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Estimating the geographic range of a threatened shark in a data-poor region: *Cetorhinus maximus* in the South Atlantic Ocean

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Abstract The distribution of the planktivorous basking shark *Cetorhinus maximus* is influenced by zooplankton abundance at small scales and temperature at medium scales in the North Atlantic. Here, we estimate the distribution of basking sharks on South Atlantic continental shelves, and the relative importance of chlorophyll concentration, as a proxy for zooplankton abundance, and temperature in determining habitat suitability for basking sharks at large scales. We used maximum entropy (MaxEnt) and maximum likelihood (MaxLike) species distribution modelling to test three hypotheses: the distribution of basking sharks is determined by (1) temperature, (2) chlorophyll concentration, or (3) both chlorophyll and temperature, while considering other factors, such as oxygen and salinity. Off South America, basking shark habitat included subtropical, temperate and cool-temperate waters between approximately 20°S and 55°S. Off Africa, basking shark habitat was limited to cool-temperate waters off Namibia and southern South Africa. MaxLike models had a better fit than MaxEnt models. The best model included minimum chlorophyll concentration, dissolved oxygen concentration, and sea surface temperature range, supporting hypothesis 3. However, of all variables included in the best model, minimum chlorophyll concentration had the highest influence on basking shark distribution. Unlike the North Atlantic distribution, the South Atlantic distribution of basking sharks includes subtropical and cool-temperate waters. This difference is explained by high minimum chlorophyll concentration off southern Brazil as compared to North Atlantic subtropical areas. Observations in other regions of the world support this conclusion. The highest habitat suitability for basking sharks is located close to nearshore areas that experience high anthropogenic impact [*Current Zoology* 61 (5): 811–826, 2015].

Keywords Basking shark, Chondrichthyes, Geographic range, MaxEnt, MaxLike, Southern Hemisphere

Large-scale spatial distribution patterns are important for conservation planning, especially for highly mobile large pelagic animals, such as sharks. Large pelagic sharks can move long distances (thousands of km), which results in wide distributions, often ranging across entire ocean basins, and crossing multiple national jurisdictions and levels of protection (Bonfil et al., 2005; Southall et al., 2006; Saunders et al., 2011; Howey-Jordan et al., 2013; Sequeira et al., 2013). The large geographic extent of the ranges of these species complicates the assessment of habitat requirements necessary for conservation planning. For this reason, large-scale habitat suitability modelling may play an important role in pelagic shark ecological and conservation science (Sequeira et al., 2012).

The basking shark *Cetorhinus maximus* is widely distributed in temperate to cool-temperate waters in the Pacific and Atlantic Oceans at temperatures between 8 and 24°C (Compagno, 2001), with only scattered records in subtropical and tropical waters (Compagno et al., 2005). These sharks can move over considerable distances travelling from eastern to western North Atlantic continental shelves (Gore et al., 2008), and moving between northwest Atlantic temperate waters and equatorial mesopelagic waters (Skomal et al., 2009). However, basking sharks that have been tagged in the North

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Atlantic tended to spend the majority of their tracks in highly productive continental shelf waters (Sims et al., 2003; Skomal et al., 2004; Southall et al., 2005, 2006; Gore et al., 2008).

Factors or resources determining basking shark distribution appear to vary with scale. At small scales (0.01 to 10 km), zooplankton abundance is a highly significant predictor of basking shark distribution and abundance. Basking sharks tend to congregate in continental shelf waters with high zooplankton concentrations (Sims et al., 1997, 2003; Sims and Quayle, 1998; Soldo et al., 2008; Curtis et al., 2014). A decrease in abundance of basking sharks off western Ireland between 1949 and 1975 is thought to have been a consequence of a contemporary decline in zooplankton (Sims and Reid, 2002). At medium spatial scales (10–1000 km), temperature appears to be the most influential factor determining basking shark occurrence (Cotton et al., 2005). At these larger scales, habitat choice seems driven more by thermal optimization, which reduces metabolic costs and increase net energy gain, than food abundance (Cotton et al., 2005). These analyses have been conducted in the North Atlantic. To what extent these results can be extended to other regions is not known. In addition, factors or resources determining basking shark occurrence at larger spatial scales (1,000–10,000 km) are unknown. They may include oxygen concentration or salinity, which are well known to affect shark distribution at varying scales (e.g. Heithaus et al., 2009; Nasby-Lucas et al. 2009; Abascal et al., 2011). There is no available information on significant determinants of basking shark distribution in the Southern Hemisphere at any scale.

In the Southern Hemisphere, basking sharks have been reported in waters from all continental shelves, except Antarctica. While basking sharks are rare off southern Australia (Last and Stevens, 2009), they are common in the cool-temperate waters off New Zealand's South Island (39°–51°S), and much less common off the North Island (Francis and Duffy, 2002). Off Chile, basking sharks appear to be seasonally common (Hernández et al., 2010), and off southern Africa, basking sharks occur in cool-temperate waters of the Benguela current (Compagno et al., 1989). Off South America's east coast, basking sharks are considered to be rare. However, records indicate that they are (or historically were) relatively common off southern Brazil (Soto, 2000; Soto et al., 2007). Basking sharks have been caught occasionally in gillnet and bottom trawl fisheries off Uruguay (Domingo et al., 2008). Further south, they have been recorded off northern Argentina (Siccardi, 1960), the northern Patagonian gulfs (Lahille, 1928; Van Der Molen et al., 1998; Perier et al., 2011), and off the Malvinas/Falkland Islands' northern shore (Norman, 1937). The basking sharks is categorized as Vulnerable at a global scale (Fowler, 2005) and Endangered in the Northeast Atlantic and North Pacific (Fowler, 2009a,b) mainly because of overfishing for the international shark fin trade. This led to the inclusion of the species in CITES Appendix II, which imposes the tracking of the international trade of products derived from basking sharks. Today, the most significant threat to basking sharks is fishing for their fins, which are among the most valuable in the international trade (Clarke, 2004). Despite these regulations, a large fraction of the international trade in basking shark fins is unrecognized (Magnussen et al., 2007).

In this paper, we compiled all known confirmed records of basking sharks in the South Atlantic, including unpublished records presented here for the first time, and used them to model the geographic range of basking sharks in the region. Our objectives were (1) to estimate the geographic distribution of basking sharks on South Atlantic continental shelves, and (2) to estimate the relative importance of several factors, including chlorophyll concentration – as a proxy for zooplankton abundance – and temperature, as well as dissolved oxygen and salinity in determining habitat suitability of basking sharks on South Atlantic continental shelves.

1 Materials and Methods

1.1 Data Sources

For the southwest Atlantic we used two primary sources of records: the scientific literature, and the database of the Onboard Fishery Observers Program of the Instituto Nacional de Investigación y Desarrollo Pesquero (Argentina). This database contains information on species caught by fishing vessels covered by the program, including photographs to check species identification, from 2003 to February 2013. For the southeast Atlantic, we used data from the Fish Collection and the Shark Collection (AfroBIS) of the Iziko South African Museum, accessed from the Global Biodiversity Information Facility data portal. We inspected all data to remove duplicates (i.e. records with the same date and location).

The study area was defined according to the coverage of the various data sources used. While we are aware that basking sharks have been occasionally recorded in oceanic waters (McKinnell and Seki, 1998; Gore et al., 2008; Skomal et al., 2009), we restricted our study area to continental shelf waters because all South Atlantic records of basking sharks come from continental shelves, which may bias estimations of oceanic habitat suitability. In addition, most tracked basking sharks occur preferentially in continental shelf waters (Sims et al., 2003; Skomal et al., 2004; Southall et al., 2005, 2006; Gore et al., 2008), indicating that this habitat plays an important role in basking shark biology. Off South America, the latitudinal limits of the study area were set at 60°S, i.e. the southern limit of the Onboard Fishery Observers Program, and the northern limit approximately at 6°N, which corresponds to the northernmost extension of the Brazilian coast surveyed by Soto (2000). The western boundary of the study area was set close to the Argentinean-Chilean border, south of Tierra del Fuego (70°W); the eastern boundary at 30°W, includes South Georgia (Fig. 1). Off Africa, the study area was between 14°S (the northernmost extension of the Benguela system; Sakko, 1998) to the southernmost extension of the continental shelf, and between 2°E and the easternmost extension of the South African coast, 32.9°E, at the border between South Africa and Mozambique (Fig. 1). Within these broad areas, the analyses were further restricted to the continental shelf and upper slope, defined as the area between the shoreline and the 500 m isobath.

Environmental predictors were obtained from the Bio-ORACLE database (Tyberghein et al., 2012). This database contains high-resolution (5 arcmin or 9 km) layers of multiple environmental variables of the ocean that were used in the models of the species distribution. We initially selected a set of variables potentially important in determining basking shark distribution on the basis of previously published information, i.e. mean, minimum, maximum, and range chlorophyll concentration, mean dissolved oxygen concentration, mean, minimum, maximum, and range sea surface temperature, and mean salinity. We interpreted mean values of all variables as a measurement of the mean effect of these variables on basking shark distribution. Maximum and minimum sea surface temperature can influence thermal upper and lower limits of the distribution of basking sharks. Range sea surface temperature is a measurement

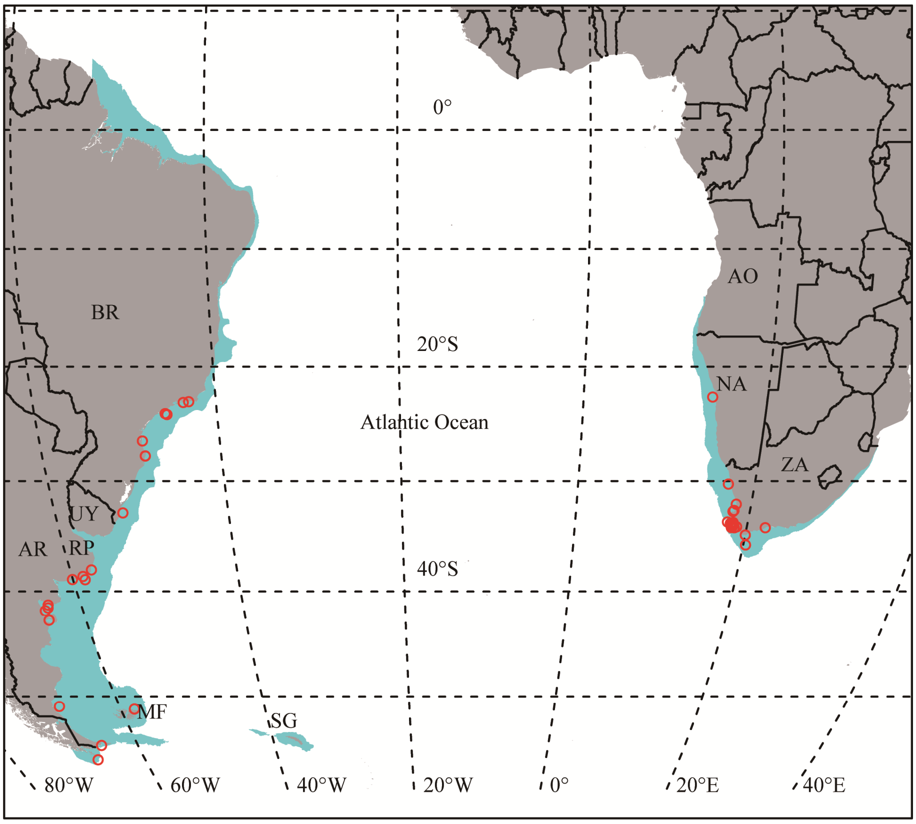

Fig. 1 Map of the South Atlantic Ocean showing continental shelves (0–500 m depth) included in the study area (cyan-colored area) to estimate the geographic range of basking sharks *Cetorhinus maximus*

Known records of basking sharks used in the analyses are shown as red circles. AO = Angola, AR = Argentina, BR = Brazil, MF = Malvinas/Falkland Islands, NA = Namibia, RP = Río de la Plata, SG = South Georgia, UY = Uruguay, ZA = South Africa. Map projection is Mollweide equal area.

of the variability in temperature that is usually associated to frontal areas. We used chlorophyll *a* concentration as a proxy for zooplankton abundance – the main food of basking sharks, given the general positive correlation between phyto- and zooplankton biomass (Irigoien et al., 2004). Maximum and minimum chlorophyll *a* concentration could be indicative of the influence of an abundance and a scarcity of food on basking shark distribution. Range in chlorophyll *a* concentration was included as an indicator of variability in food supply to basking sharks. While the focus of our work was to evaluate the relative importance of temperature and chlorophyll *a* concentration (as a proxy of planktonic productivity), we included other available variables known to affect the distribution of elasmobranchs, such as mean dissolved oxygen concentration (Nasby-Lucas et al., 2009; Abascal et al., 2011) and mean salinity (Cortés et al., 2011; Drymon et al., 2013).

1.2 Modelling

We postulated three competing hypotheses explaining basking shark distribution in South Atlantic shelf waters: (1) chlorophyll is the most important determinant, (2) temperature is a key determinant, and (3) both variables affect basking shark distribution. To test these hypotheses, we built three kinds of models: (1) Models containing only chlorophyll variables, plus other covariates, i.e. dissolved oxygen and salinity, (2) models containing only temperature variables, plus other covariates, and (3) Models containing both temperature and chlorophyll variables, plus their interaction and other covariates. After fitting the models we selected the one with the best fit to the data as the best hypothesis explaining basking shark distribution on South Atlantic continental shelves.

We used two modelling approaches to test our hypotheses, both based on presence and background data: one based on maximum entropy estimation (MaxEnt; Phillips et al., 2006; Elith et al., 2011) and another based on maximum likelihood (MaxLike; Royle et al., 2012). MaxEnt uses a sample of environmental data, called the background. Then, it determines the geographic range by finding a function that maximizes the information entropy between the distribution of the background subject to constraints imposed by the presence records. MaxLike uses all background data of the study area to estimate the probability of occurrence of a species. It accomplishes this by maximizing the likelihood conditioned on the probability of observing a cell given the species is present.

Prior to fitting models, we inspected the relationships between each pair of predictors in order to avoid multicolinearity. Variable pairs that had a correlation coefficient > 0.5 were not included together in the same model.

We implemented the MaxEnt modelling in MaxEnt version 3.3.3k within the library 'dismo' (Hijsmans et al., 2013) in the statistical software R, version 12.5.2 (R Core Team, 2012). MaxEnt generates maps of habitat suitability scaled from 0 (lowest suitability) to 1 (highest suitability) (Phillips et al., 2006; Elith et al., 2011).

We ran each MaxEnt model 100 times (the maximum number of replicates allowed by our computing power) (Dambach and Rödder, 2011), then, we obtained a mean response model from the 100 runs. Each time, a random sample of 33% of the dataset (i.e. 15 presence records) was saved to test the model. Model fit was evaluated by means of the True Skill Statistic (TSS), as recommended by Allouche et al. (2006). TSS ranges between -1 and 1, with 1 indicating perfect fit and values of 0 or less indicate a performance not better than random (Allouche et al., 2006). The threshold used in the calculation of TSS maximized the sum of sensitivity and specificity (Liu et al., 2013).

MaxLike modelling was conducted using the library 'maxlike' version 0.1.5 (Royle et al., 2012) in R, version 12.5.2. Before fitting MaxLike models all variables were standardized, as recommended by Royle et al. (2012). The Akaike Information Criterion (AIC) was computed for each MaxLike model and the model with the lowest AIC was chosen as the one with the best fit. Akaike weight (*w*) was also calculated for each model to determine the relative importance of each variable included in the best model. The Bayesian Information Criterion (BIC) was also computed for each MaxLike model.

We compared the fit of the best MaxEnt and MaxLike models with TSS.

To obtain the range map, i.e. a binary map encompassing the highest habitat suitability or probability of occurrence, a threshold was applied to the results of the best MaxEnt and MaxLike models. As before, the chosen threshold was the one that maximized the sum of sensitivity and specificity (Liu et al., 2013).

2 Results

We identified 46 confirmed records of basking sharks in the South Atlantic Ocean, 22 off southern Africa and 24 off South America (Fig. 1). Of the South American records, 4 (16%) were not reported previously. These new records substantially expanded the known geographic range of basking sharks to the southern Patagonian shelf (Table 1).

Table 1 Occurrences of basking shark *Cetorhinus maximus* used to model its distribution on continental shelves of the South Atlantic Ocean

Record number	Longitude	Latitude	Location	Source
1	-68.333	-51.042	Southern Patagonia, Argentina.	INIDEP, unpublished.
2	-67.097	-56.468	Southern Patagonia, Argentina.	INIDEP, unpublished.
3	-65.355	-54.992	Southern Patagonia, Argentina.	INIDEP, unpublished.
4	-64.683	-41.833	Golfo San Matías, Río Negro, Argentina.	Van der Molen et al.,1998
5	-64.633	-42.683	Golfo Nuevo, Chubut, Argentina.	Lahille, 1928
6	-58.133	-51.300	Between McBryde's Head and Salvador, Malvinas/Falkland Islands.	Norman, 1937
7	-57.450	-38.000	3 nautical miles off Mar del Plata, Buenos Aires, Argentina.	Siccardi, 1960
8	-58.683	-38.600	Puerto Quequén, Buenos Aires, Argentina.	Siccardi, 1960
9	-58.683	-38.600	Puerto Quequén, Buenos Aires, Argentina.	Siccardi, 1960
10	-58.533	-38.900	20 nautical miles southwest of Puerto Quequén, Buenos Aires, Argentina.	Siccardi, 1960
11	-60.067	-38.883	Claromecó, Buenos Aires, Argentina.	Photo from local newspaper “El Periodista”, unpublished.
12	-64.083	-41.300	Golfo San Matías, Río Negro, Argentina.	Perier et al., 2011
13	-64.217	-41.567	Golfo San Matías, Río Negro, Argentina.	Perier et al., 2011
14	-45.667	-24.083	Ilha de Alcatrazes, São Paulo, Brazil.	Soto, 2000
15	-43.567	-23.120	Praia do Canto, Barra de Guaratiba, Rio de Janeiro, Brazil.	Soto, 2000
16	-45.483	-24.167	Ponta da Sela, Ilhabela, São Paulo, Brazil.	Soto, 2000
17	-43.567	-23.120	Praia do Canto, Barra de Guaratiba, Rio de Janeiro, Brazil.	Soto, 2000
18	-48.567	-26.467	Barra do Sul, Araquari, Santa Catarina, Brazil.	Soto, 2000
19	-52.170	-32.860	Off southern Rio Grande do Sul, Brazil.	Soto, 2000
20	-48.490	-27.775	Pântano do Sul, Florianópolis, Santa Catarina, Brazil.	Soto, 2000
21	-48.489	-27.789	Pântano do Sul, Florianópolis, Santa Catarina, Brazil.	Soto, 2000
22	-48.490	-27.775	Pântano do Sul, Florianópolis, Santa Catarina, Brazil.	Soto, 2000
23	-48.490	-27.775	Pântano do Sul, Florianópolis, Santa Catarina, Brazil.	Soto, 2000
24	-42.960	-23.050	50 m off the beach of Itaipuaçu, Niterói, Rio de Janeiro, Brazil.	Soto et al., 2007
25	20.267	-35.733	Agulhas Bank, South Africa.	AfrOBIS
26	18.200	-34.065	Hout Bay, Western Cape, South Africa.	AfrOBIS
27	18.300	-34.083	Llandudno, Western Cape, South Africa.	AfrOBIS
28	18.800	-34.100	Strand, False Bay, Western Cape, South Africa.	AfrOBIS
29	18.200	-34.167	Gordon's Bay, False Bay, Western Cape, South Africa.	AfrOBIS
30	18.550	-34.183	Simonstown, False Bay, Western Cape, South Africa.	AfrOBIS
31	22.150	-34.182	Mossel Bay, Western Cape, South Africa.	AfrOBIS
32	17.633	-33.667	74 km WNW of Cape Town, South Africa.	AfrOBIS
33	18.000	-33.800	Blouberg Strand, Western Cape, South Africa.	AfrOBIS
34	18.200	-33.833	Near Table Bay, Western Cape, South Africa.	AfrOBIS
35	18.300	-33.717	Melkbosstrand, Western Cape, South Africa.	AfrOBIS
36	18.417	-33.900	Table Bay harbor, Western Cape, South Africa.	AfrOBIS
37	18.350	-33.800	Robben Island, Western Cape, South Africa.	AfrOBIS
38	18.220	-33.817	Dolphin Beach, Table View, Western Cape, South Africa.	AfrOBIS
39	18.150	-33.770	Bloubergstrand, Muisenberg, Western Cape, South Africa.	AfrOBIS
40	18.300	-33.967	Bakoven, Western Cape, South Africa.	AfrOBIS
41	18.050	-32.733	St. Helena, Western Cape, South Africa.	AfrOBIS
42	18.283	-32.083	Lambert's Bay, Western Cape, South Africa.	AfrOBIS
43	17.000	-30.300	Hondeklipbaai, Northern Cape, South Africa.	AfrOBIS
45	20.000	-34.840	Agulhas Bank, South Africa.	AfrOBIS
46	18.150	-32.633	St. Helena Bay, Western Cape, South Africa.	AfrOBIS
44	14.000	-22.650	Swakopmund, Erongo, Namibia.	AfrOBIS

Longitude and latitude are given in decimal degrees and negative values indicate longitudes and latitudes in Western and Southern hemispheres. INIDEP = Onboard observers database of Instituto Nacional de Investigación y Desarrollo Pesquero, Argentina. AfrOBIS = Iziko South African Museum - Fish Collection. Full citations for published records are given in References.

MaxEnt was unable to identify a single best hypothesis explaining basking shark occurrence on South Atlantic continental shelves. Several models with TSS higher than 0.5 had overlapping 95% confidence intervals (Table 2). These models were consistent with hypothesis 1 (i.e. chlorophyll is the main determinant of basking shark distribution) and 3 (i.e. both chlorophyll and temperature have an effect on basking shark distribution). However, most of these models produced inaccurate maps, for example extending the distribution of the basking shark into freshwater areas of the Río de la Plata. Of these, only model 15 (Table 2) did not predict freshwater areas as suitable habitat for basking sharks, except for a small area in the innermost Río de la Plata (Fig. 2A).

Conversely, MaxLike succeeded to identify a single

Table 2 MaxEnt models used to test three hypotheses of determinants of the distribution of basking sharks *Cetorhinus maximus* in South Atlantic continental shelves

Model number	Variables included in the model			TSS	95% CI
	Hypothesis 1: Chlorophyll as the main determinant				
1	chl a mean	oxygen		0.531	0.020
2	chl a max	oxygen		0.513	0.023
3	chl a range	oxygen		0.503	0.022
4	chl a min	oxygen		0.493	0.019
5	chl a min	salinity		0.482	0.020
6	chl a max	salinity		0.448	0.023
7	chl a range	salinity		0.423	0.024
	Hypothesis 2: Temperature as the main determinant				
8	SST mean	salinity		0.488	0.019
9	SST min	salinity		0.482	0.022
10	SST range	salinity		0.397	0.022
11	SST max	salinity		0.396	0.022
	Hypothesis 3: Both chlorophyll and temperature are determinants				
12	chl a min	salinity	SST min	0.527	0.019
13	chl a min	salinity	SST mean	0.522	0.019
14	chl a mean	oxygen	SST range	0.515	0.020
15	chl a min	oxygen	SST range	0.505	0.020
16	chl a min	salinity	SST max	0.497	0.021
17	chl a max	oxygen	SST range	0.487	0.020
18	chl a range	oxygen	SST range	0.486	0.021
19	chl a min	salinity	SST range	0.485	0.022
20	chl a max	salinity	SST mean	0.447	0.019
21	chl a max	salinity	SST min	0.445	0.018
22	chl a max	salinity	SST range	0.442	0.020
23	chl a range	salinity	SST mean	0.439	0.020
24	chl a max	salinity	SST max	0.432	0.018
25	chl a range	salinity	SST min	0.432	0.020
26	chl a range	salinity	SST range	0.422	0.022
27	chl a range	salinity	SST max	0.404	0.020

Within each hypothesis, models are ranked according to their true skill statistic (TSS); higher values of TSS indicate better fit. The interval of its 95% confidence interval (95% CI) is also given for each model. Abbreviations for variables included are: chl a min = minimum chlorophyll concentration, chl a mean = mean chlorophyll concentration, chl a max = maximum chlorophyll concentration, chl a range = chlorophyll concentration range, SST min = minimum sea surface temperature, SST mean = mean sea surface temperature, SST max = maximum sea surface temperature, SST range = sea surface temperature range, oxygen = mean dissolved oxygen concentration, salinity = mean salinity.

best model fitting the data. This was model 35 (Table 3), which included the combined effects of chlorophyll and temperature (Hypothesis 3). This model included minimum chlorophyll concentration (chl a_{min}), range of sea surface temperature (SST_{range}) and mean dissolved oxygen concentration (oxygen), and had the following parameters: intercept = 3.99, chl a_{min} = 4.91, oxygen = 4.91, SST_{range} = -3.77, chl a_{min}^2 = -1.19, $oxygen^2$ = -5.44, $oxygen^3$ = 3.05. In addition, this model had also a better fit than any MaxEnt model; it had the highest TSS value: 0.573 (95% confidence interval = 0.018) and explained 30.9% of the deviance. Therefore, we concluded that MaxLike model 35 was the best for describing the geographic distribution of basking sharks on South Atlantic continental shelves.

Variables chl a_{min}, oxygen and SST_{range} did not contribute equally to the final model. The most important variable was chl a_{min}, with a *w* of 0.616, followed by oxygen (*w* = 0.551), and SST_{range} (*w* = 0.100).

Both the best MaxEnt and MaxLike models agreed in the general extent of the basking shark range on South Atlantic continental shelves. However, the best MaxEnt model predicted a more widespread and continuous range for basking sharks than the best MaxLike model (Fig. 2A, B; Fig. 3A, B).

Based on the best MaxLike model the highest probability of occurrence of basking sharks were, generally, confined to areas south of 20°S on both sides of the Atlantic. Off South America, the highest probabilities of occurrence of basking sharks were located off southern Brazil, between Espírito Santo and Cabo de Santa Marta Grande (i.e. 20 to 28°S), off Uruguay and the Río de la Plata mouth up north to approximately 31°S, the northern Patagonian gulfs, the eastern mouth of the Strait of Magellan, and off the Malvinas/Falkland Islands (Fig. 3A). Off Africa, the highest probabilities of occurrence were located in an area ranging from off northern Namibia (just south of the Namibia-Angola border at about 20°S) to East London, Eastern Cape, South Africa, at 33°S (Fig. 3B).

Our model predictions using a threshold of 0.252 indicated that, on South Atlantic continental shelves, basking sharks inhabited cool-temperate to subtropical waters (Fig. 3). In the southwest Atlantic, basking

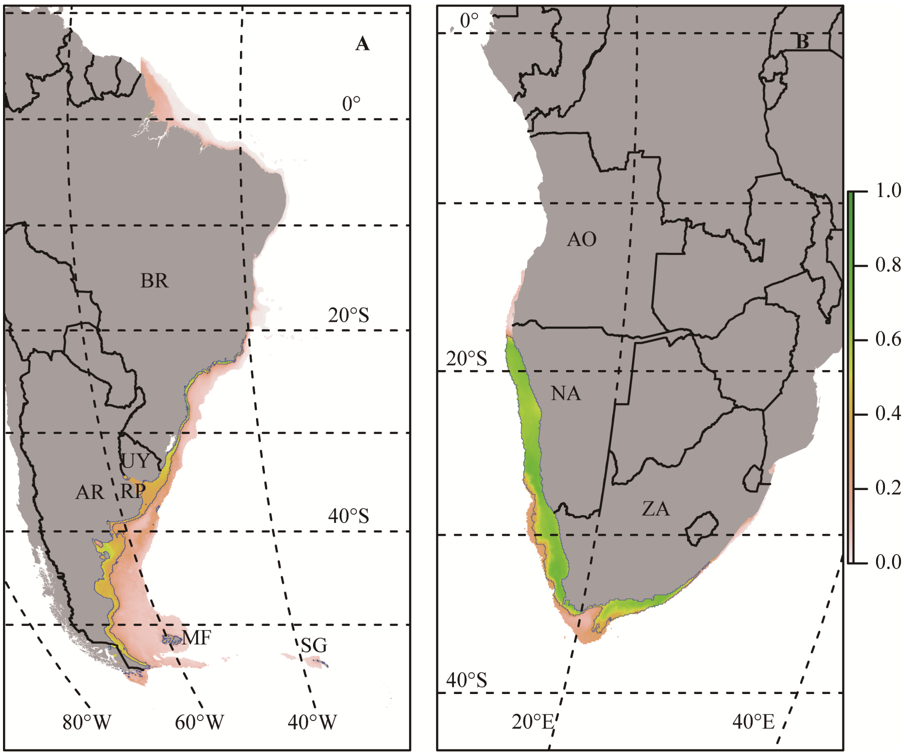

Fig. 2 Habitat suitability (from 0, lowest suitability, to 1, highest suitability) for basking sharks *Cetorhinus maximus* as estimated from a maximum entropy (MaxEnt) model including chlorophyll minimum concentration, mean dissolved oxygen concentration, and sea surface temperature range

A. Continental shelves off South America. **B**. Continental shelves of southern Africa. The blue line delimits the geographic range, estimating after applying a threshold maximizing the sum of specificity and sensitivity. AO = Angola, AR = Argentina, BR = Brazil, MF = Malvinas/Falkland Islands, NA = Namibia, RP = Río de la Plata, SG = South Georgia, UY = Uruguay, ZA = South Africa. Map projection is Mollweide equal area.

Table 3 MaxLike models used to test three hypotheses of determinants of the distribution of basking sharks *Cetorhinus maximus* in South Atlantic continental shelves

Model number	Variables included in the model	AIC	BIC
	Hypothesis 1: Chlorophyll as the main determinant		
1	chl a min + salinity + chl a min2 + salinity2 + chl a min3	896.373	905.516
2	chl a min + salinity + chl a min2 + salinity2 + chl a min3 + salinity3	898.330	909.301
3	int + chl a min + salinity + chl a min2 + salinity2 + chl a min3 + salinity3	900.287	913.088
4	chl a mean + oxygen + chl a mean2 + oxygen2 + oxygen3	900.829	909.973
5	int + chl a mean + oxygen + chl a mean2 + oxygen2 + oxygen3	902.469	913.441
6	int + chl a min + oxygen + chl a min2 + chl a min3 + oxygen3	907.383	918.354
7	int + chl a max + oxygen + oxygen2 + chl a max3 + oxygen3	907.434	918.406
8	int + chl a max + oxygen + chl a max2 + oxygen2 + chl a max3 + oxygen3	908.425	921.226
9	int + chl a min + oxygen + chl a min2 + oxygen2 + chl a min3 + oxygen3	908.812	921.612
10	int + oxygen + chl a range2 + oxygen2 + chl a range3 + oxygen3	910.735	921.707
11	int + chl a range + oxygen + chl a range2 + oxygen2 + chl a range3 + oxygen3	916.345	929.145
12	int + chl a range + salinity + chl a range3 + salinity3	936.007	945.150
13	int + chl a range + salinity + salinity2 + chl a range3 + salinity3	937.217	948.189
14	int +salinity + chl a max3 + salinity3	937.256	944.570
15	int + salinity + salinity2 + chl a max3 + salinity3	938.554	947.697
16	int + chl a range + salinity + chl a range2 + salinity2 + chl a range3 + salinity3	938.982	951.783
17	int + chl a max + salinity + salinity2 + chl a max3 + salinity3	939.720	950.692
18	int + chl a max + salinity + chl a max2 + salinity2 + chl a max3 + salinity3	941.569	954.369
19	int + chl a mean + oxygen + chl a mean2 + oxygen2 + chl a mean3 + oxygen3	943.252	956.053
	Hypothesis 2: Temperature as the main determinant		
20	salinity + SST min2	922.513	926.170
21	SST mean + salinity + SST mean2 + SST mean3	922.781	930.096
22	SST mean + salinity + SST mean2 + salinity2 + SST mean3	923.853	932.996
23	salinity + SST min2 + salinity2 + SST min3	924.655	931.970
24	int + salinity + SST min2 + salinity2 + SST min3	925.484	934.627
25	int + salinity + SST min2 + salinity2 + SST min3 + salinity3	925.645	936.617
26	int + SST mean + salinity + SST mean2 + salinity2 + SST mean3	925.850	936.822
27	int + SST min + salinity + SST min2 + salinity2 + SST min3 + salinity3	927.618	940.418
28	SST max + salinity + SST max2 + salinity2 + SST max3	932.927	942.070
29	int + SST mean + salinity + SST mean2 + salinity2 + SST mean3 + salinity3	934.770	947.570
30	SST max + salinity + SST max2 + salinity2 + SST max3 + salinity3	938.599	949.570
31	int + SST max + salinity + SST max2 + salinity2 + SST max3 + salinity3	943.413	956.213
32	int + salinity + salinity2 + SST range3 + salinity3	944.087	953.230
33	int + SST range + salinity + salinity2 + SST range3 + salinity3	946.080	957.052
34	int + SST range + salinity + SST range2 + salinity2 + SST range3 + salinity3	948.076	960.877
	Hypothesis 3: Both chlorophyll and temperature are determinants		
35	**int + chl a min + oxygen + SST range + chl a min2 + oxygen2 + oxygen3**	**890.419**	**903.219**
36	chl a min + SST min + chl a min2 + salinity2 + chl a min3 + SST min3	891.100	903.900
37	chl a range + oxygen + chl a range2 + oxygen2 + SST range2 + oxygen3 + chl a range: SST range	891.204	904.004
38	chl a min + SST min + chl a min2 + salinity2 + chl a min3 + salinity3 + SST min3	891.882	904.683
39	int + chl a min + oxygen + SST range + chl a min2 + oxygen2 + chl a min3 + oxygen3	891.957	906.586
40	int + chl a max + SST min + chl a max2 + salinity2 + SST min3	892.664	903.635

Continued Table 3

Model number	Variables included in the model	AIC	BIC
41	chl a range + oxygen + chl a range2 + oxygen2 + SST range2 + chl a range3 + oxygen3 + chl a range: SST range	892.756	907.385
42	int + chl a max + oxygen + chl a max2 + oxygen2 + SST range2 + chl a max3 + oxygen3 + chl a max: SST range	892.809	909.267
43	int + chl a min + SST min + chl a min2 + salinity2 + chl a min3 + salinity3 + SST min3	892.996	907.625
44	int + chl a min + oxygen + SST range + chl a min2 + oxygen2 + SST range2 + chl a min3 + oxygen3	893.232	907.862
45	int + chl a max + SST min + chl a max2 + salinity2 + SST min2 + SST min3	893.416	906.216
46	int + chl a min + oxygen + SST range + chl a min2 + oxygen2 + SST range2 + chl a min3 + oxygen3 + chl a min: SST range	893.485	911.771
47	int + chl a min + SST min + chl a min2 + salinity2 + chl a min3 + salinity3 + SST min3 + chl a min: SST min	894.580	911.038
48	int + chl a max + oxygen + chl a max2 + oxygen2 + SST range2 + chl a max3 + oxygen3 + SST range3 + chl a max: SST range	894.761	913.048
49	int + chl a max + SST min + chl a max2 + salinity2 + SST min2 + SST min3 + chl a max: SST min	895.012	909.641
50	int + chl a range + SST min + salinity2 + SST min2 + chl a range3 + SST min3	895.078	907.878
51	chl a min + salinity + chl a min2 + salinity2 + chl a min3 + SST mean3	895.956	906.928
52	int + chl a mean + oxygen + SST range + chl a mean2 + oxygen2 + oxygen3	896.135	908.935
53	chl a min + salinity + chl a min2 + salinity2 + SST mean2 + chl a min3 + SST mean3	896.197	908.998
54	int + chl a mean + oxygen + SST range + chl a mean2 + oxygen2 + SST range2 + oxygen3	896.317	910.946
55	chl a min + salinity + chl a min2 + salinity2 + chl a min3	896.373	911.002
56	int + chl a max + oxygen + SST range + chl a max2 + oxygen2 + SST range2 + chl a max3 + oxygen3 + SST range3 + chl a max: SST range	896.415	916.530
57	int + chl a min + salinity + SST min + chl a min2 + salinity2 + chl a min3 + salinity3 + SST min3 + chl a min: SST min	896.491	914.778
58	int + chl a max + salinity + SST min + chl a max2 + salinity2 + SST min2 + SST min3 + chl a max: SST min	896.734	913.192
59	chl a min + salinity + chl a min2 + salinity2 + SST range2 + chl a min3	896.758	907.730
60	int + chl a range + SST min + chl a range2 + salinity2 + SST min2 + chl a range3 + SST min3	897.079	911.709
61	int + chl a mean + oxygen + SST range + chl a mean2 + oxygen2 + SST range2 + chl a mean3 + oxygen3	897.134	913.592
62	chl a min + salinity + SST mean + chl a min2 + salinity2 + SST mean2 + chl a min3 + SST mean3	897.348	911.977
63	int + chl a min + oxygen + SST range + chl a min2 + oxygen2 + SST range2 + chl a min3 + oxygen3 + SST range3 + chl a min: SST range	897.615	917.730
64	int + chl a min + salinity + SST min + chl a min2 + salinity2 + SST min2 + chl a min3 + salinity3 + SST min3 + chl a min: SST min	898.422	918.537
65	int + chl a min + salinity + chl a min2 + salinity2 + SST range2 + chl a min3	898.491	911.292
66	int + chl a range + SST min + chl a range2 + salinity2 + SST min2 + chl a range3 + salinity3 + SST min3	898.648	915.105
67	int + chl a max + salinity + SST min + chl a max2 + salinity2 + SST min2 + salinity3 + SST min3 + chl a max: SST min	898.705	916.991
68	int + chl a mean + oxygen + SST range + chl a mean2 + oxygen2 + SST range2 + chl a mean3 + oxygen3 + chl a mean: SST range	898.914	917.201
69	chl a min + salinity + SST mean + chl a min2 + salinity2 + SST mean2 + chl a min3 + SST mean3 + chl a min: SST mean	899.150	915.607
70	int + chl a range + oxygen + chl a range2 + oxygen2 + SST range2 + chl a range3 + oxygen3 + chl a range: SST range	899.770	916.227
71	int + chl a min + salinity + chl a min2 + salinity2 + SST range2 + chl a min3 + chl a min: SST range	899.842	914.471
72	int + chl a range + SST min + chl a range2 + salinity2 + SST min2 + chl a range3 + salinity3 + SST min3 + chl a range: SST min	900.244	918.530
73	int + chl a max + salinity + SST min + chl a max2 + salinity2 + SST min2 + chl a max3 + salinity3 + SST min3 + chl a max: SST min	900.706	920.821
74	int + chl a mean + oxygen + SST range + chl a mean2 + oxygen2 + SST range2 + chl a mean3 + oxygen3 + SST range3 + chl a mean: SST range	900.887	921.002
75	chl a min + salinity + SST mean + chl a min2 + salinity2 + SST mean2 + chl a min3 + salinity3 + SST mean3 + chl a min: SST mean	901.059	919.346
76	int + chl a min + salinity + chl a min2 + salinity2 + SST range2 + chl a min3 + SST range3 + chl a min: SST range	901.558	918.015
77	int + chl a range + oxygen + SST range + chl a range2 + oxygen2 + SST range2 + chl a range3 + oxygen3 + chl a range: SST range	901.596	919.882
78	int + chl a range + salinity + SST min + chl a range2 + salinity2 + SST min2 + chl a range3 + salinity3 + SST min3 + chl a range: SST min	902.171	922.286
79	int + chl a min + salinity + chl a min2 + salinity2 + SST range2 + chl a min3 + salinity3 + SST range3 + chl a min: SST range	902.467	920.754

Continued Table 3

Model number	Variables included in the model	AIC	BIC
80	int + chl a min + salinity + SST mean + chl a min2 + salinity2 + SST mean2 + chl a min3 + salinity3 + SST mean3 + chl a min: SST mean	903.027	923.142
81	int + chl a range + oxygen + SST range + chl a range2 + oxygen2 + SST range2 + chl a range3 + oxygen3 + SST range3 + chl a range: SST range	903.530	923.645
82	int + chl a min + salinity + SST range + chl a min2 + salinity2 + SST range2 + chl a min3 + salinity3 + SST range3 + chl a min: SST range	903.784	923.899
83	int + SST mean + salinity2 + SST mean2 + chl a max3 + salinity3 + SST mean3 + chl a max:SST mean	908.564	923.193
84	int + chl a min + salinity + SST max + chl a min2 + salinity2 + SST max2 + chl a min3 + salinity3 + SST max3 + chl a min: SST max	909.175	929.290
85	int + chl a max + SST mean + salinity2 + SST mean2 + chl a max3 + salinity3 + SST mean3 + chl a max: SST mean	911.463	927.921
86	int + chl a range + salinity + SST mean + salinity2 + SST mean2 + chl a range3 + salinity3 + SST mean3 + chl a range: SST mean	911.535	929.822
87	int + chl a range + salinity + salinity2 + SST range2 + salinity3 + SST range3 + chl a range:SST range	912.149	926.778
88	int + chl a range + salinity + salinity2 + SST range2 + chl a range3 + salinity3 + SST range3 + chl a range :SST range	912.745	929.203
89	int + chl a range + salinity + chl a range2 + salinity2 + SST range2 + chl a range3 + salinity3 + SST range3 + chl a range: SST range	913.572	931.859
90	int + chl a range + salinity + SST range + chl a range2 + salinity2 + SST range2 + chl a range3 + salinity3 + SST range3 + chl a range: SST range	914.801	934.916
91	int + chl a max + salinity + chl a max2 + salinity2 + SST range2 + salinity3 + SST range3 + chl a max: SST range	916.915	933.373
92	int + chl a max + salinity + SST range + chl a max2 + salinity2 + SST range2 + salinity3 + SST range3 + chl a max: SST range	919.948	938.234
93	int + chl a max + salinity + SST range + chl a max2 + salinity2 + SST range2 + chl a max3 + salinity3 + SST range3 + chl a max: SST range	921.665	941.780
94	int + chl a max + salinity + SST max + salinity2 + SST max2 + chl a max3 + salinity3 + SST max3 + chl a max: SST max	921.847	940.133
95	int + chl a range + salinity + SST max + chl a range2 + salinity2 + SST max2 + chl a range3 + SST max3	926.692	943.150
96	int + chl a range + salinity + SST max + chl a range2 + salinity2 + SST max2 + chl a range3 + SST max3 + chl a range: SST max	927.634	945.921
97	int + chl a range + salinity + SST mean + chl a range2 + salinity2 + SST mean2 + chl a range3 + salinity3 + SST mean3 + chl a range: SST mean	928.686	948.801
98	int + chl a range + salinity + SST max + chl a range2 + salinity2 + SST max2 + chl a range3 + salinity3 + SST max3 + chl a range: SST max	929.622	949.737
99	int + chl a max + salinity + SST mean + salinity2 + SST mean2 + chl a max3 + salinity3 + SST mean3 + chl a max: SST mean	932.518	950.804
100	int + chl a max + salinity + SST mean + chl a max2 + salinity2 + SST mean2 + chl a max3 + salinity3 + SST mean3 + chl a max: SST mean	934.512	954.627
101	int + chl a max + salinity + SST max + chl a max2 + salinity2 + SST max2 + chl a max3 + salinity3 + SST max3 + chl a max: SST max	939.254	959.369

Within each hypothesis, models are ranked according to their Akaike Information Criterion (AIC); lower values of AIC indicate a better fit. Bayesian Information Criterion (BIC) is also given. The best model is shown in bold. Abbreviations for variables included are: chl a min = minimum chlorophyll concentration, chl a mean = mean chlorophyll concentration, chl a max = maximum chlorophyll concentration, chl a range = chlorophyll concentration range, SST min = minimum sea surface temperature, SST mean = mean sea surface temperature, SST max = maximum sea surface temperature, SST range = sea surface temperature range, oxygen = mean dissolved oxygen concentration, salinity = mean salinity. Variable names numbered 2 and 3 mean that variable to the second or third power, respectively.

sharks occurred on continental shelves from off Tierra del Fuego (Argentina) to about 20°S (Brazil), including Uruguay's eastern shore and coastal waters of the Malvinas/Falkland Islands. The model also indicated a few scattered locations suitable for basking shark occurrence in coastal waters of South Georgia (Fig. 3A). In the southeast Atlantic, basking sharks inhabited the cool waters from off southern South Africa to northern Namibia, and were absent in the subtropical waters off northeastern South Africa, and in tropical waters off southern Angola (Fig. 3B). Unlike the southeast Atlantic range, the southwest Atlantic range of basking sharks comprised cool temperate, warm temperate and subtropical waters.

3 Discussion

We found support for an effect of both chlorophyll minimum concentration and sea surface temperature range in determining the distribution of basking sharks on South Atlantic continental shelves. However, of all three variables included in the best model, chlorophyll minimum concentration had the highest contribution. We propose that the importance of chlorophyll minimum concentration on basking shark distribution likely reflects a positive correlation with phytoplankton abundance, which in turn affects the abundance of the zooplanktonic prey of basking sharks. A positive correlation of chlorophyll concentration and zooplankton abundance at large scales has been observed before (Irigoien et al., 2004; Ware and Thomson, 2005). In the study area, sectors of high zooplankton abundance coincide with areas of high phytoplankton abundance, as estimated by chlorophyll concentration (Verheye 2000; Sabatini and Álvarez Colombo, 2001; Acha et al., 2004). Our finding agrees with results at smaller scales, where zooplankton concentration is a major determinant of basking shark occurrence and abundance (Sims et al., 1997, 2003; Sims and Quayle, 1998; Soldo et al., 2008; Siders et al., 2013). The results of our model likely reflect the distribution of concentrations of basking sharks, which are generally located in areas with high food availability (Sims, 2008; Siders et al., 2013).

Evidence is increasing that dissolved oxygen concentration plays an important role in determining the distribution of large sharks. It is not surprising that dissolved oxygen concentration could limit the vertical and horizontal distribution of endothermic sharks, which have high metabolic rates and oxygen demands, such as shortfin mako *Isurus oxyrinchus* (Abascal et al., 2011), and white sharks *Carcharodon carcharias* (Nasby-Lucas et al., 2009), but it also has a large effect on ectothermic species, such as the bull shark *Carcharhinus leucas* (Heithaus et al., 2009). We hypothesize that the importance of dissolved oxygen as a determinant of the distribution of basking sharks on South Atlantic continental shelves reflects the importance of frontal, well oxygenated systems as primary habitat for this species.

We have confirmed the geographic distribution of basking sharks on southern African continental shelves and shown that the subtropical South American continental shelf between 20°S and 30°S is (or was) an area of regular occurrence of basking sharks, not previously included in any map. Compagno (1984) depicts a map where basking sharks occur in the South Atlantic south of 30°S, restricted on continental shelves on both sides of the Atlantic. Later, Compagno (2001) extends north the African range of basking sharks to 20°S, along the Namibian coast, and includes the open ocean between

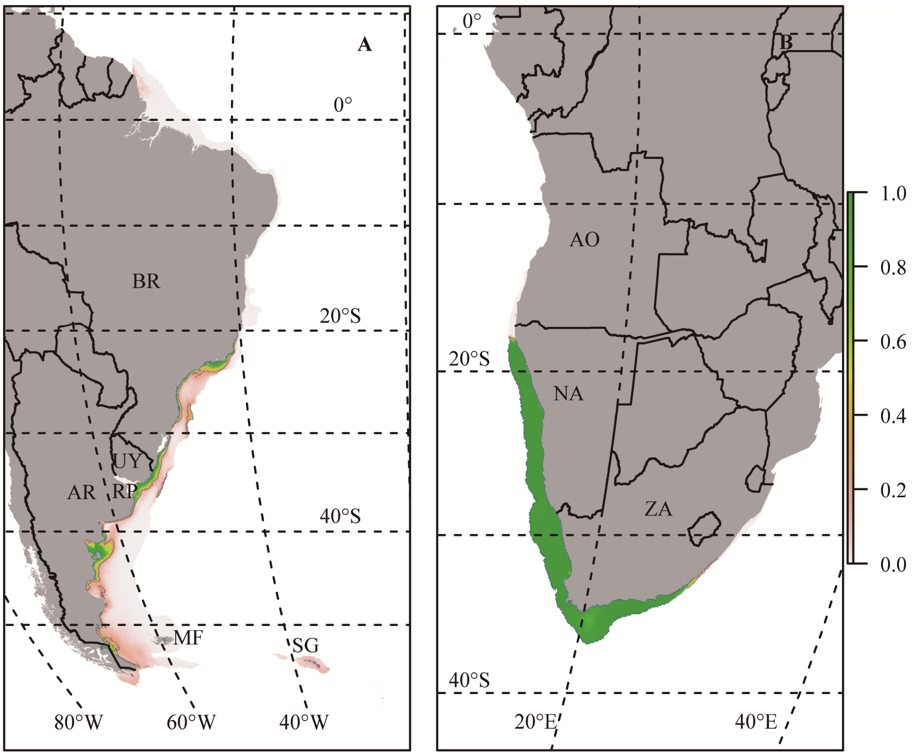

Fig. 3 Habitat suitability (from 0, lowest suitability, to 1, highest suitability) for basking sharks *Cetorhinus maximus* as estimated from a maximum likelihood (MaxLike) model including chlorophyll minimum concentration, mean dissolved oxygen concentration, and sea surface temperature range

A. Continental shelves off South America. **B**. Continental shelves of southern Africa. The blue line delimits the geographic range, estimating after applying a threshold maximizing the sum of specificity and sensitivity. AO = Angola, AR = Argentina, BR = Brazil, MF = Malvinas/Falkland Islands, NA = Namibia, RP = Río de la Plata, SG = South Georgia, UY = Uruguay, ZA = South Africa. Map projection is Mollweide equal area.

South America and Africa between 30°S and 50°S in the west and 20°S and 40°S in the east, as a potential area of occurrence of basking sharks. More recently, Ebert et al. (2013) show a map keeping essentially the same limits of the distribution of basking sharks on South Atlantic continental shelves as Compagno (2001); although they extend the distribution to oceanic waters between Africa and South America.

Eastern (i.e. African) and western (i.e. South American) parts of the South Atlantic geographic range of basking sharks are dissimilar in their habitat suitability. The southwest African shelf appears to have higher and more continuous habitat suitability than the South American shelf. This could be a result of both the high oceanographic heterogeneity of the South American shelf (Acha et al., 2004) and the extremely high productivity (second in the world) of the southwest African shelf (Waldron and Probyn, 1992). South American continental shelves include a mosaic of areas of high productivity scattered among areas of lower primary and secondary production (Acha et al., 2004). On the other hand, on the southwest African shelf, areas of high productivity are more homogeneously distributed, forming a vast frontal system – the Benguela system. Given the importance of primary production in determining basking shark distribution in the South Atlantic, it is expected a more continuous habitat suitability on the southern African shelf than off South America.

The geographic range of basking sharks on South Atlantic shelves has some marked differences with the distribution on North Atlantic shelves. In the North Atlantic outside the Gulf of Mexico, basking sharks occur mainly in high latitudes (Compagno, 2001), wandering into subtropical shelf waters (e.g. east coast of Florida, USA) only occasionally (Compagno, 2001; Compagno et al., 2005). However, regular occurrence of basking sharks in subtropical shelf waters appears to be a common pattern in some areas, like off Fujian (China), where basking sharks were common enough as to support a harpoon fishery (Lam and Sadovy de Mitcheson, 2011), and off northwestern Florida, where repeated interannual sightings of basking sharks have been reported (Hoffmayer et al., 2011). The situation off Fujian resembles the case off southern Brazil, where basking sharks used to be common and its occurrence as predictable as to support small-scale gillnet fisheries (Soto et al., 2007). Minimum chlorophyll concentration is a major driver explaining the presence of basking sharks in southern Brazilian subtropical waters, as compared to eastern Florida or KwaZulu-Natal (South Africa) waters. From the Bio-ORACLE database (Tyberghein et al., 2012), minimum chlorophyll concentration is about an order of magnitude higher off southern Brazil than off eastern Florida (Table 4). Interestingly, minimum chlorophyll concentration off Fujian and off northwestern Florida – the other subtropical areas with a known regular occurrence of basking sharks – is similar to the one off southern Brazil (Table 4). Waters off KwaZulu-Natal – the subtropical area within our study area with zero basking shark occurrences – have a minimum chlorophyll concentration lower than those off southern Brazil, Fujian, or northwestern Florida (Table 4). Thus, we propose that the regular presence of basking sharks in subtropical shelf waters is limited by food (zooplankton) availability. In fact, a positive association of food availability and abundance or occurrence has been reported in basking sharks (Sims et al., 1997; Sims and Reid, 2002; Siders et al., 2013) and other planktivorous elasmobranchs (e.g. Anderson et al., 2011; Jaine et al., 2012; McKinney et al., 2012).

In general, the most suitable habitats for basking sharks on South Atlantic continental shelves coincide with the northward branches of the Antarctic Circumpolar Current, which produce upwelling areas rich in zooplankton and dissolved oxygen, and with steep horizontal gradients in sea surface temperature. The highest habitat suitability for basking sharks are located in frontal systems, such as the Benguela upwelling off western South Africa and Namibia, the upwelling areas off Cabo Frio and Cabo de Santa Marta Grande off southern Brazil, the Río de la Plata estuary front and the shelf-break front off northern Argentina and Uruguay, the tidal front off the northern Patagonian gulfs, and the Patagonian cold estuarine front off the mouth of the Strait of Magellan. Fronts increase primary production by re-suspending nutrients in the euphotic zone, increasing zooplankton concentration (Muelbert et al., 2008),

Table 4 Minimum chlorophyll a concentration (mg/m^3) median and interquartile range values for five subtropical regions with different sighting frequency of basking sharks *Cetorhinus maximus*

Region	Median	Interquartile range
northwestern Florida	0.546	0.329–2.786
southern Brazil	0.534	0.282–1.207
Fujian	0.402	0.195–0.828
KwaZulu-Natal	0.152	0.133–0.344
eastern Florida	0.064	0.053–0.099

Data taken from the Bio-ORACLE database (Tyberghein et al., 2012).

which, in turn, increases the abundance of predators (Etnoyer et al., 2004; Royer et al., 2004; Campagna et al., 2006). Among elasmobranchs, it is well known that the abundance of both zooplankton feeders (Sims and Quayle, 1998; Luiz Jr. et al., 2009; McKinney et al., 2012) and higher-level predators (Campana and Joyce, 2004; Weltz et al., 2013) increases at fronts, making these areas hotspots of species richness (Worm et al., 2003; Lucifora et al., 2012). The congruence of the areas of highest habitat suitability for basking sharks and the location of marine fronts agree with previous observations of marine fronts as important habitats for basking sharks (Choy and Adams, 1995; Sims and Quayle, 1998; Hoffmayer et al., 2011).

Copepods and large planktonic crustaceans are the main components of the basking shark diet (Compagno, 2001; Sims, 2008). Accordingly, foraging areas of basking sharks are characterized by a predominance of these prey, particularly copepods (Sims and Merrett, 1997). Copepods are the most abundant zooplankton in frontal areas off southern Brazil (Montú et al., 1997; Lopes et al., 1999; Muelbert et al., 2008), and off Argentina (Sabatini and Álvarez Colombo, 2001; Acha et al., 2004), as well as off southwest Africa (Verheye et al., 1998). This indicates that the zooplankton community of the areas identified as suitable habitat for basking shark in the South Atlantic contains the most important prey groups for basking sharks.

The best model predicts that basking sharks might occur both in areas with historical basking shark records but without precise data, and in areas lacking any previous record of basking sharks. One of these areas is the eastern Uruguayan coast. Although we were not able to obtain the precise locations of basking shark occurrences in this area, these sharks are known to occur off eastern Uruguay (de Buen, 1950), where they are occasionally caught in gillnet fisheries (Domingo et al., 2008). Accordingly, our model predicts the occurrence of basking sharks in the same area where the species has been recorded along the Uruguayan coasts. Other areas in which the model predicts suitable habitat for basking sharks but no actual records have been confirmed include a few scattered coastal areas of South Georgia. Basking sharks have not been recorded around South Georgia waters (Duhamel and Compagno, 1985; Compagno, 1984, 2001; Ebert et al., 2013). However, the presence of basking sharks in high-latitude areas in the Northern Hemisphere (*e.g.* Barents Sea, White Sea) and the frequency of other commonly co-occurring species in South Georgia (e.g. porbeagle sharks, *Lamna nasus*) (Duhamel and Compagno, 1985; Figueroa, 1997) suggest that the habitat suitability predicted by the model may be correct. The current absence of basking sharks around South Georgia may be a result of lack of data or an actual absence due to the remoteness of this area.

There are some potential issues that might affect or limit our results. First, the opportunistic nature of our records is an obstacle that impedes the use of stronger presence-absence modelling frameworks. Modelling techniques incorporating presences and absences are known to perform better than presence-background techniques (Brotons et al., 2004). Thus, these techniques are preferred when standardized surveys are available (Brotons et al., 2004). In our case, our sources of data were records from museum collections, fishery catches and fishery observer programs. The only way of amalgamating all these records is through presence-background modelling techniques, such as those used here, which have performances close to presence-absence techniques (MacLeod et al., 2008; Royle et al., 2012), as has been done previously for basking (Siders et al., 2013) and other sharks (McKinney et al., 2012; Sequeira et al., 2012). Second, the available records had a distribution biased to coastal waters, while it is known that basking sharks spend considerable amounts of time in the open ocean at mesopelagic depths (Skomal et al., 2009). We addressed this problem by limiting our analyses to continental shelf waters. Also, our results identify offshore areas as suitable habitat for basking sharks despite most records being close to shore. This suggests that, within the neritic realm, our results could be unbiased. However, much remains to be done concerning the distribution of basking sharks in open waters of the South Atlantic Ocean.

The areas identified as most suitable for basking sharks are close to shore and in highly productive areas (fronts). Nearshore marine habitats are more affected by anthropogenic effects (e.g. pollution, habitat destruction, fishing) than offshore areas (Halpern et al., 2008). Highly productive South Atlantic marine fronts tend to accumulate fish biomass, which makes them a target of commercial fisheries (Sakko, 1998; Tyedmers et al., 2005; Lucifora et al., 2012; Alemany. 2013). Hence, in these areas basking sharks are exposed to high anthropogenic impacts. Basking sharks appear to be highly vulnerable to even low levels of human-induced mortality (Sims, 2008). Thus, regulation of fishing methods known to affect basking sharks must be monitored in areas containing suitable habitat for this species. Also, fishing crews could be instructed on the most appropriate ways of releasing basking sharks caught incidentally, although the success of such a measure will depend on post-release survival.

We have shown how habitat suitability modelling may inform about the geographic distribution of a threatened shark in a large area with little available information. Our model explains why basking sharks occur regularly in some subtropical shelf areas (e.g. southern Brazil, Fujian, northwest Florida) while being absent in other subtropical regions (i.e. east Florida, KwaZulu-Natal), and predicts the presence of basking sharks in areas with known occurrences of the species but no precise data (i.e. Uruguay east coast). Our results provide quantitative evidence of habitat suitability useful for historical baseline estimation, conservation and recovery planning.

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