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Dusky dolphin: modeling habitat selection

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1 The use of habitat selection models to predict the likely occurrence of wild populations is an important tool in conservation planning and wildlife management. The goal of our study was to build habitat selection models for the dusky dolphin (*Lagenorhynchus obscurus*) in Golfo Nuevo, Argentina. Random transects were surveyed by boat in 2002–2007. A grid of 1.5 × 1.5-km squares (cells) was constructed for the study area. We characterized each cell by depth, slope, distance from shore, sea-surface temperature, concentration of chlorophyll *a*, presence–absence of dolphins, and a coefficient of use by dusky dolphins. Models were developed for warm and cold seasons and for all data combined. Data collected during 2002–2005 were pooled to develop the model, and data collected during 2006–2007 were used for cross-validation. Logistic regression with a binomial error structure and a logit-link function were used to relate the presence of dolphins to habitat variables. Models with gamma structure and log-link function were used to relate area use to habitat variables. Models were selected with deviance analysis and Akaike's information criterion. All predictor variables significantly influenced distribution of dolphins, which preferred steep areas at depths of 50–60 m, distance from shore of 3–5 km, and higher values of chlorophyll. In the warm season dolphins preferred colder waters and avoided deeper and warmer areas. Dusky dolphins in Golfo Nuevo are exploited as a tourism resource, and selected models should be considered when deciding the impact of dolphin-watching activities on management. DOI: 00.0000/00-MAMM-X-000.1

Key words: distribution modeling, dusky dolphin, generalized linear model, habitat selection, *Lagenorhynchus obscurus*, logistic regression

Habitat selection is a hierarchical process involving a series of innate and learned behavioral decisions made by an animal about what habitat it would use at different scales of the environment (Hutto 1985). Animals actively select where they live within the constraints of their physiology and life-history strategies or passively persist in certain habitats; therefore habitat selection is a behavioral consequence (Boyce and McDonald 1999). Availability of resources generally is not uniform in nature and use can change as availability changes. Therefore, habitat resources that are used should be compared to further available resources to reach valid conclusions concerning resource selection. When resources are used disproportionately to their availability, use is said to be selective (Manly et al. 2002).

The use of habitat selection models to predict the likely occurrence or distribution of wild populations is an important tool in conservation planning and wildlife management. Habitat models allow analysis of resource selection and prediction of the occurrence of a species. For example, Gross et al. (2002) developed habitat models from observation of mountain goats (*Oreamnos americanus*) in alpine habitats near Mt. Evans, Colorado. These models provided a way to use readily available data and simple techniques to identify suitable habitat quickly over large geographical areas. Poirazidis et al. (2004) modeled nesting preference for the Eurasian black vulture (*Aegypius monachus*) in Dadia Nature Reserve, northeastern Greece. In this area future changes in the habitat suitable for black vulture nesting are expected due to human activities and natural causes. Olivera-Gómez and Mellink (2005) constructed habitat models for the Antillean manatee (*Trichechus manatus manatus*) in Bahía de Chetumal, México. With the selected model the authors showed that preservation of current freshwater sources and their quality, and insuring that they are accessible to manatees, should be an obligatory element in the management and conservation of coastal ecosystems in the region. Predictive habitat modeling is a well-used tool for terrestrial animals (Gibson et al. 2004; Hill 1999; Jeganathan et al. 2004; Rushton et al. 2004) but has been applied only recently to cetaceans, and it is still in the early stages of development (Redfern et al. 2006).

Many cetacean species are wide-ranging and respond to interannual variability in marine ecosystems by changes in distribution pattern (Forney 2000) rather than with changes in survival or reproductive success or both. Habitat models are useful in predicting occurrence of cetaceans when interannual environmental variability is the primary concern. However, other temporal scales of environmental variability are relevant, for example, interdecadal variability. No consensus exists about how these types of models will perform to predict
2 cetacean distribution in light.

Authors have used cetacean habitat models for establishing protected marine areas (Cañadas et al. 2002; Hooker et al. 1999), improvement of abundance estimates (Forney 2000; Reilly and Fiedler 1994), understanding cetacean–fisheries interactions (Kaschner 2004; Torres et al. 2003), and studying habitat segregation of ecologically similar species or different ecotypes (Reilly 1990; Waring et al. 2001). Significant relationships between distributions of populations and bathymetric variables such as bottom depth, bottom slope, and distance to shore have been observed for many cetaceans, including dusky dolphins (*Lagenorhynchus obscurus*) in Golfo Nuevo, Argentina (Garaffo et al. 2007), bottlenose dolphin (*Tursiops truncatus*) ecotypes in the northwestern Atlantic (Torres et al. 2003), and harbor porpoises (*Phocoena*
3 *phocoena*) off northern California (Carretta et al. 2001).

Off the Patagonian coast of Argentina the dusky dolphin is one of the most common small cetaceans. This species has been caught incidentally in fishing nets off the coast at unsustainable levels since at least the 1980s (Dans et al. 2003). At the same time, dusky dolphins are the target of cetacean-watching activities in Golfo Nuevo. These activities were developed 12 years ago, particularly during the summer months when the dusky dolphin has become an alternative focal animal to the southern right whale (*Eubalaena australis*), which is present in the area only in winter. At present, dolphin watching in the area is still unregulated (Coscarella et al. 2003).

Coscarella et al. (2003) showed that dusky dolphins change their behavior, including interrupting feeding, when approached by boats, with unknown long-term effects for the populations. In addition, Dans et al. (2008) showed that boats can disrupt the normal sequence of dolphin behaviors in Golfo Nuevo, and interpretations of these results suggest long-term effects and the possibility of a higher impact if dolphin watching expands. Garaffo et al. (2007) also found clear evidence that dusky dolphins are not evenly distributed throughout the environment of Golfo Nuevo. They showed that the location of animals varied in the gulf between years and that different parts of the gulf were used by animals in different years. Therefore, predictive habitat models would be useful in knowing which areas present a greater probability of occurrence of dusky dolphins and thus need a conservation strategy.

To date, habitat-use patterns of dusky dolphins in the region have been studied in relation to physiographic variables (slope, depth, and distance from the coast—Garaffo et al. 2007). The goal of the present work is to build habitat selection models for dusky dolphins considering an expanded set of environmental variables: depth, slope, distance from shore, sea-surface temperature (sst), and concentration of chlorophyll *a*. Areas with lower sst and high chlorophyll concentrations can reveal upwelling areas. These areas could be concentrating prey of the dusky dolphin.

Materials and Methods

Study area.—Golfo Nuevo (42°20′–42°50′S, 64°20′–65°00′W; Fig. 1) in Argentina is surrounded by Península Valdés, a protected area that was declared a World Heritage Site by the United Nations Educational, Scientific, and
Cultural Organization in 1999. The area of the gulf is 4
2,500 km^2, and its maximum depth is 184 m (Mouzo et al. 1978). It is a semienclosed basin approximately 70 km long and 60 km wide. It is connected to the Atlantic Ocean by shallow waters of an average depth of 44 m and length of 16 km (Mouzo et al. 1978). The gulf represents a small portion of the distribution range of the dusky dolphin in the southwestern South Atlantic. The range in depth within the gulf is similar to that of the continental shelf habitat, and group sizes of dolphins are similar to those sighted in open waters (Coscarella et al. 2003; Crespo et al. 1997).

Golfo Nuevo is homogenous in its superficial layer with respect to temperature from May to November (cold season) when lower temperatures occur. However, it is spatially variable between December and April (warm season), with lower temperatures along the southern coast. Low temperatures also can occur along the northern coast. The highest temperatures occur in the central area of the gulf. In the summer a cyclonal movement of the water can be observed in satellite images (D. A. Gagliardini, Teledetection Laboratory, Centro Nacional Patagónico, pers. comm.; Fig. 2).

Survey procedures.—Random transects were surveyed by a boat in 2002–2007. Way points were recorded from a global positioning system every 2 min. Surveys were conducted at least twice a week, between 0800 and 2000 h, when weather conditions allowed. Timing of surveys was consistent across years. Two research vessels were used: a 6-m fiberglass boat with a 50-horsepower outboard engine in 2002 and 2003 and a 7-m fiberglass boat with a 105-horsepower outboard engine from 2004 to 2007. Search speed was 10 knots.

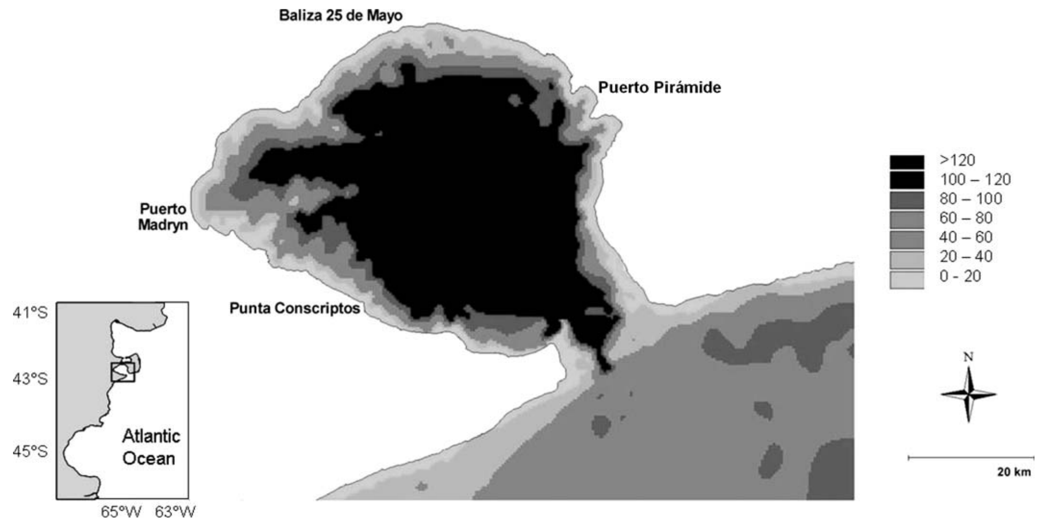

Fig. 1.—Map of Golfo Nuevo, Argentina, showing its bathymetry (m). Surveys were done from Puerto Madryn and Puerto Pirámide.

Once a group of dolphins was found it was followed as long as possible. A group was defined as any group of animals engaged in the same activity and moving in the same direction (Shane et al. 1986). Dolphin positions were obtained from global positioning system points every 2 min. All group follows continued until weather conditions became prohibitive or animals were no longer visible. If acceptable weather conditions persisted, we returned to the transect to look for another group. Our field protocol followed the guidelines of the American Society of Mammalogists (Gannon et al. 2007).

Environmental and biological data.—A grid of 1.5 × 1.5-km squares (cells) was constructed of the study area. A typical group of dusky dolphins occupies an area less than 1.5 × 1.5 km. Each cell of the grid was characterized by depth, slope, distance from shore, sst, and concentration of chlorophyll *a*. A nautical chart (H-218, 1:110000; Naval Hydrographic Service, Buenos Aires, Argentina) was used as the source of data on depth, slope, and distance from shore. Mean depth within a cell was calculated by averaging values of depth given by the chart. Slope was calculated as $(D_{max} - D_{min})/DI$, where D_{max} is maximum depth in the cell, D_{min} is minimum depth in the cell, and DI is distance (m) between the points of maximum and minimum depth, expressed in units of meters per kilometer (Cañadas et al. 2002; Garaffo et al. 2007). Distance from shore was calculated as the distance from the central point of the cell to the closest point on the coastline.

Mean sst data for each season were extracted from 2000 to 2005 from satellite images without clouds (NOAA Advanced Very High Resolution Radiometer; htpp://www.conae.gov.ar) at a spatial resolution 1.1 km^2 and overlaid on the grid. Monthly and seasonal averages were calculated, and each cell of the grid was characterized for sst. Concentration of chlorophyll *a* (mg/m^3) was extracted from *Red ANTARES*
(http://www.antares.ws). SeaWiFS images were used by this 5
source. Spatial resolution was 1.1 km^2. Satellite images from 2004 to 2007 were inspected at 1-month intervals. Seasonal averages were calculated, and each cell of the grid was characterized for chlorophyll concentration. Finally, each cell of the grid was characterized by presence or absence of dolphins. A coefficient of area use (AU) was calculated as:

$$AU = D_i/T_i,$$

where D_i is the cumulative time spent following dolphins in cell i and T_i is the total time of effort in cell i.

Data analysis.—Taking into account sst patterns, data were divided into those for the warm season (December–April) and

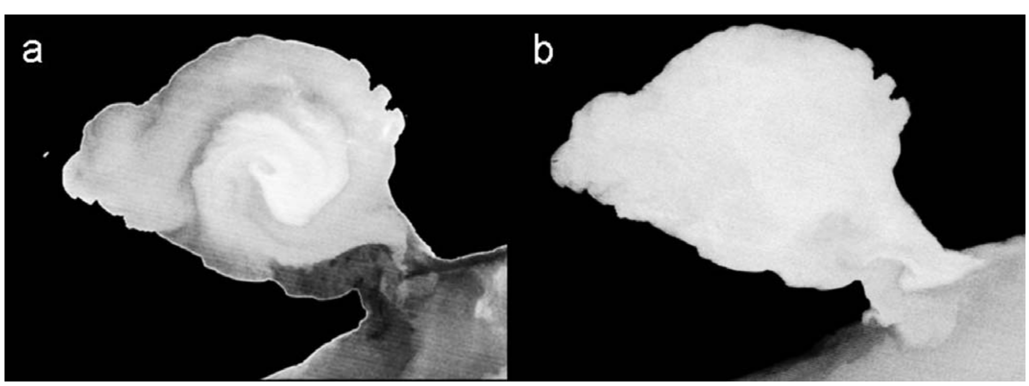

Fig. 2.—Sea surface temperature (Brightness Temperature derived from channel 6 of LANDSAT satellite images) during: a) warm season and b) cold season. Darker areas indicate colder water.

those for the cold season (May–November). Models were developed for each season, and then for the entire data set. Data collected during 2002–2005 were pooled to form the model-fitting data set. Data collected during 2006–2007 were used for cross-validation of the model.

Because dolphin occurrence in each cell was measured 2 ways (presence or absence of dolphins and AU), 2 types of generalized linear models were developed. First, to relate the presence or absence of dolphins to habitat variables and given that data on dolphin presence behave as a binary variable (i.e., presence versus absence), logistic regression models with a binomial error structure and logit-link function were used (Venables and Dichmont 2004). The logistic regression was a resource selection probability function (Manly et al. 1993) of the form:

$$p_{\mathrm{i}} = e_{\mathrm{i}}^{\mathrm{y}}/(1+e_{\mathrm{i}}^{\mathrm{y}})$$

and

$$\mathrm{y_i} = \beta_0 + \beta_1 \mathrm{x_{i1}} + \beta_2 \mathrm{x_{i2}} + \ldots + \beta_p \mathrm{x_{ip}},$$

where p_{i} is the probability of dolphins being present at site i, β_0 is the intercept and β_1 to β_p are the coefficients of the explanatory variables x_1 to x_p, respectively. The probability of dolphins being absent at site i was $1 - p_{\mathrm{i}}$. Second, to relate AU to habitat variables, models with a gamma error structure and log-link function were used, given that AU has positive values and an asymmetric distribution (McCullagh and Nelder 1983).

The evaluated explanatory variables were depth, slope, distance from shore, sst (only in the warm season), concentration of chlorophyll *a* (chlorophyll), depth^2, slope^2, distance from shore^2, sst^2, chlorophyll^2, depth^3, slope^3, distance from shore^3, sst^3, chlorophyll^3, and all interactions among the variables. Year was not used as a general proxy variable because inclusion of this term would preclude prediction in a novel year (Redfern et al. 2006).

Two approaches were used to address selection of the best models. The 1st approach used the deviance difference ($D_i - D_{i+1}$) between model *i* and model (*i* + 1), where model (*i* + 1) included all the parameters contained in model *i* plus some additional parameters; that is, model *i* was nested in model (*i* + 1). If $D_i - D_{i+1}$ is significantly large in comparison with a chi-square distribution with degrees of freedom equal to the number of additional parameters included in model (*i* + 1) but not in model *i*, then the extra parameters in model (*i* + 1) are considered to be necessary to describe the data (Harraway 1995). This procedure was used to test for improvement in model buildup when adding additional parameters. The best model is the one for which there is no significant improvement by fitting more parameters (Manly et al. 1993). SPSS 15 (SPSS, Inc., Chicago, Illinois) was used to fit the models.

In the 2nd approach the importance of each added term was evaluated using an information-theoretical approach based on Akaike's information criterion (AIC—Akaike 1973). Models 6 with a difference in AIC (delta AIC) <2 were considered to have equivalent support from the data (Burnham and Anderson 2002), and in such circumstances the most-parsimonious model was chosen.

Cross-validation is a tool to assess whether the selected models reflect not only the pattern in the data from which they were derived but also succeed in capturing a persisting biological relationship between environmental variables and dolphin presence (Burnham and Anderson 2002; Olden et al. 2002). The predictive performance was evaluated using cross-validation on an independently collected data set (2006–2007).

Confusion matrices of predicted and observed values based on each selected model were constructed. A confusion matrix contains information about actual and predicted classifications performed by a classification system. Performance of such systems is commonly evaluated using the data in the matrix. In addition, correct classification rate (proportion of all sites correctly predicted), sensitivity (proportion of positive sites correctly predicted), and specificity (proportion of negative sites correctly predicted) were calculated. These indices are threshold-dependent measures (selected cutoff value probability); therefore, additional method threshold-independent measures for evaluating models were used. A classification approach called the receiver operating characteristic was used. This approach is independent of probability cutoff level. Next, the area under curve was calculated. When the area under curve is >0.7, the model is considered useful (Fieldings and Bell 1997; Pearce and Ferrier 2000). SPSS 15 (SPSS, Inc., Chicago, Illinois) was used to calculate the receiver operating characteristic and area under curve.

Model assessment involves comparing derived probabilities with observed categories (i.e., the real absence–presence data). Most studies use thresholds to define absence (below threshold) and presence (above threshold) in the predictions (e.g., kappa statistic and classification tables—Gregr and Trites 2001; Hastie et al. 2005; Rushton et al. 2004). Threshold methods are highly sensitive to sample size and fail if the value of the number of absences exceeds that of presence values and are based on an arbitrarily chosen threshold value. In this study cross-validation was evaluated using the receiver operating characteristic in addition to classification tables; this method is threshold-independent.

Results

A total of 1,720 km^2 was surveyed in the research area between 2002 and 2007. A total of 763 cells were sampled for all years (2002–2005) and only 27.5% showed dolphin presence (Table 1). A total of 284 groups of dusky dolphins was sighted (47 groups in 2006–2007).

Models with a binomial error structure.—The analysis for whole year selected a model with distance to shore, chlorophyll^2, distance to shore^2, depth^2, distance to shore^3, and the interactions chlorophyll × slope and depth × slope. The best model for cold season included distance to shore, depth, slope, distance to shore^2, depth^2, slope^2, depth^3, and the interactions distance to shore × slope and depth × slope. The model for warm season included chlorophyll, sst, chlorophyll^2, sst^2, slope^2, chlorophyll^3, and sst^3 (Table 2).

Table 1.—Number of cells sampled and cells with dusky dolphins present for each season and all year. 7

		All year	Warm season	Cold season
Data for models (2002–2005)	Sampled	763	596	636
	Dolphins present	210	180	45
Data for validation (2006–2007)	Sampled	562	452	402
	Dolphins present	47	35	12

Models with a gamma error structure.—The analysis for whole year selected a model with chlorophyll, distance from shore, slope, distance from shore^2, chlorophyll^3, distance from shore^3, and the 3 interactions chlorophyll × distance from shore, distance from shore × depth, and distance from shore × slope. The best model for cold season included distance from shore, slope, and the 3 interactions distance from shore × depth, distance from shore × slope, and depth × slope. The model for warm season included chlorophyll, distance from shore, depth, sst, chlorophyll^2, distance from shore^2, chlorophyll^3, distance from shore^3, sst^3, and the 4 interactions chlorophyll × distance from shore, chlorophyll × depth, distance from shore × depth, and distance from shore × sst (Table 3).

Table 2.—Results of the best habitat model (generalized linear model with binomial error structure and logit-link function) relating environmental variables to presence of dusky dolphins for whole
8 year, cold season, and warm season.

Term	β	*SE*	*P*
Whole year			
Intercept	−6.971	0.748	0.0000
Distance from shore (Dfs)	2.174	0.227	0.0000
Chlorophyll^2 (C^2)	1.095	0.156	0.0000
Distance from shore^2 (Dfs^2)	−0.186	0.023	0.0000
Depth^2 (D^2)	−0.0002	0.00003	0.0000
Distance from shore^3 (Dfs^3)	0.005	0.0007	0.0000
C × slope (S)	0.040	0.012	0.0007
D × S	−0.0005	0.0002	0.0362
Cold season			
Intercept	−3.243	0.816	0.0000
Distance from shore (Dfs)	1.018	0.452	0.0243
Depth (D)	−0.134	0.049	0.0059
Slope (S)	0.137	0.046	0.0030
Distance from shore^2 (Dfs^2)	−0.063	0.028	0.0281
Depth^2 (D^2)	0.002	0.0008	0.0052
Slope^2 (S^2)	−0.001	0.0006	0.0931
Depth^3 (D^3)	−0.00001	0.0000	0.0051
Dfs × S	−0.027	0.009	0.0042
D × S	0.001	0.0006	0.1251
Warm season			
Intercept	−1,193.250	9.795	0.0000
Chlorophyll (C)	18.890	4.113	0.0000
Sea-surface temperature (sst)	−6.730	1.674	0.0000
Chlorophyll^2 (C^2)	−101.390	0.518	0.0000
sst^2	−0.140	0.145	0.0032
Slope^2 (S^2)	0.0001	0.0002	0.0996
Chlorophyll^3 (C^3)	0.760	0.214	0.0004
sst^3	−0.100	0.227	0.0045

In general, the 2 types of models suggested that dusky dolphins showed a clear preference for steep areas between 30 and 70 m deep and 3–5 km from shore. In addition, they avoided deeper areas (>100 m, in the central area of the gulf) and showed a preference for areas with higher concentration of chlorophyll *a*. In the warm season dolphins showed a preference for colder waters (Figs. 3–5). Predictive maps for 10
warm season, cold season, and whole year (Fig. 6) show that for the cold season the area of greater predicted probability of occurrence is a narrow portion nearer the coast than for the warm season.

Table 3.—Results of the best habitat model (generalized linear model with gamma error structure and log-link function) relating environmental variables to area use of dusky dolphins for whole year,
9 cold season, and warm season.

Term	β	*SE*	*P*
Whole year			
Intercept	−0.489	0.117	0.0000
Chlorophyll (C)	0.336	0.089	0.0002
Distance from shore (Dfs)	0.073	0.023	0.0011
Slope (S)	0.003	0.001	0.0001
Distance from shore^2 (Dfs^2)	−0.006	0.001	0.0000
Chlorophyll^3 (C^3)	−0.022	0.007	0.0021
Distance from shore^3 (Dfs^3)	0.0002	0.00005	0.0001
C × Dfs	0.018	0.010	0.0779
Dfs × D	−0.0002	0.00005	0.0001
Dfs × S	−0.0006	0.0002	0.0000
Cold season			
Intercept	0.008	0.018	0.6805
Distance from shore (Dfs)	0.014	0.007	0.0329
Slope (S)	0.002	0.0007	0.0054
Dfs × D	−0.0001	0.00004	0.0140
Dfs × S	−0.0008	0.0002	0.0001
D × S	0.00004	0.00001	0.0005
Warm season			
Intercept	221.4142	51.61614	0.0000
Chlorophyll (C)	1.4367	0.37012	0.0001
Distance from shore (Dfs)	1.7406	0.39588	0.0000
Depth (D)	−0.0077	0.00194	0.0001
Sea-surface temperature (sst)	−18.7628	4.39074	0.0000
Chlorophyll^2 (C^2)	−0.4927	0.14262	0.0006
Distance from shore^2 (Dfs^2)	−0.0182	0.00276	0.0000
Chlorophyll^3 (C^3)	0.0546	0.01764	0.0020
Distance from shore^3 (Dfs^3)	0.0005	0.00007	0.0000
sst^3	0.0197	0.00470	0.0000
C × Dfs	−0.0434	0.01246	0.0005
C × D	0.0023	0.00067	0.0005
Dfs × D	0.0003	0.00014	0.0335
Dfs × sst	−0.0837	0.02162	0.0001

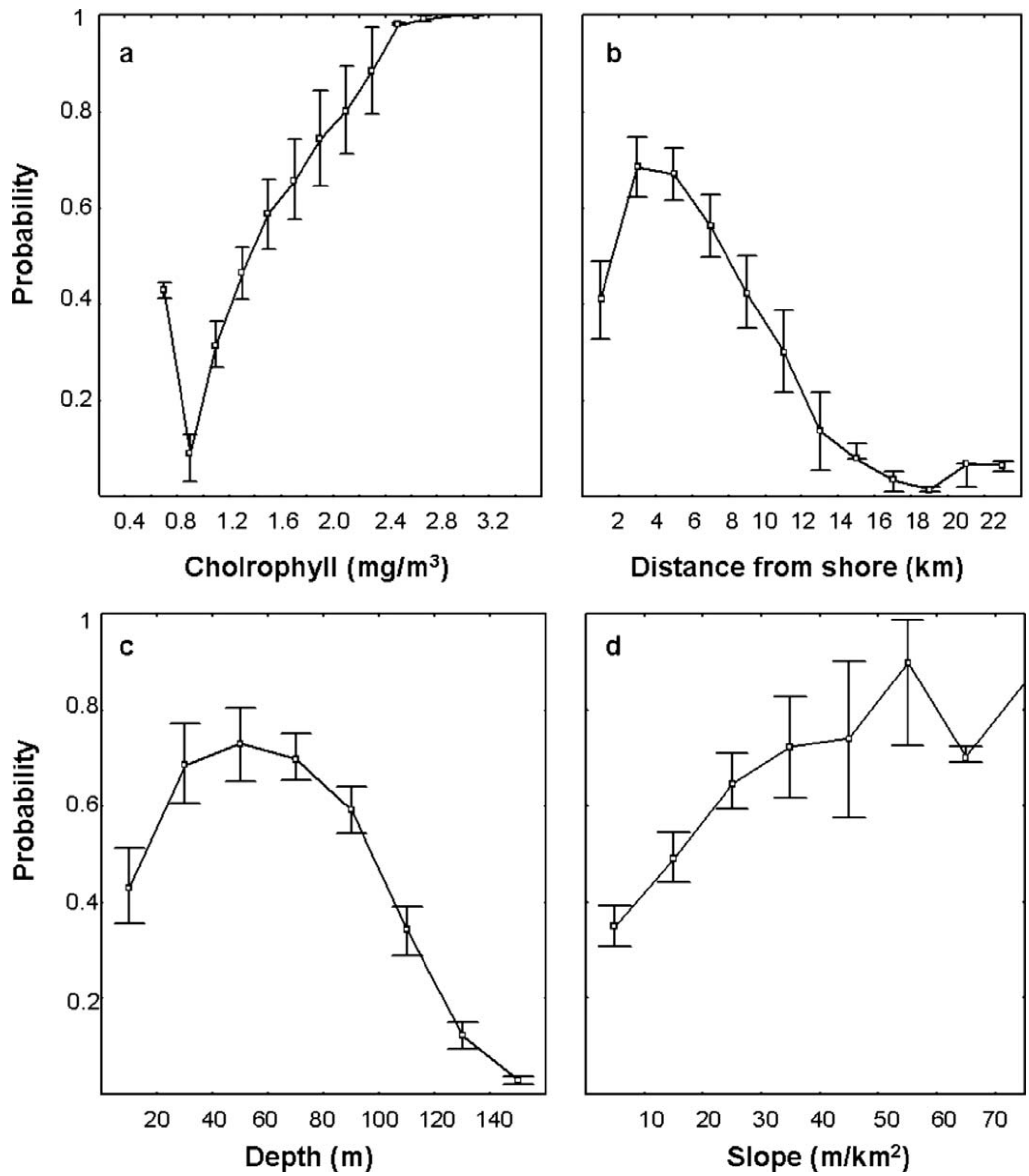

FIG. 3.—Mean probability of presence of dusky dolphins for differences in a) concentrations of chlorophyll *a*, b) distance from shore, c) depth, and d) slope for the whole model. Error bars indicate nonoutlier ranges.

Cross-validation.—Cross-validation for models with a binomial error structure showed that the selected models had correct classification rates >0.5 (Table 4). In addition, sensitivity for the whole year and the warm season was >0.7, indicating that the models work well to predict the presence of dusky dolphins in the area.

Cross-validation for generalized linear models with a gamma error structure showed that the selected models for warm season and cold season had correct classification rates >0.5 (Table 4). However, the selected model for whole year had a correct classification rate <0.5. Sensitivity for the whole year and the cold season models was >0.7, indicating that the models work very well in predicting presence of dolphins. However, only values of the area under curve >0.7 indicate that the models can be considered useful; therefore only the warm-season model could be considered useful (Table 5).

DISCUSSION

Habitat modeling is a powerful analytical tool for investigating where animals are found, why they might occur there, and where they could be expected to occur (Boyce and McDonald 1999; Rushton et al. 2004). This study provides an analysis of habitat selection by dusky dolphins based on a number of environmental parameters at sites where these cetaceans were observed and at sites where they were not observed. Such modeling of habitat selection allows a more holistic approach by incorporation of any measured variable and interactions of variables (Bräger et al. 2003). It also represents a great improvement over using simple measures of animal occurrence such as cumulative distribution maps. Cross-validation and model evaluation as done here are critical steps frequently omitted from habitat modeling.

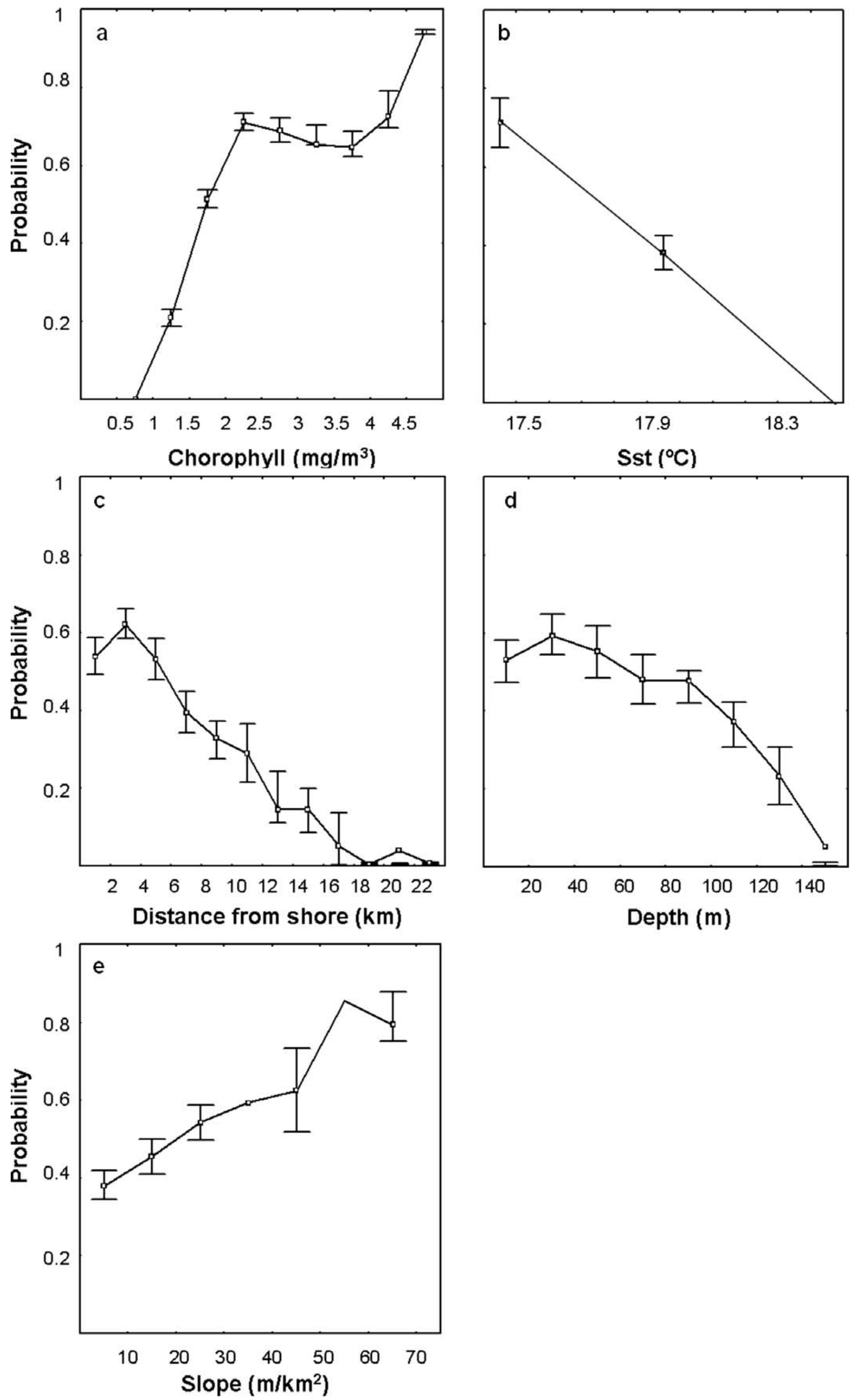

Fig. 4.—Mean probability of presence of dusky dolphins for differences in a) concentrations of chlorophyll *a*, b) sea-surface temperature (sst), c) distance from shore, d) depth, and e) slope for the warm-season model. Error bars indicate nonoutlier ranges.

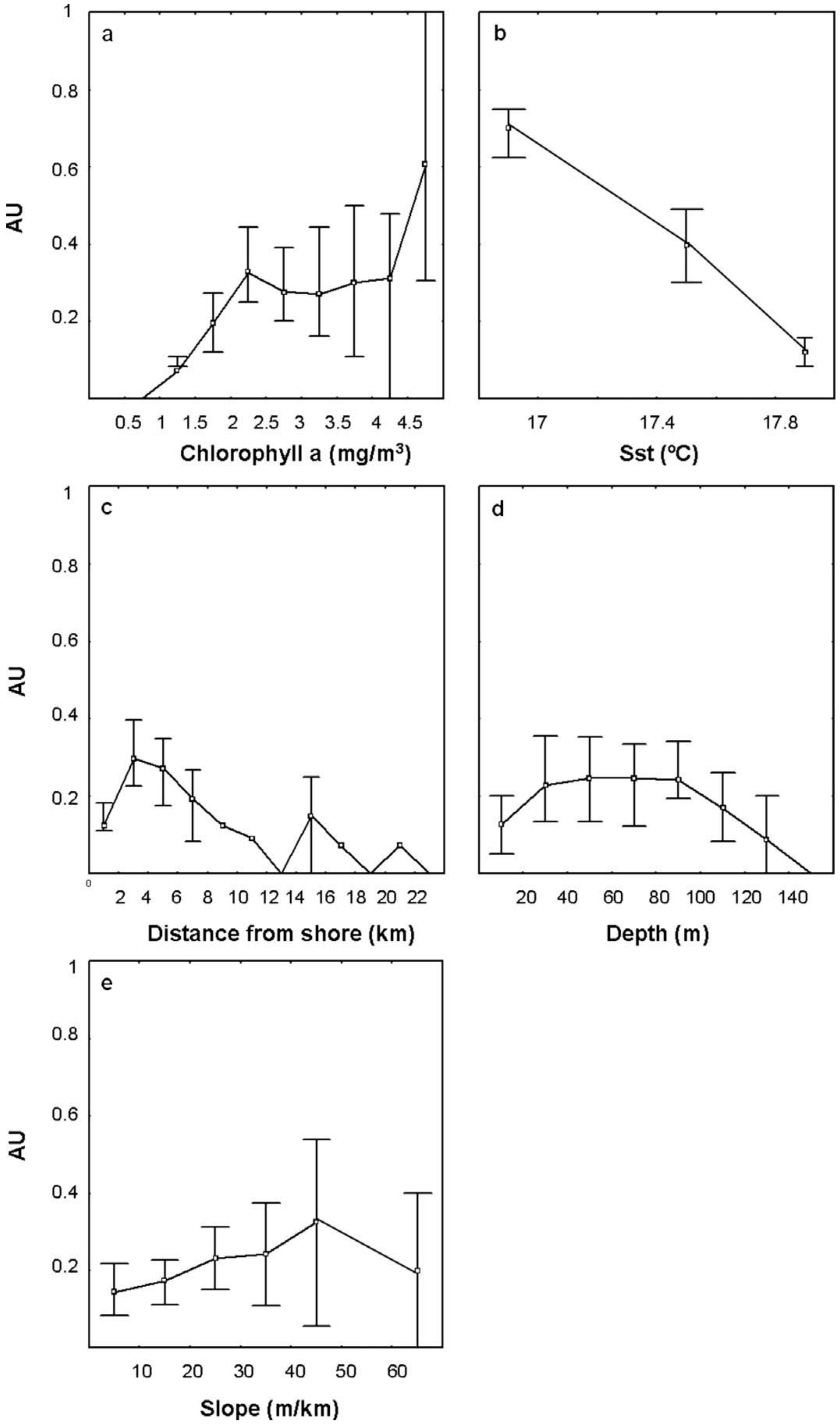

Fig. 5.—Mean predicted area use (AU) by dusky dolphins for difference in a) concentrations of chlorophyll *a*, b) sea-surface temperature (sst), c) distance from shore, d) depth, and e) slope for the warm-season model. Error bars indicate nonoutlier ranges.

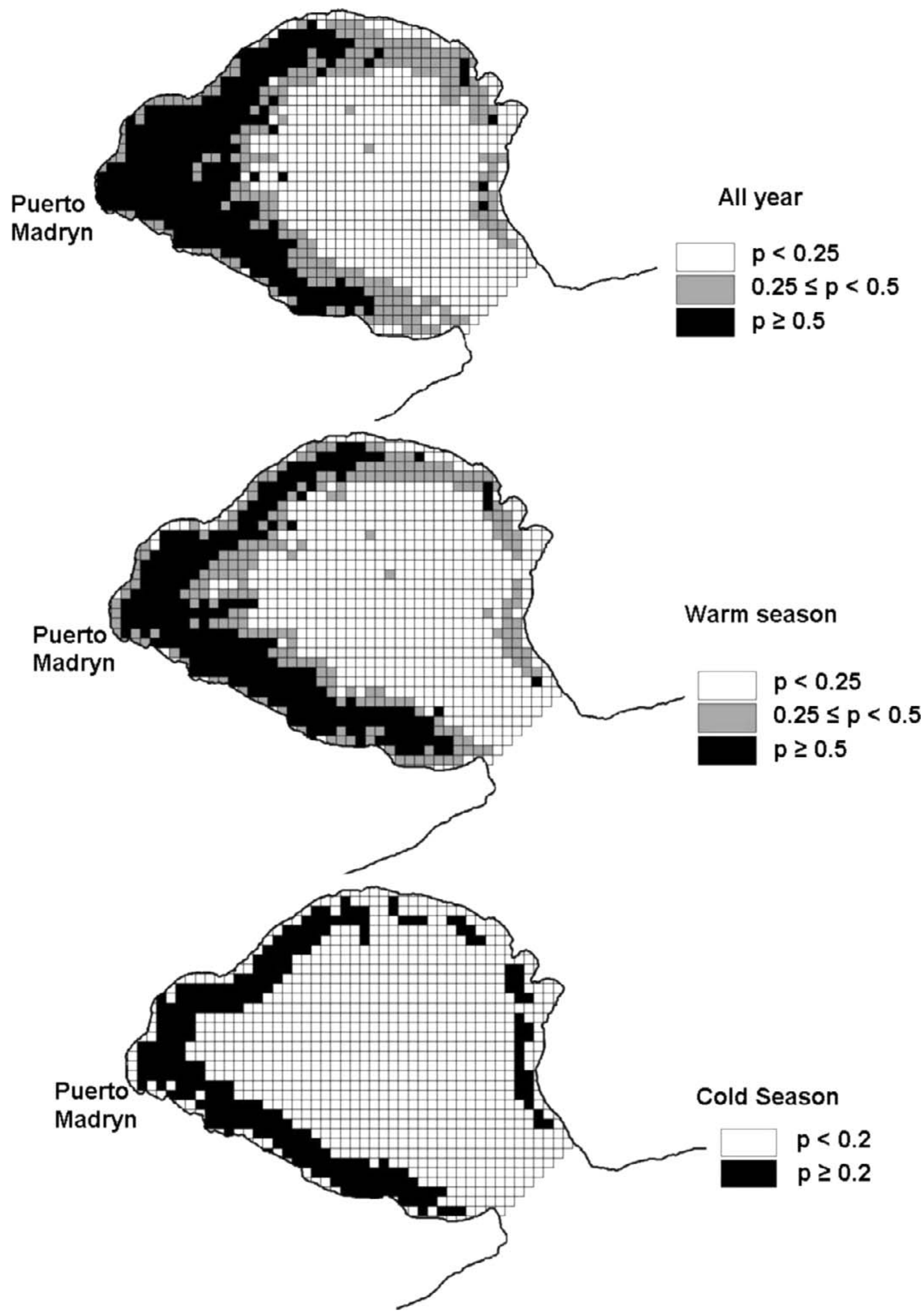

FIG. 6.—Predicted probability of occurrence for dusky dolphins in Golfo Nuevo, Argentina, by season and for all year.

Dusky dolphins show a clumped distribution in coastal areas of Golfo Nuevo (Garaffo et al. 2007). The variables included in this study significantly influence their habitat selection. The dolphins prefer waters between 50 and 60 m deep, steep slopes, distances from shore between 3 and 5 km, and areas with higher values of chlorophyll. In the warm season colder areas are preferred. These environmental variables may influence the animals directly, for example, through thermoregulatory and energetic demands, or indirectly, by acting upon other biotic factors such as prey availability and predator avoidance (Scott et al. 1990; Wells et al. 1980).

Given that dusky dolphins seem to spend approximately 16–20% of their diurnal time foraging (Dans et al. 2008; Degrati et al. 2008b), the distribution of potential prey could be an important factor underpinning the observed patterns of habitat selection. The principal prey item of dusky dolphins is the

TABLE 4.—Results of cross-validation A) for each generalized linear model with a binomial error structure and logit-link function and B) for each generalized linear model with a gamma error structure and log-link function.

	Correct classification rate	Sensitivity	Specificity
A)			
Whole year (cutoff = 0.5)	0.60	0.82	0.51
Warm season (cutoff = 0.5)	0.6	0.92	0.54
Cold season (cutoff = 0.2)	0.54	0.61	0.54
B)			
Whole year (cutoff = 1.5)	0.40	1	0.29
Warm season (cutoff = 1.5)	0.84	0.53	0.87
Cold season (cutoff = 1)	0.50	1	0.46

Argentine anchovy (*Engraulis anchoita*—Koen Alonso et al. 1998). The distribution and abundance of the anchovy in Golfo Nuevo have been studied recently with acoustic surveys (Degrati et al. 2008a). Schools of anchovy showed a contagious coastal distribution on the study area. This distribution was similar to the area of greater probability of occurrence of dusky dolphins. During the surveys in the warm season the anchovy schools were recorded mainly off the southern coast of the gulf, within the area of greater probability of occurrence of dolphins predicted by the selected model for that season. Important are the lower temperatures during the warm season that the southern coast of the gulf showed.

Sea-surface temperature (sst) was an important predictive variable during the warm season. However, during the cold season, the gulf is homogenous with respect to sst. Therefore, we might predict dolphins to be more dispersed. However, they were not more dispersed during the cold season. The variables included here are not likely to be the only factors determining habitat selection in dusky dolphin. Other factors, such as the biological variables prey availability, predators, and social structure, could be important.

Occurrence models show some limitations. Even good potential habitats will not always be used. Conversely, the chance of sighting dolphins at one site compared to another depends not only on habitat quality but also on the number of animals using the area and their group structure. Areas of high predicted occurrence indicate preference but do not provide information on behavior or density. Areas that might be used only occasionally but for critical purposes most likely will be underpredicted by occurrence models (Heinrich 2006).

In general, in this study the models with binomial error structure had higher area under curve values than those with gamma error structure (dependent variable: coefficient of area use [AU]). Therefore, the former would be more useful for predicting the potential area used by the dolphins. Cross-validation on an independent data set indicated that the models for whole year and the warm season are useful to predict the occurrence, and they should be considered when making
11 conservation and management decisions. Dusky dolphins in Golfo Nuevo are exploited as a tourism resource mainly during the summer austral months. Interactions between whale- and dolphin-watching vessels and wild dolphins have been shown to produce both short-term (Constantine et al. 2004; Coscarella et al. 2003; Lusseau 2003) and long-term (Bejder et al. 2006) disturbances, such as changes in occurrence and local abundance. The definition of appropriate restricted times or areas where only authorized boats or interactions would be permitted is a potentially powerful way to reduce these impacts on cetacean populations (Bejder et al. 2006; Lusseau and Higham 2004).

TABLE 5.—Area under curve values for each selected model for 2 types of models. GLM = generalized linear model.

	GLM with binomial error structure	GLM with gamma error structure
Whole year	0.70	0.62
Warm season	0.86	0.78
Cold season	0.55	0.5

Golfo Nuevo is a relatively small area within the distribution range of dusky dolphins in the southwestern South Atlantic. Outside Golfo Nuevo (continental shelf) areas can be found that present environmental characteristics similar to those in the areas preferred by dusky dolphins inside the gulf. Dusky dolphins are affected by incidental mortality from fisheries along the Argentinian coast (outside Golfo Nuevo). In particular, annual mortality from trawl nets was estimated to be near threshold levels (Dans et al. 2003). Therefore, Golfo Nuevo is a critical area for the dusky dolphin. At present, Península Valdés constitutes a protected area with managed resources. However, only the northern portion of Golfo Nuevo is included in this area. Obviously, this plan does not take into account the movements of dusky dolphins. Inside Golfo Nuevo the southern portion has colder waters. The selected models show that these areas have a greater probability of occurrence of dusky dolphins. However, this portion of the gulf is not included in the protected area. Therefore, because the selected models in this study can be considered useful, these should be considered when deciding the integrated management scheme.

RESUMEN

La utilización de modelos de selección de hábitat para predecir la ocurrencia de poblaciones salvajes es una herramienta importante para el manejo y conservación de la vida silvestre. El objetivo de este trabajo es construir modelos de selección de hábitat para el delfín oscuro considerando las siguientes variables: profundidad, pendiente, distancia a la costa, temperatura superficial del mar y clorofila. Se realizaron transectas al azar con embarcación (2002–2007). Se construyó una grilla con celdas de 1.5 × 1.5 km sobre el
área de estudio. Se utilizó un SIG para integrar la información 12
de las variables con la grilla. Cada celda fue caracterizada por profundidad, pendiente, distancia a la costa, temperatura superficial del mar, clorofila, presencia–ausencia de delfines y
por un índice (AU) de uso por parte de los delfines que 13

considera el esfuerzo realizado. Se desarrollaron modelos para cada estación (fría y cálida) y 1 para todos los datos juntos. Los datos colectados durante 2002–2005 se agruparon y se usaron para el ajuste del modelo y los datos colectados durante 2006–2007 se utilizaron para la validación cruzada. Se utilizó regresión logística con estructura de error binomial y función de enlace logit para relacionar la presencia de los delfines con las variables. Además se utilizó un modelo con estructura de error gamma y function de enlace log para relacionar el AU
14 con las variables. Se utilizó un análisis de deviance y AIC para seleccionar los modelos. Todas las variable predictoras influenciaron significativamente la distribución de los delfines. Los delfines oscuros mostraron una clara preferencia por áreas con pendientes pronunciadas, profundidades entre 50 y 60 m de profundidad, distancias a la costa entre 3 y 5 km y áreas con valores más altos de clorofila. Durante la estación cálida los delfines prefirieron aguas más frías. Los delfines evitaron las áreas más profundas y más cálidas. Los delfines oscuros son explotados como un recurso turístico en el Golfo
15 Nuevo. Por lo tanto, los modelos seleccionados son de gran utilidad y deberían se considerados cuando se decida el esquema de manejo para la actividad comercial de avistamiento de delfines.

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Literature Cited

Akaike, H. 1973. Information theory and an extension of maximum likelihood principle. Pp. 267–281 in International Symposium on Information Theory (B. N. Petran and F. Csàaki, eds.). Akadèemiai Kiadi, Budapest, Hungary.

Bejder, L., A. Samuels, H. Whitehead, N. Gales, and J. Mann. 2006. Interpreting short-term behavioural responses to disturbance within a longitudinal perspective. Animal Behaviour 72:1149–1158.

Boyce, M. S., and L. L. McDonald. 1999. Relating populations to habitats using resource selection functions. Trends in Ecology & Evolution 14:268–290.

Bräger, S., J. A. Harraway, and B. J. F. Manly. 2003. Habitat selection in a coastal species (*Cephalorhynchus hectori*). Marine Biology 143:233–244.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference. 2nd ed. Springer-Verlag, New York.

Cañadas, A., R. Sagarminaga, and S. García-Tiscar. 2002. Cetacean distribution related with depth and slope in the Mediterranean waters off southern Spain. Deep Sea Research Part I 49:2053–2073.

Carretta, J. V., B. L. Taylor, and S. J. Chivers. 2001. Abundance and depth distribution of harbor porpoise (*Phocoena phocoena*) in northern California determined from a 1995 ship survey. Fishery Bulletin 99:29–39.

Constantine, R., D. H. Brunton, and T. Dennis. 2004. Dolphin-watching tour boats change bottlenose dolphin (*Tursiops truncatus*) behaviour. Biological Conservation 117:299–307.

Coscarella, M. A., S. L. Dans, E. A. Crespo, and S. N. Pedraza. 2003. Potential impact of unregulated dolphin watching activities in Patagonia. Journal of Cetacean Research and Management 5:77–84.

Crespo, A. E., et al. 1997. Distribution of dusky dolphins *Lagenorhynchus obscurus* (Gray, 1828) in the southwestern Atlantic Ocean with notes on the size of herds. International Whaling Commission Report 47:693–698.

Dans, S. L., E. A. Crespo, M. Koen Alonso, and S. N. Pedraza. 2003. Incidental catch of dolphins in trawling fisheries off Patagonia, Argentina: can populations persist? Ecological Appli-
cations 13:754–762. 19

Dans, S. L., E. A. Crespo, S. N. Pedraza, M. Degrati, and G. V. Garaffo. 2008. Dusky dolphins and tourist interaction: effect on diurnal feeding behavior. Marine Ecology Progress Series 365:273–285.

Degrati, M., S. L. Dans, E. A. Crespo, G. V. Garaffo, and A. Cabreira. 2008a. Asociación entre delfines oscuros y anchoitas, su disposición espacial en el Golfo Nuevo, Argentina. 13° Reunión de Especialistas en Mamíferos Acuáticos de América del Sur,
Montevideo, Uruguay. 20

Degrati, M., S. L. Dans, S. N. Pedraza, E. A. Crespo, and G. V. Garaffo. 2008b. Diurnal behaviour of dusky dolphins, *Lagenorhynchus obscurus*, in Golfo Nuevo. Journal of Mammalogy 89:1241–1247.

Fieldings, A. H., and J. F. Bell. 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. Environmental Conservation 34:38–40.

Forney, K. A. 2000. Environmental models of cetacean abundance: reducing uncertainty in population trends. Conservation Biology 14:1271–1286.

Gannon, W. L., R. S. Sikes, and the Animal Care and Use Committee of the American Society of Mammalogists. 2007. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. Journal of Mammalogy 88:809–823.

Garaffo, G. V., S. L. Dans, S. N. Pedraza, E. A. Crespo, and M. Degrati. 2007. Habitat use by dusky dolphin in Patagonia: how predictable is their location? Marine Biology 152:165–177.

Gibson, L. A., B. A. Wilson, D. M. Cahill, and J. Hill. 2004. Spatial prediction of rufous bristlebird habitat in a coastal heathland: a GIS-based approach. Journal of Applied Ecology 41:213–223.

Gregr, E. J., and A. W. Trites. 2001. Predictions of critical habitat for five whale species in the waters of coastal British Columbia. Canadian Journal of Fisheries and Aquatic Sciences
58:1265–1285. 21

Gross, J. E., M. C. Kneeland, D. F. Reed, and R. M. Reich. 2002. GIS-based models for mountain goats. Journal of Mammalogy 83:218–228.

Harraway, J. 1995. Regression methods applied. University of Otago Press, Dunedin, New Zealand.

Hastie, G. D., R. J. Swift, G. Slesser, P. M. Thompson, and W. R. Turrell. 2005. Environmental models for predicting oceanic dolphin habitat in the northeast Atlantic. ICES Journal of Marine Science 62:760–770.

Heinrich, S. 2006. Ecology of Chilean dolphins and Peale's dolphins at Isla Chiloé, southern Chile. Ph.D. dissertation, University of St.
22 Andrews, St. Andrews, Scotland, United Kingdom.

Hill, J. K. 1999. Butterfly spatial distribution and habitat requirements in a tropical forest: impacts of selective logging. Journal of Applied Ecology 36:564–572.

Hooker, S. K., H. Whitehead, and S. Gowans. 1999. Marine protected area design and the spatial and temporal distribution of cetaceans in a submarine canyon. Conservation Biology 13:592–602.

Hutto, R. L. 1985. Habitat selection by nonbreeding migratory land birds. Pp. 455–476 in Habitat selection in birds (M. L. Cody, ed.). Academic Press, Orlando, Florida.

Jeganathan, P., et al. 2004. Modelling habitat selection and distribution of the critically endangered Jerdon's courser *Rhiptilus bitorquatus* in scrub jungle: an application of a new tracking method. Journal of Applied Ecology 41:224–237.

Kaschner, K. 2004. Modelling and mapping of resource overlap between marine mammals and fisheries on a global scale. Ph.D. dissertation, University of British Columbia, Vancouver, British Columbia, Canada.

Koen Alonso, M., E. A. Crespo, N. A. García, S. N. Pedraza, and M. A. Coscarella. 1998. Diet of dusky dolphins, *Lagenorhynchus obscurus*, in waters of Patagonia, Argentina. Fishery Bulletin 96:366–374.

Lusseau, D. 2003. The effects of tour boats on the behavior of bottlenose dolphins: using Markov chains to model anthropogenic impacts. Conservation Biology 17:1785–1793.

Lusseau, D., and J. E. S. Higham. 2004. Managing the impacts of dolphin-based tourism through the definition of critical habitats: the case of bottlenose dolphin (*Tursipos* spp.) in Doubtful Sound,
23 New Zealand. Tourism Management 25:657–667.

McCullagh, P., and J. A. Nelder. 1983. Generalized linear models.
24 Chapman and Hall, London, United Kingdom.

Manly, B. J. F., L. L. McDonald, and D. L. Thomas. 1993. Resource selection by animals. Chapman and Hall, London, United Kingdom.

Manly, B. J. F., L. L. McDonald, D. L. Thomas, T. L. McDonald, and W. P. Ericsson. 2002. Resource selection by animals. 2nd ed.
25 Kluwer Academic Publishers, Dordrecht, Netherlands.

Mouzo, F. H., M. L. Garza, J. F. Izquierdo, and R. O. Zibecchi. 1978. Rasgos de la geología submarina del Golfo Nuevo. Acta
26 Oceanográfica Argentina 2(1) : 15—32.

Olden, J. D., D. A. Jackson, and P. R. Peres-Neto. 2002. Predictive models of fish species distributions: a note on proper validation and chance predictions. Transactions of the American Fisheries Society 131:329–336.

Olivera-Gómez, L. D., and E. Mellink. 2005. Distribution of the Antillean manatee (*Trichechus manatus manatus*) as a function of habitat characteristics, in Bahía de Chetumal, México. Biological Conservation 121:127–133.

Pearce, J., and S. Ferrier. 2000. Evaluating the predictive performance of habitat models developed using logistic regression. Ecological Modelling 113:225–245.

Poirazidis, K., V. Goutner, T. Skartsi, and G. Stamou. 2004. Modelling nesting habitat as a conservation tool for the Eurasian black vulture (*Aegypius monachus*) in Dadia Nature Reserve, northeastern Greece. Biological Conservation 118:235–248.

Redfern, J. V., et al. 2006. Techniques for cetacean-habitat modeling. Marine Ecology Progress Series 310:271–295.

Reilly, S. B. 1990. Seasonal changes in distribution and habitat differences among dolphins in the eastern tropical Pacific. Marine Ecology Progress Series 66:1–11.

Reilly, S. B., and P. C. Fiedler. 1994. Interannual variability of dolphin habitats in the eastern tropical Pacific. I. Research vessel surveys 1986–1990. Fishery Bulletin 92:434–450.

Rushton, S. P., S. J. Ormerod, and G. Kerby. 2004. New paradigms for modeling species distribution? Journal of Applied Ecology 41:193–200.

Scott, M. D., R. S. Wells, and A. B. Irvine. 1990. A long-term study of bottlenose dolphins on the west coast of Florida. Pp. 235–244 in The bottlenose dolphin (S. Leatherwood and R. R. Reeves, eds.). Academic Press, San Diego, California.

Shane, S. H., R. S. Wells, and B. Würsig. 1986. Ecology and social organization of the bottlenose dolphin: a review. Marine Mammal
Science 2:34–63. 27

Torres, L. G., P. E. Rosel, C. D'Agrosa, and A. J. Read. 2003. Improving management of overlapping bottlenose dolphin ecotypes through spatial analysis and genetics. Marine Mammal
Science 19:502–514. 28

Venables, W. N., and C. M. Dichmont. 2004. GLMs, GAM and GLMMs: an overview of theory for applications in fisheries research. Fisheries Research 70:319–337.

Waring, G. T., T. Hamazaki, D. Sheehan, G. Wood, and S. Baker. 2001. Characterization of beaked whale (*Ziphiidae*) and sperm whale (*Physeter macrocephalus*) summer habitat in shelfedge and deeper waters off the northeast US. Marine Mammal Science
17:703–717. 29

Wells, R. S., A. B. Irvine, and M. D. Scott. 1980. The social ecology of inshore odontocetes. Pp. 263–317 in Cetacean behavior: mechanisms and processes (L. M. Herman, ed.). Wiley, New York.

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