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The Southwestern Atlantic Southern Right Whale, *Eubalaena australis*: updated population rate of increase

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The Southwestern Atlantic Southern Right Whale, *Eubalaena australis*: updated population rate of increase

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INTRODUCTION

Right whales have been very important as a resource for the human society. With increasing human population they became very important from the commercial point of view, something that drove them almost to the border of extinction around the mid19th 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 Ocean they started in 1772 with a few whales but in the mid19th century a minimum of 29,570 whales had been taken (Du Pasquier 1982; Best 1987; Richards 1993).

The IWC conducted a major review of the status of SRW in 1998 where 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 modelling (IWC 2001). Two workshops carried out in 2010 and 2011 analysed 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.

For the first time the population dynamics of the SRW from the south-western Atlantic Ocean at the regional level to measure numerically the effect of whaling and estimate the population trend and recovery level after depletion. Romero *et al.* (2022) reconstructed the catch history of whaling for the period 1670-1973 by an extensive review of different literature sources and developed a Bayesian state-space model to estimate the demographic

parameters. The population trajectory indicated that the pre-exploitation abundance was close to 58,000 individuals (median = 58,029; 95% CI = 33,378–100,997). The abundance dropped to its lowest abundance levels in the 1830s when less than 2,000 individuals remained. The current population abundance was estimated at 4,749 whales (95% CI = 3,840–6,048), suggesting that the SRW population remains small relative to its pre-exploitation abundance (median depletion P_{2021} 8.2%). The authors estimated that close to 36% of the SRW population visits the waters of the Península Valdés every year, the main breeding ground. These results provide insights into the severity of the whaling operation in the southwestern Atlantic along with the population's response at low densities, contributing to understand the observed differences in population trends over the distributional range of the species worldwide.

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 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, it was calculated that the rate of increase was 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 years before the workshop, to around 5.0% (Cooke, pers. comm. 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 a coastal strip known as the “whale road” (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, 3) evaluate changes in the use of the coastal zone by age and sex classes throughout time, 4) evaluate changes in distribution at the regional level.

MATERIALS AND METHODS

Study area and aerial surveys

A monitoring area was defined from the mouth of the Chubut River (42°30'S) to Puerto Lobos (42°00'S), totalling a coastal strip 620 km long (Fig. 1). The area was consistently flown at an altitude of 500 feet (152.4 m) while average speed of the aircraft remained constant at 90 knt (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 45-50 days, depending on weather conditions. Ideally, 7 to 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 79 flights were carried out between May 1999 and October 2019. Due to financial support, not every year had the same number of flights, and hence effort differed by year.

Particularly, during 2020 the flights were not performed because of the restrictions imposed by the national government to cope with the COVID-19 pandemic. During 2021 and 2022 after the pandemic, surveys were resumed and three complete flights were done in each survey area.

Age and sex classes

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 sub-adult individuals
- c) 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 analysed using a Generalized Linear Model (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 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 over dispersion 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 SRW.

As predictor variables, we included Year and Month as continuous variables (Month 1-12; Year 1999-2022). Monthly variation in number of whales was also modelled using Month², allowing the models to explore a nonlinear relationship between numbers of whales and temporal variables. Another set of models included the Year, the Julian day, and Julian day² as predictor variables. Models were selected using Akaike Information Criteria

(AIC). We modelled four response variables: a) the total number of whales; b) the number of calves; c) the number of Solitary Individuals and d) the number of individuals in the Breeding Groups. All the response variables were modelled within the same frame using the package MASS in R software (R Core Team 2022).



Fig. 1. Monitoring area for southern right whales around the breeding ground of Península Valdés and Golfo San Matías

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.

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 sub-adult whales and around 150 new-born calves. In later years (2005-2017), the number of whales in the peak of the breeding season reached 1,200 adult and sub-adult individuals and 500 new-born calves. The number of whales peaked during 2018, with a total count of 1605 whales and 710 new-born calves. Numbers were lower in 2019. In the 2021 censuses a peak of 1139 was recorded including 448 calves, while for the 2022 the values are similar with total of 1114 whales including 390 calves (Fig. 2 and 3). 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. In addition, some whales are found in deeper waters far from the coastal zone, which 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 (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 $\Delta AICc$ 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 rate of increase is 0.32 (95% IC= -1.45% - 2.08%), and the ΔAIC between both models is 1.88. The weight of these two models combined is 1.

When analysing 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 includes the Year yielding an increasing rate of 2.55% (95% CI = 0.47% - 4.63%). Nevertheless, the second best does not include the Year as a predictor variable. The ΔAIC between the two first models is 3.51, well above the threshold of 2. The combined weight of both models is more than 0.99, but the best-fitted model has an AIC weight of 0.85.

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).

For the whole population models the Julian day is the predictive variable that presents the main influence on the number of whales counted (Coef. Est. = 0.165, $p < 0.001$) and the Julian day² also has an important influence (Coef. Est. = -0.001, $p < 0.001$), indicating that the temporal relationship with the number of counted whales is not linear. 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 its minimum in January. The model for the number of calves shows a similar pattern, increasing from July onwards, and also the Julian day is the most influential variable. 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; and the first two models for each group presented a combined weight of 0.999. Both observed response variables are best supported by the same model structure as the Total number of whales and the Calves (data not shown). Nevertheless, a marked decrease in the number of breeding groups is observed with a rate of -9.75% (95%CI = -14.16 - -5.41%). For the solitary individuals the decreasing rate is less steeped, being estimated in -1.41% (95%CI = -3.58 - 0.10%). Breeding groups and Solitary individuals are becoming less common in PV.

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 year 2008-2022 were adjusted (Fig. 4). For 2007, the rate of increase was 8.20% and decrease at a rate of -0.604% annually (Linear regression, $P < 0.001$). For the calves, the rate of increase fluctuated from 7.45% to a 2.55% during the same period. The regression model shows a milder decrease in the trend for the calves increasing rate (-0.336% annually; Linear regression, $P = 0.009$).

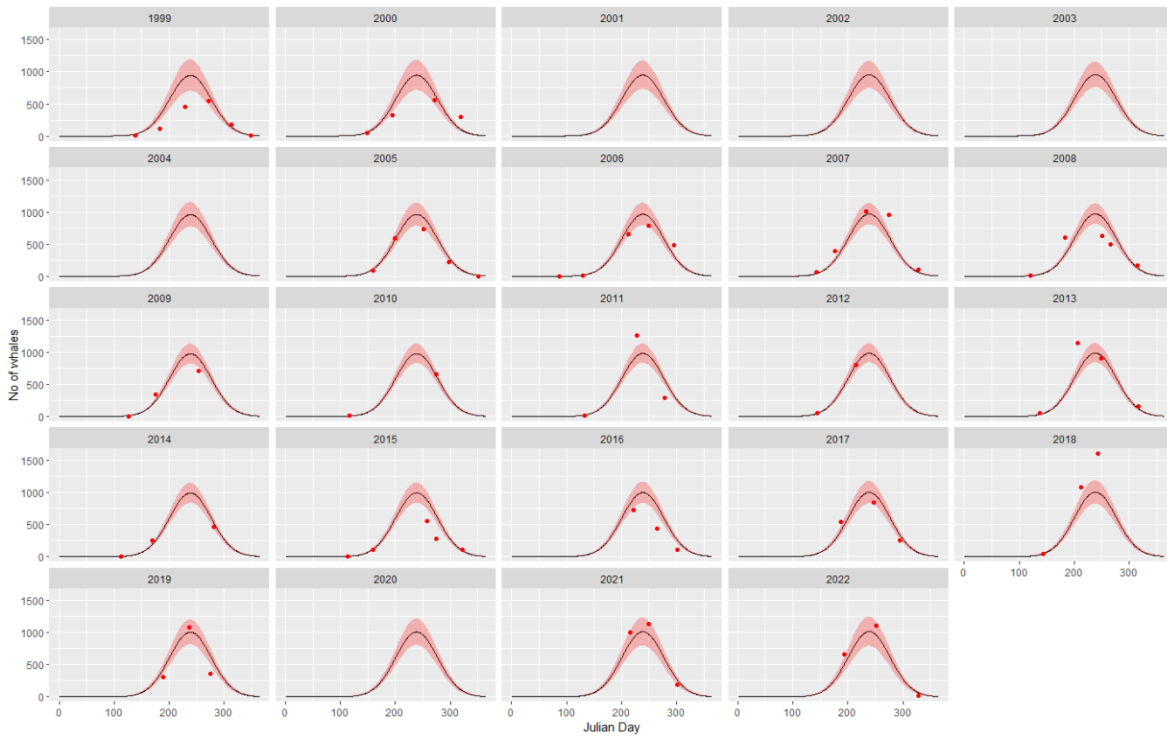


Fig. 2. Total Number of whales predicted by the best-fitted model 1999-2022. Red dots are actual observations and pink shadow area represents IC 95% for the estimates.

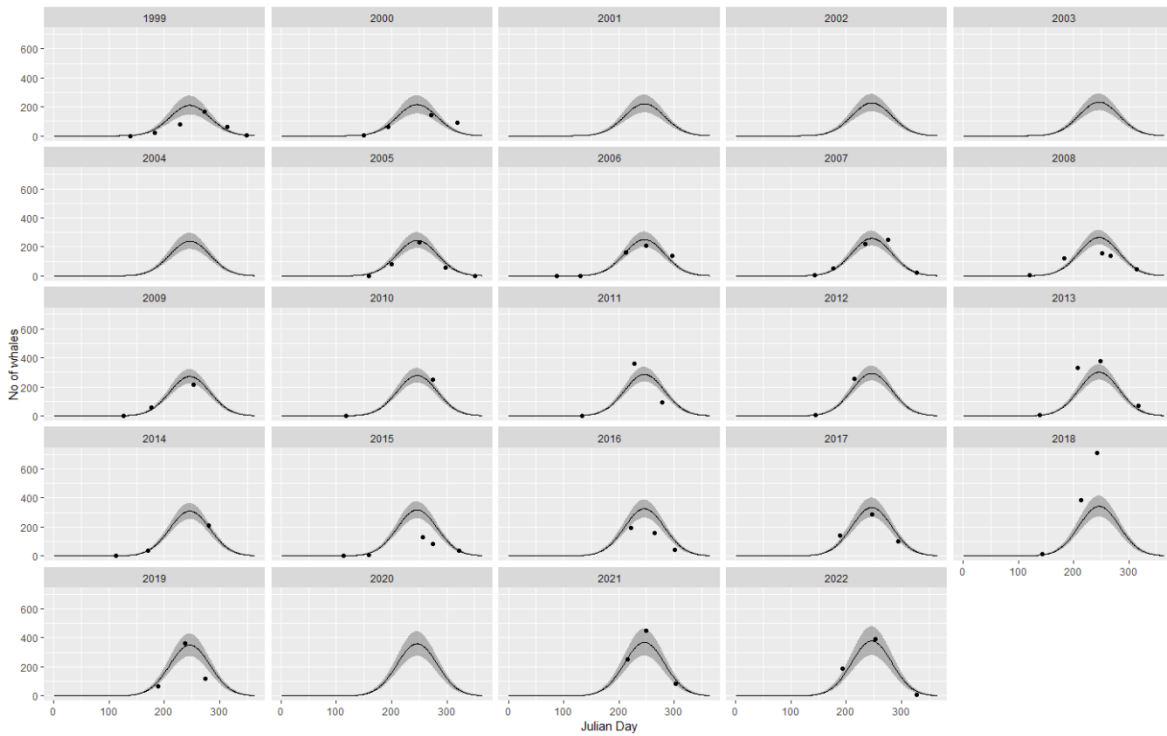


Fig. 3. Total Number of calves predicted by the best-fitted model 1999-2022. Black dots are actual observations and gray shadow area represents IC 95% for the estimates.

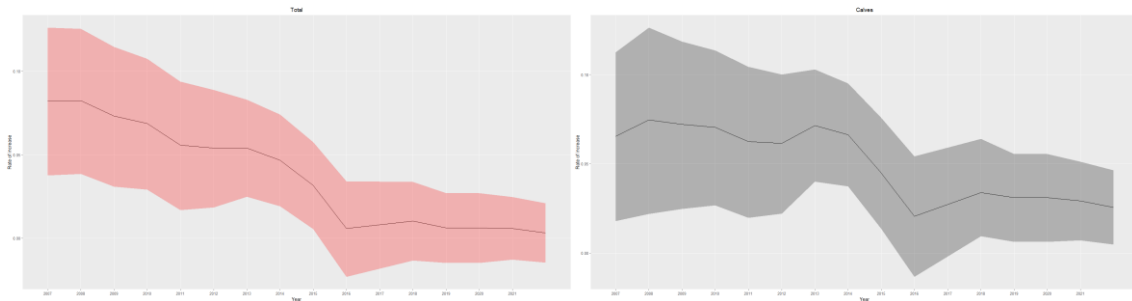


Fig. 4. Declining rate of increase from the best-fitted models adding data from years 2007-2022 sequentially. a) Total population. b) Calves. Pink and grey shadow areas indicate the CI 95% for the estimates.

Table 1. 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	Δ AIC	AICw
1	JD+JD2	Negative binomial	-	-	836.01	0	0.72
2	Y + JD + JD2	Negative binomial	0.23 %	-1.46 -2.09	837.88	1.87516141	0.28
3	Y+ M + M2	Negative binomial	0.25 %	-2.10 2.59	874.72	38.7084139	0.00
4	Y +M	Negative binomial	4.15%	0.01 – 8.26	978.55	142.540111	0.00
5	Y + JD	Negative binomial	4.49 %	0.03 – 8.62	979.22	143.209033	0.00
6	Y	Negative binomial	3.92 %	-0.01 – 8.14	984.56	148.547286	0.00

Table 2. The best fitted 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	Δ AIC	AICw
1	Y + JD + JD2	Negative binomial	2.55%	0.47% - 4.63%	663.53	0.00	0.85
2	JD+JD2	Negative binomial	-	-	667.04	3.51	0.15
3	Y+ M + M2	Negative binomial	2.53%	-0.01% - 5.18%	694.23	30.70	0.00
4	Y + JD	Negative binomial	7.36%	2.74% - 11.97%	783.14	119.61	0.00
5	Y +M	Negative binomial	6.85%	2.26% - 11.41%	782.82	119.30	0.00
6	Y	Negative binomial	6.01%	1.13% - 10.85%	795.28	131.75	0.00

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 BG model uses as response variable the individuals counted in Breeding Groups.

Response variable	Variables	Error distribution	Effect of the Year	95 % CI	AIC
SI	JD +JD2	Negative binomial	-	-	727.32
SI	Y + JD +JD2	Negative binomial	-1.42%	-3.58% - 0.1%	727.64
MG	Y + JD +JD2	Negative binomial	-9.75%	-14.16% - 5.41%	519.80
MG	JD +JD2	Negative binomial	-		535.11

DISCUSSION

The models predict the presence of whales in the area from April to December from 1999 to 2022, a wider period than that recorded in previous published information (Payne 1986; Rowntree *et al.* 2001). The behaviour 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 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 and also with mean El Niño region 4 SST anomalies delayed by 6 years. 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 no longer increasing in the nursing area around PV. Although the number of whales in the surveyed area can vary reaching peaks as in 2018, the rate of increase has decreased in the last decade, having reached a confidence interval that includes 0 as a possible value since 2016. This trend continues when incorporating the 2022 surveys. Density also has been increasing as whales have been expanding their distribution into deeper waters during the last decade (Crespo *et al.* 2019). However, density has not increased homogeneously in the area (Sueyro *et al.* 2018). In addition, mortality rates had been increasing since the early 1970s (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. These results coupled with the fact that the solitary individuals and the breeding groups are decreasing since this study started in 1999, leads us to hypothesize that the most likely future scenario includes a relocation 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 (see Fig. 1) (Arias *et al.*, 2018; Crespo *et al.*, 2019). 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 regards to the rate of increase, the inclusion of the 2022 survey indicates for the sixth consecutive year that the population as a whole is no longer increasing in PV. Instead, including 2022 survey data the confidence interval for the rate includes the 0 as possible value, as it has been the case since 2016 (Crespo and Coscarella, 2018). Contrary to what has been reported previously (Crespo *et al.* 2017) the solitary individuals and the breeding groups are decreasing in the area. Some reports make clear that a fraction of the population is moving to other peripheral areas, as shown by the changes in the distribution and density in PV (Sueyro *et al.* 2018) and the number of breeding groups and solitary individuals sighted in Golfo San Matías (Arias *et al.* 2018). This could be due to an unstable age structure within this population (Caughley 1977).

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). Information gathered with satellite tracking devices indicate that all groups are using extensively the deeper waters of the gulfs, and that during the same breeding season individuals can move from one gulf to another using deep waters (Zerbini *et al.* 2015; 2018). 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.

In the former years of our population monitoring the survey area was restricted to Península Valdés. However, in the last ten years the SRW expanded their territory to Golfo San Matías. While PV retained the area for parturition and nursing calves, in GSM started to increase the number of groups performing mating behaviours.

A change in the spatial distribution through the years along the coast of GSM was recorded (Fig. 1). In 2007, most whales were found around Puerto Lobos, near Península Valdés, and few whales were recorded on the north coast of GSM. Afterwards (2013-2016) the areas in which the whales concentrate have changed and expanded. The SRW distribution was mainly confined to the northwest coast of the GSM (Arias *et al.*, 2018). The dominant group type in the coastal strip were solitary individuals. Mother-calf pairs and

breeding groups were mainly concentrated in the area around Puerto Lobos, near Península Valdés, and in the sector between shallow waters of Bahía San Antonio (Arias *et al.*, 2018).

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