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Habitat selction of Southern Right Whales (Eubalaena australis) in the breeding ground Peninsula Valdés.

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Habitat selction of Southern Right Whales (*Eubalaena australis*) in the breeding ground Peninsula Valdés.

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Abstract

Keywords

Bayesian spatial models, Cetacean distributions, Conservation

Introduction

The Southern Right Whale (*Eubalaena australis*, hereafter SWR) was the object of a commercial exploitation between the 18th and 20th centuries that brought this species to the brink of extinction (Richards 2009). The species was protected for the first time in 1936 and additionally, in 1986, the moratorium on commercial catch established by the International Whaling Commission (IWC) came into force. By the mid-1970's, after almost 10 - 12 years of protection, several populations of SWR have shown evidence of recovery (Bannister 2001, Best *et al.* 2001, Cooke *et al.* 2001). Indeed, since the moratorium, populations throughout the southern hemisphere have experimented a recovery at a rate of 8% (Payne 1986, Payne *et al.* 1981, Payne *et al.* 1990, Whitehead *et al.* 1986, Crespo *et al.* 2019).

Even so, in Peninsula Valdés (Argentina) it has been observed that the growth rate is decreasing in recent years from near 7% in 2007 to a 0.06% for 2016. This is an indication of a decrease at a rate of -0.45% per year in the growth population rate (Crespo et al. 2019). However, the reduction in the growth rate was not uniform across the different groups that comprise the population (i.e. offspring, mother-calf, others). The estimate of the growth rate for the number of offspring born in the Peninsula Valdés was 5.54% per year between 1999 and 2017 (Crespo et al. 2019), almost doubling the growth rate for the whole population during the same period. On the contrary, the growth rate of the *Other* groups (formed by *Solitary Individuals* and *Breeding* groups) is now close to 0% (Crespo et al. 2019). This decrease in the growth rate of the *Other* group could be related to the displacement of these individuals from the shore to other locations.

The Peninsula Valdés coastal strip is not occupied homogeneously, because some parts of coast that are used for transit from one place to another, while in others the whales can be found throughout the breeding season (Crespo et al. 2019, Payne 1986, Rowntree *et al.* 2001, Sueyro *et al.* 2018). Indeed, these shallow water areas are now mostly occupied by *Mother-calf* pairs (Sueyro et al. 2018), displacing the *Other* groups, suggesting that the Peninsula Valdés coastal zone (within 2km from shore) could be close to its carrying capacity (Crespo et al. 2019). Nevertheless, the displacements of the *Other* group did not take place towards the unused coastal zones within Península Valdés, but rather to deeper farther from the coast waters or to new areas outside the current breeding ground (Arias *et al.* 2018a, Sueyro et al. 2018). There is evidence that the new observed occupied areas are locations that were occupied prior to commercial exploitation (Arias et al. 2018a). Given that the Southern Right Whales is recolonizing places used prior to exploitation or deeper waters within Península Valdés, it is worth to explore which are the environmental conditions that whales seek to establish.

Correlative species distribution models (SDMs) can be generated from relatively simple distributional data combined with environmental information to produce a geographic description of the potential distribution of a species (Elith & Leathwick 2009, Guisan & Thuiller 2005, Guisan & Zimmermann 2000). Given their wide applicability, they have been described as the main predictive tool in ecology (Bellard *et al.* 2012, Dawson *et al.* 2011). In a conservation context, they can help identify priority areas for additional sampling of rare species (e.g.(Engler *et al.* 2004, Guisan *et al.* 2006)) or support conservation planning efforts. SDMs have even been used specifically to guide management decisions affecting threatened whale populations (e.g. (Bombosch *et al.* 2014, Garrison *et al.* 2012, Gowan & Ortega-Ortiz 2014, Mannocci *et al.* 2014, Monsarrat *et al.* 2015, Monsarrat *et al.* 2016), sometimes on the basis of historical exploitation data (Monsarrat et al. 2015, Monsarrat et al. 2016, Torres *et al.* 2013). SDMs can be extrapolated across space (e.g. for predicting the potential distributions of invasive species; (Ficetola *et al.* 2007, Peterson & Vieglais 2001)), across time (e.g. for predicting range shifts under future climate scenarios; (Araújo *et al.* 2005, Garcia *et al.* 2012, Thuiller *et al.* 2005)) and even across species (e.g. to identify areas likely to harbour still undescribed species.

Within this contest, we use SDMs to predict the SRW distribution in the Peninsula Valdés incorporating environmental data and collected by the CENPAT Marine Mammal Laboratory in four different periods of time: 1999-2000, 2004-2007, 2008-2012 and 2013-2016. Predictions maps were then used to assess if there was a shift of the SRW distribution in the Peninsula Valdés trough the time and if it was related with the population growth.

Methods

The censuses were carried out from a single-engine high-wing CESSNA B-182 aircraft, flying at a constant height of 500 feet (152 m) and at 80/90 knots every 45 days from April to December each year (Crespo *et al.* 2018). In each survey a distance of 620 km was covered in 5 hours of flight, flying from south to north along the coast. The surveyed area (Figure 1) is located between the mouth of the Rio Chubut and Puerto Lobos on the border with the province of Rio Negro. The width of the strip is composed by 500 meters from the coast plus approximately 1000 meters from the plane to the open sea, composing a surveyed strip of 1500 meters (Crespo et al. 2018). This strip is set to cover the "whale-road" as described by Payne (1986), where more than 90% of the whales in the area concentrate near the coast in shallow waters.

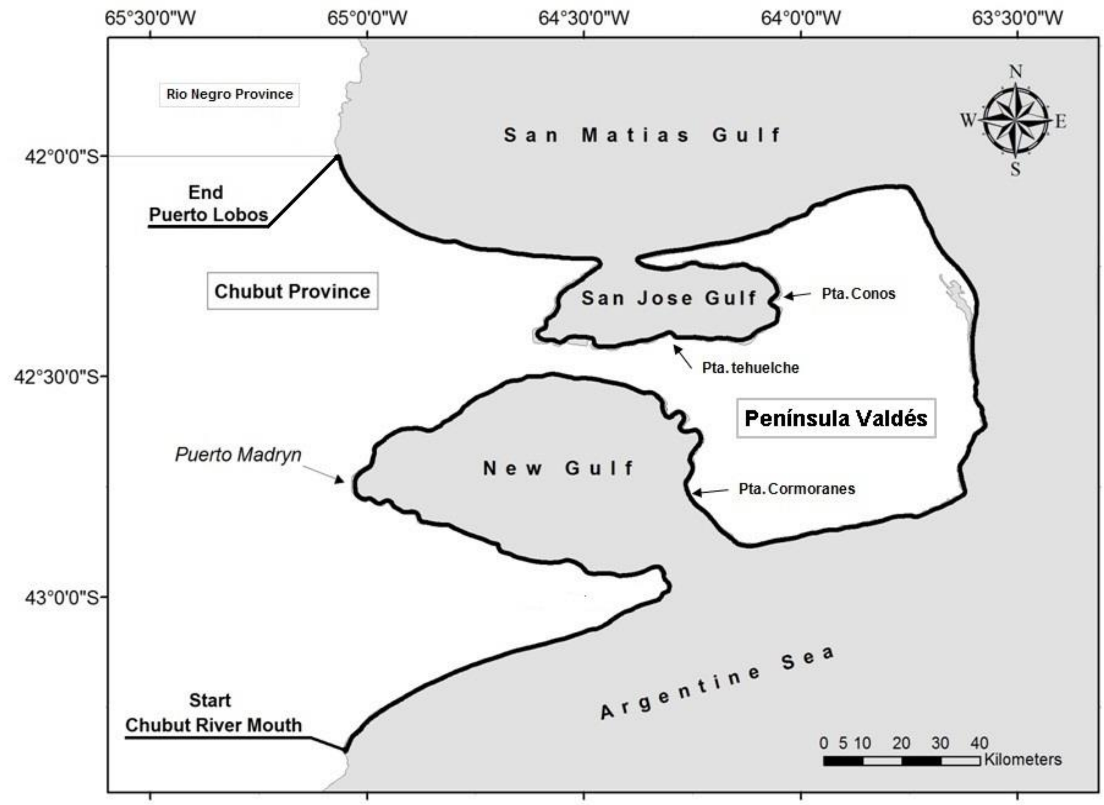

Figure 1: Sampling area. The thick black line along the coast represents the surveyed area.

The team comprised a pilot, a recorder sitting next to the pilot and two observers in the rear seats, one on the left and one on the right side of the aircraft (Crespo et al. 2018). The observations were made with the naked eye, and the information was recorded in spreadsheets or tablet applications developed *ad-hoc* with Cyber Tracker ™. Information on the on the group composition was recorded, including *Mother-calf* pairs, *Solitary Individuals* or *Breeding* groups comprising n-1 males and one female (Crespo et al. 2018). *Solitary Individuals* and *Breeding* groups were pooled in *Other* groups, as a group category opposite to the *Mother-calf* pairs. Along with the type of group we recorded the position registered with a handheld GPS, the number of individuals and the sea state on the Beaufort scale. Flights were suspended when the visibility conditions were not optimal, either because of fog or the sea state exceeded the level 3 of Beaufort scale. The information was introduced into a database developed specifically for this purpose.

The information was clumped into four periods, making each period as similar as possible considering the number of flights. A total of 58 air surveys were clumped in four periods: period 1 from 1999 and 2000 (8 flights) and the other 3 periods comprised from 2004 to 2007 for period 2 (18 flights), period 3 from 2008 to 2012 (17 flights) and period 4 from

2013 to 2016 (15 flights). For each period, the average density per group type was calculated for the entire sampling area.

Environmental variables

Bathymetry, roughness of the seabed and wave energy were used as potential predictors for selection of Southern Right Whales. Bathymetry was obtained using the Nautical Chart No. 58 of the Argentine Naval Hydrography Service (http://www.hidro.gov.ar/). This nautical chart was digitized and geo-referenced through the program QGis®2.18 using the spline method with a spatial resolution of 0.00254 x 0.00254 degree. Roughness of the seabed was derived from the bathymetry map using the terrain function of the raster (Hijmans & Graham 2006) in the R software (R-CoreTeam 2017). This method effectively captures the variability and roughness of the seabed slope in a single measurement (Sappington *et al.* 2007). Commonly, unconsolidated seabed, such as mud and sand, corresponds to low roughness values, thus, high roughness values are associated with potentially rocky substrate. Roughness is considered to be a useful surrogate for benthic diversity in the absence of detailed information on sediment type and structure (Fonseca *et al.* 2017).

To estimate the wave energy, the WEMo 4.0 program (Wave Exposure Modeling) was used. The program carries out computations using one-dimensional numerical models, in which the generation and propagation of the wave is only considered while the wave is traveling along one direction. The total energy of the wave is represented in Joules / meter. Using the WEMo requires both bathymetric and wind data from the region. The bathymetry explained above was used. In the case of winds, information was gathered from the winds database for the period 1999-2016 (Puerto Madryn station of the National Meteorological Service). The wave energy was estimated for each day a flight was performed using RWE (Representative Wave Exposure) routine of the WEMo 4.0. With the energy estimates obtained at each point, an interpolation was performed using the "Natural Neighbor" algorithm (Sibson 1981) within the study polygon.

The environmental variables were explored for collinearity, outliers, and missing data before their use in the models (Zuur *et al.* 2009). Finally, after an exploratory analysis, in order to better interpret, both the direction (positive or negative) and magnitudes (effect sizes) of parameter estimates in relation to the others, the explanatory variables were standardized (difference from the mean divided by the corresponding standard deviation) (Gelman 2008).

Statistical analysis

Bayesian hierarchical spatial model (BHSM) were applied to identify which environmental variables mostly affect the Southern Right Whales distribution in northern Patagonia and to predict their probability of occurrence in un-sampled locations. The model estimation and prediction were performed for each one of the time periods (i.e., period1: 1999-2000; period2: 2004-2007; period3: 2008-2012; period4: 2013-2016) to evaluate changes in the SWR distribution in the area. Particularly, the response variable Y_i represents the species occurrence (1 being yes; 0 being no). Consequently, the conditional distribution of the data is $Y_{ij} \sim Ber(\pi_{ij})$, where π_{ij} is the probability of occurrence at location *i* (i 1, . . . n), assuming that observations are conditionally independent given π_{ij}. These probabilities were modelled using the following hierarchical model:

$$Y_{st} \sim Ber(\pi_{ij}),$$

$$logit(\pi_{ij}) = \beta X_i + W_i,$$

where β is the vector of regression parameters, X_i is the matrix of the explanatory covariates at location *i*; W_i is the spatially structured random effect at location *i* which account for the spatial autocorrelation in the latent probabilities of occurrence. Following Bayesian reasoning, all model parameters are considered as random variables where their estimations are achieved through marginal posterior distributions. To do so, we relied on the Integrated Nested Laplace Approximation (INLA) (Rue *et al.* 2009) methodology and respective R-package (www.r-inla.org) within the R platform to estimate all fixed and random parameters.

INLA implements the Stochastic Partial Differential Equations (SPDE) approach (Lindgren *et al.* 2011, Martínez-Minaya *et al.* 2018) for the spatial effect (W), which approximates a continuously indexed Gaussian Field (GF) with a Matérn covariance function (Q) by a Gaussian Markov Random Field (GMRF). The spatial effect is a numeric vector linking each observation to a spatial location, and thus it accounts for independent region-specific noise that cannot be explained by the available covariates (Munoz *et al.* 2013). As recommended by Lindgren and Rue (2015), multivariate Gaussian distributions with mean zero and a spatially-structured covariance matrix were assumed for the spatial component. For the fixed effect vague Gaussian distribution with a zero mean and a standard deviation of 100 were assigned.

Model selection

Model selection was held following a forward-stepwise approach where the null model (containing only intercept without spatial effect) was used as a base model and covariates were added subsequently. To evaluate the goodness-of-fit and predictive quality of the models, we considered the Watanabe Information Criterion (WAIC) (Watanabe & Opper 2010) and the averaged logarithmic score of the Conditional Predictive Ordinate (LCPO) (Roos & Held 2011). Specifically, smaller WAIC and LCPO values indicate better fit and predictive quality respectively. Thus the best models were selected based on the compromise between the low WAIC and LCPO values (Fonseca et al. 2017).

Model validation

Model predictions were validated using the cross-validation procedure. The original dataset was randomly split into two subsets: a training dataset including 80% of the total observations, and a validation dataset containing the remaining 20% of the data (Fielding & Bell 1997). The first one was used to model the relationship between observed data and the explanatory variables while the second one was used to assess the quality of predictions. We repeated the validation procedure 10 times for the best model of each data source. Model performance was assessed using the area under the receiver-operating characteristic curve (AUC) (Fielding & Bell 1997), the "True Skill Statistic" (TSS) (Allouche *et al.* 2006), the specificity (i.e. ability to correctly predict absences) and sensitivity (i.e. ability to correctly predict presence). All these indicators range from 0 to 1, and values closer to 1 indicate better predictions (Pennino *et al.* 2016).

Results

A total of 58 flights were used in the analysis. In every period, when counting the number of raster cells with presence of whales, always the number of presences largely exceeded the number of cells without whales (Table 1).

Table 1. *Data on the number of flights, presences and absences for each period*

Period	N° flights	Presences	Absences
1	8	938	235
2	18	2839	710
3	17	2549	638
4	15	2400	600
Total	58	8726	2183

Exploratory analysis highlighted that the bathymetry and the roughness were highly correlated (r =0.57) and for this reason were not included together in the models.

Variable selection was performed using the entire dataset to make them comparable among the four time periods. In Table 2 are reported the most relevant models fitted and their scores in terms of WAIC and LCPO.

Table 2 *Selection of 5 models ordered according to WAIC and with their DIC and LCPO value. The abbreviations of the predictors are: W = spatial effect, B = bathymetry, R = roughness, WE = wave energy.*

N°	Models	WAIC	DIC	LCPO
1	**b_0 + R + WE + W**	5354.460	5368.751	0.2454470
2	**b_0 + WE + W**	5358.681	5372.605	0.2456404
3	**b_0 + W**	5367.272	5381.414	0.2460443
4	**b_0 + B + WE + W**	5370.148	5380.130	0.2461527
5	**b_0 + R + W**	5370.346	5384.352	0.2461748

Among all the combination tested, the selected model included the roughness, wave energy and spatial effect. This model was then used to perform the analysis in each of the periods. Table 3 shows the numerical summary of the estimated models. Overall, the roughness showed a positive relationship with the SWR occurrence with exception of the last period (Table 3). In the first three period SWR preferred consolidated seabed, while in the fourth period the areas selected by SWR individuals were on potentially rocky substrate.

The wave energy showed a negative relationship with the SWR occurrence in all the periods of time, except the second one. This means that overall SWR occur in areas where the wave energy is lower, while from 2004 to 2007 individuals were present in areas with relatively higher wave energy (Table 3).

Looking at the magnitude of the estimated effects, the wave energy is more relevant for the SWR occurrence than the roughness of the seabed.

Table 3. *Numerical summary of the posterior marginal distribution of the fixed effects for period 1 (years 1999-2000), period 2 (years 2004-2007), period 3 (years 2008-2012) and period 4 (years 2013-2016) Bayesian hierarchical spatial model (BHSM). For each variable, the mean, standard deviation, and a central credible interval of 95% (Q0.025 - Q0.975) are provided, which contains 95% of the probability under the posterior distribution. The acronyms of the predictors are: W = spatial effect, R = roughness, WE = wave energy.*

Model	Period	Variable	Mean	Sd	Q0.025	Q0.975
b_0 + R + WE + W	**1**	**Roughness**	0.0354	0.0225	-0.0089	0.0795
		Wave Energy	-0.1777	0.0284	-0.2336	-0.1774
	2	**Roughness**	0.0554	0.0640	-0.0701	0.1809
		Wave Energy	0.0134	0.0535	-0.0917	0.1184
	3	**Roughness**	0.1270	0.0968	-0.0637	0.3165
		Wave Energy	-0.3138	0.1159	-0.5432	-0.0881

	4	**Roughness**	-0.1312	0.1067	-0.3420	0.0771
		Wave Energy	-0.2398	0.0798	-0.3961	-0.0828

The predictive performance of the model was higher in the first period, compared to the others (Table 4). However, all the models present a good performance in terms of AUC and TSS, as well as the sensitivity and specificity. Overall, the models had higher values of specificity, which means that better predict absences.

Table 4. Predictive power of the model

Period	TSS	AUC	Sd	Sensitivity	Sd	Specificity	Sd
1	0.334324	0.615458	0.022850	0.480173	0.0230164	0.828801	0.026474
2	0.106522	0.527748	0.014374	0.403545	0.0130233	0.698991	0.019378
3	0.106522	0.527748	0.014374	0.403545	0.0130233	0.698991	0.019378
4	0.106522	0.527748	0.014374	0.403545	0.0130233	0.698991	0.019378

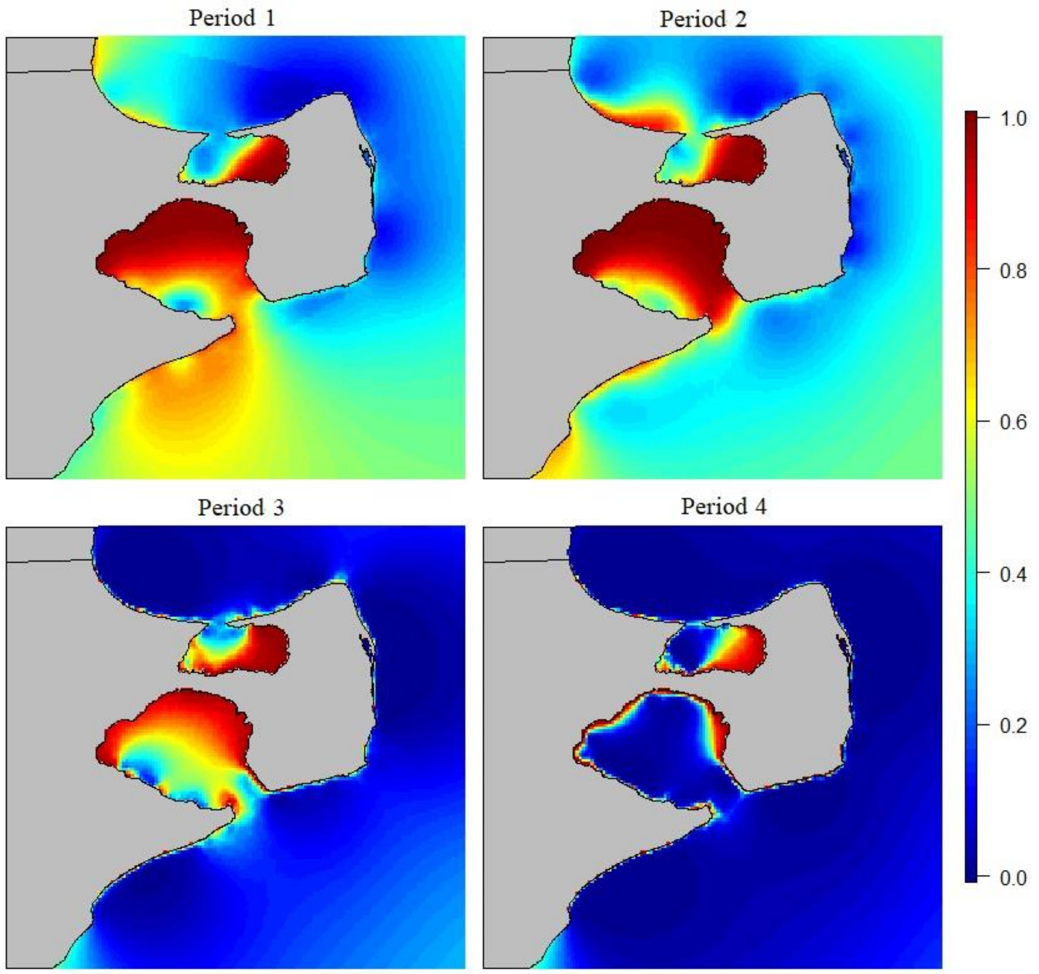

Figure 2. Posterior probability of occurrence of the SWR in the Peninsula Valdés for the four time periods: period 1 (years 1999-2000), period 2 (years 2004-2007), period 3 (years 2008-2012) and period 4 (years 2013-2016).

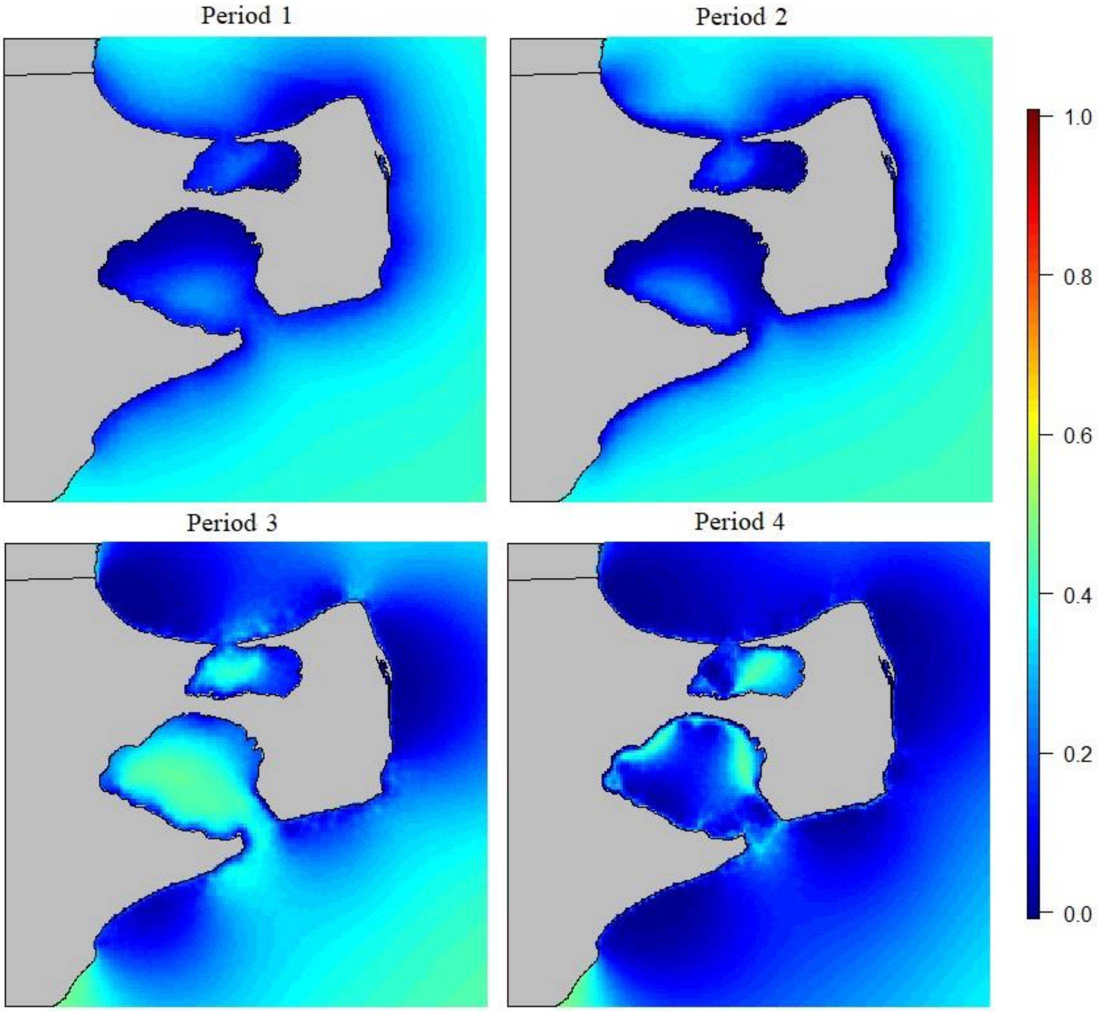

Figure 3 standard deviation of posterior probability of occurrence of the SWR in the Peninsula Valdés for the four time periods: period 1 (years 1999-2000), period 2 (years 2004-2007), period 3 (years 2008-2012) and period 4 (years 2013-2016).

Figure 2 shows the posterior probability of occurrence of the SWR in the Peninsula Valdés area. The probability of occurrence of the SRW decreased trough the time series, getting very costal in the last period (2013-2016). Figure 3 shows the posterior standard deviation of the response variable. Overall, the standard deviation was low, and the variability decreased along the periods. These results indicate that during the first period the area where the whales were found changed from one flight to the next and could be found almost in most coastal areas inside the gulfs, but their location was variable. As the time passed, the selection of coastal areas, related to the wave energy and roughness of the seabed was more evident.

Discussion

This is the first study to implement spatial models to assess the spatial selection of the SRW in the context of population growth. Figure 2 shows the probability of occurrence of the SRW in the Peninsula Valdés area, as the population increases the probability of finding a SRW in the coastal area increase. Period 4 is the time in which there are more SRW in the area and the highest probability of SRW occurrence is the most coastal of the four periods.

The selection movements of the different areas in the Peninsula Valdés was previously recorded in the 70's, 80's and 90's (Rowntree et al. 2001). In those decades there was a movement of SRW from the outer ridge of the Peninsula Valdés towards the interior of the Nuevo and San Jose Gulfs (Rowntree et al. 2001). The same kind of movement was also observed on the coasts of the San Matias Gulf (Arias et al. 2018a).

The censuses to estimate the relative abundance of SRW by means of coastal flights started in the Peninsula Valdés area in the late 90s; and by that time there was a strong evidence of a population growth. Later during the 2000 and the 2010 decades this population growth rate decreased, but the number of individuals recorded has increased since in the breeding and calving area (Cooke *et al.* 2015, Crespo et al. 2019). A dense-dependence process was proposed, since observations suggested that groups comprised only by adults (namely Solitary individuals and Breeding groups) were displaced from coastal areas towards deeper waters (Crespo et al. 2019). This also led to a process of expansion of these groups to other coasts (Arias et al. 2018a, Sueyro et al. 2018).

In recent years, the presence of a higher numbers and proportion of mothers with calves replacing other type of groups, had as a possible consequence the increase in the probability of finding the whales in some restricted coastal area. This is in agreement with the findings of other studies that did not analyzed the spatial component of the system (Arias et al. 2018a, Sueyro et al. 2018)(Crespo et al 2019); with mothers with calves preferring these coastal areas, increasing its use. The period 4 model results are also in agreement with these studies, suggesting that a density-dependence process is underway int the breeding area. The coastal breeding areas of Peninsula Valdes could be reaching their carrying capacity, so it is expected that in the coming years an increase in the number of mothers with calves will be observed in other areas, such as the Bay of San Antonio in the Gulf San Matias.

The distribution changes observed are also reflected in the selected physical variables of our models. Indeed, SRW individuals prefer coastal areas with low roughness seabed (sandy beach or small pebbles) and with low wave energy. These results are in agreement with what was suggested previously, but is now confirmed by modelling (Lanfiutti 2000, Payne 1986, Payne et al. 1990).

Pontones (2014) carried out an analysis of the wave energy relationship and the presence of SRW where they select coasts with high wave energy. The biggest caveat to the Pontones's study is that an average wave energy from the entire spring season was used. The SRW individuals that remain in the area are in constant movement within the area (Zerbini 2016). Due to the variation of the wind conditions in the area, the wave energy varies in the different coasts, consequently the whales move depending upon these conditions.

The obtained results also reflect the long-term movement of whales in the breeding area, giving us a hint on the recolonization process. Whales during the first period were fund in lesser numbers in a much wider area, including coastal and deeper waters. As the whales explore the area and find the most suitable area, they tend to return to these beaches year after year, being more predictable as the time passes. Arias *et al.* (2018b) suggested that the recolonization process includes the exploratory behavior by the juveniles, as it is common in other mammals (Greenwood 1980). The changes observed in the probability of finding whales along the different periods reflect the changes occurred due to the population growth. Despite having more whales in Península Valdés, the reduced probability of finding whales off the coast and more in new coastal areas outside the established breeding ground, gives us an indication that southern right whales are near the carrying capacity in the core area.

It is important to expand this kind of models to predict the future possible expanding areas for SRW in the South Western Atlantic Ocean, in order to be able to avoid potential future conflicts with human activities, such as new harbors or to predict future areas where sustainable endeavors such as whale watching can take place in the future.

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