




The southwestern Atlantic southern right whale, *Eubalaena australis*, population is growing but at a decelerated rate

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ABSTRACT

This paper reports on aerial surveys conducted to estimate the relative abundance and trend in growth of the southern right whale (*Eubalaena australis*) population from Península Valdés. The number of whales counted tripled from 1999 to 2016. We modeled the number of whales, the number of calves, the number of solitary individuals and the number of individuals in breeding groups using as predictive variables the year, Julian day, and Julian day² by means of generalized linear models. The rate of increase decreased from near 7% in 2007 to 0.06% and 2.30% for total number of whales and number of calves, respectively for 2016. Trends in the rates of increase for total number of whales and number of calves were negative (−0.732% and −0.376%, respectively). The habitat use of the whales changed along the years, with mothers and calves using more heavily the near-shore strip, resulting in a decreasing trend for solitary individuals and breeding groups in near-shore waters. We conclude that whales are still increasing their abundance, while the rate of increase is decreasing. Differences in the rates of increase of the group types and changes in habitat use are thought to be the consequence of a density-dependence process.

Key words: southern right whales, rate of increase, population trend, *Eubalaena australis*, Península Valdés, southwestern Atlantic.

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Right whales have been very important as a resource for human society. With increasing human population they became very important commercially, something that drove them almost to extinction around the mid-19th century. Catches of southern right whales (*Eubalaena australis*) (SRW) in the Southern Hemisphere were carried out by American, British, French, and Spanish whalers. In the South Atlantic they started in 1772 with a few whales but in the mid-19th century a minimum of 29,570 whales were taken (Du Pasquier 1986, Best 1987, Richards 1993).

The IWC conducted a major review of the status of SRW in 1998, from which a hypothetical original population size was established between 60,000 and 100,000 whales in the Southern Hemisphere, depending on the rate of increase used in the modeling (IWC 2001). Two workshops carried out in 2010 and 2011 analyzed the status and trend of all SRW stocks (IWC 2010, 2011). Following severe historical depletion by commercial whaling, the main breeding populations (Argentina/Brazil, South Africa, and Australia) of SRW have shown evidence of strong recovery, with a doubling time of 10–12 yr (Bannister 2001, Best *et al.* 2001, Cooke *et al.* 2001). Other breeding populations like the Southeast Pacific are still very small, and data are insufficient to determine whether they are recovering. Estimated total population 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) (IWC 2001), and the three main populations have continued to increase at a similar rate since then.

Regarding the western South Atlantic stock, illegal Soviet catches (mainly in the 1960s) were carried out in international waters off Península Valdés (PV), Argentina. The total catch was over 3,300 individuals, and in only one season (1961–1962) the Soviets took 1,300 whales (Tormosov *et al.* 1998). These catches probably delayed recovery for some time, but overall the population appears to have grown strongly since then.

Payne and colleagues carried out long-term studies of SRW around PV beginning in the early 1970s. Population size and other parameters were estimated from 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 at 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% (IWC 2001). More recently, it was decided to carry out a series of population trajectory calculations following essentially the same procedures as outlined in detail in the report of the 1998 right whale meeting (IWC 2001:26). During the workshop, which was carried out in Buenos Aires in 2011, the rate of increase was calculated to be between 6% and 7%. However, it was also suggested that there has been a substantial decline in the rate of increase for this population over the last 10 yr before the workshop, of around 5.0% (Cooke, personal communication to the 2011 SRW Workshop).

The process of gathering the information from photo-id data is time consuming, and late in the 1990s there was an urgent need for the PV management officers to have a quick and relatively inexpensive methodology to estimate abundance and population trend (Crespo *et al.* 2011, Cooke *et al.* 2015). For this reason, aerial surveys of the coastal zone were chosen as the optimum approach. The method was based on the assumption that around 95% of the whales are found within the 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.

Therefore, the objectives of this work were (1) to estimate the relative abundance along the coastal zone of PV, (2) to estimate the rate of increase in the area, and (3) to evaluate changes in the use of the coastal zone by age and sex classes throughout time.

MATERIALS AND METHODS

Study Area and Aerial Surveys

A monitoring area was defined from the mouth of the Chubut River ($42^{\circ}30'S$) to Puerto Lobos ($42^{\circ}00'S$), totaling a coastal strip 620 km long (Fig. 1). The area was consistently flown at an altitude of 500 ft (152.4 m) while average speed of the aircraft remained constant at 90 knots (Crespo *et al.* 2011, 2014, 2015) from south to north, taking off at approximately 1000 to avoid variation due to the time of the day. Flights were only carried out if the Beaufort Sea State was between 0 and 3 (Crespo *et al.* 2011, 2014). The period between surveys ranged from 45 d to 50 d, depending on weather conditions. Ideally, 7–8 flights were done in a given year but the actual number each year depended on weather conditions and financial support.

The surveys were carried out using high-wing, single-engine aircraft (Cessna B-182). Each survey involved a crew of four: the pilot, one recorder, and one observer on each side of the plane. Flight path was maintained at approximately 500 m from the coastline on the left (onshore) side of the plane. From measurements carried out with a clinometer, the effectively covered strip to the right (offshore) side of the plane (deeper water) was about 1,000 m.

The sea depth in the monitoring area under the plane was less than 20 m. 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 differed by year.

Age and Sex Classes

Whales from the air can be distinguished in three groups: (1) mother-calf pairs (MC), which are one adult female and a calf; (2) solitary individuals (SI), which can be either adult males or females or subadult individuals; and (3) breeding groups (BG), which are assumed to be formed by one adult female and several males.

Rate of Increase Estimated Using Generalized Linear Models Procedures

The full data set was analyzed using a generalized linear model (GLM) framework, which extends the standard linear regression model by assuming a nonnormal 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 with count data (Zuur *et al.* 2009). We used a negative binomial regression, which can be considered 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,

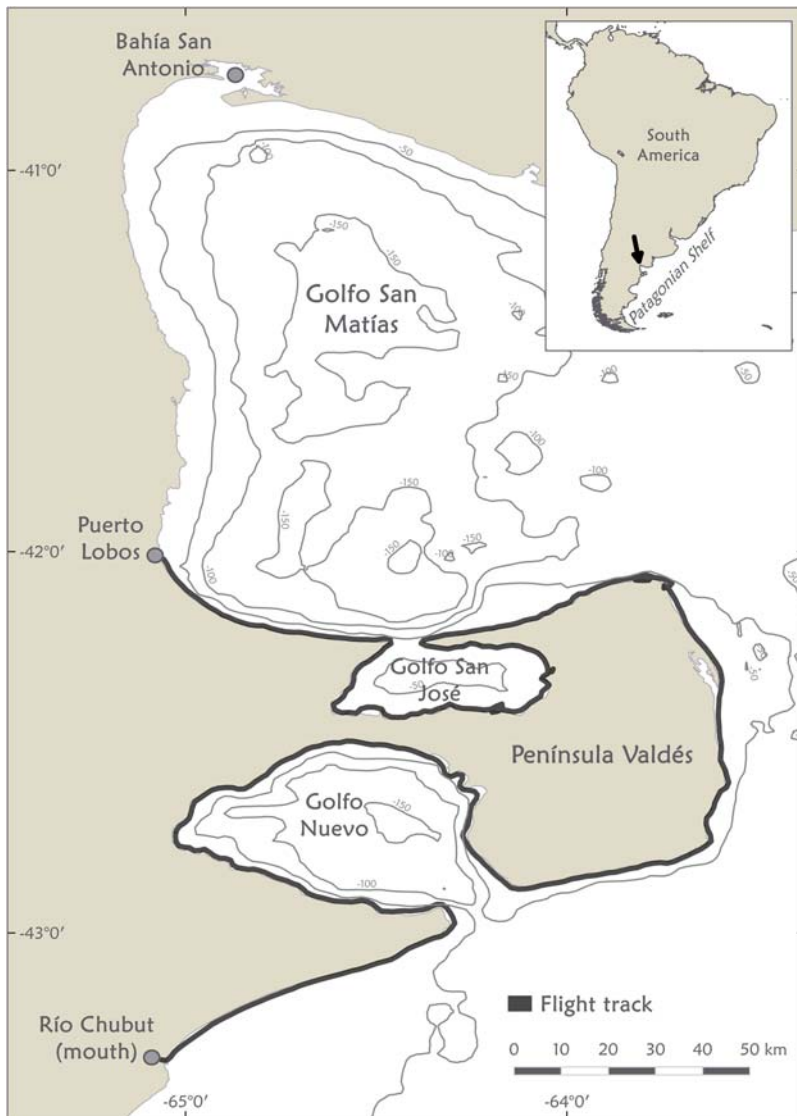


Figure 1. Monitoring area for southern right whales around the breeding ground of Península Valdés.

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 the census data for SRW in the PV area. As predictor variables, we included year and month as continuous variables (months 1–12; years 1999–2016). Monthly variation in number of whales was also modeled using month², allowing the models to explore a nonlinear relationship between numbers of whales and temporal variables. Another set of

models included year, Julian day, and Julian day² as predictor variables. Models were selected using Akaike information criteria (AIC). We modeled four response variables: (1) the total number of whales, (2) the number of calves, (3) the number of solitary individuals, and (4) the number of individuals in the breeding groups. All of the response variables were modeled within the same frame using the package MASS in R software (R Core Team 2013).

Other 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 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 dependent process in which the mother and calf pairs remained preferentially closer 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 models were built, one for the left side and one for the right side (Zuur *et al.* 2009). 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

Relative Abundance of Whales

Whales arrive at PV early in April or later in May and remain in the area up to November or later in December. The length of the season varies from year to year. Some years a few whales are still seen in January. The peak of the season is usually at the end of August or in mid-September, but it has occurred at the end of July as well. In the earlier years of the survey (1999–2000) the total number of whales counted during a flight reached around 400 adult and subadult whales and around 150 newborn calves. In later years (2005–2016), the number of whales in the peak of the breeding season reached 1,200 adults and subadults and 450 newborn calves. These figures correspond to an instantaneous count and thus are not the number of whales that pass through the area given that the residence time of individual whales is always less than the length of the breeding season (Rowntree *et al.* 2001). In addition, some whales are found in deeper waters far from the coastal zone, and these whales remain to be estimated.

Estimated Rate of Increase

The set of models built using the total number of whales including calves as a response variable is shown in Table 1, while Table 2 shows the same models for the number of calves. Table 3 considers the number of solitary individuals and breeding groups. The results for other models (Tables 1, 2) are presented in terms of Δ AIC, 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 Δ AIC values that are more than ten should receive little consideration (Burnham and Anderson 2002).

The selected model for the census of SRW in PV indicates that there is no influence of the year (Table 1). The second best model includes the year, the estimated

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 year	95% CI	AIC	Δ AIC
1	JD + JD ²	Negative binomial	—	—	601.05	1.77
2	Y + JD + JD ²	Negative binomial	0.06%	-2.15%–3.51%	602.82	29.13
3	Y + M + M ²	Negative binomial	0.08%	-2.84%–4.56%	630.18	102.79
4	Y + M	Negative binomial	3.41%	-3.34%–9.91%	703.84	102.96
5	Y + JD	Negative binomial	3.85%	-2.93%–10.00%	704.01	107.94
6	Y	Negative binomial	2.76%	-4.21%–9.46%	708.99	2,466.23
7	Y + JD + JD ²	Poisson	0.07%	0.04%–1.32%	3,067.28	2,494.12
8	JD + JD ²	Poisson	—	—	3,095.17	3,791.17
9	Y + M + M ²	Poisson	1.61%	1.35%–1.88%	4,392.22	15,446.46
10	Y + M	Poisson	2.79%	2.52%–3.07%	16,047.51	15,569.48
11	Y + JD	Poisson	2.86%	2.58%–3.13%	16,170.53	17,367.29
12	Y	Poisson	2.42%	2.14%–2.69%	17,367.29	16,766.24

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 year	95% CI	AIC	Δ AIC
1	JD + JD ²	Negative binomial	—	—	463.912	
2	Y + JD + JD ²	Negative binomial	2.30%	-0.98%–5.56%	464.050	0.137
3	Y + M + M ²	Negative binomial	2.97%	-1.25%–7.14%	488.228	24.313
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	84.956
6	Y	Negative binomial	4.59%	-3.55%–12.32%	558.730	94.815
7	Y + JD + JD ²	Poisson	2.17%	1.64%–2.70%	1,313.997	850.082
8	JD + JD ²	Poisson	—	—	1,377.251	913.336
9	Y + M + M ²	Poisson	2.89%	2.37%–3.40%	1,723.256	1,259.341
10	Y + M	Poisson	4.64%	4.11%–5.17%	4,933.856	4,469.940
11	Y + JD	Poisson	4.73%	4.2%–5.62%	5,002.132	4,538.2165
12	Y	Poisson	4.15%	3.61%–4.69	5,648.578	5,184.6629

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 breeding groups.

Response variable	Variables	Error distribution	Effect of year	95% CI	AIC
SI	JD + JD ²	Negative binomial	—	—	526.9151
SI	Y + JD + JD ²	Negative binomial	-0.012	-0.042%–0.022%	528.8969
MG	Y + JD + JD ²	Negative binomial			380.2897
MG	JD + JD ²	Negative binomial	-0.050%	-0.111%–0.0814%	381.0706

rate of increase is 0.60% (95% IC = -2.15%–3.51%), and the Δ AIC between both models is less than 2. The weight of these two models combined is 0.99. When analyzing the data set, from 1999 to 2015 without including 2016, the population has increased in 3.15% annually (95% IC = 0.53%–5.75%). Inclusion of the 2016 census rendered a rate of increase of 0, but the analysis of the influence of individual observations (leverage analysis) shows that this data point does not influence the outcome of the model more than expected (Cook 1977, Laurent and Cook 1993).

When analyzing the number of calves of SRW born in PV, the results are consistent with those obtained for the census counting the total number of whales. The selected model does not include the year, and the second best yields an increasing rate of 2.30% (95% CI = -0.98%–5.56%). When analyzing the data from 1999 to 2015 (without 2016), the estimated increasing rate is 4.48% per year (95% CI = 1.35%–7.57% per year). The Δ AIC between both models is 0.137, well below the threshold of 2. The combined weight of both models is also 0.99.

For both response variables (whole population and calves), no other model presents a Δ AIC < 2, hence no other model but the selected one was supported by the data (Tables 1 and 2). Models with a Poisson error distribution were less supported than models with negative binomial error distribution. The Julian Day is the predictive variable that presents the main influence on the number of whales counted (coefficient estimate = 0.161, $P < 0.001$) and the Julian Day² also has an important influence (coefficient estimate = 0.003, $P < 0.001$), indicating 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.

The negative binomial model with the lowest AIC score for both response variables 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). In recent years, the number of whales starts to decrease from September to December, reaching it minimum in January. The model for 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).

Regarding the models for the other two response variables (solitary individuals and breeding groups), the results are summarized in Table 3. Both observed response variables are best supported by the same model structure as the total

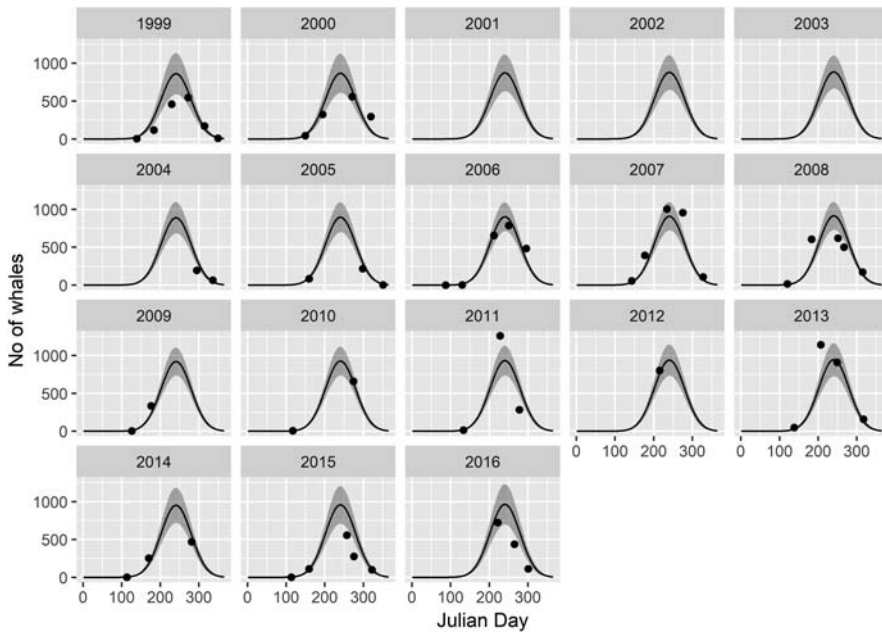


Figure 2. Total number of whales predicted by the best-fitted model. Red dots are actual observations and green shadow area represents IC 95% for the estimates.

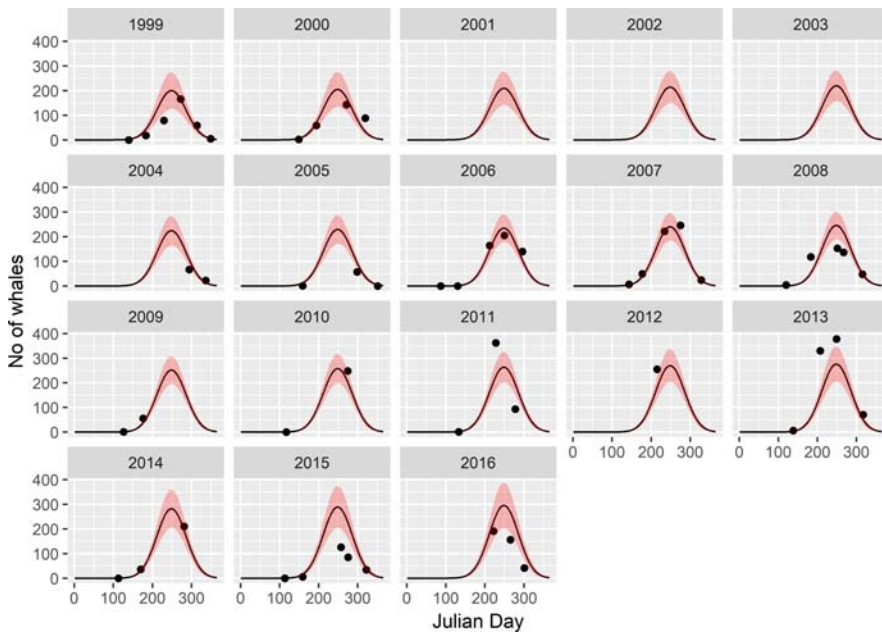


Figure 3. Total number of calves predicted by the best-fitted model. Black dots are actual observations and red shadow area represents IC 95% for the estimates.

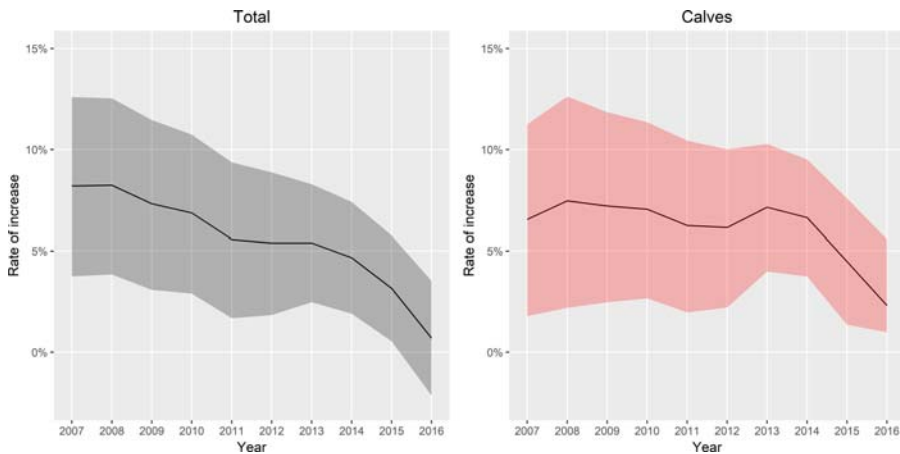


Figure 4. Rate of increase from the best-fitted models adding data from years 2007–2016 sequentially. Gray and red shadow area indicates the 95% CI for the estimates.

number of whales and the calves (data not shown), and again the effect of the year is not significant.

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 that selected for the whole set (Table 1), including the year, the Julian day, and the Julian day² and a negative binomial error distribution. The first estimate is for the year 2007 (from 1999), and sequentially models including the years 2008–2016 were adjusted (Fig. 4). For 2007, the rate of increase was 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 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, $P = 0.020$).

Inference on Density Dependent Process

When testing the hypothesis that the type of groups observed on each side of the transect changed across years, the 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 on each side. At the beginning of the study, the model estimates roughly a 26% chance of observing a mother with calf on the left side (Fig. 5 left panel), and while there seems to be a small decrease, there is no trend. On the contrary, solitary individuals presented a steep trend as the breeding groups did for the same period. On the other hand (Fig. 5 right panel), an increasing trend could be found in both mother-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 that observed on the left side.

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

	df	AIC	Δ AIC
Right side of the strip			
Year * Type of group	7	2,474.792	
Year + Type of group	5	2,640.679	165.887
Type of group	4	2,899.740	424.948
Year	2	4,048.292	1,573.500
Left side of the strip			
Year * Type of group	7	2,790.352	
Year + Type of group	5	2,862.862	72.510
Type of group	4	3,007.620	217.268
Year	2	5,956.698	3,166.346

DISCUSSION

The model predicts the presence of whales in the area from April to December from 1999 to 2016, a wider period than that recorded in previous published information (Payne 1986, Rowntree *et al.* 2001). The behavior of the model predicts that the maximum number of whales could be reached from August to September (exceptionally late July), not during September as has been assumed (Rowntree *et al.* 2001). Our data show that depending upon the actual 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 PV area. The information required for doing so is not available now, but mean monthly sea surface temperature in the South Georgia Islands area, or productivity, are candidate variables to model this temporal variation.

In this sense, Leaper *et al.* (2006) found a strong relationship between SRW calving output and SST anomalies at South Georgia in the autumn of the previous year

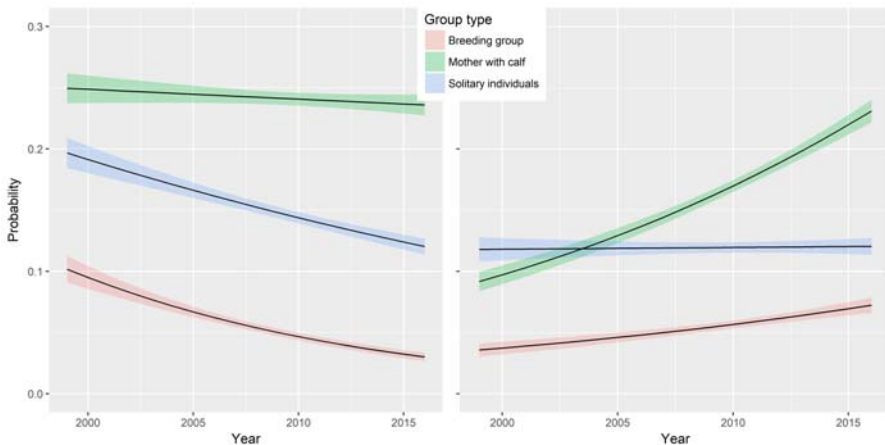


Figure 5. Probability of observing a particular type of group on each side of the strip surveyed. Left pane: left side of the strip. Right Pane: right side of the strip. Shadow areas are the confidence interval of 95% as predicted by the model.

and also with mean El Niño region 4 SST anomalies delayed by 6 yr. These results extend similar observations from other krill predators and show clear linkages between global climate signals and the biological processes affecting whale population dynamics. Seyboth *et al.* (2016) also found that global climate indices influence SRW breeding success in southern Brazil by determining variation in krill availability. Therefore, increased frequency of years with less krill availability due to global warming is likely to reduce chances of SRW recovery from exploitation.

Our results support that the SRW population is increasing in the nursing area around PV. In spite of the fact that the number of whales in the surveyed area is increasing, the rate of increase is steadily decreasing, having reached a confidence interval that includes 0 as a possible value in 2016 for the first time since this study started. Density also has been increasing as whales have been expanding their distribution into deeper waters during the last decade (Crespo *et al.* 2014), and mortality rates since the early 1970s show an increase (Crespo *et al.* 2015). All these facts together are consistent 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 in SRW.

Although the growth rate for the whole population is near a steady state rate, the calves are increasing at a rate that is much lower than that previously reported (Crespo *et al.* 2011). These results coupled with the fact that the solitary individuals and the breeding groups are no longer increasing, lead us to hypothesize that the most likely future scenario includes a redistribution of the whales in the PV area. Mother-calf pairs are still occupying the coastal zone (presumably their optimal habitat), while solitary individuals and breeding groups are forced to use deeper waters or to move out of the region, in particular to Golfo San Matías. The trend could be an indication that the area is getting close to its carrying capacity as optimal habitat. This coupled with the fact that more whales are sighted each year outside the surveyed area leads us to propose that the South Atlantic population is still growing at a high rate. Whales are recolonizing previously occupied areas, both along the Argentine coasts as in southern Brazil (Groch *et al.* 2005) and Uruguay (Costa *et al.* 2007, Danilewicz *et al.* 2016). For the surveyed area, we propose that over the next few years solitary individuals and breeding groups will be found in deeper waters inside both gulfs and the outer ridge of PV. In addition, we can expect to observe density-dependent effects on population parameters, including perinatal and calf mortality.

With regard to the rate of increase, although the inclusion of the 2016 survey rendered 0 as a possible value for the rate of increase, the calves are still increasing, contrary to what we have observed for solitary individuals and the breeding groups, which show no increase. These differences could 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 (Arias *et al.* 2017). This could be due to an unstable age structure within this population (Caughley 1977).

It should be noted that the analysis of GLM models take into account the total number of whales and newborn calves counted in the coastal strip. Previously, we have reported a shift in the proportion of the different groups recorded from each side of the plane, and the proportion of MC 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 the proportion of MC pairs practically remained unchanged in the last 18 yr on the left side of the strip. This increase in numbers in the area has also increased the proportion of this kind of group on the right side. The number of breeding groups decreased on the left side

and shows a reverse pattern on 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 recent years, mother-calf pairs (which 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 and a less preferred habitat. The solitary individuals tell a different story because the proportional decrease of this group is mostly on the left side, but contrary to other type of groups, they 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 5 m corridor or “whale road” proposed by Payne (1986) is no longer the only place where SRW are to be found in large numbers. Further information is needed to clarify 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 mainly on copepods (D’Agostino *et al.* 2016). An extensive survey should be undertaken, including both high- and low-density areas inside the gulfs, 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 PV as the optimum habitat, once it becomes saturated, the rate of growth in the area should decrease (as observed), and the whales should start moving to other less dense regions, in which the rate of growth could be higher. There are clues to suggest that this is the case, as shown by the number of whales occupying deeper waters in PV, 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 rate of increase in the population will be a combination of growth in the optimal habitat and the rate of expansion in peripheral areas.

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LITERATURE CITED

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