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Capture-recapture estimates of abundance of Antarctic blue whales

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ABSTRACT

Photo-identification data of Antarctic blue whales from 2003/2004 to 2018/2019 were used in a capture-recapture analysis to produce estimates of population abundance and growth rate for the circumpolar Antarctic. Photographs were collected during IWC-SOWER, IWC-SORP, ICR, and SAABWS cruises and also made available by opportunistic contributors. Separate capture-recapture estimates were made using photos taken of the right and left sides of the whales. Two capture-recapture models, POPAN and Pradel, were applied to these data to estimate superpopulation abundance (N), recruitment-immigration ($pent$), and probability of capture (p) from the POPAN model and probability of capture and population growth rate (λ) from the Pradel model. The fits of a series of pre-specified apparent survival rates from 0.75 to 1 were compared using $\Delta AICc$. Derived parameters of annual abundances and population growth rate were calculated from the POPAN models. A wide range of annual survival rates were consistent with the capture-recapture data based on $\Delta AICc$ scores. Four different best-fitting configurations of left side data, right side data, POPAN, and PradLambda had survival rates of 0.94, 0.87, 0.97 and 0.9 (mean 0.92). The best superpopulation estimates from POPAN for the left and right sides were 3,488 (95% CI = 1754, 7178) and 3,659 (95% CI = 1906, 7241) whales, respectively. Assigning a survival rate of 0.92 to the combined and right and left side models produced an abundance estimate for the last year, 2018/2019 (2,050 whales ; CI = 1,135 to 3,704) that was lower than the projected abundance for 2019 from Branch (2004) (9,608 whales (CI = 1257 to 26,060 whales)). Assigning a higher survival rate of 0.99 for the POPAN models produced higher annual estimates of abundance although still less than the projections from Branch (2004). Population growth rates from Pradel, POPAN and Branch (2007) were also compared. Estimated population growth rates from the Pradel and POPAN models during 2003/2004 – 2018/2019 were at the upper end of the Branch (2007) growth estimates for 1997/1998. The Pradel and POPAN models suggested annual population growth was slowing by the end of the time series instead of increasing exponentially.

KEYWORDS: ANTARCTIC, PHOTO-ID, MARK-RECAPTURE, ABUNDANCE ESTIMATE

INTRODUCTION

During the first half of the 20th Century, the population of Antarctic blue whales (*Balaenoptera musculus intermedia*) was reduced by whaling from an estimated pre-exploitation size of 239,000 (95% CI=202,000-311,000) to less than 1% of its former abundance (Branch, 2007). To date the population has not recovered to its pre-exploitation size, although Branch *et al.* (2004) provides evidence that the population is increasing. Antarctic blue whales are listed as Critically Endangered by the International Union for the Conservation of Nature (Reilly *et al.*, 2008). In 2006 the IWC Scientific Committee initiated an in-depth assessment of this population and Branch (2007) produced estimates of abundance from each of the three circumpolar sets of surveys¹ conducted under the IWC IDCR/SOWER² program. Branch's (2007) work provides the most recent population abundance estimate accepted by the IWC, 2,280 (CV=0.36), and is based on data from the last IDCR/SOWER circumpolar series, CPIII. The estimate was based on the CPIII midpoint year 1997/1998. Currently the Scientific Committee is planning a new in-depth assessment of this population (IWC, 2022).

¹ CPI (1978/79-1983/84), CPII (1985/86-1990/91), CPIII (1991/92-2003/04)

² International Decade of Cetacean Research/Southern Ocean Whale Ecosystem Research

The Antarctic Blue Whale Catalogue (Olson *et al.*, 2020) contains photo-identification data available for analysis in a capture-recapture estimate of abundance. Previously we conducted capture-recapture estimates with these data (Olson *et al.* 2018; 2021), and in addressing comments from the Committee in response to those estimates we have reworked the analysis here. We used right and left side photographs to calculate separate circumpolar estimates for the number of blue whales present from 2003/2004 to 2018/2019.

METHODS

Field methods

Research cruises conducted by year are given in Table 1. During IWC-SOWER and ICR³ cruises, photo-identification effort was conducted ancillary to the primary cruise objectives, thus the amount of effort varied by year (Matsuoka *et al.*, 2003; Matsuoka and Pastene, 2009; Olson, 2010). Photo-ID was most often conducted from the bow of the research vessel in conjunction with biopsy sampling. Blue whale research was the primary objective of the IWC-SORP and SAABWS⁴ voyages where photo-ID was also conducted in conjunction with biopsy sampling (Double *et al.*, 2013; Double *et al.*, 2015; Double *et al.*, 2021; Findlay, *et al.* 2014). The 2013 IWC-SORP voyage operated an inflatable boat for approaches as well as the larger ship.

Both right and left sides of the whales were photographed whenever possible, but not all whales were approachable on both sides. 35mm SLR cameras using black and white film were used through 2004/2005, overlapping in use with digital SLR cameras beginning in 2003/2004. Digital SLR cameras were used exclusively starting with the 2005/2006 season. Cameras had zoom lenses with maximum focal lengths ranging from 200-400mm.

Photo-ID data

Digital SLR cameras substantially improved the quality of identification photographs and resulted in larger sample sizes starting in 2003/2004. Previous explorations of the photo-ID data including the earlier years with film photographs (1990/1991 – 2002/2003) resulted in capture-recapture models with problems of convergence and extremely high uncertainty in the estimates for annual abundances in the earliest years (Olson *et al.*, 2018; 2021). Therefore, the time period 2003/2004 – 2018/2019 was selected for the analysis here.

Identification photographs of Antarctic blue whales were available from 6 IWC-SOWER cruises, 3 IWC-SORP voyages, 10 ICR cruises, and 1 SAABWS voyage from a 16-year period, 2003/2004 through 2018/2019. The IWC-sponsored Southern Hemisphere Blue Whale Catalogue (Galletti Vernazzani *et al.*, 2022) facilitated the collaborative use of photographs. Photographs that were collected opportunistically by scientists working on other projects in the Antarctic and from citizen scientists aboard tourist vessels were also made available to the catalogue. Good quality opportunistic photographs come from six seasons 2009/2010 through 2018/2019.

Photographs from all sources were obtained during the Austral summer.

Antarctic blue whale photographs were examined for unique natural markings and identified as individuals following methods outlined in Gendron and Ugalde de la Cruz (2012) and Sears *et al.* (1990). The methods required the presence of the dorsal fin in the photo. Identification photos were selected for each whale, an identification number assigned, and the photos compiled into a photo-ID catalogue. (Identifications from the ICR and SAABWS photo collections were cross-referenced.) Identification photographs were compared within and between years. The Antarctic Blue Whale Photo-identification Catalogue is maintained at the Southwest Fisheries Science Center in the USA (Olson, 2010).

Identification photos (the best right side and best left side for each individual whale) were coded for quality using a four-tier system representing photo quality ranging from excellent (code 1) to poor (code 4) (Olson *et al.*, 2021). Photo quality was based on three features: angle to the subject, exposure and focus. Photos with the top three codes were used in capture-recapture analysis (and weighted equally).

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⁴ South African Antarctic Blue Whale Survey

Capture-recapture analysis

Given the uncertainty of population identity of blue whales north of 60°S, only photographs obtained south of 60°S were used in the analysis. All Antarctic blue whales were treated as a single population assumed to mix freely throughout the Southern Ocean south of 60°S. Individual Antarctic blue whales have been documented to move at least 6,550km within the Southern Ocean between inter-annual re-sightings (Olson *et al.*, 2016).

Each research season (year) was considered a sampling occasion. The database is an array of ones and zeros indicating the number of individuals identified (rows) by the number of sampling occasions (columns). Thus, each row represents an identified individual with a "1" in the occasion(s) it was sighted and a "0" during sampling occasions when that individual was not sighted. Within-year re-sightings were ignored.

Capture-recapture modeling was conducted using the R package 'RMark' version 3.0.0 (Laake and Rexstad, 2011) as an interface to the program 'Mark' version 10.0 (Cooch and White, 2011). Two open-population implementations of the Jolly-Seber model, POPAN and PradLambda, were applied to the capture-recapture data for each side. These models allow births, deaths, immigration and emigration during the time period of the study. POPAN can estimate four population parameters: apparent survival (**Phi**) (this can include emigration); the probability of capture (**p**) given that an individual is present; the probability of entry (**pent**), which can be a combination of recruitment and immigration; and the superpopulation (**N**), the total number of individuals estimated to be present during the period of sampling. In the POPAN model the first year value of pent is derived as 1-sum (estimated pents from all subsequent years), with a MLogit link function insuring that the sum of the pent values for all years equals one. Derived estimates of the annual numbers of individual whales can be calculated once these four estimated parameters are obtained from POPAN. We estimated the population growth rate from 2003/2004 to 2018/2019 from the first and last of these annual abundances as:

$$(N_t/N_0)^{1/n_t} - 1$$

where

N_t is abundance in 2018/2019, the final year,

N_0 is abundance in 2003/2004, the first year,

n_t is the number of years (15) when $N_0 = 2003/2004$.

PradLambda is a variant of the Pradel capture-recapture model that estimates three parameters: **Phi**, **p** and **Lambda** (λ). Phi and p represent survival and probability of capture as described above. Lambda is the realized population growth rate. Unlike the POPAN model, the Pradel model estimates growth rate as a proportion without estimating abundance.

Initial trials supplying the blue whale capture-recapture data to POPAN and PradLambda models indicated that not all parameters were simultaneously identifiable. A series of models representing the right and left side photos was therefore supplied with pre-specified survival rates, Phi, from 0.75 to 1. The p, pent, N and λ parameters were then estimated from the POPAN and PradLambda models for the right and left side survival series, and the best of the two models for each side and Phi value were chosen using the ΔAIC_c score. The best four models for each of these configurations (left POPAN, right POPAN, left PradLambda, right PradLambda) were identified based on these comparisons.

The mean of the four survival rates from the best model-data configurations was calculated. The estimates of models using this mean Phi were compared to the estimates from the models with the best Phi value for the individual model and data configurations. The growth rate calculated from the POPAN abundances was compared to the Pradel estimate of Lambda.

The right and left side sample sizes in the capture-recapture POPAN estimates were similar (right side = 225 whales, left side = 214 whales). For comparison with the Branch projections for 2003/2004 – 2018/2019, annual mean abundances (\hat{N}) and variances ($Var(\hat{N})$) were calculated for the combined left and right sides using inverse-variance weightings as $\hat{N} = \frac{\sum_i N_i / \sigma_i^2}{\sum_i 1 / \sigma_i^2}$ and $Var(\hat{N}) = \frac{1}{\sum_i 1 / \sigma_i^2}$, where side is indexed by i .

The CV for the combined sides was:

$$CV = e^{\left(1.96 \sqrt{\ln\left(1 + \left(\frac{SE(N_t)}{N_t}\right)^2\right)}\right)}$$

where

N_t = the annual abundance estimates for the combined sides,

$SE(N_t)$ = the standard errors of annual abundances for the combined sides.

The combined lower and upper confidence intervals were calculated as:

$$95\% \text{ CI} = (N_t / CV, N_t CV).$$

where

N_t = the mean of the right and left side abundance estimates,

CV = the combined CV.

RESULTS

Photo-ID

For the time period 2003/2004 – 2018/2019, 225 right side and 214 left side individual blue whale photos met the criteria for the top three quality codes (Table 1), with 12 recaptures for the right side and 10 recaptures for the left side (Table 2). Whales were photo-identified in all six IWC Management Areas.

Table 1. Numbers by year of left and right side Antarctic blue whale identification photographs, 2003/2004 – 2018/2019, quality codes 1-3, used in the capture-recapture analyses. (Photographs of recaptured whales appear more than once.) Opportunistic = photos contributed from collegial and citizen scientists.

Season	No. left side photos	No. right side photos	Source
2003/2004	5	9	IWC
2004/2005	12	7	IWC, ICR
2005/2006	31	29	IWC, ICR
2006/2007	58	65	IWC, ICR
2007/2008	7	3	IWC, ICR
2008/2009	9	8	IWC, ICR
2009/2010	4	7	ICR, opportunistic
2012/2013	32	33	IWC-SORP, ICR
2013/2014	6	4	SAABWS, opportunistic
2014/2015	24	29	IWC-SORP, ICR, opportunistic
2015/2016	15	13	ICR, opportunistic
2016/2017	4	3	ICR
2017/2018	1	4	opportunistic
2018/2019	16	21	IWC-SORP, opportunistic

Table 2. Recaptured Antarctic blue whales, 2004/2005 – 2018/2019.

Whale ID	Side	Capture season	Recapture season	Interval (years)
0622	left	2006	2007	1
0623	left	2006	2007	1
0761	left	2005	2007	2
0607	left	2006	2008	2
0738	left	2007	2010	3
0802	left	2008	2013	5
0758	left	2007	2013	6
1306	left	2013	2019	6
1313	left	2006	2013	7
1322	left	2006	2013	7
0623	right	2005	2006	1
0623	right	2006	2007	1
0622	right	2006	2007	1
0761	right	2005	2007	2
1343	right	2013	2015	2
0104	right	2001	2004	3
1005	right	2010	2013	3
0802	right	2008	2013	5
0758	right	2007	2013	6
1313	right	2006	2013	7
1322	right	2006	2013	7
J062	right	2003	2015	12

Capture-recapture

Most of the four model series' of configurations with pre-specified survival values from 0.75 to 1 were within 2 ΔAIC_c of one another, indicating the wide range of plausible survival values consistent with these capture-recapture data (**Figure 1, Supplementary Tables 1 to 4**). The best-fitting (lowest ΔAIC_c) of the four model combinations of left side data, right side data, POPAN, and PradLambda were at four different survival values: 0.94, 0.87, 0.97 and 0.9 (left side POPAN, right side POPAN, left side PradLambda, and right side PradLambda, respectively). The mean of these four values of survival was 0.92 (95% CI = 0.83, 1). The corresponding best superpopulation estimates from POPAN for the left and right sides were 3,488 (95% CI = 1754, 7178) and 3,659 (95% CI = 1906, 7241) whales, respectively.

The realized population growth rates from the best PradLambda models were 1.13 (95% CI = 0.98, 1.31) from the left side (best Phi = 0.97) and 1.14 (95% CI = 0.98, 1.131) for the right side (best Phi = 0.9) (**Figure 2**). After adding 1 to compound growth rates to make them comparable with Lambda rates, the POPAN derived mark-recapture growth rates were 1.10 (left) and 1.13 (right). The comparable growth rate from Branch (2007) was $1.0 + 0.082 = 1.082$ (95% CI = 1.016, 1.148). Thus the POPAN and Pradel growth rates were near the upper limit of the Branch (2007) confidence interval for population growth rate.

Derived values of the annual abundances from the POPAN models with different best-fitting Phi values for each side (0.94 left, 0.87 right) (**Figure 3A, Supplementary Tables 5, 6**) and the mean Phi value of 0.92 (**Figure 3B, Supplementary Tables 7, 8**) produced similar patterns of increasing abundance from 2004 to 2019 from the two data sets.

The best POPAN models for both the right and left sides estimated a time-constant probability of entry (pent) of 0.06 for each of the years 2004/2005 – 2018/2019. The pent value for year 2003/2004 was derived as $1 - \text{sum}(15 \times 0.06) = 0.1$, making the sum of the 16 years of pent estimates equal to 1.

The 1998 abundance estimates from Branch (2004) projected forward to 2003/2004 – 2018/2019 were higher than the capture-recapture estimates for the same period (**Figure 4**). The Branch projection for the mean population size in 2018/2019 was 9,608 whales (CI = 1257, 26,060). The left and right side combined capture-recapture abundance in 2018/2019 was 2,050 whales (CI = 1135, 3704) when survival was 0.92 (**Figure 4A**). When survival was increased to 0.99 the combined capture-recapture estimates increased to 3,683 whales, with overlapping confidence intervals during the last half of the projection period (**Figure 4B**, **Supplementary Tables 11, 12**).

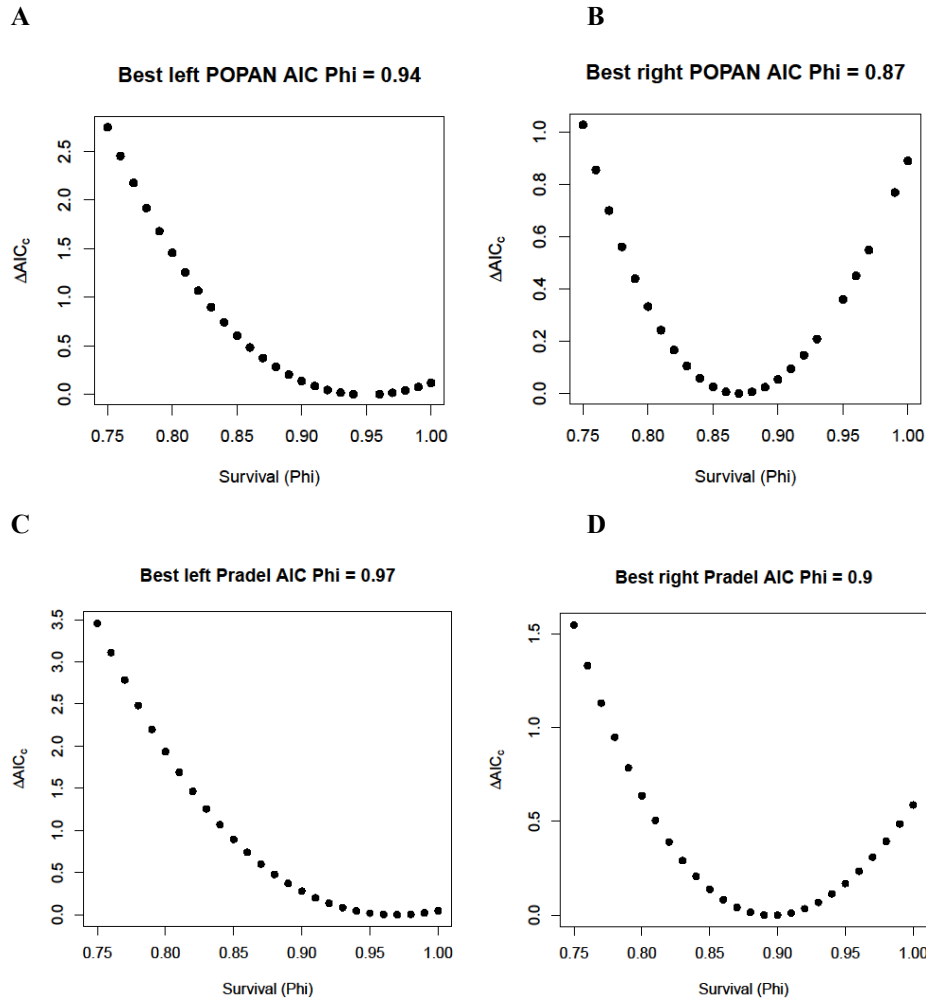


Figure 1. ΔAIC_c scores of capture-recapture configurations with pre-specified Phi (survival) values for: **A** left side POPAN; **B** right side POPAN; **C** left side Pradel and **D** right side Pradel models. Missing sections in the POPAN plots represent model non-convergence or ΔAIC_c scores greater than 3.5 at those Phi values.

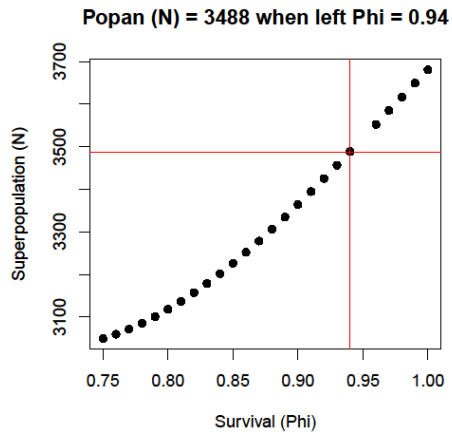
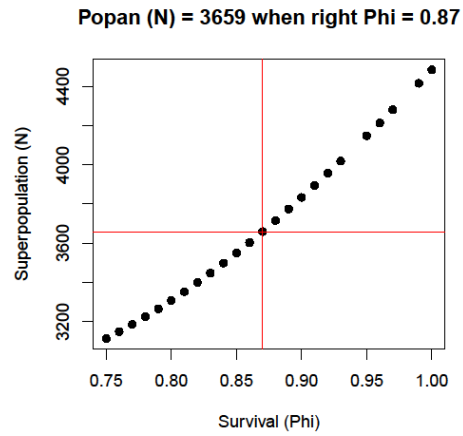
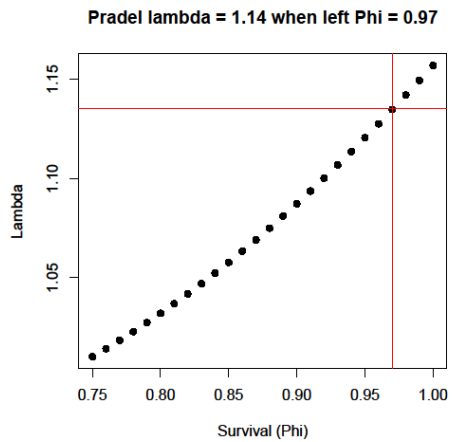
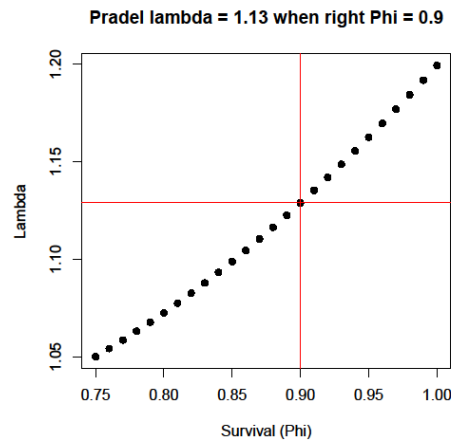
A**B****C****D**

Figure 2. Capture-recapture estimates using pre-specified survivals (Phi) for: **A** the superpopulation (N) from left side POPAN; **B** the superpopulation (N) from right side POPAN; **C** the finite population growth rate Lambda (λ) from left side Pradel; **D** the finite growth rate from right side Pradel models. Red lines indicate the best ΔAIC_c -selected models.

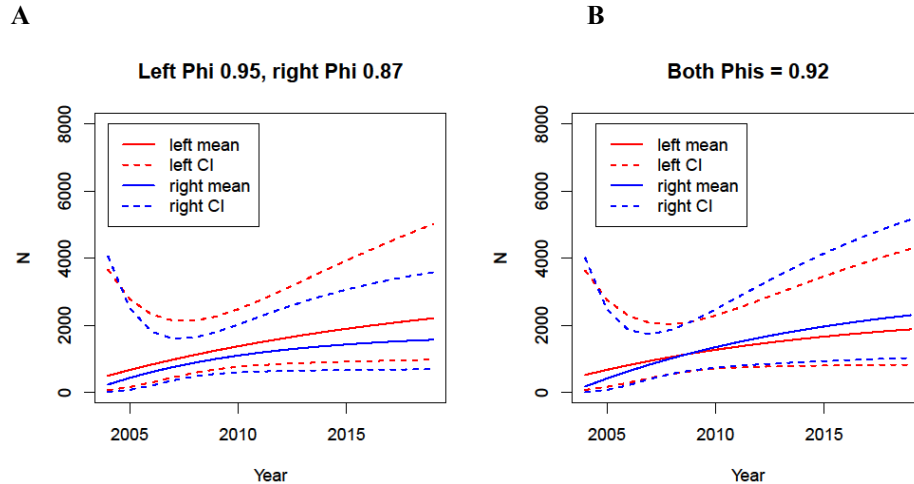


Figure 3. Means and confidence intervals of left side (red) and right side (blue) estimates of annual abundance of Antarctic blue whales derived from POPAN models using (A) the best ΔAIC_c -selected left and right side specific Phi values of 0.95 and 0.87, respectively, and (B) mean Phi values of 0.92 for both left and right sides.

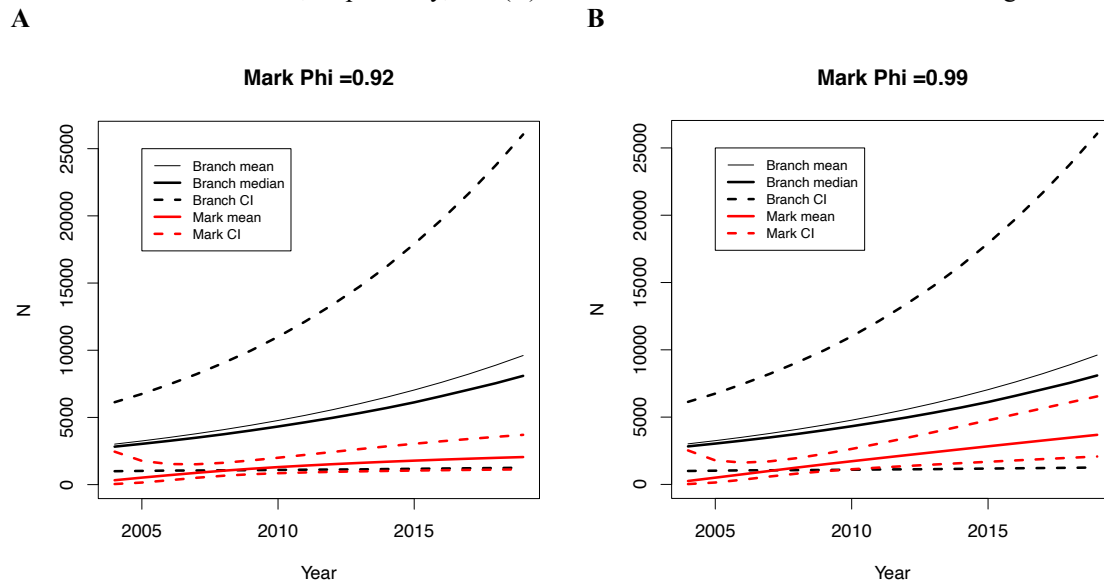


Figure 4. Means and confidence intervals of annual abundance estimates for Antarctic blue whales for 2003/2004 – 2018/2019 projected from Branch (2004) estimates (black) and from the combined left and right side mark-recapture models with (A) apparent survival = 0.92 and (B) apparent survival = 0.99.

DISCUSSION

Capture-recapture estimates using photo-ID data of population scale and trends provide an alternative, lower estimate of the population size of Antarctic blue whales for 2003/2004 – 2018/2019 to projections from the Branch (2004) estimates for 1997/1998. Without additional line-transect and photo-ID surveys these differences may be difficult to resolve. One option for current management could be to combine the 1997/1998 projections from Branch (2007) with the 2003/2004 – 2018/2019 mark-recapture estimates analogously as was implemented in this study for the right and left side photo-ID estimates. Use of prior distributions in a Bayesian approach using these capture-recapture data is another option.

Although the population growth rates of 13-14% estimated by the best Pradel models and 10-13% derived from the best POPAN models were greater than the 8.2% estimated by Branch (2007), examination of the POPAN annual abundances (Figures 3, 4; Supplementary Tables 5-8) show even higher growth rates at the start of the time series,

with decreasing growth in the latter portion of the series. POPAN-derived growth rates from 2003/2004 to 2004/2005 exceeded 50% in some cases, a biologically implausible rate.

The life span of blue whales is 80-90 years (Sears and Perrin, 2018). Beyond their potential use in estimating the current abundance of the population, some of the individual Antarctic blue whales identified in this study will continue to be recognizable in future decades. The Antarctic blue whale photo-id database will enable these individuals to be re-identified in future studies of population abundance, movement and behavior.

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Supplementary Table 1. Left side POPAN model estimates of the superpopulation (N) from configurations supplied with pre-specified survival rates (Phi) from 0.75 to 1 and the associated AIC_c and Δ AIC_c scores.

Phi	N	AICc	deltaAICc
0.75	3049	201.1203	2.74437
0.76	3059	200.8249	2.44892
0.77	3071	200.5486	2.17259
0.78	3085	200.2909	1.91498
0.79	3101	200.0517	1.67573
0.8	3118	199.8304	1.45443
0.81	3136	199.6267	1.25069
0.82	3157	199.4401	1.0641
0.83	3179	199.2702	0.89423
0.84	3202	199.1166	0.74066
0.85	3226	198.9789	0.60295
0.86	3252	198.8566	0.48065
0.87	3278	198.7493	0.3733
0.88	3306	198.6564	0.28042
0.89	3335	198.5775	0.20155
0.9	3364	198.5122	0.13619
0.91	3394	198.4598	0.08385
0.92	3425	198.42	0.04404
0.93	3456	198.3922	0.01626
0.94	3488	198.376	0
0.95	2586	202.7361	4.36015
0.96	3552	198.376	7.00E-05
0.97	3585	198.3914	0.01541
0.98	3617	198.4163	0.0403
0.99	3650	198.4502	0.07425
1	3680	198.4928	0.11681

Supplementary Table 2. Right side POPAN model estimates of the superpopulation (N) from configurations supplied with pre-specified survival rates (Phi) from 0.75 to 1 and the associated AIC_c and Δ AIC_c scores.

Phi	N	AICc	deltaAICc
0.75	3115	190.0697	1.02816
0.76	3150	189.8972	0.85568
0.77	3186	189.7419	0.70031
0.78	3225	189.6032	0.56166
0.79	3266	189.4809	0.43936
0.8	3309	189.3745	0.333
0.81	3354	189.2837	0.24217
0.82	3401	189.208	0.16647

0.83	3449	189.147	0.10548
0.84	3499	189.1003	0.05877
0.85	3550	189.0675	0.02592
0.86	3604	189.048	0.00647
0.87	3659	189.0415	0
0.88	3716	189.0476	0.00605
0.89	3775	189.0657	0.02418
0.9	3834	189.0955	0.05392
0.91	3895	189.1364	0.09482
0.92	3957	189.188	0.14642
0.93	4018	189.2498	0.20827
0.94	2994	196.3848	7.34321
0.95	4148	189.4024	0.36088
0.96	4213	189.4923	0.45076
0.97	4280	189.5906	0.54909
0.98	2511	195.2474	6.20584
0.99	4415	189.8109	0.7694
1	4483	189.9321	0.89054

Supplementary Table 3. Left side Pradel model estimates of population growth rate (λ) from configurations supplied with pre-specified survival rates (Φ) from 0.75 to 1 and the associated AIC_c and Δ AIC_c scores.

Phi	lambda	AICc	deltaAICc
0.75	1.01	1106.373	3.5022
0.76	1.014	1106.025	3.1543
0.77	1.019	1105.698	2.8272
0.78	1.023	1105.392	2.5207
0.79	1.027	1105.105	2.2342
0.8	1.032	1104.838	1.9675
0.81	1.037	1104.591	1.7202
0.82	1.042	1104.363	1.4918
0.83	1.047	1104.153	1.2819
0.84	1.052	1103.961	1.09
0.85	1.058	1103.787	0.9157
0.86	1.063	1103.629	0.7585
0.87	1.069	1103.489	0.6177
0.88	1.075	1103.364	0.493
0.89	1.081	1103.255	0.3838
0.9	1.087	1103.16	0.2895
0.91	1.094	1103.08	0.2095
0.92	1.1	1103.014	0.1433
0.93	1.107	1102.961	0.0904
0.94	1.114	1102.921	0.0501

0.95	1.12	1102.893	0.022
0.96	1.128	1102.876	0.0055
0.97	1.135	1102.871	0
0.98	1.142	1102.876	0.005
0.99	1.149	1102.891	0.02
1	1.157	1102.915	0.0445

Supplementary Table 4. Right side Pradel model estimates of population growth rate (λ) from configurations supplied with pre-specified survival rates (Φ) from 0.75 to 1 and the associated AIC_c and ΔAIC_c scores.

Phi	lambda	AICc	deltaAICc
0.75	1.05	1136.956	1.5458
0.76	1.054	1136.74	1.3293
0.77	1.059	1136.541	1.1304
0.78	1.063	1136.359	0.9489
0.79	1.068	1136.195	0.7844
0.8	1.073	1136.047	0.6367
0.81	1.078	1135.916	0.5054
0.82	1.083	1135.8	0.3902
0.83	1.088	1135.701	0.2907
0.84	1.093	1135.617	0.2066
0.85	1.099	1135.548	0.1373
0.86	1.105	1135.493	0.0826
0.87	1.11	1135.452	0.0419
0.88	1.116	1135.425	0.0149
0.89	1.123	1135.411	0.0011
0.9	1.129	1135.41	0
0.91	1.135	1135.421	0.0112
0.92	1.142	1135.444	0.0342
0.93	1.149	1135.479	0.0685
0.94	1.156	1135.524	0.1137
0.95	1.163	1135.58	0.1693
0.96	1.17	1135.645	0.2348
0.97	1.177	1135.72	0.3098
0.98	1.184	1135.804	0.3939
0.99	1.192	1135.897	0.4866
1	1.199	1135.998	0.5874

Supplementary Table 5. Derived estimates of annual abundance from the best-fitting ($\Phi = 0.94, \Delta AIC_c = 0$) POPAN model for the left-side data.

yr	estimate	se	lcl	ucl
2004	496	670	67	3653
2005	665	558	159	2780

2006	825	468	293	2323
2007	975	407	445	2138
2008	1116	380	583	2135
2009	1249	387	689	2261
2010	1373	422	762	2474
2011	1490	474	811	2738
2012	1600	535	846	3027
2013	1704	599	873	3327
2014	1801	665	894	3628
2015	1893	729	913	3924
2016	1979	792	930	4212
2017	2059	852	945	4489
2018	2135	910	959	4756
2019	2207	965	972	5010

Supplementary Table 6. Derived estimates of annual abundance from the best-fitting (lowest AIC_c) POPAN model for the right-side data ($\Phi = 0.87$, $\Delta AIC_c = 0$).

yr	estimate	se	lcl	ucl
2004	233	633	13	4059
2005	431	481	74	2512
2006	604	368	201	1815
2007	754	300	355	1599
2008	884	283	479	1632
2009	998	306	554	1797
2010	1096	350	595	2019
2011	1182	400	620	2255
2012	1257	450	636	2483
2013	1322	497	648	2695
2014	1378	539	658	2888
2015	1428	577	666	3061
2016	1470	611	673	3214
2017	1508	641	679	3350
2018	1540	667	684	3470
2019	1568	690	688	3576

Supplementary Table 7. Derived estimates of annual abundance from the POPAN model for the left-side data when $\Phi = 0.92$ ($\Delta AIC_c = 0.044$).

yr	estimate	se	lcl	ucl
2004	519	672	74	3632
2005	671	554	164	2755
2006	811	459	289	2279
2007	940	393	428	2066
2008	1059	361	552	2030

2009	1168	363	644	2117
2010	1268	390	703	2286
2011	1360	433	740	2501
2012	1445	484	763	2738
2013	1523	538	778	2981
2014	1595	591	790	3222
2015	1661	643	799	3456
2016	1722	693	806	3679
2017	1778	739	813	3890
2018	1830	783	819	4089
2019	1877	824	824	4275

Supplementary Table 8. Derived estimates of annual abundance from the POPAN model for the right-side data when $\Phi = 0.92$ ($\Delta AIC_c = 0.146$).

yr	estimate	se	lcl	ucl
2004	173	601	7	4005
2005	412	471	69	2473
2006	631	374	215	1850
2007	833	323	400	1733
2008	1018	323	555	1869
2009	1189	365	661	2140
2010	1346	428	733	2472
2011	1491	499	787	2824
2012	1624	572	831	3174
2013	1746	643	868	3513
2014	1859	711	901	3834
2015	1962	774	931	4136
2016	2058	834	958	4419
2017	2145	889	983	4683
2018	2226	941	1006	4928
2019	2300	989	1026	5155

Supplementary Table 9. Derived estimates of annual abundance from the POPAN model for the left-side data when $\Phi = 0.99$ ($\Delta AIC_c = 0.074$).

yr	estimate	se	lcl	ucl
2004	448	669	54	3739
2005	657	571	151	2859
2006	864	493	305	2445
2007	1068	442	490	2330
2008	1271	429	668	2419
2009	1472	454	815	2658
2010	1671	512	929	3005
2011	1867	591	1019	3423

2012	2062	685	1094	3887
2013	2255	786	1161	4380
2014	2446	893	1223	4892
2015	2635	1002	1282	5415
2016	2822	1113	1339	5946
2017	3007	1225	1395	6481
2018	3191	1337	1450	7019
2019	3372	1449	1505	7557

Supplementary Table 10. Derived estimates of annual abundance from the POPAN model for the right-side data when $\Phi = 0.99$ ($\Delta AIC_c = 0.769$).

yr	estimate	se	lcl	ucl
2004	112	576	3	3969
2005	398	468	64	2474
2006	681	390	240	1935
2007	961	360	472	1956
2008	1238	388	679	2256
2009	1513	462	842	2716
2010	1784	563	976	3264
2011	2053	678	1093	3858
2012	2320	801	1202	4477
2013	2583	927	1306	5110
2014	2844	1055	1407	5750
2015	3103	1184	1506	6393
2016	3359	1314	1603	7036
2017	3612	1443	1699	7677
2018	3862	1571	1794	8316
2019	4111	1699	1888	8952

Supplementary Table 11. Derived estimates of annual abundance from the POPAN model for the combined-side data when $\Phi = 0.92$.

yr	estimate	se	lcl	ucl
2004	327	448	44	2453
2005	521	359	153	1767
2006	703	290	323	1529
2007	876	250	507	1515
2008	1036	241	661	1624
2009	1178	257	772	1799
2010	1303	288	849	2000

2011	1416	327	906	2214
2012	1520	369	950	2431
2013	1615	413	986	2644
2014	1703	454	1018	2848
2015	1784	495	1046	3041
2016	1859	533	1072	3225
2017	1928	568	1095	3395
2018	1992	602	1116	3555
2019	2050	633	1135	3704

Supplementary Table 12. Derived estimates of annual abundance from the POPAN model for the combined-side data when $\Phi = 0.99$.

yr	estimate	se	lcl	ucl
2004	255	437	26	2526
2005	502	362	141	1784
2006	751	306	349	1619
2007	1004	279	588	1714
2008	1253	288	803	1954
2009	1492	324	980	2272
2010	1722	379	1125	2637
2011	1947	446	1251	3032
2012	2171	521	1366	3451
2013	2392	600	1475	3880
2014	2612	682	1580	4320
2015	2830	765	1682	4762
2016	3046	849	1782	5208
2017	3260	934	1880	5653
2018	3473	1018	1978	6097
2019	3683	1102	2074	6540