Modeling habitat use for dusky dolphin and Commerson's dolphin in Patagonia

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ABSTRACT: Several species of small cetaceans inhabit the coastal area of Patagonia (Argentina), but little is known about their distribution and the degree of overlap between them. The goal of the present study was to build habitat-selection models for small cetaceans in order to assess areas of particular importance for the different species. These models were constructed using physiographic and remotely sensed variables. From 1994 to 2007, 13 aerial surveys were conducted along the Patagonian coast (from Golfo San Matías: 40°40′–42°14′S, 65°00′–63°47′W to Bahía de los Nodales: 48°00′S, 65°35′W). A grid of 0.5° × 0.5° cells was constructed for the study area. Each cell was characterized by environmental variables and by the encounter rate (ER) for each cetacean species. The ER of each species was investigated in relation to environmental variables using generalized linear models, and model averaging (multimodel inference) was used to obtain a predicted ER for the different species. The correlation between the ER of different species was analyzed by Spearman rank correlation. The environmental variables that were found to be significant predictors of species distribution differed between species. The ERs of dusky dolphin *Lagenorhynchus obscurus* and Peale's dolphin *L. australis* showed a positive relationship. Commerson's dolphin *Cephalorhynchus commersonii* presented a more coastal distribution than the other species, and individuals were more often found feeding in estuarine zones. Knowledge of the patterns of distribution of small cetaceans along the Patagonian coast provides baseline knowledge of how these species interact with each other and their environment. Such information should be considered when managing potential areas of conflict between coastal small cetaceans and human activities.

KEY WORDS: Distribution modeling · Dolphins · Generalized linear model · Habitat selection · Patagonia

INTRODUCTION

The coastal area of Patagonia, Argentina, is a highly productive environment, and is therefore very important for both regional and local economies and marine life. Many species of seabirds, marine mammals, migratory birds, fishes, mollusks, and crustaceans breed and forage along these coasts. Several species of small cetaceans inhabit these waters. Among the most abundant are the dusky dolphin *Lagenorhynchus obscurus*, Peale's dolphin *L. australis*, Commerson's dolphin *Cephalorhynchus commersonii*, the common

dolphin *Delphinus delphis*, the bottlenose dolphin *Tursiops truncatus*, Burmeister's porpoise *Phocoena spinipinnis*, and the spectacled porpoise *P. dioptrica*. Little is known about the distribution of these species within the Patagonian shelf and the degree of overlap between them. A considerable degree of sympatry between the dusky dolphin and Peale's dolphin exists, although these species may use different habitats (Crespo et al. 1997a, Brownell et al. 1998).

Co-occurrence of 2 or more species in the same geographic area, i.e. sympatry, is common in marine environments, where important resources such as prey are grouped and patchily distributed. When different species require similar resources and these resources are limited, temporal or spatial segregation may occur to reduce competition (Roughgarden 1976). Such habitat partitioning has been observed in many marine species (Gowans & Whitehead 1995). Alternatively, species may be able to coexist as a result of dietary differences or by using the area for different functions, so that they do not exert a strong competitive pressure on each other (Bearzi 2005).

While knowledge of a species' distribution is a fundamental part of ecological studies, being able to predict the distribution is essential for conservation and population management (Boyce & McDonald 1999, Hill 1999, Cabeza et al. 2004, Gibson et al. 2004, Jeganathan et al. 2004). Predictive habitat models can provide a powerful tool for assessing areas of high relative density, and for determining the factors that influence distribution (Redfern et al. 2006). In turn, the identification of these key areas for each species provides a focus for conservation action and appropriate management. Marine mammals are potential indicator species, in that their protection should also ensure the health of other key components of a marine ecosystem (Hooker & Gerber 2004).

Small cetaceans are subject to a wide variety of anthropogenic effects, including direct mortality (e.g. bycatch or whaling), competition for prey, contamination from chemical compounds, degradation and loss of important habitat, and effects from global climate change (Whitehead et al. 2000, Bjørge 2001, Evans 2002). Many authors have used cetacean habitat models to establish marine protected areas (Hooker et al. 1999, Cañadas et al. 2002, Bailey & Thompson 2009), predict which areas present a greater probability of occurrence of species (Garaffo et al. 2010), improve abundance estimates (Reilly & Fiedler 1994, Forney 2000), understand cetacean-fisheries interactions (Torres et al. 2003, Kaschner 2004), or to study habitat segregation of ecologically similar species or different ecotypes (Reilly 1990, Waring et al. 2001). Several studies have described cetaceans' distribution and habitat preferences by linking their presence to different habitat variables (Forcada 2002). Such variables include sea temperature (Brown & Winn 1989, Baumgartner et al. 2001, Cañadas et al. 2005, Panigada et al. 2008, Garaffo et al. 2010), bathymetric and physiographic variables (Baumgartner 1997, Carretta et al. 2001, Cañadas et al. 2002, 2005, Torres et al. 2003, Panigada et al. 2005, 2008, Garaffo et al. 2007, 2010, Ingram et al. 2007, Bailey & Thompson 2009, Embling et al. 2010), currents and frontal systems (Tynan 1998, Mendes et al. 2002, Johnston et al. 2005a,b, Pedraza 2008), primary production (Littaye et al. 2004, Panigada et al. 2008, Garaffo et al. 2010), and prey distribution (Jaquet & Gendron 2002, Baumgartner et al. 2003, Macleod et al. 2004).

In the Patagonian waters of Argentina, the main threats to small cetaceans are incidental mortality in fishing gear, indirect effects of fisheries, tourism interactions, and more recently, offshore oil exploration (Corcuera et al. 1994, Crespo et al. 1994, 1997b, 2000, Goodall et al. 1995, Dans et al. 1997, 2003, 2008, Coscarella et al. 2003). The dusky dolphin, Peale's dolphin, Commerson's dolphin, the common dolphin, the bottlenose dolphin, and Burmeister's porpoise are species that suffer both direct and indirect effects from interaction with fisheries operating in the Argentine Sea (Corcuera et al. 1994, Crespo et al. 1994, 1997b, 2000, Goodall et al. 1995, Dans et al. 1997, 2003). In addition, the dusky dolphin is a target of commercial whale watching in the Golfo Nuevo, as is Commerson's dolphin near the Chubut River and the estuary of Puerto Deseado (Coscarella et al. 2003, Dans et al. 2008).

Predictive habitat models for different species can provide a background for empirically based recommendations for cetacean conservation. Habitat-selection models have been used successfully for the dusky dolphin in Golfo Nuevo (~2500 km^2 in area) (Garaffo et al. 2010), showing that physiography, sea surface temperature (SST), and chlorophyll *a* (Chl *a*) concentration were all important in determining which areas would have a higher probability of dusky dolphin occurrence. The goal of the present work was to build habitat-selection models for the 2 most abundant small cetacean species (dusky dolphin and Commerson's dolphin) in the Patagonian marine system (from Golfo San Matías to Bahía de los Nodales), using both physiographic (depth and distance from shore [Dfs]) and remotely sensed environmental variables (SST and Chl *a*). This is the first large-scale spatial study to use habitat-selection models for small cetaceans in the southwest Atlantic Ocean, and the results will help differentiate among the species' habitat preferences, which in turn is useful for conservation and management.

MATERIALS AND METHODS

Data collection. From 1994 to 2007 (see Table 1), 13 aerial surveys were conducted along Patagonian coastal and neritic waters (from Golfo San Matías: 40° 40′–42° 14′ S, 65° 00′–63° 47′W to Bahía de los Nodales: 48° 00′ S, 65° 35′ W; ~53 000 km² in area; Fig. 1). The surveys were carried out using 2 different high-wing twin-engine aircrafts, depending on the year of the survey: a CASA C-212 belonging to Prefectura Naval Argentina (National Coast Guard of Argentina) and a Cessna 337 Super-Skymaster. On each flight in the Cessna 337, 3 trained people traveled: 1 recorder and 2 observers (1 on each side of the plane); and 5 trained people traveled on each flight in the CASA C-212: 4 observers and 1 recorder. Each survey design was planned in advance to be between the shoreline and a distance of ~100 km from the coast and at a height of 150 m. The design was based on both the availability, the cost and the range of the aircraft, and on the weather conditions for safety and security. Surveys were undertaken on days with a calm sea state (Beaufort ≤3). Data on survey effort and cetacean locations were recorded using a GPS (Fig. 1). The original aim of these surveys was to estimate the abundance of the cetacean species. However, given the quality of information obtained, it was possible to use these surveys to relate the distribution of different species to environmental variables.
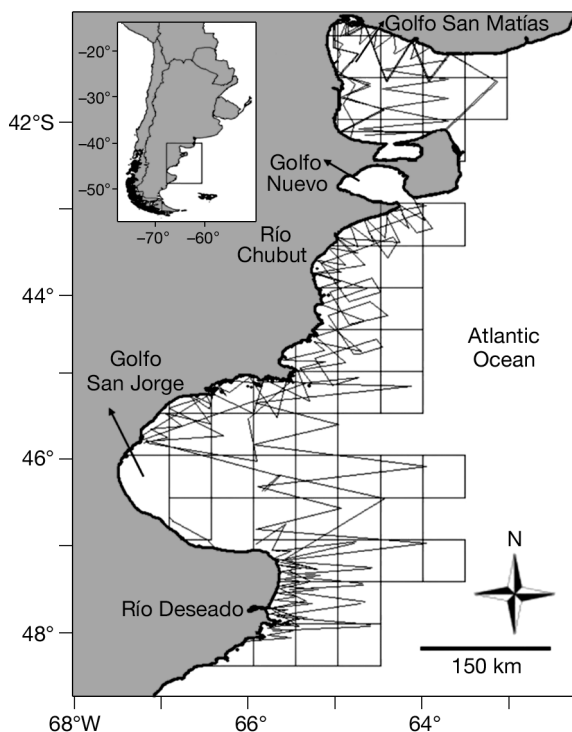

Fig. 1. Study area showing aerial survey transects conducted from 1994 to 2007 (effort) and 0.5° × 0.5° grid cells

Environmental and biological data. A grid of 0.5° × 0.5° squares (~2300 km² cell⁻¹) was constructed on the study area. Each cell of the grid was characterized by depth, Dfs, SST, Chl a, and distance to the nearest large river mouth (Drm). Because 2 of the 13 aerial surveys were conducted during the cold season (May and August), cells were also characterized according to seasonal variability in SST (SST_{var}) and Chl a (Chl a_{var}). Depth and Dfs data were obtained from a nautical chart (H-50, Naval Hydrographic Service, Buenos Aires). Mean depth was calculated by averaging all values within a cell, and Dfs was calculated as the distance from the central point of the cell to the closest point on the coastline.

Mean annual and seasonal SST data were obtained from Piola (2008a). The original data were extracted from satellite images (National Oceanic and Atmospheric Administration, NOAA) (http://podaac.jpl.nasa.gov). SST_{var} in each cell was calculated as: mean summer SST – mean winter SST. The annual SST map and SST_{var} were overlaid on the grid. Mean annual and seasonal concentrations of Chl a (mg m⁻³) were obtained from Piola (2008b). SeaWiFS images were extracted from http://oceancolor.gsfc.nasa.gov. Chl a_{var} in each cell was calculated as: mean summer Chl a – mean winter Chl a. The annual Chl a concentration map and Chl a_{var} were overlaid on the grid. Then, each cell of the grid was characterized for annual SST, annual Chl a, SST_{var}, and Chl a_{var}. Finally, each grid cell was characterized by the encounter rate (ER) for each small cetacean species. The ER in each cell was calculated as:

$$ER = (Number\ of\ sighted\ groups\ /\ km\ of\ survey\ effort) \times 100$$

Because the cells intercepted by the coast were smaller than open-water cells, ER was corrected by the proportion of effective area of the cell (surface ratio with respect to a whole cell) as follows:

$$ER_{corrected} = ER\ /\ proportion\ of\ effective\ area\ of\ cell$$

A group was defined as any group of animals closely engaged in the same activity and moving in the same direction. The survey effort was quantified as the sum of kilometers traveled in each cell during the whole study (from 1994 to 2007).

Data analysis. Generalized linear models (GLMs; Dobson 2002) were used to investigate the distribution of each small cetacean species in relation to environmental variables. The explanatory variables evaluated were depth, Dfs, SST, Chl a, Drm, SST_{var}, Chl a_{var}, depth², Dfs², SST², Chl a^2, Drm², SST_{var}^2, Chl a_{var}^2, and all interactions among them. Candidate variables were chosen based on their hypothesized biological importance and were then treated as continuous covariates. SPSS version 15 statistical software was used for data analyses.

The response variable was the ER of a given species within each cell. The models for each species were fitted assuming a Poisson error distribution, with a log-link function. In the case of existing overdispersion, the standard errors of the parameter estimates and related statistics were computed taking into account the overdispersion (McCullagh & Nelder 1989). The best model was selected for each species using the Akaike information criterion (AIC) (Akaike 1973). Models with a difference in AIC (ΔAIC) <2 were considered to have equivalent support from the data (Burnham & Anderson 2002). ΔAIC and Akaike weights (w_i) were calculated for each model. When >1 model had substantial support, model averaging (a form of multimodel inference) was used (Burnham & Anderson 2002). Part of multimodel inference includes ranking the fitted models from the best to the worst based on the AIC, and then scaling to obtain the relative plausibility of each fitted model by a weight of evidence (in this case w_i) relative to the selected best model (lowest AIC). Then, a weighted estimate of the predicted value, weighting the predictions by w_i, was computed. Therefore, this method allows formal statistical inference from all models in the set. The model fit and the selection of predictive variables deemed to be important often reflect the selection process more than biological relevance (MacNally 2000). In the present study, the fit and complexity of the models were evaluated in successive steps to avoid overfitting, until a model with sufficient predictive power was obtained.

Spearman rank correlation (Siegel & Castellan 1995) was used to investigate the correlation between the ER of different species. In this way, an indicator of species overlap was retrieved.

RESULTS

A total of 10 600 km was surveyed (Fig. 1) during 13 aerial surveys. Six dolphin species were recorded, including 101 groups of dusky dolphin and 65 groups of Commerson's dolphin (Table 1). Thirty groups of common dolphin were sighted; however, the present study only covered a small portion (the most southern part) of this species' distribution. Therefore, no analysis of its relationship with environmental variables was made due to the bias in the surveys; this species is very common along the coast of Buenos Aires province and north of Patagonia, with the southernmost sightings recorded in Golfo Nuevo. In addition, <15 groups in total were recorded for bottlenose dolphin, Burmeister's porpoise, and Peale's dolphin; no analyses of their relationships with environmental variables were made due to the small sample size.

The environmental variables that were found to be significant predictors of distribution differed between dusky and Commerson's dolphins. Table 2 shows the models with ΔAIC <2 for the dusky dolphin. The model with the lowest AIC value shows that ER was significantly related to SST_{var}, Dfs, Dfs^2, SST^2, and Chl a^2, and to the interaction between Dfs and Chl a, and between SST and Chl a. However, this model was not clearly the best as w_i = 0.093, which is a very low value. A model can be considered the best when w_i is ~1. and so the average model was calculated. Following model averaging, the highest predicted values of ER occurred in cells with high temporal variability in SST (Fig. 2a), between 30 and 60 km from shore (Fig. 2b, SST between 12 and 13°C (Fig. 2c), and cells with intermediate values of Chl a (Fig. 2d). The highest ER of dusky dolphin was therefore predicted to occur in the central zone of the study area (Fig. 3).

Table 3 shows the models with ΔAIC <2 for Commerson's dolphin. The model with the lowest AIC value shows that ER was significantly related to Drm, Drm^2, SST, SST^2, and Chl a^2. However, this model was not clearly the best (w_i = 0.089, see previous paragraph) and so the model averaging was done. Model averaging showed that the highest predicted values of ER occurred in areas close to the river mouth (Fig. 4a) and in cells with high values of Chl a (Fig. 4b). The relationship with SST was bimodal, peaking in colder areas of 9 to 10°C and in warmer areas of 12 to 13°C (Fig. 4c). The highest ER was predicted to occur in the surrounding area of both Chubut and Deseado river mouths (Fig. 5).

Among all species, only the correlation between ER of the dusky dolphin and ER of Peale's dolphin was significant (Spearman rank correlation: r_s = 0.357, n = 60, p = 0.0051).

Table 1. *Lagenorhynchus obscurus* and *Cephalorhynchus commersonii*. Survey effort and number of groups of each species recorded for each aerial survey, from 1994 to 2007

Date	Survey effort (km)	No. of groups	
		Dusky dolphin	Commerson's dolphin
17 Nov 94	800	0	21
25 Nov 94	700	0	1
9 May 95	770	4	0
31 Aug 95	770	2	0
8 Nov 95	1040	46	3
27 Nov 95	1200	16	3
12 Dec 95	730	0	12
4 Dec 96	780	6	0
14 Feb 00	510	16	9
7 Feb 03	850	3	12
9 Feb 03	950	1	0
4 Oct 07	570	0	0
29 Nov 07	930	7	4
Total		101	65

Table 2. *Lagenorhynchus obscurus*. Models with ΔAIC <2. All were generalized linear models with a Poisson error structure and log-link function, relating environmental variables to the encounter rate for dusky dolphin. AIC = Akaike information criterion, w_i = Akaike weight, Chl *a* = chlorophyll *a* concentration, Chl a_{var} = temporal variability in Chl *a*, Dfs = distance from shore, SST = sea surface temperature, SST_{var} = temporal variability in SST. The symbol ':' means an interaction between variables

| Model	AIC	ΔAIC	w_i
SST_{var} Dfs Dfs^2 SST^2 Chl a^2 Dfs:Chl *a* SST:Chl *a*	184.127	0.000	0.093
SST_{var} Dfs SST Dfs^2 SST^2 Chl a^2 Dfs:Chl *a* SST:Chl *a*	184.238	0.111	0.088
Dfs Dfs^2 SST_{var}^2 SST^2 Chl a^2 Dfs:Chl *a* SST:Chl *a*	184.323	0.195	0.085
Dfs SST SST_{var}^2 Dfs^2 SST^2 Chl a^2 Dfs:Chl *a* SST:Chl *a*	184.393	0.266	0.082
SST_{var} Dfs SST Chl a_{var}^2 Dfs^2 SST^2 Chl a^2 Dfs:Chl *a* SST:Chl *a*	185.165	1.038	0.055
SST_{var} Dfs Chl *a* Dfs^2 SST^2 Chl a^2 Dfs:Chl *a* SST:Chl *a*	185.279	1.152	0.052
Dfs SST SST_{var}^2 Chl a_{var}^2 Dfs^2 SST^2 Chl a^2 Dfs:Chl *a* SST:Chl *a*	185.339	1.212	0.051
SST_{var} Dfs SST Chl *a* Dfs^2 SST^2 Chl a^2 Dfs:Chl *a*	185.340	1.213	0.051
Dfs SST Chl *a* SST_{var}^2 Dfs^2 SST^2 Chl a^2 Dfs:Chl *a*	185.468	1.341	0.048
SST_{var} Dfs Chl *a* Dfs^2 SST^2 Dfs:Chl *a* SST:Chl *a*	185.483	1.356	0.047
Dfs Chl *a* SST_{var}^2 Dfs^2 SST^2 Chl a^2 Dfs:Chl *a* SST:Chl *a*	185.531	1.404	0.046
SST_{var} Dfs SST Chl *a* Chl a_{var}^2 Dfs^2 SST^2 Chl a^2 Dfs:Chl *a*	185.785	1.658	0.041
SST_{var} Dfs SST_{var}^2 Dfs^2 SST^2 Chl a^2 Dfs:Chl *a* SST:Chl *a*	185.848	1.720	0.039
Dfs Chl *a* SST_{var}^2 Dfs^2 SST^2 Chl a^2 Dfs:Chl *a* SST:Chl *a*	185.858	1.731	0.039
SST_{var} Dfs SST SST_{var}^2 Dfs^2 SST^2 Chl a^2 Dfs:Chl *a* SST:Chl *a*	185.892	1.765	0.039
Dfs SST Chl *a* Chl a_{var}^2 SST_{var}^2 Dfs^2 SST^2 Chl a^2 Dfs:Chl *a*	185.932	1.805	0.038
Chl a_{var} SST_{var} Dfs SST Dfs^2 SST^2 Chl a^2 Dfs:Chl *a* SST:Chl *a*	186.036	1.908	0.036
SST_{var} Dfs Chl a_{var}^2 Dfs^2 SST^2 Chl a^2 Dfs:Chl *a* SST:Chl *a*	186.048	1.921	0.035
Chl a_{var} SST_{var} Dfs Dfs^2 SST^2 Chl a^2 Dfs:Chl *a* SST:Chl *a*	186.117	1.990	0.034
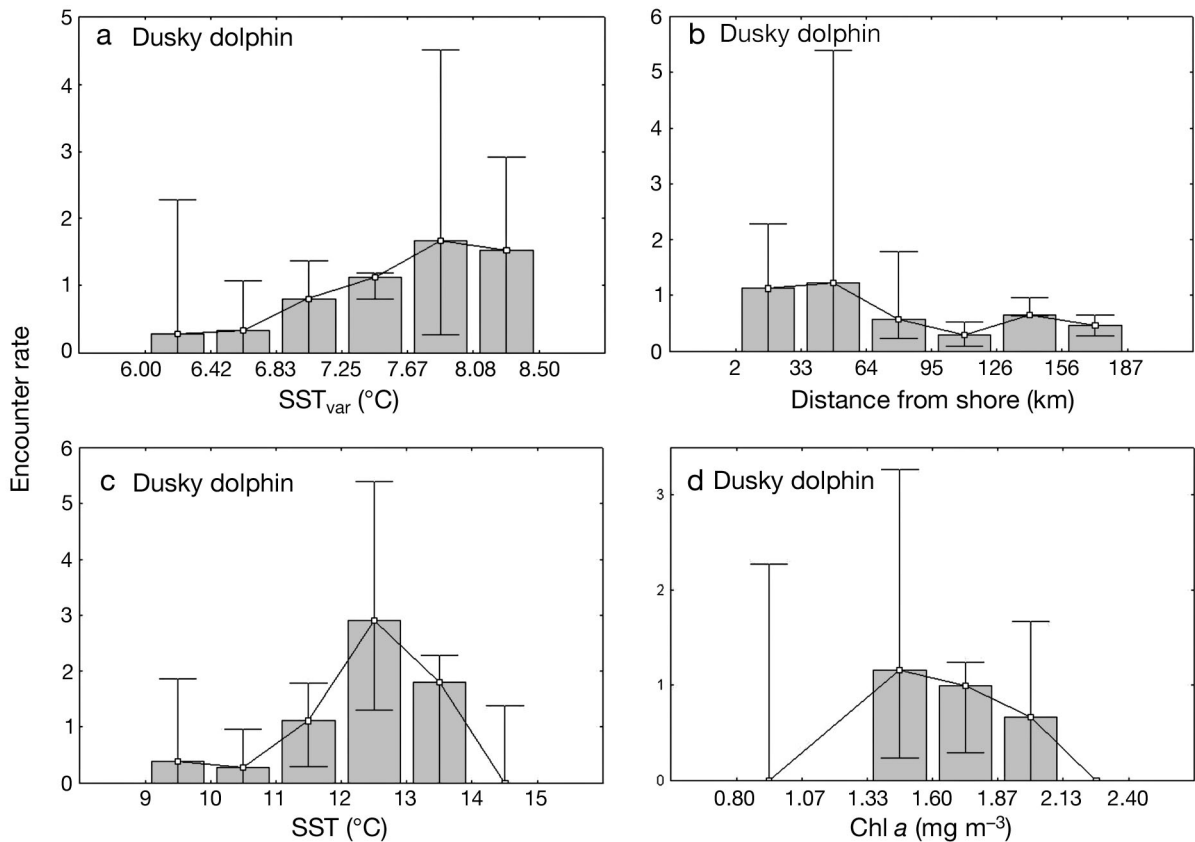
Fig. 2. *Lagenorhynchus obscurus*. Mean predicted encounter rate for dusky dolphin by average model for differences in (a) temporal variability in sea surface temperature (SST_{var}), (b) distance from shore, (c) sea surface temperature (SST), and (d) chlorophyll *a* concentration (Chl *a*). Error bars indicate non-outlier ranges
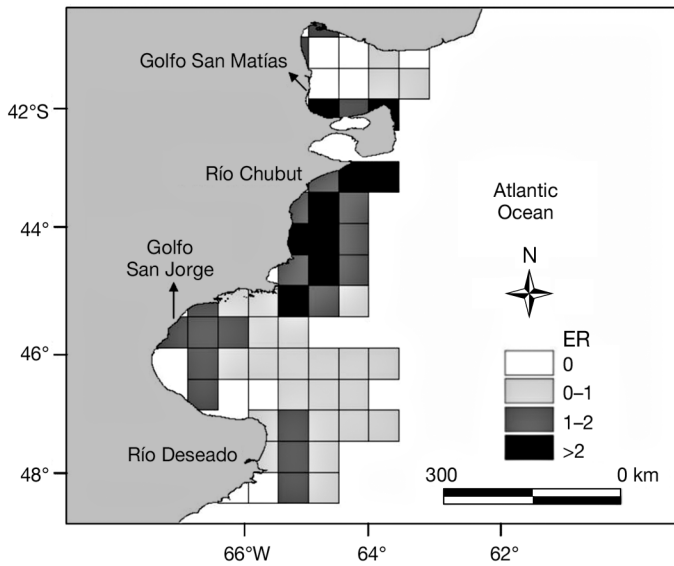
Fig. 3. *Lagenorhynchus obscurus*. Predicted encounter rates (ER; according to average model) within 0.5° × 0.5° grid cells

Table 3. *Cephalorhynchus commersonii*. Models with ΔAIC <2. All were generalized linear models with a Poisson error structure and log-link function, relating environmental variables to the encounter rate for Commerson's dolphin. AIC = Akaike information criterion, w_i = Akaike weight, Chl a = chlorophyll a concentration, Chl a_{var} = temporal variability in Chl a, Dfs = distance from shore, Drm = distance to the river mouth, SST = sea surface temperature, SST$_{var}$ = temporal variability in SST. The symbol ':' means an interaction between variables

Model	AIC	ΔAIC	w_i
Drm SST Drm^2 SST^2 Chl a^2	148.287	0.000	0.089
Drm Depth SST Drm^2 Depth^2 SST^2	148.764	0.477	0.070
Drm SST Drm^2 SST^2 Chl a^2	148.881	0.594	0.066
Drm SST Chl a Drm^2 SST^2 Chl a^2	149.070	0.784	0.060
Drm SST Drm^2 SST^2 SST:Chl a	149.219	0.932	0.056
Drm Depth Depth^2	149.301	1.015	0.054
Depth SST Depth^2 SST^2	149.317	1.031	0.053
Drm SST Drm^2 SST^2 Chl a^2 SST:Chl a	149.476	1.189	0.049
Drm SST Drm^2 SST^2	149.493	1.206	0.049
Drm SST Drm^2 SST^2 Chl a^2 Dfs:Chl a	149.623	1.335	0.046
Drm Depth SST Drm^2 SST^2	149.696	1.410	0.044
Depth Depth^2 SST^2	149.817	1.530	0.042
Depth Drm^2 Depth^2	149.862	1.575	0.041
SST$_{var}$ Drm SST Drm^2 SST^2 Chl a^2	149.934	1.647	0.039
Drm SST Chl a Drm^2 SST^2 Chl a^2 Dfs:Chl a	150.104	1.8175	0.036
Drm SST Drm^2 SST^2 Dfs:Chl a	150.133	1.847	0.035
SST$_{var}$ Drm Depth SST Drm^2 Depth^2 SST^2	150.160	1.874	0.035
Drm Drm^2 Chl a^2	150.204	1.917	0.034
Drm SST Drm^2 SST^2 Chl a^2	150.245	1.958	0.034
Drm Depth SST Drm^2 SST^2 Chl a^2	150.262	1.975	0.033
Chl a_{var} Drm SST Drm^2 SST^2 SST:Chl a	150.275	1.988	0.033

DISCUSSION

The present study offers the first assessment of the distribution and occurrence of small cetaceans in the marine system of Patagonia in relation to environmental variables. ERs for cetaceans were modeled using GLMs in order to select covariates driving the cetacean presence in the area and then model averaging (a form of multimodel inference) was performed. This approach has practical advantages. Where a model-averaged estimator can be used, it appears to have better precision and reduced bias compared to the estimator from the selected 'best' model (Burnham & Anderson 2002).

Sightings of different species were not distributed evenly within the study area. The environmental variables that significantly predicted cetaceans' distribution differed between species, which allows us to make inferences about species' habitat preferences. When a resource is used in a way that is disproportionate to how it is available in the environment, this can be used to infer species' preferences. So, when analyzing several species simultaneously in the same area, a differential use of the environment by each species may be seen. Modeling of habitat selection allowed for a more holistic approach and the correlation test revealed overlaps between the different species.

In general, studies of correlation between environmental variables and sightings of dolphins use data from the same month of a survey. In the present study, SST and Chl a concentration maps (annual and seasonal) extracted from Piola (2008a,b) were used to characterize the area. This data treatment is considered valid because records of SST and Chl a for the Southwest Atlantic Ocean, and especially for our study area, have shown a stable interannual pattern (Acha et al. 2004, Piola 2008c, Rivas 2010). Even though the data employed in th present study for SST (1985 to 1997) were gathered >10 yr ago, only minimal if any changes in oceanographic patterns caused by global warming have been reported since then (Piola 2008c). Indeed, recent studies (Belkin 2009, Rivas 2010) have shown that the increment in SST in the Patagonian shelf ecosystem during the 1982–2006 period was negligible, ranging between 0.06 and 0.08°C decade^{-1}.
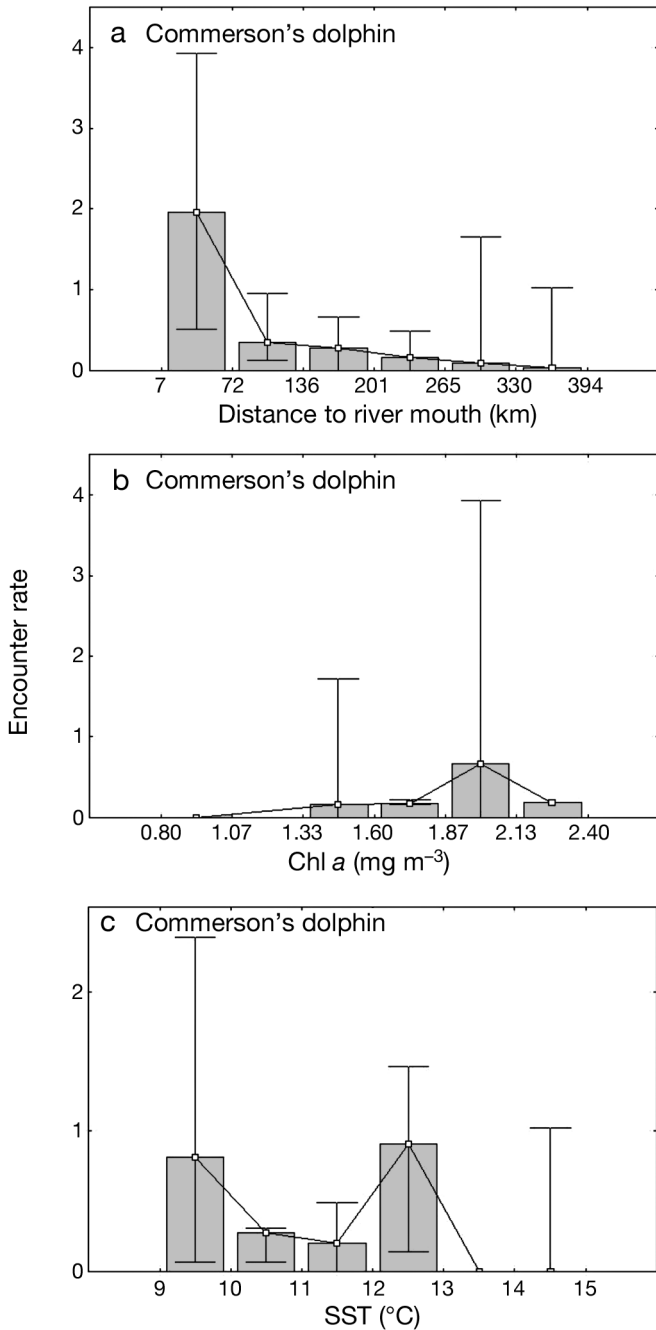
Fig. 4. *Cephalorhynchus commersonii.* Mean predicted encounter rate for Commerson's dolphin by average model for differences in (a) distance to river mouth, (b) chlorophyll *a* concentration (Chl *a*), and (c) sea surface temperature (SST). Error bars indicate non-outlier ranges

Fig. 5. *Cephalorhynchus commersonii.* Predicted encounter rates (ER; according to average model) within 0.5° × 0.5° grid cells

been frequently sighted in a large area between 42° and 55°S, overlapping in at least part of their distribution (Van Waerebeek 1992, Goodall et al. 1997). The results of the present study support the hypothesis of an overlapping distribution for these 2 species. However, they exploit different subdivisions of habitat and have clearly different social and feeding strategies (Brownell et al. 1998). This would indicate that these 2 species share space but use different food resources. On the Patagonian coast, Peale's dolphin is associated with coastal kelp *Macrocystis pyrifera* beds (de Haro & Iñiguez 1997, Lescrauwaet 1997). The fishes associated with this kelp have been found in Peale's dolphin's diet. Its main prey are the pink cusk-eel *Genypterus blacodes*, shrimp (*Pleoticus muelleri*), squids (*Loligo gahi* and *Illex argentinus*), common hake *Merluccius hubbsi*, and small octopuses (Schiavini et al. 1997). However, these diet studies were conducted with individuals from Tierra del Fuego (further south than our study area), so this information should be treated with caution until information on diet for the whole study area is available.

Brownell et al. (1998) indicated that despite the extensive overlap in their distribution, dusky and Peale's dolphins differ in their habitat use, and the dusky dolphin has a wider offshore distribution. However, recent data from a survey conducted in November 2009 shows that groups of Peale's dolphins were sighted near the continental slope between 41 and 43°S (authors' unpubl. data). On the other hand, the dusky dolphin is a mesopelagic feeder whose main prey is Argentine anchovy *Engraulis anchoita* (Koen

The distribution of dusky dolphin and Peale's dolphin would be expected to be similar, since the ERs of these species showed a positive relationship. Even though Brownell (1974) and Mitchell (1975) proposed that dusky and Peale's dolphins showed an allopatric distribution in the Atlantic Ocean, both species have
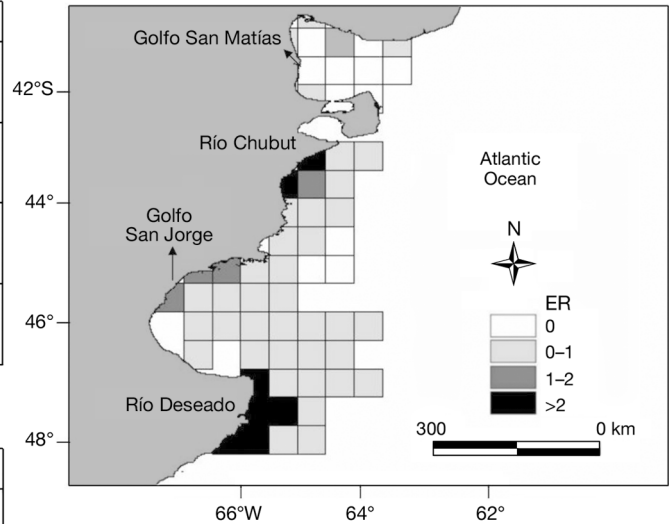
Alonso et al. 1998). The highest ER of the dusky dolphin was predicted to occur in the central zone of our study area; this zone coincides with the location of the coastal fraction of the highest densities of Patagonian anchovy stock (Hansen et al. 2001, Buratti et al. 2006).

In the present study, Commerson's dolphin presented the most coastal distribution. The habitat preferences found for this species corresponded to the warm months. No sightings of Commerson's dolphin were made in the colder months (May, August, and October), suggesting maybe a different habitat preference in colder seasons. Pedraza (2008) found that depth does not seem to influence the distribution of this species, which is often found feeding at the mouths of the Patagonian rivers Chubut, Deseado, Coy Gallegos, and Bahía San Julián, all places with intense tide flows. In northern Patagonia, this dolphin shows pelagic and opportunistic feeding habits. But in areas with large tidal amplitudes (parts of the coast of the provinces of Santa Cruz and Tierra del Fuego), it uses benthic resources (Bastida et al. 1988). Therefore, there are differences in habitat use compared to the other species in the present study.

In the present study, the habitat models were not only explanatory (i.e. to understand what variables are important in habitat selection) but also predictive (i.e. to predict where dolphins are likely to occur given certain habitat types). From an ecological perspective, environmental variables are those of direct interest as they represent proxies for biological features that determine habitat quality (Heinrich 2006). The direct causal relationships underlying the observed distribution and habitat selection patterns are currently unknown. As is common in cetacean habitat studies, environmental features are considered proxies for the availability and distribution of critical resources, such as prey, mates, and shelter from predators, all of which are inherently difficult to determine or quantify reliably (Gowans & Whitehead 1995, Fiedler et al. 1998, Reilly et al. 1998, Griffin & Griffin 2003, Macleod et al. 2004, Croll et al. 2005).

Habitat modeling is a powerful analytical tool to investigate where animals are found, why they might occur there, and where they could be expected to occur (Boyce & McDonald 1999, Rushton et al. 2004). However, the results from habitat models need to be evaluated carefully before conclusions are drawn or generalizations are made. It is important to consider that grid size affects the amount of effort and number of sightings within each cell. At larger grid sizes, the sighting rate is higher but the environmental conditions are averaged over a larger area (Hamazaki 2002, Redfern et al. 2006). An advantage of the use of habitat-selection models is that they can be refitted to incorporate both new sightings and expanded environmental data to clarify effects and to explore whether

habitat use appears to be changing. It also provides a focus for more detailed studies to explore the mechanisms determining cetacean distribution and hence a better prediction of the effects of anthropogenic factors on conservation status (Cañadas et al. 2005).

The selected models could be improved by evaluating several spatial and temporal scales, because some predictor variables may have different significance at different scales. In addition, environmental predictor variables such as SST and Chl *a* vary between months. Therefore, including temporal variability may also improve descriptions of habitat use. Finally, knowledge of the distribution patterns and occurrence of small cetaceans in the Patagonian marine system provides a baseline understanding of how these species interact with each other and their environment. Such information should be considered when potential areas of conflict between coastal cetaceans and human activities are being planned. The main threats for small cetaceans in Patagonian waters are incidental mortality in fishing gear, indirect effects of fisheries, tourism interactions, and more recently, offshore oil exploration (Corcuera et al. 1994, Crespo et al. 1994, 1997b, 2000, Goodall et al. 1995, Dans et al. 1997, 2003, 2008, Coscarella et al. 2003). Habitat-preference modeling identified areas with higher rates of encounter for the species of small cetaceans studied, which therefore by implication are the areas more important for their conservation. These areas should be considered in future designs of marine protected areas.

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