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INTRODUCTION

The IWC conducted its last major review of the status of southern right whales (SRW) (*Eubalaena australis*) in 1998 (IWC 2001) and more recently in 2010 (IWC 2010) and 2011 (IWC 2011). Following severe historical depletion by commercial whaling, several breeding populations (Argentina/Brazil, South Africa, and Australia) of SRW have shown evidence of strong recovery, with a doubling time of 10-12 years (Bannister 2001, Best *et al*. 2001, Cooke *et al*. 2001). The other breeding populations are still very small, and data are insufficient to determine whether they are recovering. Estimated total size for the species in the Southern Hemisphere in 1997 was 7,500 animals (of which 1,600 were mature females, including 547 from Argentina and 659 from South Africa), and the three main populations have continued to increase at a similar rate since then.

Regarding the Atlantic stock, illegal Soviet catches (mainly in the 1960s) were carried out in the South Atlantic in international waters in front of Península Valdés. The catch was over 3300 individuals and in only one season (1961-1962) the soviets took 1300 whales (Tormosov et al. 1998). They temporarily inhibited recovery, but overall the population appears to have grown strongly since then.

Payne and colleagues carried out long term studies in SRW around Península Valdés (Argentina) since the early 70´s and estimated population size and other parameters derived mark recapture models based on individual recognition of whales by their pattern of callosities (Payne 1986). For this population the rate of increase r was estimated close to 8% (Payne et al., 1983, 1990; Whitehead et al., 1986). Whereas in 1998 the assumed average growth rate for all populations of SRW throughout the Southern Hemisphere was 7.5%. During the workshop carried out in Buenos Aires in 2011 it was agreed that the rate of increase was between 6% and 7%. However, Cooke suggested that there has been a substantial decline in the rate of increase for this population in recent years, around 5.0% over the last 10 years (Cooke, pers. comm. to the 2011 SRW Workshop).

However, the process of gathering the information from photo-id data bases is time consuming, and there was a need from the local management officers to have a quick and relatively cheap methodology to estimate abundance and population trend (Crespo et al., 2011; Cooke et al., 2015). This is the main reason why we decided to develop a method based on direct counts of whales on the coastal zone from aerial surveys.

Therefore, the objectives of this work were: 1) to estimate the relative abundance in the monitoring zone, 2) to estimate the rate of increase in the area, 3) evaluate changes in the use of the coastal zone by age and sex classes throughout time, 4) evaluate the trend of mortality rates.

MATERIALS AND METHODS

We developed a method for monitoring the population, which could lead to study seasonal changes within and among years. The method was based on the assumption that around 95% of the whales are found within a coastal strip (Payne 1986; Payne et al., 1983, 1990) and the number of whales in the strip can be considered a measure of relative abundance in the whole PV area. However, during the study period the whales started to occupy deeper waters in the gulfs and it was a need to estimate the number of those whales by complementary methods. The breeding season lasts for several months, from May to December, but each whale arrives to the area and stays a period of time shorter than the whole breeding season, this means that not all the whales arrive and leave at the same time (Rowntree et al., 2001).

Study area and aerial surveys

A monitoring area was defined from the mouth of Chubut River (42°30´) to Puerto Lobos (42°) totalling a coastal strip of 350 nm long (620km) (Fig. 1) flying the coastal zone parallel to the coastline at an altitude of 500 feet (Crespo et al., 2011, 2014, 2015). The area was consistently flown from south to north always taking off around 10:00am in order to avoid any variation in the numbers/visibility due to the time of the day.

Aerial surveys were selected to be the best method to count whales in the monitoring area. The period between flights ranged from 45-50 days depending on weather conditions. Ideally, 7 to 8 flights would be done in a given year. Flights were carried out if the Beaufort Sea State was between 0 and 3 (Crespo et al., 2011, 2014).

The surveys were carried out using high-wing single-engine aircrafts Cessna B-182. A crew of four flew in every survey: the pilot, one recorder and one observer on each side of the plane.

Figure 1: Monitoring area designed for counting SRW

Distance to the coast (on the left side of the plane) was constant at 500 m. From measures carried out with a clinometer, the effectively covered strip to the right side of the plane (deeper waters) was about 1000m. Then the monitoring zone covers the coastal waters from the mouth of Chubut River to Puerto Lobos, in a water strip of about 1500m from the shore.

Average speed of the aircraft remained constant at 90 kn and height within 500 ft (≈ 152.4 m). The depth under the plane was less than 20m. Abundance was estimated by counting the total number of whales within the monitoring area which gives a relative measure of abundance. A total of 65 flights were carried out between May 1999 and December 2000 and June 2005 and November 2016. Due to financial support not every year had the same number of flights, and hence effort differs yearly.

Age and sex classes to be count

Whales from the air can be distinguished in three groups.

a) Mother-calf pairs (MC) which are one adult female and a calf

b) Solitary individuals (SI) which can be either adult males or females or subadult individuals

c) Breeding groups (BG) which is usually formed by one adult female and several males.

Rate of increase estimated using Generalized Linear Models procedures

The full data set was analysed using a GLM framework, which extends the standard linear regression model by assuming a non-Normal error structure and using a “link” function

(McCullagh and Nelder, 1989; Zuur et al., 2009). The GLM framework has been applied successfully in ecology because some of the exponential family distribution can cope with the problems associated to count data (Zuur et al., 2009). We used a Negative binomial regression, which can be considered as an extension of the Poisson regression model when the overdispersion parameter is known. This parameter allows the variance to be larger than the mean, estimating more accurate standard errors for the parameters (Ward et al 2011). While the Poisson distribution assumes that data are randomly distributed, the negative binomial can estimate the parameters for aggregated data such as the censuses for the southern right whale.

Both Poisson and negative binomial models were applied to data of censuses of SRW in Península Valdés Area. As predictor variables we included the Year and the Month, considered as continuous variables (Month 1-12; Year 1999-2016). Monthly variation in number of whales was modelled using also the $Month^2$, allowing the models to explore a non-linear relationship between numbers of whales and temporal variables. Another set of models included as predictor variables the Year and the Julian Day, using also Julian Day^2. Models were selected using Akaike Information Criteria (AIC), allowing evaluating which error structures and predictors are best supported by the data. We modelled four response variables: a) the total number of whales; b) the number of calves; c) the number of solitary individuals and c) the number of mating groups. All of the response variables were modelled within the same frame using the package MASS in R software (R Core Team, 2013).

Many more models were evaluated for the full data set, including models that treated the predictor Month as a categorical variable, models estimating the parameters using a quasi-Poisson distribution and models using a normal distribution, but only the best fitting model and several related models are presented.

Using the data gathered from each side of the plane, we tested the hypothesis that the type of groups observed in each side of the transect line changed through time, due to a density dependence process in which the mother and calf pairs remained preferentially closest to the shore than the rest of the groups. Using as a response variable the proportion of whales counted for each type of groups in each side of the plane from the total number of whales counted in a particular flight two Logit Regression model were built, one for the left and one for the right side (Zuur et al , 2007). The predictors were both the year (continuous) and the type of group (categorical). The models were implemented in R, using the package MASS (R Core Team, 2013).

RESULTS

Estimated rate of increase

The set of models built using the total number of whales as a response variable is shown in Table 1, while Table 2 shows the same models for the number of calves. Table 3 consider the number of Solitary Individuals and Breeding Groups. The results for other models (Table 1 and 2) are presented in terms of ΔAIC, and as a rule of thumb values that are less than two should be given consideration in addition to the selected model, while models with ΔAICc values that are more than ten should receive little consideration (Burnham and Anderson, 2002).

The selected model for the census of SRW in Península Valdés indicates that there is no influence of the Year (Table 1). The second best model includes the Year and the estimated rate of increase is 0.60% (95% IC= -2.15 - 3.51%), and the ΔAIC between both models is less than 2. The weight of these two model combined is 0.99. When analysing the data set spanning from 1999 until 2015 indicates that the population has increased in 3.15% annually (95% IC= 0.53 - 5.75). The inclusion of the 2016 census rendered a 0 rate of increase, but the analysis of the leverage shows that this data point doesn't influence the outcome more than the expected (data not shown).

When analysing the number of calves of SRW born in Peninsula Valdés, the results are consistent with those obtained for the census counting the total number of whales. The selected model dos not include the Year, and the second best yields and increasing rate of 2.30% (95%CI

= -0.98 - 5.56%). When analysing the data from 1999 until 2015, the estimated increasing rate is 4.48% per year (95% CI = 1.35 – 7.57% per year). The ΔAIC between both models is 0.137, well below the two unit threshold. The combines weight of both models is also 0.99.

For both response variables (whole population and calves), no other model presents a ΔAIC less than 2, hence no other model, but the selected one, was supported by the data (Table 1 and 2). Every model that assumes a Poisson error distribution are less supported that the Negative Binomial distribution of errors used. The Julian day is the predictive variable that presents the main influence on the number of counted whales (data not shown), and also, the Julian Day^2 has an important influence, suggesting that the temporal relationship with the number of counted whales is not linear. The later can be deduced from the fact that the best fitting models irrespectively of the error distribution includes this term.

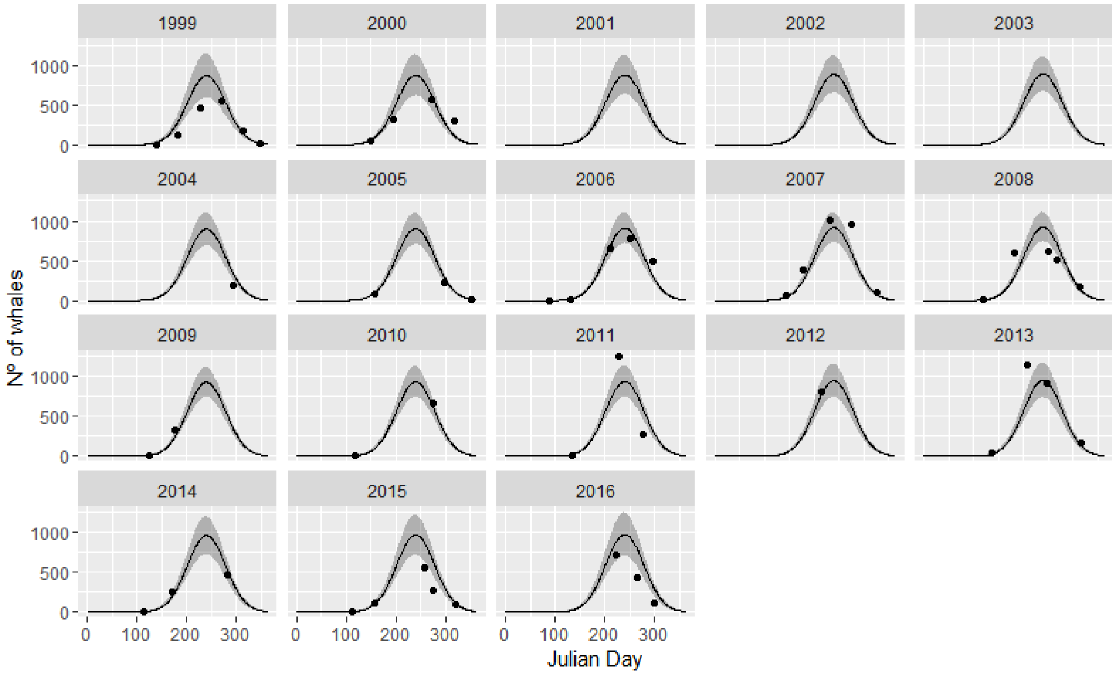

Figure 2: Total Number of whales predicted by best fitted model. Red dots are actual observations and green shadow area represents IC 95% for the estimates.

The negative binomial model with the lowest AIC score for both response variable treated Julian day dependence as quadratic. For the whole population the sightings increase from June to September, reaching approximately the same expected number of whales for August and September (Fig. 2). The number of whales lately starts to decrease from September to December, reaching it minimum in January. The model that uses as response variable the number of calves shows a similar pattern, increasing from July onwards. The maximum number of calves in the area is attained during September, and decreases abruptly until December (Fig. 3).

Table 1: Poisson and Negative binomial models for SRW censuses, using year (Y) and month (M) and year and Julian day (JD) as predictor variables. For each model, the effect of the variable Year is expressed as an annual increase rate and its associated 95% confidence interval (CI). The models are ordered according to the support given by the data assessed by the AIC.

Model	Predictors	Error distribution	Effect of the Year	95 % CI	AIC	ΔAIC
1	JD+JD2	Negative binomial	-	-	601.05	
2	Y + JD +JD2	Negative binomial	0.06%	-2.15 - 3.51%	602.82	1.77
3	Y+ M + M2	Negative binomial	0.08%	-2.84 - 4.56%	630.18	29.13
4	Y +M	Negative binomial	3.41%	-3.34 - 9.91%	703.84	102.79
5	Y + JD	Negative binomial	3.85%	-2.93 - 10.00%	704.01	102.96
6	Y	Negative binomial	2.76%	-4.21 - 9.46%	708.99	107.94
7	Y + JD +JD2	Poisson	0.07%	0.04 - 1.32%	3.067.28	2.466.23
8	JD+JD2	Poisson	-	-	3.095.17	2.494.12
9	Y+ M + M2	Poisson	1.61%	1.35 - 1.88%	4.392.22	3.791.17
10	Y+M	Poisson	2.79%	2.52 - 3.07%	16.047.51	15.446.46
11	Y + JD	Poisson	2.86%	2.58 - 3.13%	16.170.53	15.569.48
12	Y	Poisson	2.42%	2.14 - 2.69%	17.367.29	16.766.24

Regarding the models supported for the other two additional response variables (Solitary individuals and Mating groups), the results are summarized in Table 3. Both observed response variables are best supported by the same model structure as the Total number of whales and the Calves (data not shown), and again the effect of the year is non-significant.

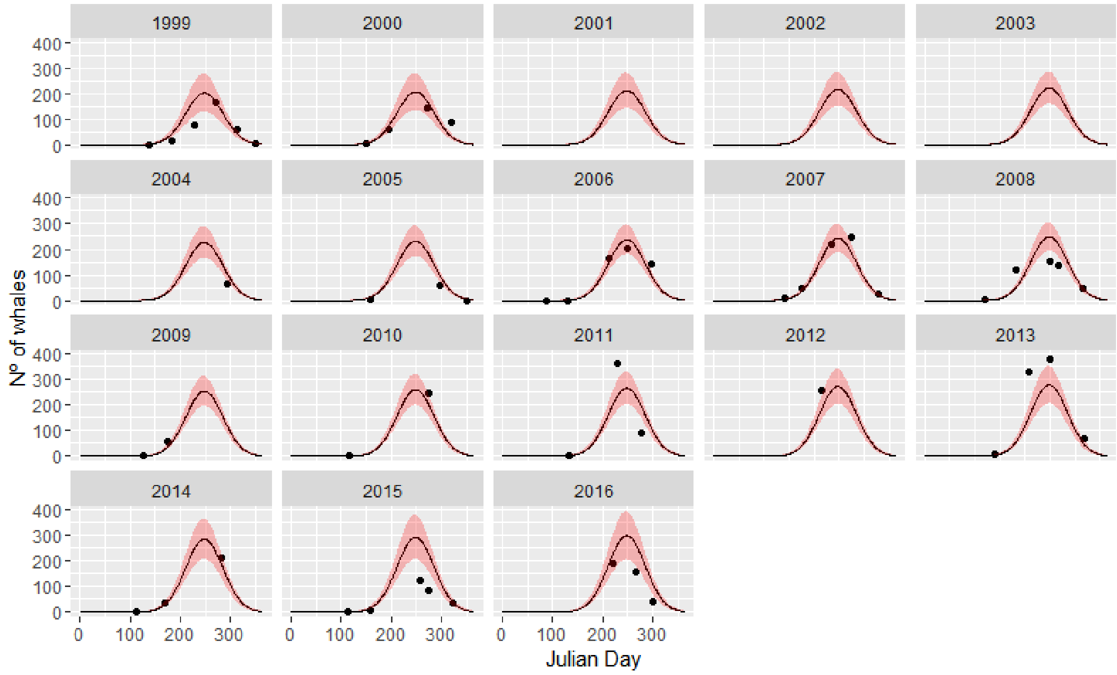

Figure 3: Total Number of calves predicted by best fitted model. Black dots are actual observations and red shadow area represents IC 95% for the estimates.

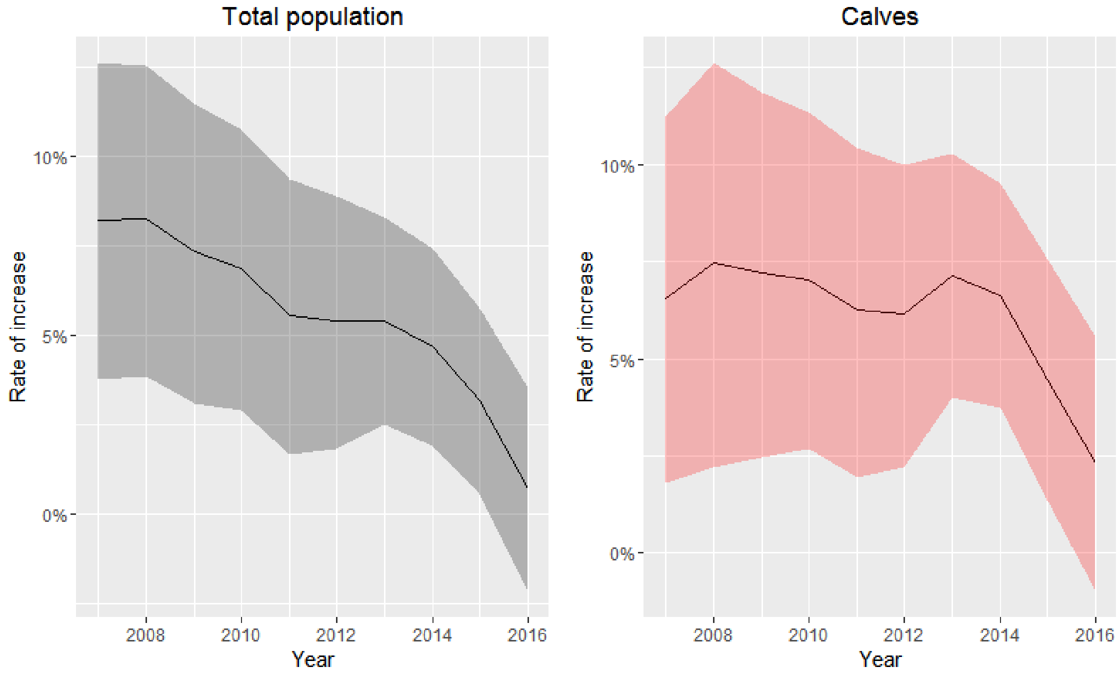

Figure 4: Rate of increase from the best fit models adding sequentially data from years 2007-2016. Grey and pink shadow area indicates the CI 95% for the estimates.

Table 2: Poisson and negative binomial models for SRW calves censuses, using year (Y), month (M) and Julian day (JD) as predictor variables. For each model, the effect of the variable Year is expressed as an annual increase rate and its associated 95% confidence interval (CI). The models are ordered according to the support given by the data assessed by the AIC.

Model	Predictors	Error distribution	Effect of the Year	95 % CI	AIC	ΔAIC
1	JD+JD2	Negative binomial	-	-	463.912	
2	Y + JD +JD2	Negative binomial	2.30%	-0.98 - 5.56%	464.050	0.137
3	Y+ M + M2	Negative binomial	2.97%	-1.25 - 7.14%	488.228	24.3131
4	Y + JD	Negative binomial	6.66%	-1.03 - 14.00%	548.781	84.866
5	Y +M	Negative binomial	5.88%	-1.78 - 13.19%	548.872	84.9567
6	Y	Negative binomial	4.59%	-3.55 - 12.32%	558.730	94.8149
7	Y + JD +JD2	Poisson	2.17%	1.64 - 2.70%	1.313.997	850.0816
8	JD+JD2	Poisson	-	-	1.377.251	913.3361
9	Y+ M + M2	Poisson	2.89%	2.37 - 3.40%	1.723.256	1259.3412
10	Y+M	Poisson	4.64%	4.11 - 5.17%	4.933.856	4469.9407
11	Y + JD	Poisson	4.73%	4.2 - 5.62%	5.002.132	4538.2165
12	Y	Poisson	4.15%	3.61 - 4.69	5.648.578	5184.6629

In order to detect a trend in the rate of increase, estimates using the same model selection procedure were performed, using the information available. The best fit model for every data set was the same as the selected for the whole set (Table 1), including the year, the Julian day and the Julian Day^2 and a negative binomial error distribution. The first estimate is for the year 2007 (from 1999), and sequentially models including the year 2008-2016 were adjusted (Fig. 4). For 2007 the r=8.20% and decreased at a rate of -0,732% annually (Linear regression, $p< 0.001$). For the calves, the rate of increase fluctuated from 7.45% to a 2.30% during the same period. The regression model show a milder decrease in the trend for the calves increasing rate (-0.376% annually; Linear regression, $p=0.02$).

Table 3: Negative binomial models for SRW censuses, using year (Y), month (M) and Julian day (JD) as predictor variables. For each model, the effect of the variable Year is expressed as an annual increase rate and its associated 95% confidence interval (CI). SI model uses as a response variable the Solitary individuals and MG model uses as response variable the individuals counted in Mating Groups.

Response variable	Variables	Error distribution	Effect of the Year	95 % CI	AIC
SI	JD +JD2	Negative binomial	-	-	526.9151
SI	Y + JD +JD2	Negative binomial	-0.012	-0.042 – 0.022%	528.8969
MG	Y + JD +JD2	Negative binomial			380.2897
MG	JD +JD2	Negative binomial	-0.050%	-0.111 – 00814%	381.0706

Inference on density dependent process

When testing the hypothesis that the type of groups observed in each side of the transect, changed along the years, the built models included separately for each side the variables Year and Type of group. Selected models included for both sides a first order interaction between both variables. Table 4 presents the selected model for each side. Figure 5 shows the estimated probability of observing a particular type of group for each year in each side. At the beginning of the study, the model estimates that on the left side, roughly a 26% chance of observing a mother with calf pair on the left side (Fig. 5 left panel), and while there seems to be a small decrease, there is no trend. Contrary, Solitary individuals presented a steep trend as the Breeding groups did for the same period. On the other hand (Fig. 5 right panel), and increasing trend could be found in both Mothers with calf pairs and breeding groups, while a downward trend is observed for Solitary individuals. The former trend in Solitary individuals is not as pronounced as the observed on the left side.

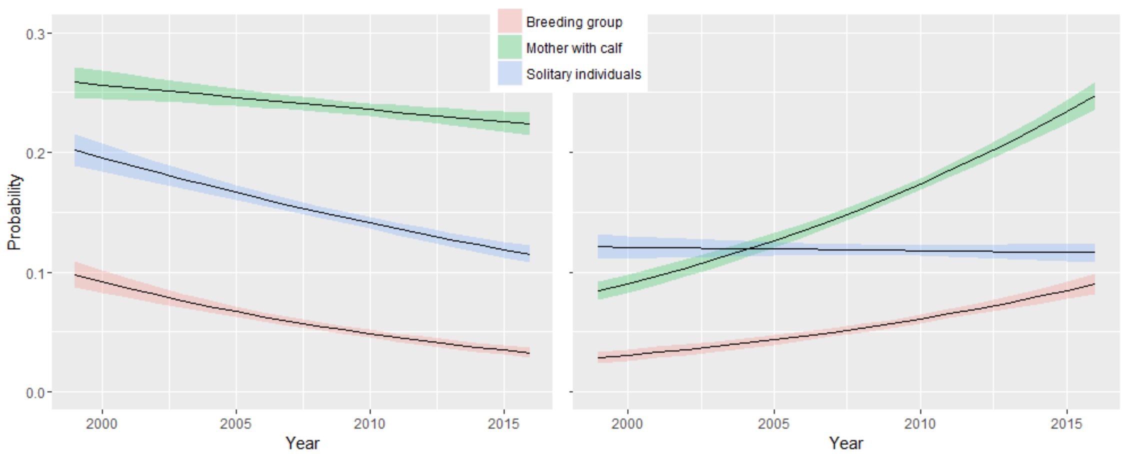

Figure 5. Probability of observe a particular type of group on each side of the strip surveyed. Left pane: left side of the strip. Right Pane: right side of the strip. Shadow areas are the confidence interval of 95%

as predicted by the model.

Table 4: Logistic regressions for the proportion of whales by group type.

	df	AIC	∆ AIC
Right side of the strip			
Year * Type of group	7	2474.792	
Year + Type of group	5	2640.679	165.887
Type of group	4	2899.740	424.948
Year	2	4048.292	1573.500
Left side of the strip			
Year * Type of group	7	2790.352	
Year + Type of group	5	2862.862	72.510
Type of group	4	3007.620	217.268
Year	2	5956.698	3166.346

DISCUSSION

The model predicts the presence of whales in the area from April to December. This behaviour of the model is consistent with the previous published information, but it predicts that the maximum number of whales could be reached from August to September, not during September as it always was assumed (Rowntree et al., 2001). Our data shows that depending upon the Year, the bulk of whales can arrive early or later during the season.

The proposed models are not able to cope with the year-related variation in the arrival of the whales to Península Valdés area. The information required for doing so is not available at the moment, but mean monthly STT in South Georgia Islands area, or productivity are candidate variables to model this temporal variation.

The analysis of the information presented in this paper supports that the SRW population is increasing in the nursing area around Península Valdés. In spite that the number of whales in the surveyed area is increasing, the rate is steadily decreasing, having reached the year 2016 for the first time since this study started an increasing rate with an interval confidence that includes the 0 as a possible value. Density has been also increasing and whales have been expanding their distribution to deeper waters during the last decade (Crespo et al., 2014) while the analysis of mortality rates since the early 70´s show an increase (Crespo et al., 2015). All these facts together are coherent with a density-dependence response. The same effect was also shown by Rowntree et al., (2013) when they compared the increase in calf mortality with the increase of living calves.

Although the rate for the whole population is near a steady state rate, the calves are increasing at a rate that is much smaller than the previously reported. These results coupled with the fact that the Solitary Individuals and the Mating Groups are no longer growing, is leading us to hypothesize that the most likely scenario includes a relocation of the whales in the Península Valdés area. Mother-calf pairs are still occupying the coastal zone (presumably their optimal habitat), while Solitary Individuals and Mating groups are forced to use deeper waters or to move out of the gulfs, in particular to the Golfo San Matías. The trend found could be an indication that the area is getting close to its carrying capacity for the optimal habitat. This coupled with the fact that more whales are sighted each year outside the surveyed area, leading us to propose that the south Atlantic population still grows at a high rate. Whales are recolonizing pre-depletion areas, both along the argentine coasts as in southern Brazil and Uruguay (Groch et al. 2005). For the surveyed area, we propose that in the next few years the Solitary Individuals and the Mating Groups will be found in deeper waters inside both gulfs and the outer ridge of Península Valdés. Also, in the surveyed area, we can expect to observe density-dependent effects on population parameters, including perinatal and calf mortality.

With regards to the rate of increase, although the inclusion of the 2016 survey rendered the 0 as a possible value for the rate of increase, the calves are still increasing, contrary to what we have observed for the Solitary Individuals and the Mating Groups which show no increase. These differences could also be explained by the fact that some adult whales could be moving to other peripheral areas as shown by the number of breeding groups and solitary individuals sighted in Golfo San Matías. This could be due to a non-stable age structure within this population (Caughley, 1977).

It should be considered that the analysis of GLM models take into account the total number of whales and calves born counted in the coastal strip. Previously we have reported a shift in the proportion of the different groups type recorded from each side of the plane, and the proportion of mother-calf pairs is higher than expected on the coastal side (Crespo et al., 2014). The models built in this paper using the number of whales in each type of group by each side indicate that while the proportion of Mother and calf pairs practically remained unchanged in the last 18 years in the left side of the strip. This increase in numbers in the area has also increased the proportion of this kind of groups in the right side. The proportion of breeding groups decreased from the left side, and shows a reverse pattern in the right side of the strip. The scenario presented by the models indicate that while areas very close to the shore are preferred by all kind of groups, in the last years, the Mother with calf pairs (that can be regarded as the most vulnerable population segment) have become proportionally the most abundant type of group in the area. The breeding groups have moved to the right side of the strip, not so close to shore to a less preferred habitat. The Solitary individuals tell a different story because the proportional decrease of the kind of group is the steeped on the left side, but contrary to the other type of groups do not increase on the right side of the strip. Hence, the proportion of solitary individuals has decreased in the survey area. This could be an indication that these individuals are using a deeper area (not surveyed) of the gulfs or are moving to other adjacent areas. This new information along with the estimates of the number of whales in the deeper waters of Golfo Nuevo are a clear indication that the 5m corridor or “whale road” proposed by R. Payne is no longer the only place where SRW are to be found in large numbers (Payne, 1986). Further information is needed to clarify is the proportion of whales that can be found in deeper waters. Also, it is clear that whales are not evenly distributed in deeper waters, with more whales surrounding the areas of high density in the coastal zone and areas recently described where whales were observed feeding on copepods (D’Agostino et al., 2016). An extensive survey must be undertaken, including both high and low density areas inside the gulfs, for us to be able to make accurate estimates of the population size.

The surveyed area for the SRW includes most of the population off the coast of Argentina, and could be considered as the optimum habitat for the species on its breeding grounds. Considering that Península Valdés as the optimum habitat, once it becomes saturated, the rate of growth in the area should decrease (as observed), and the whales should start to move to other regions, less dense and in which the rate of growth could be higher. There are clues that indicate that this could be the case, as shown by the number of whales occupying deeper waters in Península Valdés, the increasing number of whales spotted in Golfo San Matías, Buenos Aires, Uruguay and Santa Catarina in southern Brazil (Groch, et al 2005, IWC. 2010). The actual population rate of increase would be a combination of the growth in the optimal habitat and the rate of expansion to more peripheral areas.

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