables that were present in the final delphinid encounter rate and group size GAMs, and in the error analysis for the models. In particular, the model fits describing the relationship between slope and group size, and those relating encounter rate to longitude, offshore distance, depth, sea surface salinity, surface chlorophyll concentration, and thermocline depth were all nonlinear. The error analysis showed that differences between observed and predicted values were small and that the ratios of pooled predicted to pooled observed values were close to 1.0. Furthermore, in the geographically stratified analysis comparing model predictions to observed values, encounter rate and group size pre-

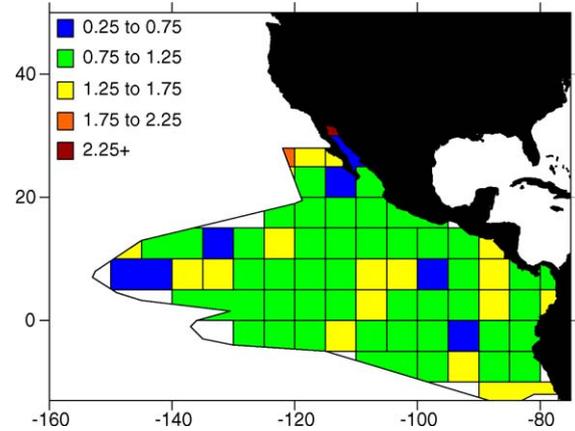


Fig. 7. Geographic distribution of residuals for delphinid encounter rates measured as the ratio $R_{ER} = [\text{sum}(\text{predicted})/\text{sum}(\text{observed})]$. Predictions were based on observed oceanography data from Southwest Fisheries Science Center cetacean line-transect survey cruises in 1986–1990 and 1993.

dictions in the majority of the strata were within 25% of the observed values. Overall, we were effectively able to increase the resolution of density predictions by using more of the information from the SWFSC survey cruises in the ETP, relating delphinid density to several environmental predictors in a relatively simple process, and allowing finer resolution of the patterns in delphinid density than is available using a conventional stratified line-transect analysis.

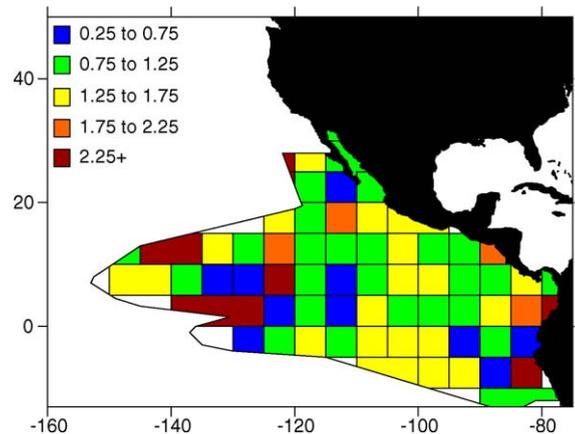


Fig. 8. Geographic distribution of residuals for delphinid group sizes measured as the ratio $R_{GS} = [\text{sum}(\text{predicted})/\text{sum}(\text{observed})]$. Predictions were based on observed oceanography data from Southwest Fisheries Science Center cetacean line-transect survey cruises in 1986–1990 and 1993.

The error analysis addressed the question of how well the models fit the data on which they were built, but the predictive performance on completely novel data (i.e., data from a future ETP survey) needs to be addressed further. Most of the predictor variables that we considered were proxies for characteristics of the environment that potentially relate more directly to delphinid density, such as prey concentrations. The predictive performance of these delphinid density models when applied to new data may be improved if more information about the prey were available.

One drawback to GAM methodology is that estimating variance in predictions is not simple. The sources of uncertainty in the ETP analysis are numerous and not fully understood. Several sources of uncertainty include: (1) survey design, because changing the spatial or temporal specifications of the shipboard survey tracklines would have produced a different set of delphinid and oceanographic observations; (2) error in the measurement of environmental variables; (3) stochasticity inherent in the Poisson sampling process generating the encounter rates; (4) parameter estimation error in the model fitting process; (5) model selection error associated with choosing the appropriate variables and corresponding degrees of freedom; (6) errors due to a disassociation between the animals' distribution and the predictor variables used to try to understand the ecology of the system. Hedley et al. (1999) and Hedley and Buckland (2004) have addressed the problem of estimating two sources of variance in GAM predictions by applying parametric and nonparametric bootstrap methods to estimate the variance associated with line-transect parameter estimation (number 4 above) and stochasticity in encounter rates (number 3 above). Work is ongoing to understand the various sources of uncertainty and to estimate their magnitude (Ferguson, 2005).

We consider these GAMs to be a first step in predictive modeling of cetacean densities because our analysis posed more questions than it answered. Three lines of active research involve issues of scale, autocorrelation, and model implementation. The question of scale permeates all aspects of the model-building process: the spatial resolution of raw oceanographic data; the unit (i.e., line segment, circle, or sphere) and distance used to define neighborhoods in which the environment influences the habitat of a given point;

whether environmental effects are transmitted as a constant function or decay with distance from a point; the appropriate size of the study area, which should be large enough to encompass meaningful contrasts but small enough to thoroughly sample; the taxonomic level (population, species, genus, or family); and the temporal scale (seasonal, annual, multi-year, decadal). We showed that there was no pattern in the residuals on the $5^\circ \times 5^\circ$ scale, but it is unknown whether autocorrelation exists on smaller scales. Assessing whether autocorrelation exists in the model residuals is important for accurately quantifying the variance in the model predictions and, from an ecological perspective, for accurately identifying which environmental variables are associated with observed patterns in animal density. The main issue regarding model implementation is obtaining quality environmental data on which to make predictions. Remotely sensed data and predictions from physical and biological oceanographic models are advantageous because they are synoptic and available for all seasons. Nevertheless, remotely sensed data are limited to surface observations and they do not provide direct information on cetacean prey. Furthermore, both remotely sensed data and modeled data should be ground-truthed before they are relied upon as input into predictive models. A further detail related to implementing these encounter rate and group size models to predict densities involves the estimation of $f(0)$. The values of $f(0)$ were based upon stratified estimates for the survey region. In some situations, it may be more appropriate to incorporate values of $f(0)$ that are functions of sighting conditions, location, etc. (e.g., Marques, 2001; Gerrodette and Forcada, 2002a, 2002b).

It is important to keep in mind that predictions from cetacean-habitat models such as ours implicitly assume a particular population size and set of environmental conditions for some specified study area. Just as it would be unwise to use a model built on cetacean and oceanographic data from the ETP to predict cetacean densities in the Gulf of Alaska, it would also be unwise to use a model built on cetacean data gathered when the overall population size was large or climatic conditions were significantly different to predict cetacean densities in the same region when the overall population size is small. Density dependent effects and unknown environmental effects may significantly alter ecosystem, community, or population dynamics, and blind adher-

ence to model predictions could result in significant errors. Therefore, we advocate an iterative approach to predictive modeling where large-scale abundance estimates are used to inform models that predict densities at smaller scales, which, in turn, may be used to fine-tune the large-scale abundance estimates.

In summary, GAM-based methods have the potential to predict cetacean densities on smaller spatial scales than conventional line-transect analyses. Future work should focus on understanding the ecology of delphinid prey and on addressing questions of variance estimation, scale, autocorrelation, and model implementation. In addition, we can test the performance of our GAMs by evaluating how well they predict delphinid densities observed on future surveys. The model fits from this GAM analysis also provide starting points for testing hypotheses about ecological associations between the cetaceans and their environment, leading to more insight into the mechanisms that structure cetacean distributions. Finally, there is value in comparing predictions from different types of models, and work should continue on developing new and better frameworks for spatial modeling of cetacean density. Even though the truth may never be known, such a comparative analysis may reveal biases associated with each method, increasing our understanding of the ecological system along the way.

Acknowledgements

We would like to thank the marine mammal observers, cruise leaders, and crew of the David Starr Jordan and the McArthur who collected the valuable data sets that we used in our analysis. We are also grateful to A. Jackson and V. Andreassi for bringing the data into user-friendly formats. Thanks to J. Carretta, K. Forney, T. Chereskin, P. Dayton, D. Goodman, L. Haff, J. Leichter, and P. Smith for providing intellectual stimulation and guidance through the early days of this analysis. We appreciate S. Hedley's help in answering programming questions. S. Martin helped write the program to plot the survey effort in Fig. 1. This manuscript was improved by comments from E. Becker. Finally, many thanks to J. Redfern for catching errors before they caught us. Funding for this research came from the Department of Navy through the Office of Naval Research and the Strategic Environmental Research

and Development Program and from the National Science Foundation, which supported M. Ferguson under a Graduate Research Fellowship.

References

- Au, D.W.K., Perryman, W.L., 1985. Dolphin habitats in the eastern tropical Pacific. *Fish. Bull.* 83 (4), 623–643.
- Barlow, J., Gerrodette, T., Perryman, W., 1998. Calibrating group size estimates for cetaceans seen on ship surveys. Administrative Report LJ-98-11, Available from Southwest Fisheries Science Center, P.O. Box 271, La Jolla, CA 92038, 73 pp.
- Buckland, S.T., Anderson, D.R., Burnham, K.P., Laake, J.L., Borchers, D.L., Thomas, L., 2001. Introduction to Distance Sampling: Estimating Abundance of Biological Populations. Oxford University Press, Oxford, 432 pp.
- Chambers, J.M., Hastie, T.J., 1991. *Statistical Models*. Chapman & Hall/CRC Press, Boca Raton, 608 pp.
- Ferguson, M.C., 2005. Cetacean population density in the eastern Pacific Ocean: analyzing patterns with predictive spatial models. Ph.D. Dissertation. University of California San Diego, Scripps Institution of Oceanography, 221 pp.
- Ferguson, M.C., Barlow, J., 2001. Spatial distribution and density of cetaceans in the eastern Pacific Ocean based on summer/fall research vessel surveys in 1986–1996. Administrative Report LJ-01-04, Available from National Marine Fisheries Service (NMFS), Southwest Fisheries Science Center, P.O. Box 271, La Jolla, CA 92038, 61 pp.
- Fiedler, P.C., 2002. The annual cycle and biological effects of the Costa Rica Dome. *Deep-Sea Res.* 1 49, 321–338.
- Fiedler, P.C., Philbrick, V.A., 2002. Environmental change in the eastern tropical Pacific Ocean: observations in 1986–1990 and 1998–2000. Administrative Report LJ-02-15, Available from National Marine Fisheries Service (NMFS), Southwest Fisheries Science Center, P.O. Box 271, La Jolla, CA 92038, 18 pp.
- Fiedler, P.C., Talley, L.D., 2006. 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. Stat. Soc. Suppl.* 7, 155–161.
- Forney, K.A., 1999. Trends in harbour porpoise abundance off central California, 1986–1995: evidence for interannual changes in distribution? *J. Cetacean Res. Manage.* 1 (1), 73–80.
- Forney, K.A., 2000. Environmental models of cetacean abundance: reducing uncertainty in population trends. *Conserv. Biol.* 14 (5), 1271–1286.
- Gerrodette, T., Forcada, J., 2002a. Estimates of abundance of western/southern spotted, whitebelly spinner, striped and common dolphins, and pilot, sperm and Bryde's whales in the eastern tropical Pacific Ocean. Administrative Report LJ-02-20, Available from National Marine Fisheries Service (NMFS), Southwest Fisheries Science Center, P.O. Box 271, La Jolla, CA 92038, 24 pp.
- Gerrodette, T., Forcada, J., 2002b. Estimates of abundance of north-eastern offshore spotted, coastal spotted, and eastern spinner

- dolphins in the eastern tropical Pacific Ocean. Administrative Report LJ-02-06, Available from National Marine Fisheries Service (NMFS), Southwest Fisheries Science Center, P.O. Box 271, La Jolla, CA 92038, 41 pp.
- Gerrodette, T., Perryman, W., Barlow, J., 2002. Calibrating group size estimates of dolphins in the eastern tropical Pacific Ocean. Administrative Report LJ-02-08, Available from Southwest Fisheries Science Center, P.O. Box 271, La Jolla, CA 92038, 73 pp.
- Guisan, A., Edwards Jr., T.C., Hastie, T., 2002. Generalized linear and generalized additive models in studies of species distributions: setting the scene. *Ecol. Modell.* 157, 89–100.
- Hamazaki, T., 2004. Modeling species–habitat relationship in the marine environment: a response to Gregr (2004). *Marine Mammal Sci.* 20 (2), 356–358.
- Hastie, T.J., Tibshirani, R.J., 1999. *Generalized Additive Models*. Chapman & Hall/CRC Press, Boca Raton, 335 pp.
- Hedley, S.L., Buckland, S.T., 2004. Spatial models for line transect sampling. *J. Agric. Biol. Environ. Stat.* 9 (2), 181–199.
- Hedley, S.L., Buckland, S.T., Borchers, D.L., 1999. Spatial modelling from line transect data. *J. Cetacean Res. Manage.* 1 (3), 255–264.
- Kessler, W.S., 2006. The circulation of the eastern tropical Pacific: a review. *Prog. Oceanogr.*, in press.
- Kinzev, D., Olson, P., Gerrodette, T., 2000. Marine mammal data collection procedures on research ship line-transect surveys by the Southwest Fisheries Science Center. Administrative Report LJ-00-08, Available from Southwest Fisheries Science Center, P.O. Box 271, La Jolla, CA 92038, 32 pp.
- Lehmann, A., Overton, J.M.C., Leathwick, J.R., 2003. GRASP: generalized regression analysis and spatial prediction. *Ecol. Modell.* 160, 165–183.
- Lierheimer, L.J., Fiedler, P.C., Reilly, S.B., Pitman, R.L., Ballance, L.T., Thomas, G.G., Behringer, D.W., 1989a. Report of ecosystem studies conducted during the 1988 eastern tropical Pacific dolphin survey on the research vessel David Starr Jordan. NOAA Technical Memorandum NOAA-TM-NMFS-SWFSC-131, Available from Southwest Fisheries Science Center, P.O. Box 271, La Jolla, CA 92038, 125 pp.
- Lierheimer, L.J., Fiedler, P.C., Reilly, S.B., Pitman, R.L., Ballance, L.T., Behringer, D.W., 1989b. Report of ecosystem studies conducted during the 1988 eastern tropical Pacific dolphin survey on the research vessel McArthur. NOAA Technical Memorandum NOAA-TM-NMFS-SWFSC-132, Available from Southwest Fisheries Science Center, P.O. Box 271, La Jolla, CA 92038, 121 pp.
- Lierheimer, L.J., Fiedler, P.C., Reilly, S.B., Pitman, R.L., Ballance, L.T., Beavers, S.C., Behringer, D.W., 1990a. Report of ecosystem studies conducted during the 1989 eastern tropical Pacific dolphin survey on the research vessel McArthur. NOAA Technical Memorandum NOAA-TM-NMFS-SWFSC-140, Available from Southwest Fisheries Science Center, P.O. Box 271, La Jolla, CA 92038, 123 pp.
- Lierheimer, L.J., Fiedler, P.C., Reilly, S.B., Pitman, R.L., Ballance, L.T., Beavers, S.C., Thomas, G.G., 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 Technical Memorandum NOAA-TM-NMFS-SWFSC-139, Available from Southwest Fisheries Science Center, P.O. Box 271, La Jolla, CA 92038, 118 pp.
- Marques, F.F.C., 2001. Estimating wildlife distribution and abundance from line transect surveys conducted from platforms of opportunity. Unpublished Ph.D. Thesis. University of St. Andrews, Scotland.
- Moisen, G.G., Frescino, T.S., 2002. Comparing five modeling techniques for predicting forest characteristics. *Ecol. Modell.* 157, 209–225.
- Neter, J., Wasserman, W., Kunter, M.H., 1990. *Applied Linear Statistical Models*, 3rd ed. R.D. Irwin, Inc., Homewood, IL.
- Olivier, F., Wotherspoon, S.J., 2005. GIS-based application of resource selection functions to the prediction of snow petrel distribution and abundance in East Antarctica: comparing models at multiple scales. *Ecol. Model.* 89 (1–2), 105–129.
- Perrin, W.F., 1969. Using porpoise to catch tuna. *World Fish.* 18 (6), 42–45.
- Philbrick, V.A., Fiedler, P.C., Reilly, S.B., Pitman, R.L., Ballance, L.T., Behringer, D.W., 1991a. Report of ecosystem studies conducted during the 1990 eastern tropical Pacific dolphin survey on the research vessel McArthur. NOAA Technical Memorandum NOAA-TM-NMFS-SWFSC-161, Available from Southwest Fisheries Science Center, P.O. Box 271, La Jolla, CA 92038, 132 pp.
- Philbrick, V.A., Fiedler, P.C., Reilly, S.B., Pitman, R.L., Ballance, L.T., Thomas, G.G., 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 Technical Memorandum NOAA-TM-NMFS-SWFSC-160, Available from Southwest Fisheries Science Center, P.O. Box 271, La Jolla, CA 92038, 117 pp.
- Reilly, S.B., 1990. Seasonal changes in distribution and habitat differences among dolphins in the eastern tropical Pacific. *Marine Ecol. Prog. Series* 66, 1–11.
- Reilly, S.B., Fiedler, P.C., 1994. Interannual variability of dolphin habitats in the eastern tropical Pacific. I. Research vessel surveys, 1986–1990. *Fish. Bull.* 92, 434–450.
- Reilly, S.B., Fiedler, P.C., Gerrodette, T., Ballance, L.T., Pitman, R.L., Borberg, J.M., Holland, R.C., 2002. Eastern tropical Pacific dolphin habitats – interannual variability 1986–2000. Administrative Report LJ-02, Available from National Marine Fisheries Service (NMFS), Southwest Fisheries Science Center, P.O. Box 271, La Jolla, CA 92038, 43 pp.
- Ryther, J.H., 1969. Photosynthesis and fish production in the sea. *Science* 166, 72–76.
- Seoane, J., Bustamante, J., Diaz-Delgado, R., 2004. Are existing vegetation maps adequate to predict bird distributions? *Ecol. Modell.* 175, 137–149.
- Smith, R.J., 1993. Logarithmic transformation bias in allometry. *Am. J. Phys. Anthropol.* 90, 215–228.
- Smith, T.D., Casey, J.G., 1992. The distribution and ecological role of large marine predators in the north temperate Atlantic: a proposal for coordinated study. *ICES C.M.* 1992/N:23.
- Thayer, V.G., McDonald, B.G., Ellingson, J.M., Oliver, C.W., Behringer, D.W., Reilly, S.B., 1988a. Report of ecosystem studies conducted during the 1986 eastern tropical Pacific dolphin survey

- on the research vessel McArthur. NOAA Technical Memorandum NOAA-TM-NMFS-SWFSC-104, Available from Southwest Fisheries Science Center, P.O. Box 271, La Jolla, CA 92038, 112 pp.
- Thayer, V.G., Pitman, R.L., Rittmaster, K.A., Thomas, G.G., Behringer, D.W., 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 Technical Memorandum NOAA-TM-NMFS-SWFSC-105, Available from Southwest Fisheries Science Center, P.O. Box 271, La Jolla, CA 92038, 106 pp.
- Thayer, V.G., Reilly, S.B., Fiedler, P.C., Pitman, R.L., Thomas, G.G., Behringer, D.W., 1988c. Report of ecosystem studies conducted during the 1987 eastern tropical Pacific dolphin survey on the research vessel David Starr Jordan. NOAA Technical Memorandum NOAA-TM-NMFS-SWFSC-115, Available from Southwest Fisheries Science Center, P.O. Box 271, La Jolla, CA 92038, 94 pp.
- Thayer, V.G., Reilly, S.B., Fiedler, P.C., Oliver, C.W., Behringer, D.W., 1988d. Report of ecosystem studies conducted during the 1986 eastern tropical Pacific dolphin survey on the research vessel McArthur. NOAA Technical Memorandum NOAA-TM-NMFS-SWFSC-114, Available from Southwest Fisheries Science Center, P.O. Box 271, La Jolla, CA 92038, 114 pp.