



Original Investigation

At-sea abundance and spatial distribution of South American sea lion (*Otaria byronia*) in Chilean Northern Patagonia: How many are there?L. Bedriñana-Romano^{a,b}, F.A. Viddi^{a,b}, J.P. Torres-Florez^b, J. Ruiz^{a,b}, M.F. Nery^b, D. Haro^b, Y. Montecinos^b, R. Hucke-Gaete^{a,b,*}^a Instituto de Ciencias Marinas y Limnológicas, Universidad Austral de Chile, Casilla 567, Valdivia, Chile^b NGO Centro Ballena Azul, c/o ICML, UACH, Casilla 567, Valdivia, Chile

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ABSTRACT

The South American sea lion (*Otaria byronia*) (SSL) is a widespread opportunistic predator that inhabits waters ranging from Southern Ecuador to Southern Chile in the Pacific Ocean and from Southern Brazil to Southern Argentina in the Atlantic. SSL abundance estimates, as for many pinniped species, have relied on shore censuses, with the uncertainty that an indeterminate number of individuals at sea might remain uncounted. The proportion of the population that remains at sea during censuses and their distribution patterns are not clear and has been scarcely assessed. We used line transect sampling to gather information about at-sea abundance, density and spatial distribution of SSL in coastal waters off the Chilean Northern Patagonia. A total of 123 groups were sighted while on-effort, with an estimated density of 0.393 ind./km² (95%CI = 0.262–0.591) and a total abundance, for the surveyed area, of 13,721 individuals (95%CI = 9127–20,627). Even when our survey was rather restricted in spatial range, generalized additive model results showed that depth, distance to SSL rookeries, coastline complexity and geographical coordinates had a significant influence on SSL spatial distribution. The results on abundance and spatial distribution of SSL at sea are discussed in terms of current population estimates. Our substantial at-sea abundance estimate suggests that shore censuses might have been historically biased. Several aspects should be taken into account in further research on SSL abundance, such as including pelagic waters and undertaking simultaneously on-rookery and marine SSL abundance estimates. The results presented here provide valuable insights for revisiting and possibly improve population estimates of SSL and other pinnipeds species worldwide. This is particularly relevant when management and conservation actions need to be taken on those species that have strong interactions with fisheries and aquaculture.

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Introduction

The South American sea lion (*Otaria byronia*) (herein referred to as SSL) is a widespread predator that inhabits waters ranging from Southern Ecuador to Southern Chile in the Pacific Ocean and from Southern Brazil to Southern Argentina in the Atlantic, including Falkland/Malvinas Islands (King, 1983; Félix, 2002). Overall abundance of this species has been estimated to reach 500,000 individuals of which half are distributed off the Atlantic and the other half off the Pacific coast (Oliva et al., 2009). SSL is a generalist and opportunistic predator that shows extensive regional variation in its prey consumption (George-Nascimento et al., 1985; Harcourt, 1993; Thompson et al., 1998; Koen Alonso et al., 2000;

Campagna et al., 2001; Hückstädt and Krautz, 2004; Suarez et al., 2005; Hückstädt et al., 2007; Drago et al., 2010) and an ability to shift its foraging habits according to prey availability (Soto et al., 2006; Drago et al., 2009). In part, the plasticity to exploit local resources has fostered the occurrence of numerous type of interactions with fisheries and aquaculture, with different intensity throughout its wide distributional range (Muck and Fuentes, 1987; Crespo et al., 1997; Hückstädt and Antezana, 2003; Szteren and Páez, 2003; Szteren et al., 2004; Sepúlveda and Oliva, 2005; Sepúlveda et al., 2007; de la Torre et al., 2010; Riet-Sapriza et al., 2013; Reyes et al., 2013). These conflicts with human activities have led to illegal takes and/or claims for managed culling. This in despite of information gaps regarding population and/or sub-population trends (Dans et al., 2004; Sepúlveda et al., 2011). Under this scenario, it becomes evident that effective ecosystem-based management decisions require sound population size assessments.

As in many pinniped species, SSL abundance has been assessed by means of on-rookery censuses during reproductive and moulting

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seasons, when a large proportion of this species' population congregates on land. A major inconvenient of direct counting is that an indeterminate number of individuals remains always uncounted because they are either at sea (*i.e.*: juveniles, old animals, adults performing foraging trips), hidden (*i.e.*: between boulders or within caves/crevices, or even covered by other individuals) or excluded from sampling because of inherent logistic problems (*i.e.*: poor weather conditions and/or accessibility to rookeries). To account for these difficulties, several methods that allow quantifying the size of this "uncounted fraction" have been developed and used for pinniped censuses (Berkson and DeMaster, 1985; Crespo, 1988; Reyes et al., 1999; Calkins et al., 1999; Huccke-Gaete et al., 2004). However, fewer attempts have dealt with the direct estimation of the population fraction that remains at sea in this taxonomic group (Williams and Thomas, 2007).

Line transect sampling has been widely used for abundance assessment in many environments and species (Buckland et al., 2001) and is currently one of the two more frequently used approaches for estimating cetacean abundance (Dawson et al., 2008). This method gives enough flexibility to assess the density, abundance and distribution of multiple species by adjusting several detection curves depending on species being assessed (Williams and Thomas, 2007). Furthermore, data collected from these line transects can also be used to fit mathematical models that relate the spatial distribution of individuals to environmental variables in a predictive manner (Guisan and Zimmermann, 2000).

Line transect sampling techniques have scarcely been used for pinniped abundance estimates and distribution at sea, even when it can offer valuable information about population size (Williams and Thomas, 2007). Here, we used data from a large marine mammal survey conducted in coastal waters off southern Chile to (a) assess the at-sea abundance of SSL; and (b) determine their spatial distribution, in relation to fixed explanatory variables such as depth, distance to coast, distance to salmon farms, distance to sea-lion rookeries, coastline complexity and geographic coordinates. Results are discussed in terms of current population estimates for SSL.

Material and methods

Study region

The study was carried out off the Chilean Northern Patagonia coast (CNP, 41°30' S–45°30' S) in the Eastern South Pacific (ESP, Fig. 1). This area, within the shelf, is characterized by an intricate array of inner passages, archipelagos, channels, and fjords and deep canyons of up to 400 m, stretching along ca. 900 km of linear coastline and encloses roughly 12,000 km of convoluted and protected shoreline.

The general oceanographic conditions affecting the study region are under the direct influence of the West Wind Drift (WWD). The bulk of the oceanic west-driven currents encounter the South American continent at about latitude 41° S, one of the major fjord regions of the world, and the origin of a northbound current characterized by an equatorward flowing branch (the Humboldt Current, which in turn splits in two: coastal and oceanic) and a southbound current represented by a poleward flowing branch (the Cape Horn Current) (Longhurst, 1998). The interaction between the WWD, Sub Antarctic waters, fjord freshwaters (coastal runoffs from glacier melt, river drainage and copious precipitation) and tidal currents defines a strong salinity gradient (vertically and horizontally) (Dávila et al., 2002; Palma and Silva, 2004), which in turn has an important effect on phytoplankton and primary productivity (Iriarte et al., 2007).

Survey design and implementation

A marine mammal survey was conducted during mid February and mid March of 2009 throughout the study area, covering open coasts, gulfs, and inner channels. The survey period covered the final stage of SSL breeding season, when most adults are congregated on land, but progressively leaving reproductive rookeries (Pavés et al., 2005). The original design included a single-stratum survey extending as far as the 200 m depth contour, including approximately 1800 km of trackline and providing approximately 20 replicate transects (Fig. 1). Due to logistic constraints, stratification was not feasible, thus non-uniform coverage probability within inlets and narrow channels might have occurred (Thomas et al., 2007). The automated survey design engine in the software Distance 6.0 (Beta 5, Thomas et al., 2006) was used to evaluate the performance of parallel line and equal-spaced zigzag samplers. The equal-spaced zigzag design was chosen because it offered good coverage probability during 100 simulations while retaining high efficiency. The design axis was set to run in a roughly north-east to south-west direction, so that transect lines ran perpendicular to the coast. Poor weather precluded the planned survey from being completed in its entirety. However, the survey followed the original transect spacing and angle when displacing the offshore boundary of the survey region inshore (*i.e.* by shortening the originally planned transects), and thus coverage probability within the survey region remained acceptable. Final survey area was restricted to coastal waters with a westerly boundary that did not exceed ca. 25 km from the nearest coast, excluding therefore offshore waters where SSL presence has been documented (Hückstädt and Krautz, 2004). Logistical problems precluded surveying the Chiloe inner sea where the presence of the species is known to occur. Despite these limitations in our survey design, we were able to cover most of the study region (Fig. 1).

Field protocols followed standard line-transect survey methods (Buckland et al., 2001) on board the 17 m motor-yacht "Noctiluca" and the 17 m sailboat "Williwaw", with some modifications specific to small-boat surveys (Dawson et al., 2008; Williams and Thomas, 2007, 2009). Only one observer platform could be used (at one particular time), so all analyses assumed complete detection on the trackline (*i.e.* $g(0)=1$). Three people formed the primary observer team, namely a port and starboard observer and a data recorder, all using a platform height of 5 m (Noctiluca) and 1.63 m (Williwaw). In addition to the observers, one person sat in the wheelhouse to operate the computer. The primary observer team searched ahead of the vessel, that is, a sector from the trackline to 90° abeam, while concentrating primarily on the trackline. Each observer searched a sector spanning from 10° on one side of the trackline to 90° on the other side. The data recorder logged whenever a sighting was made, and assisted the observer with species identification or group size estimation when needed. A GPS was connected to a computer running *Logger 2000* software (International Fund for Animal Welfare) which collected geographical location every 10 s, and was used for calculating length of the covered trackline, as well as recording ship's course and speed. The computer operator entered information on sighting conditions every 15 min, or as conditions changed. The computer operator also noted the position of each team member at the beginning of every hour. Observer rotation occurred every half hour. Information collected on factors that could affect sighting conditions included sea state, cloud cover, precipitation and a subjective sightability code.

Whenever a sighting was made, a sighting number was assigned and reported to the computer operator *via* two-way VHF radio. An angle board mounted on the deck was used to measure radial angle to the group of animals, and a visual estimate was made of the range to the first sighting. In cases when a visual range was made, radial

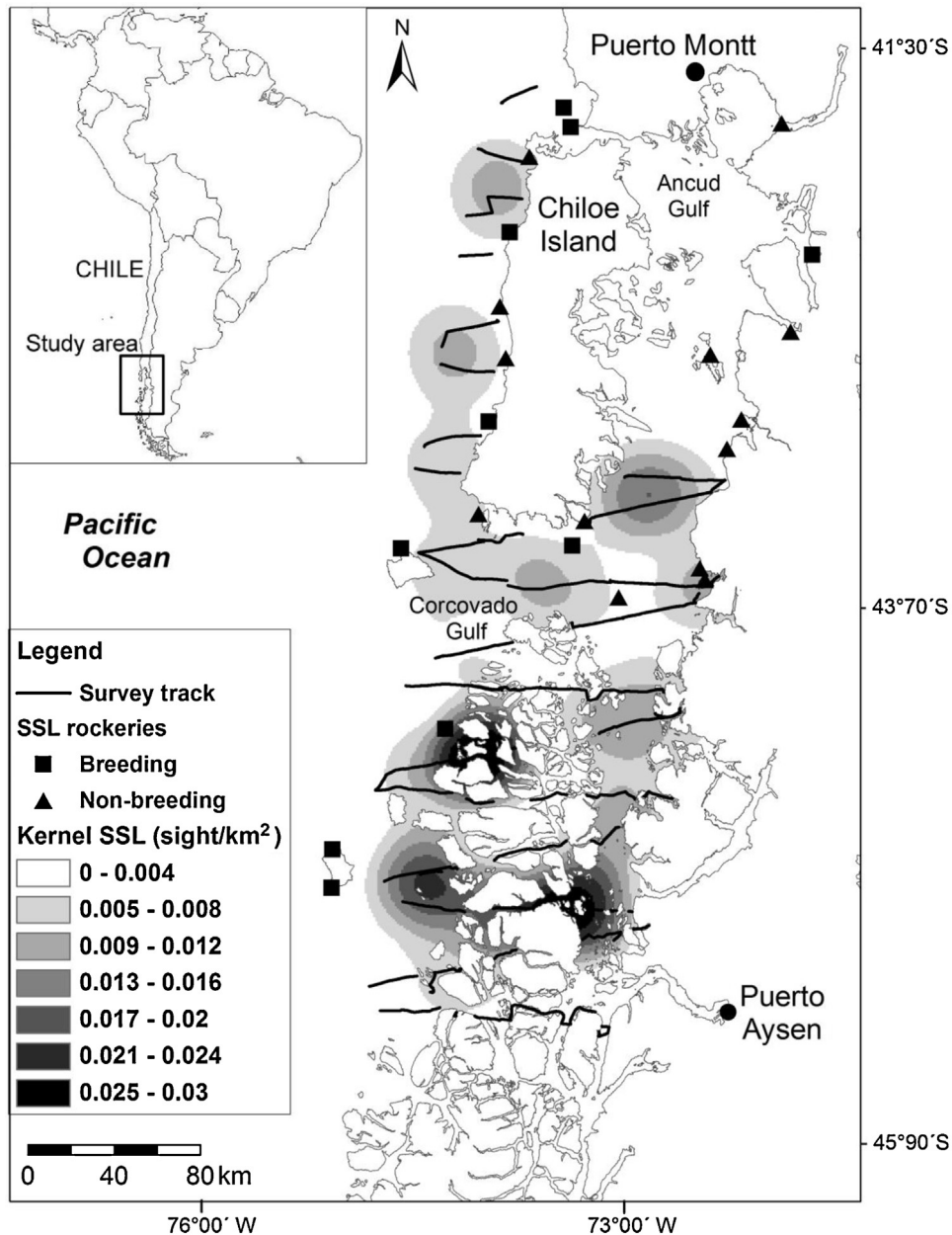


Fig. 1. Marine survey tracks in the study area showing kernel density of SSL sightings and SSL breeding (squares) and non-breeding (triangles) rookeries.

distance estimates were corrected subsequently using results from observer-specific distance estimation experiments (Williams et al., 2007). Distance estimation experiments were conducted for each observer using rangefinders and radar to measure true distance to objects within a range of 50 m–6 km, while observers recorded an estimated distance to the target. Linear regression models were fitted to the distance estimation experimental data with standard error proportional to true distance. Bias in visual estimates was addressed by dividing estimated distances by the slope of the regression through the origin.

With every sighting, data on species group size and behavioural category was recorded. Behavioural categories were defined in terms of how they might affect detection capability:

(i) Swimming/travelling: Considered as directional surfacing behaviour with no explicit heading relative to the survey vessel.

- (ii) Feeding: Consisted in fast surface movements and the confirmed observation of fish in SSL mouths and/or the presence on leaping fish nearby the group.
- (iii) Avoiding: Swimming direction of the SSL group was clearly away from the survey vessel
- (iv) Approaching: Swimming direction of the SSL group was clearly towards the survey vessel
- (v) Leaping: At least two-thirds of the body were observed out of the water often followed by a splash.

Data analysis

Abundance estimates

A “conventional distance sampling” approach, as described by Buckland et al. (2001), was followed to analyse the data, which included only at-sea sightings discarding every sighting from hauled out SSL. This method assumes that probability of detection

of animals at zero distance from the trackline is one (the so-called $g(0)=1$ assumption). The analysis can be split into three parts: (i) fitting a detection function $g(x)$, where x is perpendicular distance to observed distances of each sighting from the transect to estimate average probability of detection, p ; (ii) using observed group sizes to estimate mean group size in the population, $\hat{E}(s)$; (iii) estimation of animal density, \hat{D} , using the formula

$$\hat{D} = \frac{n\hat{E}(s)}{2wL\hat{p}}$$

where n is the number of groups seen within w ; w is the truncation distance; and L is the total length of the transects searched on effort. Estimation of detection probability mean group size and density was performed using the free software *Distance* 6.0, Release 2 (Thomas et al., 2009).

In order to obtain $g(x)$, several models were fitted to the observed distribution of distances based on the key function and series expansion formulation of Buckland et al. (2001). The uniform, half-normal and hazard-rate key functions were used, together with polynomial or cosine series expansion terms as required. The model that minimized the Akaike Information Criterion (AIC) was selected unless visual inspection of the curve suggested violation of biological expectations. The absolute fit of models was judged using diagnostic plots and the Kolmogorov–Smirnov goodness of fit test. No truncation was applied in the field, so this was the first step from the analysis. Several histograms were constructed with the data and visual inspection of them oriented the decision of where to truncate data. Finally, as suggested by Buckland et al. (2001), this truncation was done *ca.* the value of x where $\hat{g}(x) = 0.15$ and rounded to the nearest 10 m.

An unbiased estimate of group size was determined by *Distance* default method. Briefly this implied regressing the natural logarithm of group size on the estimated probability of detection at the distance the group was seen. The predicted value of $\ln(s)$ at zero distance (where detection probability is 1) was then back-transformed to provide the required estimate.

Once every parameter was obtained an estimate of density and abundance was calculated. Variances were calculated based on the empirical variance in estimated density between samples (default in current *Distance* version) described in Fewster et al. (2009).

Spatial patterns

All sightings recorded were mapped through GIS tools after correcting for angle and distance. A kernel density of sightings was generated within the survey area using a band of 1.5 km either side of the vessel's track, while a 1 km × 1 km grid was generated using the Geospatial Modelling Environment (Beyer, 2012). The extension of the band (1.5 km) was chosen because it was the maximum achieved detection distance for SSL and it was found to be the optimal size and scale for GIS and mapping analysis. For statistical analyses, a value of the density of sightings and seven explanatory variables were extracted from GIS. These variables included:

- (i) Depth: Raw data for depth (as Latitude, Longitude and z values) were obtained from the Chilean Navy (Servicio Hidrográfico y Oceanográfico), from which a Triangular Irregular Network (TIN) model was created using 3D Analyst in ArcGIS.
- (ii) Distance to coast: Distance from SSL sighting location to the nearest land point.
- (iii) Distance to salmon farms: Distance from every SSL sighting location to the nearest salmon farm facility. This variable was selected because of known negative interactions between SSL and salmon farms have been reported in the area (Sepúlveda and Oliva, 2005).

- (iv) Distance to SSL rookeries: Distance from every SSL sighting location to the nearest SSL rookery (extracted from Oliva et al., 2008). SSL rookeries holding more than 200 individuals were considered. Rookeries locations have been correlated with the proximity to feeding grounds in otariids (Call and Loughlin, 2005). Therefore distance to rookeries could be used as a proxy for the selection of certain areas.
- (v) Coastline complexity: This variable is a proxy of island concentration, convoluted bays and narrow channels measured as a density of coastline. The calculation of this variable was done by estimating the total length of coastline (in km) falling into a 1 km × 1 km cell within a searching radius of 10 km. Values equal to zero mean that no coast is found within a 10 km radius, therefore lower values represent more open waters while larger values represent enclosed waters.
- (vi) Geographical coordinates: Universal Transverse Mercator (UTM) Northing and Easting (instead of latitude and longitude) were included to test whether SSL were clumped to specific geographic coordinates. UTM Northing and UTM Easting were treated as sixth and seventh variable in the spatial model.

Generalized additive models (GAMs) were used to examine the role of explanatory variables on SSL density. GAMs allow a data-driven approach by fitting smoothed non-linear functions of explanatory variables without imposing parametric constraints (Hastie and Tibshirani, 1990). Smoother terms were derived using thin plate regression splines implemented under the “mgcv” package in R 3.0.0 (Wood, 2006; R Development Core Team, 2009). A Gaussian error distribution with the identity link function was used. Backward selection, beginning from a fully saturated model, was used to obtain the best-fitting models on the basis of their GCV scores (generalized cross validation). The GCV can be viewed as the criterion that selects the effective degrees of freedom of a model where the scale parameter is unknown and is therefore estimated by the model. The GCV operates by performing smoothing parameter selection wherein the GCV essentially finds an appropriate smoother for each covariate (Wood, 2006). A lower GCV score indicates a better-fitting GAM. From the initial full model, the covariate with the highest non-significant p -value was removed and refitted to the reduced model. If that model resulted in a lower GCV score, it was retained and again the explanatory variable with the highest p -value was removed. The procedure was repeated until the removal of any explanatory variable resulted in a higher GCV score. If at any stage removing the least significant explanatory variable resulted in an increased GCV score, then the next least significant term was removed, and so on until no further reduction in GCV could be obtained. Diagnostic plots were also made to determine the fit effectiveness of the models (Wood, 2006). We chose GAM models because they generate smoothed curves representing the relationship between the response and each explanatory variable in the model. GAMs are particularly good at identifying and describing non-linear relationships that are more typical than linear relationships in ecology (Oksanen and Minchin, 2002).

Results

Survey effort

The western boundary of the planned design proved to be impractical when faced with poor weather conditions. The realized survey effort comprised an area of 34,899 km² (Fig. 1). Effective trackline effort totalled 1278.12 km corresponding to 20 transects.

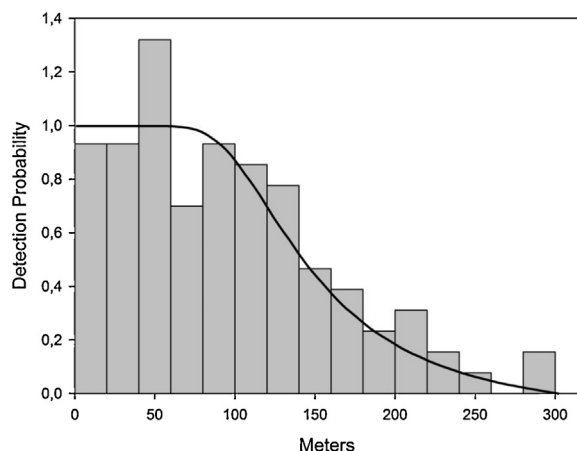


Fig. 2. Histogram of estimated distances to every SSL group sighted. Truncation was performed at 300 m and a HR function with no cosine adjustments was fitted to the data. Notice the slight spike at 50 m that could indicate some avoidance to the vessel presence by SSL.

Abundance

A total of 123 SSL groups were sighted while on-effort. Fitting the detection function required truncation of data around 300 m (where $\hat{g}(x) = 0.159$), which resulted in 17 sightings being excluded. Animal behaviour did not show any sign of responsive avoidance or attraction. Most sightings were recorded as swimming/travelling (115/123 = 93.5%), followed by feeding (3/123 = 2.4%), avoiding (3/123 = 2.4%), approaching (1/123 = 0.8%) and leaping (1/123 = 0.8%). However, visual inspection of the histogram used for fitting the detection function showed a slight signal of avoidance behaviour, with detection probability spiking around 50 m (Fig. 2).

Several detection function models with different series expansion were fitted to the corrected perpendicular sightings data. Two models minimized the AIC, a Half-Normal with no series expansion (HN) and a Hazard Rate with no series expansion (HR). The HR model was preferred over the HN, although later showed slightly lower AIC ($\Delta AIC = 1.07$) because it better fit the data, maintaining the curve steady with detection probability equal to 1 until a steep decline at around 100 m coinciding with the biological expectation that the detection function should have a wider shoulder.

SSL group size range between 1 and 30 individuals with a mean of 2.24 (%CV 19.49) and the estimated expected group size was 1.70 (%CV 7.67) (Table 1). Estimated density of SSL was 0.393 ind./km² (95%CI = 0.262–0.591) resulting in a total abundance for the surveyed area of 13,721 individuals (95%CI = 9127–20,627) (Table 1).

Spatial distribution

The explanatory variables that were found to be significant predictors of SSL included geographical coordinates (UTM Easting and Northing), depth, distance to SSL rockery, and coastline complexity. SSL distribution was spatially uneven, being observed preferentially to South and East of the study area (Fig. 3a and b). In general, model suggested that SSL had a greater preference for lower depths, predominantly around 50 and 200 m (Fig. 3c). In addition, SSL showed a clear preference for areas located within 3 km of rockeries (Fig. 3e) and avoided areas of high coastline complexity (Fig. 3d). The best model for SSL data explained 54.4% of the deviance (Table 2).

Table 1

Results of SSL at-sea abundance estimate. (a) Results from detection curve fitting, truncation distance (w), number of observation (n) (before and after truncation), fitted detection function model, p -value from Kolmogorov–Smirnov goodness of fit test, estimated mean detection probability (\hat{p}) and corresponding percentage coefficient of variation; (b) estimated expected group size and corresponding percentage coefficient of variation for SSL, plus average, CV and maximum observed group size; (c) estimated density (\hat{D}) and abundance (\hat{N}), with corresponding confidence intervals (CIs) and percentage coefficient of variation (%CV).

w (m)	n before	n after	Model	K-S p	\hat{p}	%CV (\hat{p})
(a)						
300	123	106	HR	0.999	0.548	9.01
Estimated group size		Observed group size				
\hat{E} (s)	%CV	Mean	%CV	Maximum		
(b)						
1.70	7.67	2.24	19.49	30		
\hat{D}	95%CI (\hat{D})	\hat{N}	95% CI (\hat{N})	%CV		
(c)						
0.393	0.262–0.591	13,721	9127–20,627	20.41		

Discussion

The SSL at-sea abundance was estimated here to nearly 14,000 individuals. This value corresponds to the average number of individuals that were present at sea during late summer and day time within our study area. Previous on-rockery censuses in the same area, carried out using correction factors, resulted in abundance estimates of approximately 47,000 individuals, representing ca. 33% of the entire Chilean SSL population (Oliva et al., 2008, 2009). The correction factors used by these authors were estimated from daily and weekly *circa* rhythm analyses carried out in selected rockeries from central Chile (Sepúlveda et al., 2001). After correction, total counts increased in ca. 2%, implying that only around 1000 individuals were missed during censuses because they were at sea (Oliva et al., 2008). However, there is one order of magnitude difference between our at-sea abundance estimate and that of Oliva et al. (2008). Even if not directly comparable, the large difference between estimates suggests that SSL population size in CNP might have been underestimated.

Our results are important in terms of magnitude; however, before making any further inference, it is important to highlight some caveats that could influence the results and conclusions of our study. Needless to say that these aspects should be the focus of future research efforts: (a) our survey was not specifically designed for SSL, therefore some areas recognized as hot spots for this species, such as the Northern part of the Chiloé Archipelago Inner Sea (Ancud Gulf), were not included in the survey. This consequently leads to an underestimation of the total

Table 2

Results of GAM for SSL density of sightings in Chilean Northern Patagonian fjords, including the covariates selected by the models. The best final model explained 54.4% of the deviance.

Parameter	Estimate	s.e.	t -Value	p -Value
Intercept	6.52×10^{-3}	1.59×10^{-4}	4.13	<0.001
Smoother terms		edf	F -value	p -Value
UTM Northing		8.61	31.40	<0.001
UTM Easting		5.69	10.11	<0.001
Depth		5.56	2.11	<0.05
Density of coast		2.23	2.16	<0.05
Distance to colonies		5.93	8.35	<0.001
Best final model: Density of sightings \sim s (UTM Northing) + s (UTM Easting) + s (depth) + s (density of coast) + s (distance to colonies)				
GCV Score = 1.42×10^{-3} ; $r^2 = 0.52$; $N = 531$				

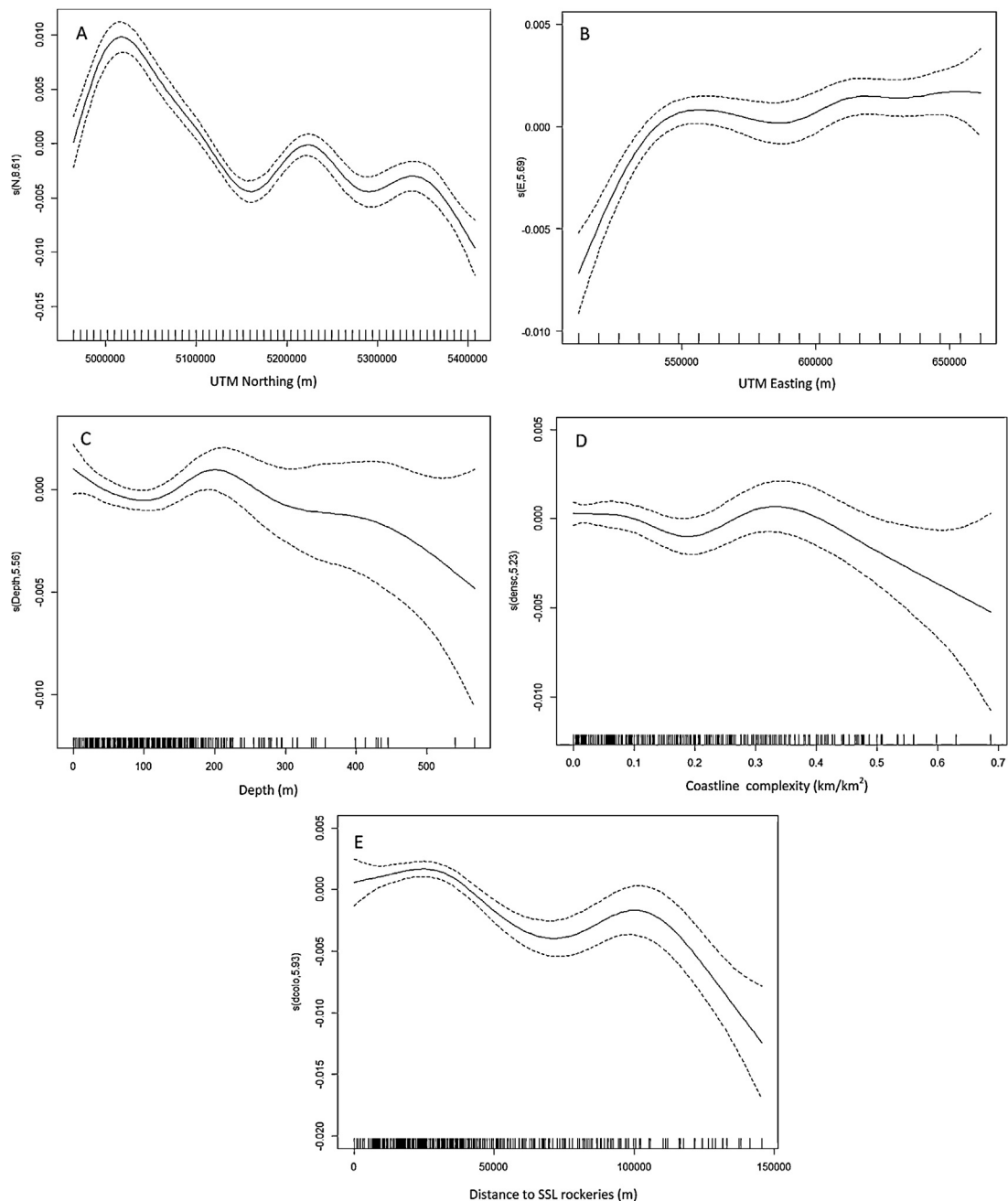


Fig. 3. GAM-predicted smooth splines of the response variable density of SSL as a function of the explanatory variables: (a) UTM Northing, (b) UTM Easting, (c) depth, (d) coastline complexity; and (e) distance to rockery. The degrees of freedom for non-linear fits are in parenthesis on the y-axis. Tick marks above the x-axis indicate the distribution of observations (with and without sightings). Dotted lines represent the 95% confidence intervals of the smooth spline functions.

at-sea abundance throughout the entire area; (b) survey design did not consider the complex geography for transect allocation, leading to yet unknown biases due to non-uniform coverage probability in inlets and narrow channels (Thomas et al., 2007); (c) a violation of the $g(0) = 1$ assumption is likely to have occurred because of some SSL avoidance reaction to the vessel was observed when fitting the detection curve, causing an abundance underestimation (Williams and Thomas, 2007); (d) our study was carried out from mid February, when most of the reproductive adults are in the breeding colonies, to mid March, when many of them have returned to the sea. This resulted in an average estimation of the at-sea abundance between two different stages in SSL life history; (e) SSL are highly mobile predators, making impossible to assure that animals sighted during the survey belong to local rockeries; and (f) shore

censuses were not conducted simultaneously to properly compare at-sea estimates with those made on land.

Three out of the six caveats described above suggest an underestimation of our SSL at-sea abundance estimate, strengthening the idea that SSL population in CNP could be larger than previously considered. The possibility that a large number of individuals were found at sea because adults were returning to the sea after breeding season should be addressed in light of previous work. On-rockery censuses carried out during summer and winter seasons in CNP have shown that, in general, there was no significant inter-season variation between total counts (Oliva et al., 2008). Instead, these authors observed a rearrangement in the distribution of some rockeries, their relative contribution to total counts and a change in age class relative abundance. In fact, Oliva et al.

(2008) found that there were three times more juveniles and the half of adult males on land during winter when compared to summer counts. This is consistent with Crespo (1988) who estimated that up to 45% of the SSL population, with a strong composition of juveniles, was at sea and thereby missed during summer censuses in Western South Atlantic (WSA). The aforementioned lack of difference in total counts between summer and winter also suggests that an increase in rookery use by juveniles during winter may compensate adults' movement to the sea. Thus, our at-sea abundance estimate is not necessarily overinflated by the assumed net seaward population exodus at the end of reproductive season.

Another argument explaining the large number of SSLs observed at sea relates to the potential entry of SSL coming from rookeries outside CNP. However, as discussed below, this argument might not stand according to previous studies on the use of coastal waters and our spatial distribution assessment.

Even when our study area was restricted to coastal waters, our GAM results showed that SSL preferred shallow waters (50–200 m). This is consistent with previous studies that characterize SSL as a shelf restricted forager with dive depths that seldom exceed 200 m (George-Nascimento et al., 1985; Thompson et al., 1998; Campagna et al., 2001; Hückstädt and Krautz, 2004; Riet-Sapriza et al., 2013; Rodríguez et al., 2013; Hückstädt et al., 2013). Our results also suggest a selection by SSLs for open water areas closer to SSL rookeries (presumably feeding grounds). This was expected because the selection for rookeries locations has been correlated with the proximity to feeding grounds in otariids (Call and Loughlin, 2005). The fact that these potential feeding grounds are located in open waters is congruent with previously depicted highly productive areas in CNP (González et al., 2011; Huckle-Gaete, 2004). Although the survey design might explain proximity to SSL rookeries, modelling assessment showed their distribution had no relation with distance to the coast, meaning that SSL had indeed preference for certain areas, most surely feeding grounds, and not just an evidence of a plain coastal at-sea distribution.

Results from our spatial distribution model are in agreement with the shelf restricted distributional pattern described above for SSL, although some differences between the WSA and the ESP should be noticed. While SSL in the WSA disperse throughout the wide continental shelf reaching hundreds of kilometres from the coastline (Campagna et al., 2001), in the ESP their movements are more restricted to coastal areas with a mean distance of 20 km from shore, with a maximum of 80 km (Hückstädt et al., 2013). Even when the maximum linear distance from the rookery in both basins is quite similar (around 300 km), SSL movements in the ESP showed a marked directionality following the north–south orientation of the Chilean narrow continental shelf (Campagna et al., 2001; Hückstädt et al., 2013). If SSL shows a more restricted coastal at-sea distribution in CNP, then our survey design limitations would be lessened, giving our spatial distribution model more consistency.

The occurrence of SSL interacting with fishing boats at distances of about 300 km from the coastline in both the WSA and the ESP do not necessarily suggest the their normal at-sea distribution, but the behaviour of specific individuals that have learnt to benefit from fishing vessels (Campagna et al., 2001; Hückstädt and Krautz, 2004). Although, the level of the interaction and the proportion of the population that is currently involved have not yet been addressed.

Finally, considering that (a) our study area lies at the centre of the area previously assessed by Oliva et al. (2008), which encompassed rookeries up to 300 km north and south from the boundaries described for our study area; (b) this distance (300 km) corresponds to the maximum recorded linear distance of an SSL individual to rookeries during a foraging trip, both in the WSA and the ESP (Campagna et al., 2001; Hückstädt et al., 2013);

and (c) given the north–south directionality of SSL movement observed in ESP (Hückstädt et al., 2013); then if individuals coming from rookeries outside our study area are preferentially using some feeding grounds within it, then it is likely that our at-sea abundance estimate might remain pertinent to the CNP.

The at-sea abundance estimate and spatial distribution model highlighted here must be taken with caution and strongly considered for future research on SSL abundance and distributional patterns. Simultaneous censuses should be developed on rookeries and at-sea over a determined period of time to properly assess the population proportion that remains at sea during censuses. Marine predators such as SSL, travel and select areas in relation to marine habitat dynamics, particularly oceanographic processes that influence prey distribution. Variables such as sea surface water temperature, currents, fronts, eddies, among others (Guinet et al., 2001; Friedlaender et al., 2006) should be considered for future habitat modelling in order to obtain a more holistic insight of SSL distributional patterns. Furthermore, robust studies that include telemetry techniques (Bjørge et al., 2002) could certainly assist widening our scope regarding this particular issue in CNP, particularly in assessing negative interactions with fisheries and aquaculture.

The possibility that SSL population in ESP could be larger than expected should not be taken as an argument supporting SSL culling in Chilean waters. Culling top predators for the sake of fisheries and aquaculture has been widely criticized, not just because of the inherent ethical dilemmas, but because the outcomes of such management decisions are highly unpredictable given current scarcity of knowledge regarding links and causal consequences of trophic interactions and cascade effects within complex ecosystems (Yodzis, 2001). The removal of one predator species could indeed release predatory pressure to a given commercial species and potentially increase fisheries yields; however, if the culled species was also preying upon an intermediate predator, the result could be the opposite of the expected and the target fishery might be affected (Yodzis, 2001). Improving our estimates about critical ecological parameters for SSL population in Chilean marine ecosystems steps up as one of the priorities under an ecosystem based management approach.

Conclusions

Our at-sea abundance estimate for SSL is one order of magnitude larger than previously considered by on-rookery censuses conducted in CNP. Here, we propose that a large proportion of the SSL population might have been omitted from censuses in the past, thus underestimating its local population size. If we consider our at-sea abundance estimation of about 14,000 individuals as a conservative estimate for the population fraction that remains at sea during on-rookery censuses, it would imply that at least 20% of the CNP population has been omitted during previous assessments. So far, the results from this study are highly consistent with previous studies regarding SSL at-sea spatial distribution. These estimates bring forward new information for revisiting current population size estimations in SSL, but it might also be applicable for other pinniped species worldwide. Further research should consider the survey caveats discussed here, such as including simultaneous censuses on rookeries and at-sea, in order to assess true SSL population size.

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