



FEATURE ARTICLE

Absence of scale dependence in dolphin–habitat models for the eastern tropical Pacific Ocean

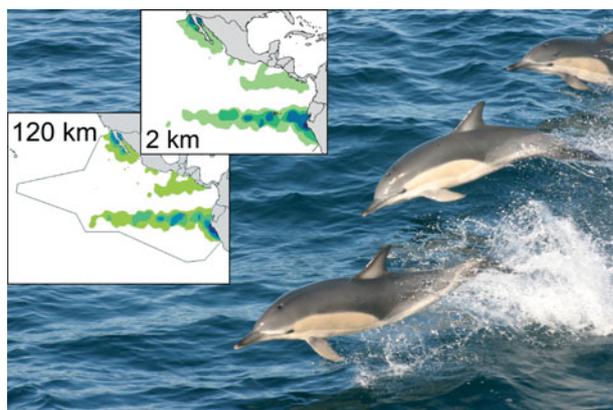
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ABSTRACT: Research into the effects of scale on cetacean–habitat relationships is limited and has produced ambiguous results. We explored the effects of spatial resolution (a component of scale) on dolphin–habitat models using 4 yr of data collected in the eastern tropical Pacific Ocean (ETP). We developed generalized additive models of dolphin–habitat relationships for 4 species at 6 spatial resolutions using oceanographic and geographic habitat variables. For all species, the ecological patterns in the models built at the different resolutions were similar: the same variables frequently occurred at multiple resolutions and had similar functional forms, and maps of predicted distributions identified similar high and low density regions. Additionally, interannual habitat variability, which is most likely related to the El Niño–Southern Oscillation, had a greater impact on the predictive power of dolphin–habitat models than spatial resolution. Although it is common to find scale dependence in species–habitat relationships, domains of scale exist in which ecological patterns do not change. The absence of scale dependence in the models for the 4 dolphin species suggests that resolutions from 2 to 120 km occur within a single domain of scale in the ETP. This domain of scale may be determined by the physical oceanography of the ETP, which is generally defined by large-scale processes. Although resolutions from 2 to 120 km appear to occur within a domain of scale, building models at the larger resolutions we investigated may reduce the noise in the data due to false absences.

KEY WORDS: Dolphin density · Habitat modeling · Striped dolphin · *Stenella coeruleoalba* · Eastern spinner dolphin · *Stenella longirostris orientalis* · Short-beaked common dolphin · *Delphinus delphis* · Risso's dolphin · *Grampus griseus*

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Modeled densities indicate scale-independence in dolphin–habitat relationships

Image: J.V. Redfern

INTRODUCTION

The influence of scale on the identification and interpretation of ecological patterns has long been a central theme in ecological research (Haury et al. 1978, Wiens 1989, Levin 1992). Of particular importance is spatial scale dependence in species–habitat relationships, which has been documented for a variety of seabird species (e.g. Logerwell & Hargreaves 1996, Logerwell et al. 1998, Fauchald et al. 2000, Davoren et al. 2002, Pinaud & Weimerskirch 2005). For example, seabird studies suggest that the strength of the correlation between seabirds and prey generally increases with increasing spatial resolution (Schneider & Piatt 1986, Heinemann et al. 1989, Erikstad et al. 1990, Piatt 1990, Hunt 1991, Hunt et al. 1992, Logerwell & Hargreaves 1996, Fauchald et al. 2000), although there are exceptions (e.g. Cairns & Schneider 1990).

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Research into the effects of scale on cetacean–habitat relationships is more limited and has produced ambiguous results. Jaquet & Whitehead (1996) analyzed a range of resolutions (i.e. the unit of analysis, a component of scale) from 80 to 640 nautical miles (n mile) (148 to 1185 km) and found that sperm whale density in the South Pacific was correlated with habitat variables only at resolutions greater than 320 n mile (593 km). Hamazaki (2002) assessed the effect of spatial resolutions ranging from 4×4 km grid cells to 96×96 km grid cells on predictive habitat models for 13 cetacean species in the mid-western North Atlantic Ocean and found no relationship between resolution and the correct classification rate of logistic regression models. While Hamazaki's (2002) results suggest that spatial resolution did not affect the predictive power of the models, ecological questions about the effect of resolution cannot be addressed because the behavior of the predictor variables at the different resolutions (e.g. the magnitude and sign of the relationship) was not examined.

We expect scale-dependent habitat relationships for cetaceans and seabirds because both are apex marine predators that must respond to the hierarchical patch structure of their prey in which high density, small-scale patches are nested within lower density, large-scale patches (Murphy et al. 1988, Fauchald 1999, Fauchald et al. 2000). Heterogeneity, which may be a driving factor in scale-dependent species–habitat relationships (Wiens 1989), occurs at every stage of this hierarchy and is coupled with biological and physical processes (Haury et al. 1978). Heterogeneity in small-scale patches (100s of m) may be driven by prey behavior or by turbulent diffusion and mixing for weakly swimming organisms; heterogeneity in meso-scale patches (10s to 100s of km) may be caused by oceanographic features such as fronts and eddies (Murphy et al. 1988, Fauchald 1999, Fauchald et al. 2000).

A primary difference between cetacean and seabird habitat studies is found in the variables used to define habitat. Cetacean habitat is often defined using oceanographic variables (Redfern et al. 2006), while seabird habitat is frequently defined using prey density. Cetacean studies may use variables such as sea surface temperature and salinity to represent physiological constraints or identify water masses typical of good prey habitat as well as variables such as thermocline depth and strength, which are expected to influence prey abundance or availability. Consequently, relationships between apex marine predators and habitat defined by oceanographic variables should be subject to scale dependencies because heterogeneity in prey patches is likely to be linked to oceanographic conditions.

In this paper, we explore the effects of spatial resolution on dolphin–habitat models using 4 yr of data collected aboard research vessels in the eastern tropical Pacific Ocean (ETP). We developed generalized additive models (GAMs) of dolphin–habitat relationships at 6 spatial resolutions by varying the unit of analysis from 2 to 120 km. Habitat was defined using physical and biological oceanographic and geographic variables. Four dolphin species were selected to represent a range of habitat types and selectivity: striped dolphin *Stenella coeruleoalba*, eastern spinner dolphin *S. longirostris orientalis*, short-beaked common dolphin *Delphinus delphis*, and Risso's dolphin *Grampus griseus*.

MATERIALS AND METHODS

Study area and data collection. The ETP (Fig. 1) is a large (19.6 million km²), oceanographically diverse area that supports at least 29 cetacean species (Wade & Gerrodette 1993). Temporal variability in the ETP exists at a range of scales, but is dominated by inter-annual variability created by the El Niño–Southern Oscillation (ENSO) (Fiedler 2002a). On a macroscale, the ETP is defined by 3 surface currents: the North Equatorial Current, the North Equatorial Countercurrent, and the South Equatorial Current (Fig. 1). The northern and southern regions of the ETP are defined by Subtropical Surface Water (Fig. 1), which has the highest salinity values (greater than 35) and lowest nutrient concentrations in the area (Fiedler & Talley 2006). The central region is defined by Tropical Surface Water north of the equator, which includes the eastern Pacific warm pool, and by Equatorial Surface Water along the equator, which includes the equatorial cold tongue (Fig. 1). Tropical Surface Water has higher surface temperatures (greater than 25°C), lower salinity values (less than 34), and lower nutrient concentrations than the Equatorial Surface Water (Fiedler & Talley 2006). The eastern boundary currents (i.e. the California Current and the Peru Current) also have high nutrient concentrations relative to surrounding regions (Fiedler & Talley 2006).

The ETP contains a number of mesoscale features that also define the habitat of this region (Fig. 1). Thermal fronts occur between the eastern boundary currents and the warm pool, as well as between the South Equatorial Current and the North Equatorial Countercurrent (Fiedler & Talley 2006). The Equatorial Front, which occurs between the Peru Current and the North Equatorial Countercurrent, is one of the most prominent, low latitude, oceanic fronts in the world. It is a permanent feature of the region, although its intensity varies both spatially and temporally. A strong, shallow

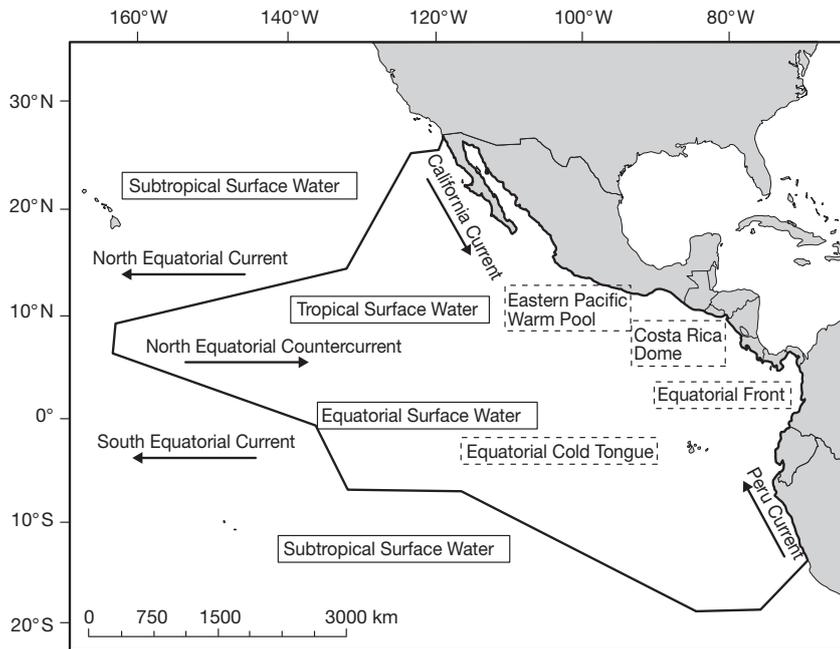


Fig. 1. Primary oceanographic features in the eastern tropical Pacific Ocean (ETP) that influence dolphin habitats. Study area is shown by the thick black line; water masses are identified by solid boxes; currents are shown with an arrow indicating the direction of flow, and other important features are identified by dashed boxes (adapted from Wyrтки 1966, 1967, Fiedler & Talley 2006)

thermocline predominates throughout the ETP, and a thermocline ridge predictably occurs between the North Equatorial Current and the North Equatorial Countercurrent. The Costa Rica Dome, a cyclonic gyre that develops at the eastern end of this ridge, is an area of regionally high surface chlorophyll from May to September (Fiedler 2002b). High productivity in the dome is supported by nutrients brought to the surface by wind mixing and upwelling. These 3 features, the Equatorial Front, the thermocline ridge, and the Costa Rica Dome, are significant for a number of seabirds and cetaceans (Ballance et al. 2006).

We used spatially referenced dolphin and oceanographic data that were collected by the Southwest Fisheries Science Center (NOAA Fisheries). The data were collected from 2 comparable oceanographic research vessels from late July until early December in 1992 and 1998 to 2000 (a third comparable vessel was also used in 1998). The 1992 survey focused on a subsection of the study area off the Middle and South American coast from

Guatemala to Colombia. Dolphin data were collected during daylight hours using line-transect methods (Buckland et al. 2001); field protocols are described in detail in Kinzey et al. (2000), Barlow et al. (2001), and Gerrodette & Forcada (2005). We used approximately 70 000 km of on-effort sampling data, which is defined as sampling conducted by the full observing team when Beaufort sea state was less than 6. The transects provided dense coverage of the study area (Fig. 2). Survey effort consisted of 2 observers searching for dolphins from the flying bridge of the ship (at a height ranging between 10 and 15 m above sea level) using pedestal-mounted 25 × 150 binoculars. A third observer served as the data recorder and searched by naked eye or with 7× handheld binoculars. Observers also regularly recorded survey conditions, including the Beaufort sea state. When dolphins were detected, the vessel approached the group as needed to identify the species and obtain group size estimates. Observers independently recorded their best

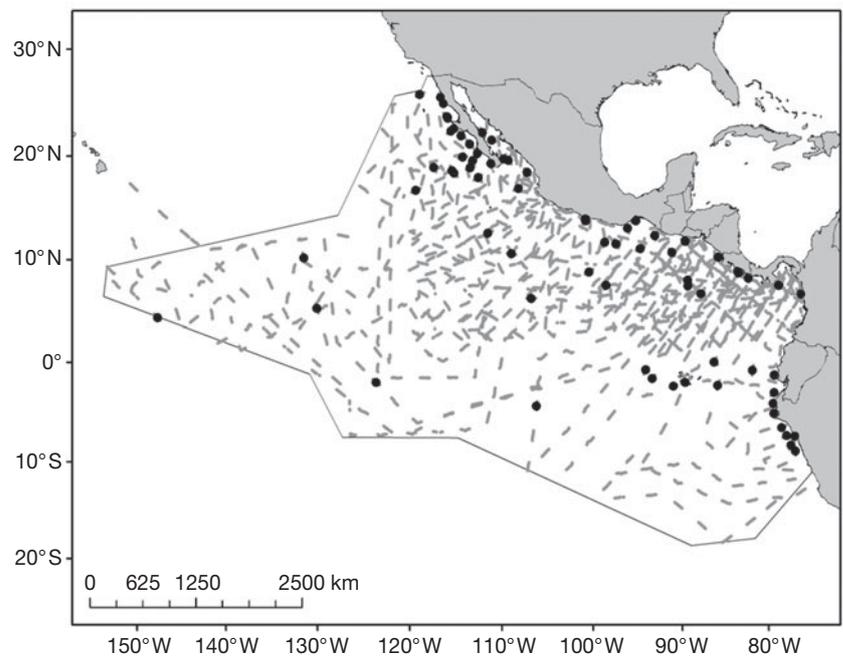


Fig. 2. Transect lines (---) used to collect dolphin and oceanographic data in the ETP. Data were collected aboard 2 research vessels from late July until early December in 1992 and 1998 to 2000 (3 vessels were used in 1998). Locations of the largest 10% of temperature fronts at the 120 km resolution are shown for all years of data (●). Fronts were defined as the difference between the minimum and maximum temperature recorded on a segment

estimate of group size, as well as high and low group size estimates, for each sighting. To obtain a single group size estimate for each sighting, we averaged the best estimate from each observer. In mixed species sightings, we averaged the estimates of the percentage of each species from each observer. We used only on-effort sightings that were identified to species in our analyses. Additionally, only those sightings for which at least 1 observer estimated a best group size and (where applicable) species percentages were included in our analyses.

Oceanographic sampling was systematically conducted during each survey (see Fiedler & Philbrick 2002 for a detailed description). Surface temperature and salinity were recorded at 2 min intervals using a thermosalinograph. Surface chlorophyll concentrations were measured at approximately 55 km intervals using a fluorometer. Water column properties, including thermocline depth and strength (i.e. midpoint of the depth interval containing the maximum temperature gradient and the value of the gradient, respectively), were derived from data collected using expendable bathythermographs (XBTs) and CTD casts. XBT drops to 760 m were conducted at approximately 55 km intervals each day and CTD casts to 1000 m were conducted before sunrise and after sunset. The seafloor depth was derived from a digital bathymetric map with a resolution of 1 to 12 km, which captures intermediate and large-scale structures of the ocean basins including canyons, ridges, and seamounts (Smith & Sandwell 1997), using ARCGIS version 9.1 (ESRI).

Data analyses. The design of the ETP cetacean and ecosystem assessment surveys resulted in transects that traversed the study area and ran parallel to each other or intersected at multiple locations. Transects in close spatial proximity may be temporally separated such that oceanographic conditions differ substantially. Consequently, a gridded representation of our data would combine temporally separated transects and was therefore deemed too coarse to adequately represent concurrent dolphin–habitat relationships. Instead, we summarized the data in 2, 10, 20, 40, 60, and 120 km segments along the transect lines; segment lengths were calculated using great circle distances from the starting point of effort each day. The 120 km resolution corresponds to a minimum amount of transect covered in a typical day; effort beyond 120 km was excluded from our analyses. The ship generally continued along the transect at night, producing a break in survey effort that is assumed to reduce dependence among daily segments. Consequently, we did not explore resolutions larger than 120 km.

Four dolphin species were included in our analyses: striped dolphin, eastern spinner dolphin, short-beaked

common dolphin, and Risso's dolphin. Encounter rate and group size models were built for each species. Dolphin encounter rates were calculated as the number of sightings of each species on a segment divided by the distance traveled on effort in that segment. When more than one sighting of a given species occurred on a segment, group sizes were averaged to obtain a single group size. We did not assess spatial autocorrelation in our dependent dolphin variables because we were concerned with the predictive power of the models, which is not affected by spatial autocorrelation.

Habitat variables used in our analyses were surface temperature and salinity, the natural logarithm of surface chlorophyll concentration (this transformation was used because the minimum and maximum measured values differed by more than an order of magnitude), thermocline depth and strength, and seafloor depth. We also approximated temperature fronts by subtracting the minimum from the maximum temperature on each segment. Large temperature differences tended to occur along the Equatorial Cold Tongue and in the coastal waters of our study area (Fig. 2). We also included Beaufort sea state as a predictor variable in our models. Although Beaufort sea state is not expected to affect the number or type of dolphins on a segment, it was included as a correction for sighting conditions because the probability of detecting dolphins decreases with increasing Beaufort sea states (Barlow et al. 2001). The product-moment correlation coefficients among all pairs of variables at the 2 km scale were between -0.5 and 0.5 .

Surface chlorophyll concentration and thermocline depth and strength were interpolated to the midpoint of the 2 km segments using inverse distance weighting; the degree of smoothing for each of these variables depended on the frequency of data collection (Fig. 3). Only 2 oceanographic measurements, the one temporally before and the one temporally after the segment midpoint, were used in the interpolation. Segments were not used in analyses unless both measurements were within 370.4 km (approximately 200 n mile) of the midpoint. All surface temperature and salinity measurements made within a segment were averaged to obtain a single value. The seafloor depth was calculated at the midpoint of each 2 km segment. Mean Beaufort sea state values, weighted by the amount of on-effort distance traveled in that state, were also calculated for each 2 km segment. Only segments for which mean Beaufort sea state was <5.5 were included in our analyses because of the difficulty in detecting dolphins at higher Beaufort sea states.

Estimates of surface chlorophyll, thermocline depth and strength, seafloor depth, and Beaufort sea state for the 2 km segments were averaged to create the corresponding values for 10, 20, 40, 60, and 120 km seg-

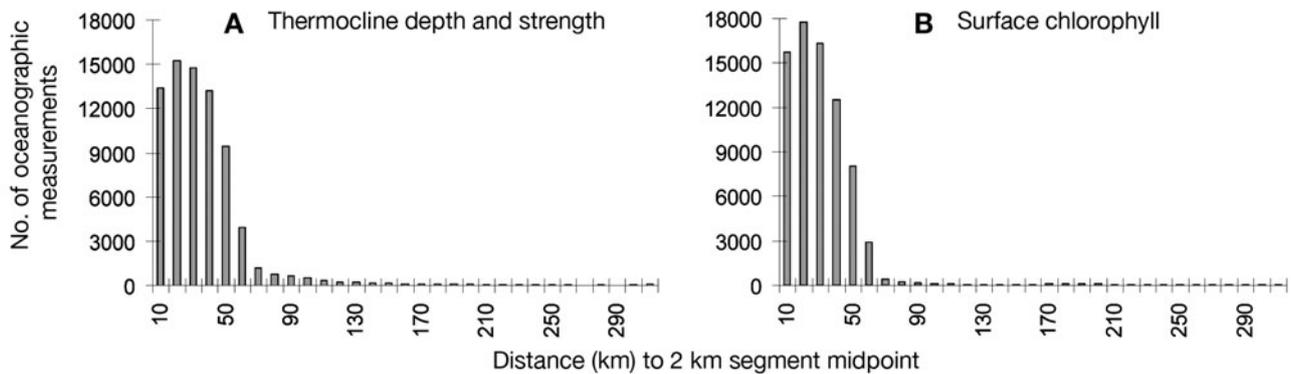


Fig. 3. Frequencies of the distances between the midpoints of the 2 km segments and the data collection locations used for the interpolation of (A) thermocline depth and strength and (B) surface chlorophyll measurements

ments. Temperature, salinity, and temperature front values were recalculated for each segment. Any larger segment containing one or more 2 km segments with a missing value for a predictor variable was also assigned a missing value. Because a single missing value at the 2 km resolution produces missing values at the larger resolutions, there are many days containing 2 km segments but no segments at the larger resolutions. To ensure consistency in the data across resolutions, only days for which the 120 km segment contained complete oceanographic data were used for all resolutions. The total number of segments, number of dolphin sightings, and mean dolphin group sizes for each resolution are presented in Table 1.

We used GAMs to explore the effects of spatial resolution on dolphin–habitat relationships in the ETP. A GAM approach was selected because it can fit a non-parametric relationship between the response and predictor variables via a scatterplot smoother; consequently, this approach allows the data to identify nonlinearities in dolphin–habitat relationships rather than imposing parametric fits through polynomial terms in a linear regression (Chambers & Hastie 1991). This approach has been applied to model cetacean–habitat relationships for delphinids (Ferguson et al. 2006a) and beaked whale species (Ferguson et al. 2006b) using data collected in the ETP from 1986 to 1990. The software package SPlus (Windows Professional Developer, version 7.0, Insightful Corp.) was used to fit the GAMs; we chose cubic smoothing splines (Hastie & Tibshirani 1990) with a maximum of 3 degrees of freedom for all predictor variables to capture non-linear relationships,

while limiting the inclusion of unrealistic detail in the shape of the function (Forney 2000).

Dolphin encounter rates are expected to follow an overdispersed Poisson distribution; therefore, encounter rate models were built using a logarithmic link and quasi-likelihood error distribution in which the variance was proportional to the mean. The distance traveled on effort for each segment was incorporated as an offset in the models. Dolphin group size models were fit using only those segments in which the species was present; models were built using a log-normal distribution. For both dolphin encounter rate and group size models, an automated forward/backward stepwise approach based on Akaike’s information criterion (AIC) was used to select the variables for inclusion in each model as well as the degrees of freedom for the cubic smoothing splines (Ferguson et al. 2006a). Each model was fitted 3 times, starting with a null model that included only the intercept. The dispersion

Table 1. Number of sightings (Sight.) and mean group size (GS) are shown for the 4 species and 6 spatial resolutions (including total number of segments for each resolution) considered in our analyses. The 120 km resolution has the highest number of encounters for several species because segments with Beaufort sea state values >5.5 were excluded from our analyses. In particular, 2 km segments containing an encounter and occurring in Beaufort sea states >5.5 may not contribute to the analyses at the smaller resolutions but may contribute at the larger resolutions if the average Beaufort sea state on the longer segment was ≤ 5.5 . Striped dolphin *Stenella coeruleoalba*, eastern spinner dolphin *S. longirostris orientalis*, short-beaked common dolphin *Delphinus delphis*, Risso’s dolphin *Grampus griseus*

| Spatial resolution (km) | Striped dolphin | | Eastern spinner dolphin | | Short-beaked common dolphin | | Risso’s dolphin | | Total no. of segments |
|-------------------------|-----------------|-------|-------------------------|-------|-----------------------------|--------|-----------------|-------|-----------------------|
| | Sight. | GS | Sight. | GS | Sight. | GS | Sight. | GS | |
| 2 | 420 | 49.03 | 161 | 96.87 | 263 | 160.93 | 134 | 21.46 | 37830 |
| 10 | 420 | 49.09 | 161 | 96.76 | 263 | 162.35 | 134 | 21.23 | 8659 |
| 20 | 421 | 48.61 | 161 | 96.87 | 264 | 163.31 | 134 | 21.86 | 4452 |
| 40 | 421 | 48.54 | 161 | 96.10 | 264 | 163.03 | 135 | 21.47 | 2262 |
| 60 | 421 | 46.30 | 161 | 95.93 | 264 | 164.26 | 135 | 19.80 | 1513 |
| 120 | 421 | 47.34 | 161 | 97.64 | 265 | 164.25 | 135 | 19.44 | 763 |

parameter from the null model was used to calculate AIC values in the algorithm `step.gam`, which tested all predictor variables for inclusion in the second model as cubic smoothing splines with 2 or 3 degrees of freedom. For the final model, the dispersion parameter from the second model was used to calculate the AIC values in the algorithm `step.gam`, which tested all predictor variables for inclusion as linear terms or cubic smoothing splines with 2 or 3 degrees of freedom.

A primary goal of our analyses was to explore the predictive power of models built at 6 different resolutions. Models built using an entire data set run the risk of being too complex (i.e. including too many variables or cubic smoothing splines with too many degrees of freedom) to enable accurate prediction of dolphin densities. Consequently, we used a 'pseudo-jackknife' cross validation approach to select our final model (Becker 2007). In particular, 4 data sets were constructed by excluding one of the 4 yr of data. Cross validation data sets were created by excluding a year of data, rather than randomly selecting the excluded data, to explore the power of the models to predict dolphin densities in a novel year—a primary conservation and management application of the models. We also needed to ensure that the final model could adequately predict each individual year; consequently we added a 'pseudo-jackknife' component to the cross validation, as explained below, to minimize the influence of oceanographic conditions and species distribution patterns in any particular year on the selection of the final model (Becker 2007).

Dolphin encounter rate and group size models for each species were built for each resolution and data set; consequently, for each species there were 4 candidate encounter rate and 4 candidate group size models for each resolution. At each resolution, the candidate models (i.e. the selected variables and degrees of freedom for each cubic smoothing spline) were re-fit to the 3 remaining cross validation data sets, e.g. the candidate model built from the 1992, 1998, and 1999 data was re-fit to the 3 data sets: (1) 1992, 1998, and 2000; (2) 1992, 1999, and 2000; and (3) 1998, 1999, and 2000. Dolphin encounter rates and group sizes were predicted for each year omitted during model building and the average squared prediction error (ASPE) was calculated. Anscombe residuals (McCullagh & Nelder 1989) were used in the ASPE calculations for the encounter rate models to account for the quasi-likelihood error distribution. A ratio estimator (Smith 1993) was used to correct the bias in group size predictions caused by reverse transforming the logarithm of group size predicted by the model (Finney 1941, Smith 1993). The sum of the ASPE values from each of the 4 fits of the 4 candidate models was used to select the best model for each species and resolution. Models having

ASPE sums within 5% of the lowest sum were considered to have equal predictive ability. In these cases, the best model was defined as the candidate model that had the lowest ASPE value when predicting the year that was excluded from model building. The best model was then re-fit using all 4 years of data to produce the final models at each resolution. The predictive power of the final models was evaluated using ratios of observed to predicted dolphin relative abundance (defined as the number of encounters multiplied by the average group size). Specifically, the observed and predicted number of dolphins were calculated for each segment and summed for all segments within a year or for all years.

Predicted dolphin densities, D , were obtained for each segment using a line-transect formula:

$$D = \frac{\text{Sightings} \times \exp(\text{LGS}) \times \text{Ratio} \times f(0)}{2 \times \text{Distance} \times g(0)}$$

where Sightings is the predicted number of sightings, LGS is the predicted logarithm of group size, Ratio is the ratio estimator used to correct for potential bias created by modeling logarithmic school sizes, Distance is distance in kilometers traveled on effort in the segment, and $f(0)$ and $g(0)$ are line-transect variables that respectively correct for a decrease in detection probability with distance from the transect and detection probabilities on the transect that are <1 (Buckland et al. 2001). Values of $f(0)$ and $g(0)$ for predicted group sizes in each segment were obtained from Ferguson & Barlow (2001); specifically, we used their estimates of $f(0)$ from the ETP region. The group-size independent $f(0)$ values reported for the 3 stocks of common dolphin were averaged.

We calculated the correlation between predicted densities at the different resolutions by assigning the predictions for the larger segments to all of the smaller segments they contained. There was a mismatch between the 40 and 60 km segments for each day; consequently, the prediction for the 40 km segment that overlapped both 60 km segments was arbitrarily assigned to the prediction for the first 60 km segment. We created a 95% confidence interval (CI) for the average of the correlation values by randomly permuting the predicted densities in the smaller segments for the entire survey data set and recalculating the correlation 1000 times; the CI was determined by the 25th and 975th ordered values of the permutation. If the observed correlation was not contained in the 95% CI, it was assumed to be statistically significant from the correlation that would be obtained from a random distribution. We mapped predicted densities at all resolutions by assigning the predicted density to the midpoint of each segment and interpolating these points in a 10×10 km grid using negative exponential distance weighting (circular neighborhood of 300 km, weights reached 0.5 at 100 km).

RESULTS

Dispersion parameters for the final encounter rate models ranged from 2.36 to 0.87; this range is appreciably different from 1, the value expected for a Poisson distribution, and justifies the use of the quasi-likelihood error distribution. The models with the lowest ASPE in our cross validation analysis were generally built using the same data subset for a majority of spatial resolutions for each species, but the data subsets tended to differ between encounter rate and group size models for each species and among species (Table 2). Typically, the best model was the candidate model that had the lowest ASPE value when predicting the year that was omitted from model building because the ASPE sums for multiple models were within 5% of one another. In general, there was no pattern in the number of variables selected at the different resolutions. The variables included in the final encounter rate and group size models for a particular

species, however, were not a random collection. The same variables frequently appeared at multiple resolutions and had similarly shaped cubic smoothing splines.

Final encounter rate and group size models are shown for all species at the 40 km resolution in Fig. 4. The patterns shown in this figure are generally indicative of the patterns observed at all scales. In general, models for all species suggest that encounter rates are influenced by temperature and the properties of the thermocline (Fig. 4). The encounter rate models for all species at all resolutions include Beaufort sea state, as expected due to the increased difficulty of detecting groups in higher Beaufort sea states. The percentage of explained deviance for the encounter rate models at the 40 km resolution ranged from 18 (striped dolphin) to 30 (eastern spinner dolphin), and from 7 (eastern spinner dolphin) to 26 (Risso's dolphin) for the group size models (Table 3). The percentage of explained deviance generally increases with increasing spatial

Table 2. Final encounter rate and group size models had the lowest average squared prediction error in the cross validation analyses (see 'Materials and methods—Data analyses' for details). The years excluded from the cross validation data sets for the final models are shown for each species and spatial resolution. Predictor variables selected in the final models are also shown; the order of variables corresponds to the consistency with which the variables were selected among resolutions. Fronts: differences between the minimum and maximum temperatures on a segment; Temp: sea surface temperature; Sal: sea surface salinity; TCD: thermocline depth; TCS: thermocline strength; Chl: natural logarithm of surface chlorophyll concentrations. Species taxa are given in Table 1

| Spatial resolution (km) | Encounter rate | | Group size | |
|------------------------------------|----------------|--|---------------|-------------------------------|
| | Excluded year | Predictor variables | Excluded year | Predictor variables |
| Striped dolphin | | | | |
| 2 | 1998 | Depth TCD TCS Beaufort | 2000 | TCD TCS |
| 10 | 1998 | Depth TCD TCS Beaufort | 2000 | TCD TCS |
| 20 | 1998 | Depth TCD Beaufort Temp | 2000 | TCD TCS Fronts |
| 40 | 1998 | Depth TCD TCS Beaufort | 2000 | TCS Fronts Temp Sal |
| 60 | 1998 | Depth TCD TCS Beaufort | 2000 | TCD TCS Temp Sal |
| 120 | 1998 | Depth TCD TCS Beaufort | 1999 | TCD TCS Sal |
| Eastern spinner dolphin | | | | |
| 2 | 1999 | Depth Temp TCD Beaufort TCS | 1999 | Temp |
| 10 | 1999 | Depth Temp TCD Beaufort | 1999 | Temp |
| 20 | 1999 | Depth Temp TCD Beaufort | 1999 | Temp |
| 40 | 2000 | Depth Temp TCD Beaufort | 1992 | Temp |
| 60 | 1998 | Depth Temp TCD Beaufort Chl | 1999 | Temp |
| 120 | 2000 | Depth Temp TCD Beaufort TCS | 1992 | Temp Fronts |
| Short-beaked common dolphin | | | | |
| 2 | 1998 | Temp TCD Beaufort Depth Chl | 1992 | Sal Chl Beaufort Depth Fronts |
| 10 | 1998 | Temp TCD Beaufort Depth | 1992 | Sal Chl Beaufort |
| 20 | 1998 | Temp TCD Beaufort Depth Chl | 1998 | Sal Chl Beaufort |
| 40 | 1998 | Temp TCD Beaufort Depth Chl Fronts TCS | 1992 | Chl Beaufort |
| 60 | 2000 | Temp TCD Beaufort Depth Chl | 1992 | Sal Beaufort Depth |
| 120 | 1999 | Temp TCD Beaufort | 1992 | Sal Chl Beaufort |
| Risso's dolphin | | | | |
| 2 | 1998 | Depth Beaufort Chl | 1992 | Beaufort |
| 10 | 2000 | Depth Beaufort Chl Temp TCD | 1998 | Beaufort Sal TCD |
| 20 | 2000 | Depth Beaufort Chl Temp TCD | 1998 | Beaufort Depth |
| 40 | 2000 | Depth Beaufort Chl Temp TCD | 1992 | Beaufort Depth |
| 60 | 1998 | Depth Beaufort | 1992 | Beaufort Depth |
| 120 | 2000 | Depth Beaufort Temp TCD Sal | 1999 | Beaufort Depth |

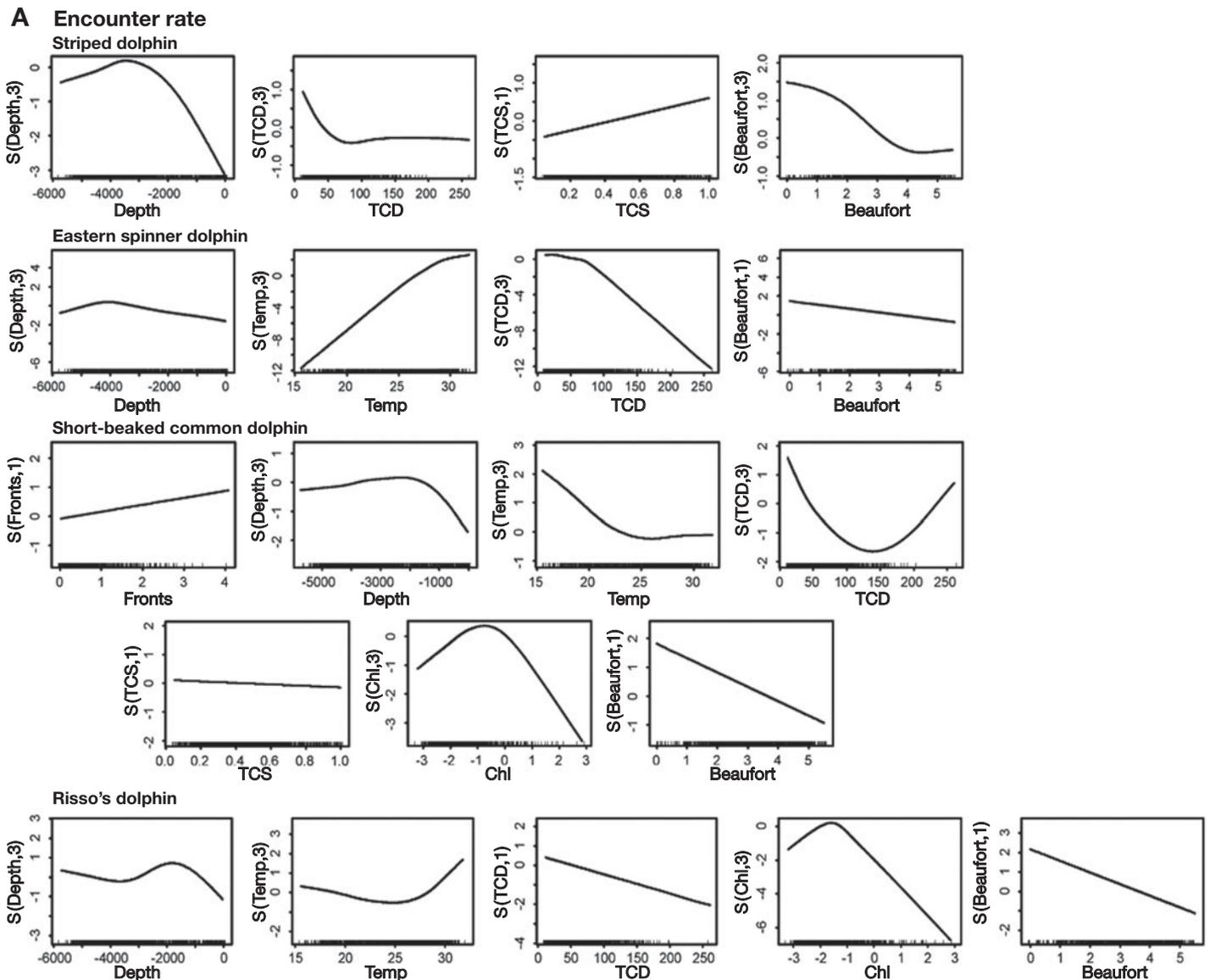


Fig. 4. (A) Final encounter rate and (B) group size models for all dolphin species at the 40 km resolution. Fronts: differences between the minimum and maximum temperatures on a segment; Temp: sea surface temperature; Sal: sea surface salinity; TCD: thermocline depth; TCS: thermocline strength; Chl: natural logarithm of surface chlorophyll concentrations. The y-axes, representing the smoothing spline function and labeled to indicate the degrees of freedom for the spline (linear terms are represented by a single degree of freedom), have been scaled across all resolutions relative to the variable having the largest y-axis range that was not influenced by a small number of outlying points; the scale of the y-axes was determined separately for the encounter rate and group size models for each species. Data points for each variable are indicated by tick marks along the x-axis. Species taxa are given in Table 1

resolution for the encounter rate models, which is likely an outcome of the larger sample size that includes a larger proportion of zeroes at the smaller resolutions. This pattern is less pronounced for the group size models, where sample size is relatively consistent because only segments containing a sighting are used to build the models.

The product-moment correlation coefficients between densities predicted at the different resolutions

were quite high (Table 4), with average values ranging from 0.77 (Risso's dolphin) to 0.92 (striped dolphin). These correlations were considered significant because the confidence interval for the average correlation from a random distribution ranged from -0.01 to 0.01 . Hence, the models built at all resolutions identified the same areas of high and low densities for each species. The 40 km model results suggest a mean density of 94 ind. per 1000 km² for striped dolphin (range:

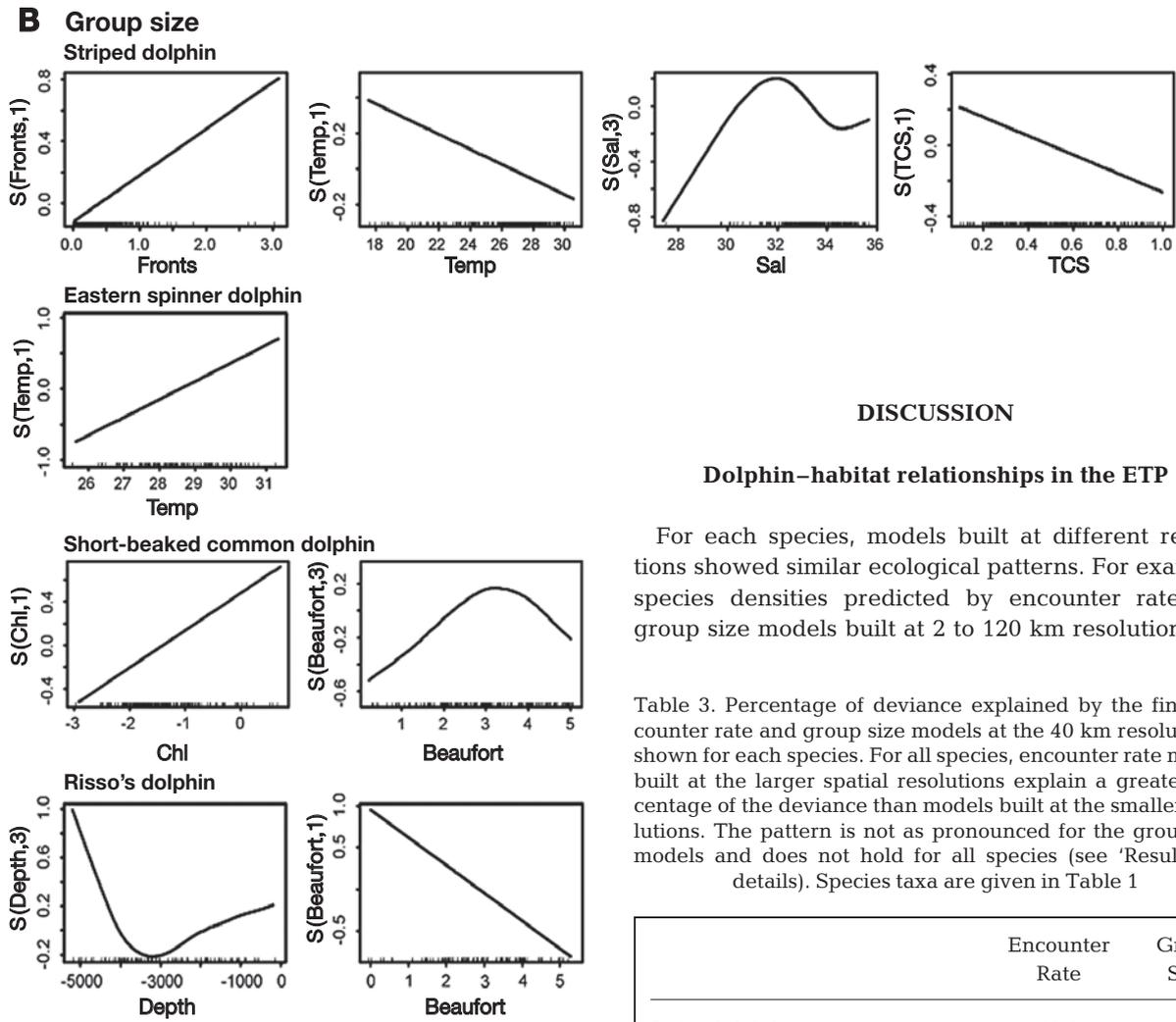


Fig. 4 (continued)

1 to 1171), 48 ind. per 1000 km² for eastern spinner dolphin (range: 0 to 1582), 177 ind. per 1000 km² for short-beaked common dolphin (range: 2 to 8512), and 29 ind. per 1000 km² for Risso's dolphin (range: 0 to 2349).

Ratios of observed to predicted relative abundance for all species summarized over all years have low bias (i.e. are within 10% of unity) and have similar precision (Table 5), suggesting that models built at all resolutions do equally well at predicting relative abundance for these species. Ratios of observed to predicted relative abundance compared among years, however, did not identify a single best resolution for any species (Table 5). Instead, the ratios clearly indicate that there is greater variability in the ratios among years than among spatial resolutions for all species.

DISCUSSION

Dolphin–habitat relationships in the ETP

For each species, models built at different resolutions showed similar ecological patterns. For example, species densities predicted by encounter rate and group size models built at 2 to 120 km resolutions are

Table 3. Percentage of deviance explained by the final encounter rate and group size models at the 40 km resolution is shown for each species. For all species, encounter rate models built at the larger spatial resolutions explain a greater percentage of the deviance than models built at the smaller resolutions. The pattern is not as pronounced for the group size models and does not hold for all species (see 'Results' for details). Species taxa are given in Table 1

| | Encounter Rate | Group Size |
|-----------------------------|----------------|------------|
| Striped dolphin | 18.3 | 7.6 |
| Eastern spinner dolphin | 30.3 | 7.0 |
| Short-beaked common dolphin | 28.7 | 9.9 |
| Risso's dolphin | 23.4 | 26.0 |

Table 4. Averages of the product-moment correlation coefficients between densities predicted for each resolution (e.g. the average of the correlation coefficients between 2 and 10, 2 and 20, 2 and 40, 2 and 60, and 2 and 120 is shown for the 2 km resolution) and all resolutions are shown. The correlation values are high, suggesting that all models identify similar areas of high and low dolphin densities. Species taxa are given in Table 1

| Spatial resolution (km) | Striped dolphin | Eastern spinner dolphin | Short-beaked common dolphin | Risso's dolphin |
|-------------------------|-----------------|-------------------------|-----------------------------|-----------------|
| 2 | 0.93 | 0.92 | 0.85 | 0.75 |
| 10 | 0.93 | 0.93 | 0.80 | 0.81 |
| 20 | 0.92 | 0.93 | 0.84 | 0.83 |
| 40 | 0.92 | 0.92 | 0.79 | 0.74 |
| 60 | 0.92 | 0.91 | 0.79 | 0.75 |
| 120 | 0.89 | 0.81 | 0.66 | 0.72 |
| All | 0.92 | 0.90 | 0.79 | 0.77 |

Table 5. Ratios of observed to predicted dolphin relative abundance are shown for all species and resolutions. Predicted relative abundance was obtained by multiplying results from the final encounter rate and group size models; ratios were calculated by summing the relative abundance for all segments within a year or for all years. The standard error of the ratios (SE) was calculated using the values from the individual years. Species taxa are given in Table 1

| | Spatial resolution | | | | | |
|------------------------------------|--------------------|-------|-------|-------|-------|--------|
| | 2 km | 10 km | 20 km | 40 km | 60 km | 120 km |
| Striped dolphin | | | | | | |
| 1992 | 1.611 | 1.602 | 1.430 | 1.594 | 1.586 | 1.572 |
| 1998 | 0.923 | 0.920 | 0.904 | 0.977 | 1.012 | 1.000 |
| 1999 | 0.785 | 0.784 | 0.770 | 0.766 | 0.794 | 0.796 |
| 2000 | 0.933 | 0.929 | 0.976 | 0.916 | 1.000 | 0.987 |
| All years | 1.001 | 0.998 | 0.979 | 1.005 | 1.047 | 1.039 |
| SE | 0.186 | 0.184 | 0.143 | 0.182 | 0.170 | 0.168 |
| Eastern spinner dolphin | | | | | | |
| 1992 | 0.653 | 0.633 | 0.634 | 0.620 | 0.635 | 0.744 |
| 1998 | 1.154 | 1.144 | 1.143 | 1.187 | 1.199 | 1.108 |
| 1999 | 0.896 | 0.850 | 0.846 | 0.872 | 0.807 | 0.680 |
| 2000 | 0.977 | 1.038 | 1.043 | 1.025 | 1.042 | 1.003 |
| All years | 0.992 | 0.987 | 0.987 | 1.002 | 0.997 | 0.938 |
| SE | 0.104 | 0.112 | 0.113 | 0.121 | 0.125 | 0.102 |
| Short-beaked common dolphin | | | | | | |
| 1992 | 1.611 | 1.686 | 1.532 | 1.395 | 1.627 | 1.802 |
| 1998 | 0.722 | 0.686 | 0.756 | 0.766 | 0.722 | 0.657 |
| 1999 | 0.949 | 0.961 | 0.917 | 0.938 | 0.910 | 0.955 |
| 2000 | 1.074 | 1.027 | 1.053 | 1.058 | 1.029 | 0.871 |
| All years | 0.988 | 0.971 | 0.980 | 0.979 | 0.967 | 0.926 |
| SE | 0.189 | 0.212 | 0.167 | 0.133 | 0.196 | 0.251 |
| Risso's dolphin | | | | | | |
| 1992 | 0.429 | 0.454 | 0.408 | 0.437 | 0.464 | 0.453 |
| 1998 | 1.223 | 1.059 | 1.053 | 1.060 | 1.354 | 1.174 |
| 1999 | 0.996 | 0.954 | 0.966 | 1.032 | 1.040 | 1.057 |
| 2000 | 0.900 | 1.077 | 1.002 | 0.951 | 0.907 | 1.010 |
| All years | 0.975 | 0.962 | 0.934 | 0.947 | 1.034 | 1.011 |
| SE | 0.167 | 0.146 | 0.151 | 0.146 | 0.185 | 0.161 |

highly correlated (Table 4). Additionally, key variables (identified by large changes in the mean response over the range of the variable) were included in encounter rate and group size models built at a majority of resolutions and had similar functional forms for each species.

Our exploration of the effect of spatial resolution on dolphin–habitat models builds on 3 decades of dolphin–habitat studies in the ETP (Au & Perryman 1985, Reilly 1990, Reilly & Fiedler 1994, Reilly et al. 2002). Our analyses used 3 of the same years of data as Reilly et al. (2002), but the technique used to assess species–habitat relationships differs as does our treatment of resolution. In particular, Reilly et al. (2002) used an ordination technique to analyze data collected in the ETP from 1986 to 1990 and 1998 to 2000, and selected a survey day as the unit of analysis; a survey day translates to a ~160 km resolution (Reilly et al. 2002); although Reilly & Fiedler (1994), who also used a survey day as the unit of analysis for data collected in the ETP from 1986 to 1990, found that the distance traveled can vary substantially (i.e. 37 to 222 km).

Reilly (1990) and Reilly & Fiedler (1994) obtained weak relationships between striped dolphin distributions and oceanographic variables. Striped dolphin encounter rate models had the lowest explained deviance among the 4 species in our study (Table 3), supporting the hypothesis that the broad distribution of striped dolphin (Fig. 5) made it difficult for the models to capture dominant habitat patterns using oceanographic variables. The variables selected in our models suggest that striped dolphin encounters decrease in depths less than 3000 m and increase when the thermocline is strong and shallow (Fig. 4). Upwelling modified waters are defined by cooler temperatures, weak and shallow thermoclines, and high surface chlorophyll concentrations in the ETP, while tropical waters are defined by warmer temperatures, strong and deep thermoclines, and lower surface chlorophyll concentrations. Hence, encounter rate models for striped dolphin relate to elements of both habitat types, similar to the findings of Reilly (1990) and Reilly & Fiedler (1994). Striped dolphin group sizes tended to be larger when the thermocline was shallow and weak, which is consistent with upwelling modified waters, although the association between larger groups and shallow thermoclines was replaced by an association with cooler, more saline

waters at the 40 km resolution (Fig. 4). While temperature only entered the group size models built at the 40 km resolution, the association between large groups and waters with higher salinities was observed at the 40 to 120 km resolutions.

All previous studies of dolphin habitat in the ETP (Au & Perryman 1985, Reilly 1990, Reilly & Fiedler 1994, Reilly et al. 2002) found spinner dolphin in tropical waters and common dolphin in upwelling modified waters. Densities of eastern spinner dolphin predicted by our models are highest along the coasts of Mexico, Guatemala, and El Salvador (Fig. 5), similar to the results of previous studies. Encounter rates and group sizes for eastern spinner dolphin increase in warm temperatures, which identifies tropical waters. Within these waters, however, higher encounters occur when the thermocline is shallow, which contrasts with previous results (Reilly & Fiedler 1994).

Maps of predicted densities for common dolphin suggest that the equatorial cold tongue, Costa Rica Dome, and areas off the coast of Baja California are important habitat (Fig. 5). Encounter rate models for

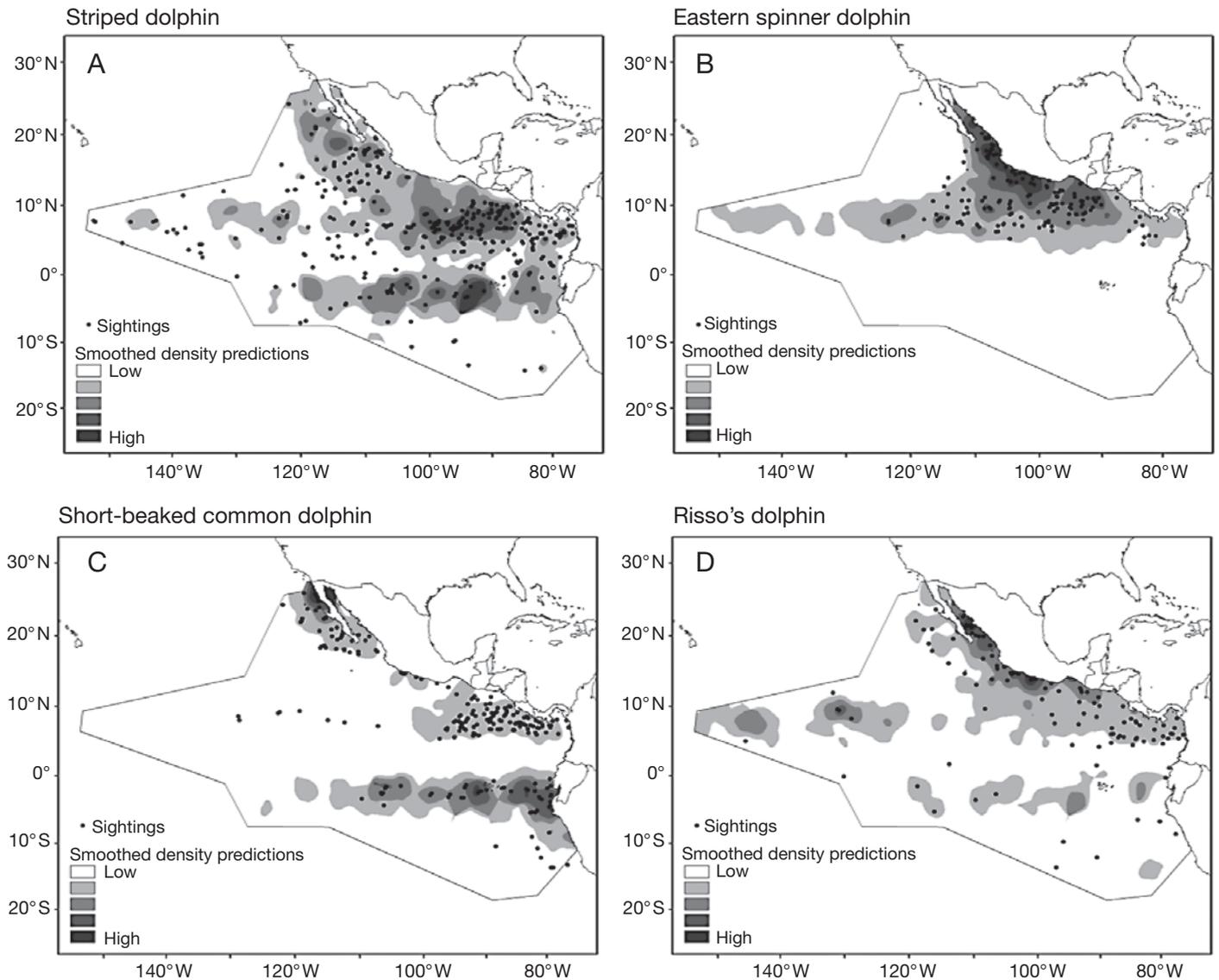


Fig. 5. Densities were predicted using the final encounter rate and group size models built at the 40 km resolution and interpolated in a 10×10 km grid using negative exponential distance weighting (see 'Materials and methods' for details) for (A) striped dolphin *Stenella coeruleoalba*, (B) eastern spinner dolphin *S. longirostris orientalis*, (C) short-beaked common dolphin *Delphinus delphis*, and (D) Risso's dolphin *Grampus griseus*. Densities scale from the lowest values shown in white to the highest values shown in dark grey; sightings of each species are shown as black dots. Density values within each shade category differ among species

common dolphin mirror this pattern with increased encounters occurring in cooler temperatures and shallow thermoclines (the increase in common dolphin encounters for thermocline depths greater than 150 m appears to be driven by a few outliers, Fig. 4). Encounters peak in intermediate chlorophyll concentrations (Fig. 4), however, which is unexpected for upwelling modified waters. Common dolphin groups tended to be largest in waters with high salinity and chlorophyll concentrations, although the association between large groups and high salinity was not found at the 40 km resolution (Fig. 4) and the association between large groups and high chlorophyll concentrations was

replaced by an association with shallow waters at the 60 km resolution.

Habitat for Risso's dolphin was only explored in the qualitative analyses of Au & Perryman (1985). They suggested that Risso's dolphin occurred in both upwelling modified and tropical waters. The high-density areas predicted by our models for Risso's dolphin overlap with high-density areas for common and eastern spinner dolphin (Fig. 5), supporting their finding. Encounters of Risso's dolphin also reflect properties of both upwelling modified and tropical waters: encounters generally increase when the temperature is warm and the thermocline is shallow and decrease in waters with higher

chlorophyll concentrations (Fig. 4). Group sizes were not generally related to any oceanographic variables, but only showed an increase with depth (Fig. 4).

The general correspondence between the models we built at all resolutions and previously documented dolphin–habitat relationships, as well as the general similarity among the models built at all resolutions, suggest that resolution, within a range of 2 to 120 km, does not affect the identification of ecological patterns in ETP dolphin–habitat models. No direct comparisons of the percentage of explained deviance were available for the species we modeled. However, Reilly et al. (2002) found that their canonical correspondence analyses of daily encounter rates using similar oceanographic variables explained 16% of the variance for striped dolphin, 8% for eastern spinner dolphin, and 50% for common dolphin. Our percentages of explained deviance at the 120 km resolution were higher for striped (27%) and eastern spinner dolphin (43%), but lower for short-beaked common dolphin (30%). Ferguson et al. (2006a) used GAMs and a ~9 km spatial resolution to relate delphinid encounter rates and group sizes to many of the oceanographic variables considered in our analyses. The percentage of explained deviance in the delphinid encounter rate models (12%, Ferguson et al. 2006a) was intermediate between the percentage of explained deviance for our striped and eastern spinner dolphin models built at the 10 km resolution (11 and 19%, respectively) and lower than the values for the striped and eastern spinner dolphin models built at the 40 km resolution (18 and 30%, respectively). The percentage of explained deviance in the delphinid group size models (5%, Ferguson et al. 2006a) was at the lower end of the percentage of explained deviance for our striped and Risso's dolphin models built at all resolutions (6 and 26%, respectively). In our analyses and Ferguson et al. (2006a), encounter rate models generally had a higher percentage of explained deviance than group size models. This result may suggest that the oceanographic variables used in these studies are not effective proxies for the complex factors influencing dolphin group sizes, such as behavior, ability to capture prey, and protection from predators. This hypothesis is supported by the analyses of Reilly & Fiedler (1994); they found that groups of all sizes occurred in the same habitats and that group size was not strongly related to oceanographic variables within a habitat.

Predictive power: the importance of interannual habitat variability

The importance of interannual variability is clearly shown in our yearly ratios of observed to predicted dol-

phin relative abundance. For all species considered in our analyses, the predictive power of the GAMs varied more among years than among spatial resolutions (Table 5). For the spatial resolutions analyzed in our study, these results suggest that interannual habitat variability has a greater impact on the predictive power of dolphin–habitat models than the resolution of the unit of analysis. ENSO produces strong interannual variability in the ETP with a period of 2 to 7 yr (Fiedler 2002a). A number of oceanographic changes associated with ENSO are expected to affect prey densities and concomitantly the density of apex marine predators. Although the relationships among interannual variability in oceanographic conditions, mid-trophic species, and apex predators are not fully understood, the patterns of interannual variability in the predictive power of our models suggests that ENSO may influence dolphin distributions and, hence, their densities within our study area.

Domains of scale in the ETP: selecting the best resolution

Although it is common to find scale dependence in species–habitat relationships for a variety of organisms in a wide range of ecosystems, domains of scale exist in which ecological patterns do not change, or change monotonically, with scale (Wiens 1989). Within a domain, patterns may be extrapolated across scales; extrapolation across domains is not possible because observed species–habitat relationships may differ among domains (Wiens 1989). The absence of scale dependence in our models suggests that resolutions from 2 to 120 km occur within a single domain of scale in the ETP.

Previous studies have found scale dependence in seabird–habitat relationships. Although differences between seabirds and dolphins, such as size, diving abilities, and energetic constraints, may contribute to the absence of scale dependence observed in our study, the absence may also be the result of differences in our study design and area. For example, we defined habitat using oceanographic variables that are expected to be proxies for prey abundance, while seabird studies frequently define habitat using direct measures of prey abundance. While it would be difficult to collect detailed prey data for a large pelagic region such as the ETP, it is possible that scale dependence among the resolutions considered here would occur in models relating dolphins to habitat variables that are trophically closer to prey species. Additionally, it is possible that resolutions larger than 120 km may occur outside of the domain of scale we observed in the ETP. Consequently, analyses conducted at larger resolutions may exhibit scale dependence.

The absence of scale dependence in our models may also be ecosystem dependent. Most scale dependent seabird–habitat relationships have been observed in temperate or high latitude ecosystems, particularly in waters on the continental shelf or around islands, where habitat is expected to change on smaller spatial scales. We examined dolphin–habitat relationships in the ETP biogeographic province, where much of the physical oceanography is defined by large-scale processes, including current systems and variability in rates of evaporation and precipitation (Fiedler & Talley 2006). It is possible that the approximately 55 km sampling scale of the water column and surface chlorophyll data fails to capture fine-scale variability and that models built using more frequently sampled oceanographic data would be scale dependent. However, we conducted analyses using only the oceanographic and geographic data that were collected at all resolutions (i.e. sea surface temperature and salinity, temperature fronts, and depth) and found similar results to those presented here. Hence, the similarity of the models at all resolutions may indicate that the dominant oceanographic variability is captured by the sampling scale or that cetaceans are not responding to fine-scale oceanographic variability in the ETP. Additional analyses are needed to examine these hypotheses. For example, oceanographic variability is expected to occur on finer scales in the northeastern Pacific, particularly in the California Current Ecosystem. It is possible that dolphin–habitat models built at resolutions from 2 to 120 km may show scale dependence in such regions.

Habitat models are potentially powerful tools for incorporating heterogeneity in marine ecosystems into the management and conservation of dolphins, many of which are substantially impacted by human activities. In the ETP, dolphin management and conservation focuses heavily on interactions between species and a variety of fisheries. Combining model predictions of dolphin density with estimates of fishing intensity can help identify areas of potentially frequent interactions that may result in dolphin bycatch or other adverse population effects. To date, quantitative dolphin–habitat models have been developed for only a small proportion of the species impacted by anthropogenic activities in the ETP.

Our dolphin–habitat models suggest that resolutions from 2 to 120 km occur within a single domain of scale in the ETP. In particular, similar results are achieved by models built using oceanographic habitat variables at any of these resolutions for species that are broadly distributed in the ETP. A plausible hypothesis is that the domain of scale is defined by the relative homogeneity of the oceanographic variables throughout these resolutions. This hypothesis suggests that the consequence of changing resolutions is a change in the

signal-to-noise ratio. Specifically, the number of segments containing a zero is drastically reduced at the larger resolutions for all species (see Table 1 for a general indication, although note that some segments may contain more than 1 encounter). The similarity of results from all models suggests that the large number of segments containing a zero at the smaller resolutions do not contain ecological information about the dolphin–habitat relationships. Consequently, it may be appropriate to develop predictive dolphin–habitat models for species that are broadly distributed in the ETP at larger resolutions when habitat is defined using oceanographic variables. There is a trade-off, however, between using larger resolutions and maximizing sample size. The total ETP data set contains 909 d of survey effort. We had to restrict our analyses to days in which the ship traveled 120 km (a total of 817 d) and days in which complete oceanographic data was collected (763 d); we also had to exclude effort that occurred outside the 120 km segment. Using intermediate resolutions, such as the 40 km resolution presented here, may provide an optimal solution to this trade-off because it minimizes false absences and allows the inclusion of more survey days and more effort per day.

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