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Capture-recapture estimates of abundance of Antarctic blue whales

Paula A. Olson¹, Douglas Kinzey², Michael C. Double³, Koji Matsuoka⁴, Ken Findlay⁵

¹Marine Mammal and Turtle Division,

²Antarctic Ecosystem Research Division,

Southwest Fisheries Science Center, NMFS/NOAA, 8901 La Jolla Shores Drive, La Jolla, CA 92037 USA

³Australian Marine Mammal Centre, Australian Antarctic Division, 203 Channel Highway, Kingston, Tasmania 7001 Australia

⁴Institute of Cetacean Research, Toyomi-cho 4-5, Chuo-ku Tokyo 104-0055, Japan

⁵Mammal Research Institute Whale Unit, University of Pretoria. [c/o Iziko SA Museum, PO Box 61, Cape Town 8000, South Africa]

Paula.Olson@noaa.gov

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 super-population abundance, from which derived estimates of annual abundances were obtained, for the circumpolar Antarctic. Photographs were collected during IWC, IWC-SORP, ICR, and SAABWS cruises and also made available by opportunistic contributors. Separate capture-recapture estimates were made using photos taken of the left and right sides of the whales. Two values of annual survival rates, 0.90 and 0.96, were supplied as model inputs. The estimates for the separate sides were similar but the assigned survival values had a larger impact on the population estimates. The circumpolar superpopulation estimates for the 0.90 survival rate were 3,912 (95% CI 1,891 to 7,930) Antarctic blue whales (left side photographs) and 4,296 (95% CI 2,095 to 9,085) (right side photographs) for the 16 year period of the study. For the 0.96 survival rate these estimates were 4,130 (95% CI 1,935 to 9,122) (left side) and 4,624 (95% CI 2,109 to 10,491) (right side). As more data become available in the future, it should be possible to estimate survival from photo-ID capture-recapture modeling in addition to the other estimated parameters.

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 indepth assessment of this population (IWC, 2017).

The population status of Antarctic blue whales is also a focus of the IWC-SORP³ Antarctic Blue Whale Project, which is aimed at improving the understanding of population structure and working toward an updated circumpolar abundance estimate (Bell, 2019). The use of photo-identification data in a capture-recapture analysis for the production of a contemporary (new) estimate of abundance of Antarctic blue whales is a component of the Antarctic Blue Whale Project (Bell, 2012). The size of the Antarctic Blue Whale Catalogue has been increasing annually, and has added 17% more identification photos since a capture/recapture was conducted in 2018 (Olson *et al.*, 2018). In order to address comments from the Committee in response to that estimate, and with more data, we conducted a capture-

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

³ Southern Ocean Research Partnership

recapture estimate of abundance using the most recent photo-ID data from the circumpolar Antarctic. We used leftside and right-side photographs to calculate separate circumpolar estimates for the number of blue whales present from 2003/2004 to 2018/2019.

METHODS

Field methods

During IDCR/SOWER and ICR⁴ cruises, photo-identification effort was conducted ancillary to the primary cruise objectives, thus the amount of effort varied by year (Matsuoka *et al.*, 2003; Matsoka 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 SAABWS⁵ 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 left and right 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 2004/05, overlapping in use with digital SLR cameras beginning in 2003/04. Digital SLR cameras were used exclusively starting with the 2005/06 season. Cameras had zoom lenses with maximum focal lengths ranging from 200-400mm.

Photo-ID data

Identification photographs of Antarctic blue whales were available from 17 IWC cruises, 16 ICR cruises, 3 IWC-SORP voyages, and 1 SAABWS voyage over the 29-year period, 1990/1991 through 2018/2019. The IWC-sponsored Southern Hemisphere Blue Whale Catalogue (Galletti Vernazzani *et al.*, 2020) facilitated the collaborative use of photographs. Black and white photographs were digitized for archiving and to facilitate comparison with digital images. 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. These photographs come from eight seasons 2004/2005 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 left side and best right 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). 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).

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.

⁴ Institute of Cetacean Research

⁵ South African Antarctic Blue Whale Survey

The R package RMark version 2.27 (Laake and Rexstad, 2011) was used as an interface to the program Mark version 9.0 (Cooch and White, 2011). The POPAN capture-recapture component of Mark is an open-population implementation of the Jolly-Seber model, allowing births, deaths, immigration and emigration during the time period of the study.

The POPAN model can potentially estimate 4 types of parameters: apparent survival (phi); probability of an encounter given an individual is in the population (p); probability of new individuals entering the population (pent); and the number of all individuals present during the sampling period including births and deaths, the superpopulation (N). The first three of these may be assigned to be either time-varying or constant during the study period. The superpopulation is a single number. The number of individuals estimated to be present each year with upper and lower confidence intervals are derived parameters.

Phi and *pent* could potentially represent permanent emigration out of and immigration into the sampling area during the study period as well as survival and recruitment, respectively. Assuming permanent immigration and emigration in the study area are negligible these parameters would estimate actual survival and recruitment to the population.

We modeled two periods of Antarctic surveys for which blue whale identification photos were available:1990/1991 to 2018/2019 and 2003/2004 to 2018/2019. The quantity and quality of identification photographs increased with the use of digital cameras, notably with the 2003/2004 season, so that was selected as the first year of the second time period. No large-scale surveys were conducted during years 2010/2011, 2011/2012, and 2017/2018, so these three years were assigned p values of 0. Right and left side photos were modeled separately. All combinations of alternative models representing both constant and annually-varying p, *pen*t, and *phi* values were conducted, with the best combination of model parameters for each side selected by AIC. In addition, two models for each side with *phi* values for Antarctic blue whales were assigned from the literature of 0.90 (Galletti Vernazzani *et al.*, 2017) and 0.96 (Branch *et al.*, 2004). Derived estimates of annual abundance are reported as well as the actual parameter estimates from the best models for the two sides.

RESULTS

Photo-ID

For the time period 1990/1991 - 2018/2019, 235 left side and 239 right side individual blue whale photos met the criteria for the top three quality codes (Table 1), with 10 recaptures for the left side and 11 recaptures for the right side (Table 2). For 2003/2004 - 2018/2019, 213 left side and 221 right met the quality criteria with 9 recaptures for the left side and 9 recaptures for the right side. 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, 1990/1991 - 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	No. right	Source
	side	side photos	
1990/1991	0	1	IWC
1991/1992	0	0	IWC
1992/1993	3	3	IWC ICR
1993/1994	0	1	ICR
1994/1995	4	1	IWC
1995/1996	1	0	IWC
1996/1997	4	1	IWC
1997/1998	2	2	IWC
1998/1999	5	2	IWC.
1999/2000	0	2	ICR
2000/2001	0	2	IWC
2001/2002	2	4	IWC. ICR
2002/2003	2	1	IWC, ICR
2003/2004	6	9	IWC. ICR
2004/2005	11	7	IWC, ICR, opportunistic
2005/2006	31	28	IWC, ICR
2006/2007	62	66	IWC, ICR
2007/2008	3	2	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,
	4 -		opportunistic
2015/2016	15	14	ICR, opportunistic
2016/2017	4	4	ICR, opportunistic
2018/2019	16	21	IWC-SORP, opportunistic

Whale ID	Side	Capture season	Recapture season	Interval (years)
0607	left	2006	2008	2
0622	left	2006	2007	1
0623	left	2006	2007	1
0738	left	2007	2010	3
0758	left	2007	2013	6
0761	left	2005	2007	2
0772	left	1995	2007	12
0802	left	2008	2013	5
1306	left	2013	2019	6
1322	left	2006	2013	7
0104	right	2001	2004	3
0622	right	2006	2007	1
J062	right	2003	2015	12
0623	right	2005	2007	2
0758	right	2007	2013	6
0761	right	2005	2007	2
0802	right	2008	2013	5
1005	right	2010	2013	3
1313	right	2006	2013	7
1322	right	2006	2013	7
1343	right	2013	2015	2

Table 2. Recaptured Antarctic blue whales, 1990/1991 – 2018/2019.

Capture-recapture

Capture-recapture models using the data from 1990/1991 to 2018/2019 exhibited problems with convergence and related issues such as extremely high uncertainty in the estimates for annual abundances in the earliest years. The left and right side models using 2003/2004 to 2018/2019 data exhibited better convergence properties when survival was assigned but not always when survival was estimated. High variance in the *phi* (survival) estimates produced high variance in the annual abundance estimates over several orders of magnitude and convergence issues for some parameter combinations. Assigning survival as either 0.90 or 0.96 improved convergence and indicates plausible ranges of annual abundances that are consistent with the model estimates for *p*, *pen*t, and the superpopulation *N* (Figure 1).

For both the left and right side photos, the best model had time-varying capture (p) probabilities and time-invariant probability of entry (pent) (Table 3). The model with assigned survivals of 0.96 had lower (better) AIC_c values than the models with survivals assigned as 0.90 for both the left and right sides (Table 3). However, some of the intermediate survival values had convergence issues so the best value for survival was not able to be determined with these data.

Annual abundances based on the right side photos began and ended higher from 2003/2004 to 2018/2019 for both *phi* values than abundances estimated by the left side photos (Table 4) but were within one another's 95% CIs (Figure 1). Survival rates of 0.96 produced higher growth rates of 0.15 (left side) and 0.13 (right side), compared to growth rates when survival was 0.09 of 0.10 (left) and 0.09 (right) (Table 4).

Model	side	npar	AIC _c
Phi(0.9)p(~time)pent(~1)N(~1)	left	15	178.1
Phi(0.9)p(~time)pent(~time)N(~1)	left	29	207.3
Phi(0.9)p(~1)pent(~time)N(~1)	left	17	312.0
Phi(0.9)p(~1)pent(~1)N(~1)	left	3	323.7
Phi(0.96)p(~time)pent(~1)N(~1)	left	15	171.4
Phi(0.96)p(~time)pent(~time)N(~1)	left	29	190.6
Phi(0.96)p(~1)pent(~time)N(~1)	left	3	332.3
Phi(0.96)p(~1)pent(~1)N(~1)	left	17	333.1
Phi(0.9)p(~time)pent(~1)N(~1)	right	15	167.5
Phi(0.9)p(~time)pent(~time)N(~1)	right	29	190.1
Phi(0.9)p(~1)pent(~time)N(~1)	right	17	316.6
Phi(0.9)p(~1)pent(~1)N(~1)	right	3	331.9
Phi(0.96)p(~time)pent(~1)N(~1)	right	15	167.2
Phi(0.96)p(~time)pent(~time)N(~1)	right	29	190.6
Phi(0.96)p(~1)pent(~time)N(~1)	right	3	332.3
Phi(0.96)p(~1)pent(~1)N(~1)	right	17	333.1

Table 3. Model configurations, number of parameters, and corresponding AIC_c scores for Phi = 0.9 and Phi = 0.96 for the left and right side photos. For *pent* and *p*, (~time) indicates annually-variable estimates of those parameters and for all estimates (~1) indicates a time-constant value was estimated.

Year	left.phi90	right.phi90	left.phi96	right.phi96
200	4 363	536	301	452
200	5 557	733	544	712
200	6 731	910	777	962
200	7 888	1070	1002	1201
200	8 1029	1214	1217	1431
200	9 1156	1343	1423	1652
201	0 1270	1459	1622	1864
201	1 1373	1564	1812	2068
201	2 1466	1658	1995	2263
201	3 1549	1743	2170	2451
201	4 1624	1820	2339	2631
201	5 1692	1888	2501	2804
201	6 1752	1950	2656	2970
201	7 1807	2006	2805	3129
201	8 1856	2056	2948	3282
201	9 1901	2101	3085	3429
Populatio growth rat	n 0.10 e	0.09	0.15	0.13

Table 4. Derived parameters of annual abundances estimated from left and right side photos at phi = 0.90 and 0.96.

The estimates for the super-population are given in Table 5. The original parameter estimates and their CIs from the best four models are reported in the Supplementary Material.

Table 5. Maximum likelihood estimates and 95% CI for the super-population (N) of all blue whales present during the study.

	Ν	phi
Left side	3912 (1891, 7930)	0.90 (fixed)
Left side	4130 (1935, 9122)	0.96 (fixed)
Right side	4296 (2095, 9085)	0.90 (fixed)
Right side	4624 (2109, 10491)	0.96 (fixed)



Figure 1. Derived estimates of Antarctic blue whale annual abundances from 2003/2004 to 2018/2019 assuming (a) a 90% survival rate; (b) a 96% survival rate. In each plot red represents the left side estimates, blue represents the right side estimates, solid lines represent mean abundances and dashed lines represent upper and lower 95% CIs.

DISCUSSION

The estimates for the super-population and annual trends from the left- and right-side circumpolar models from 2003/2004 - 2018/2019 appear plausible. However, there are still a relatively small number of recaptures in the Antarctic blue whale database and that makes these POPAN estimates very sensitive to small differences in the timing and location of each recapture. As more recapture data are collected, parameter uncertainty should be reduced. Additional covariates representing such issues as heterogeneity in effort and possible directed movements among areas could be considered as candidates for modeling.

The super-population estimates of abundance of Antarctic blue whales (Table 5) can be viewed in context with the line-transect estimates of Branch (2007), although they are not directly comparable. The line-transect estimates are for the population during a stationary point in time while the super-population is an estimate of total abundance over a number of years. When a line-transect estimate of abundance is made for a population inside a longer time interval for which super-population abundance is also estimated, the latter should be greater than the line-transect estimate because the super-population estimate does not include mortality during the longer time period over which it is estimated.

Branch (2007) estimated the circumpolar abundance of Antarctic blue whales based on the line-transect data from CPIII (1991/92-2003/04); the same surveys that provided the photo-ID data used in this study. He estimated 2,280 Antarctic blue whales for the CPIII midpoint year 1997/1998 (and the most recent estimate of abundance for Antarctic blue whales). The left side and right side mean super-population estimates of this study, 2003/2004 – 2108/2019, are greater than that of Branch for 1997/1998.

The mean rates of increase for the circumpolar population over the 16-year interval were 0.10 and 0.15 for the left side photographs (with assigned survival rates of 0.90 and 0.96, respectively) and 0.09 and 0.13 for the right side photographs (Table 4). These rates are higher than previously reported Antarctic blue whale growth rates of 0.082 (Branch, 2007) and 0.073 (Branch *et al.*, 2004).

With additional photo-ID data from surveys in the future, we expect the estimability of all parameters, including the survival rate (*phi*), to improve.

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SUPPLEMENTARY MATERIAL

parameter years	estimate	se	lcl	ucl
p0 t2004	0.017	0.031	0.000	0.418
p1 t2005	0.020	0.020	0.003	0.128
p2 t2006	0.042	0.026	0.013	0.133
p3 t2007	0.071	0.030	0.030	0.158
p4 t2008	0.002	0.002	0.000	0.009
p5 t2009	0.008	0.004	0.003	0.019
p6 t2010	0.003	0.002	0.001	0.010
p9 t2013	0.020	0.009	0.009	0.046
p10 t2014	0.004	0.002	0.001	0.011
p11 t2015	0.014	0.007	0.006	0.035
p12 t2016	0.009	0.004	0.003	0.023
p13 t2017	0.002	0.001	0.001	0.008
p15 t2019	0.008	0.004	0.003	0.023
N t2004-t2019	3811.9	1455.4	1891.4	7930.1
pent t2005-t2019	0.060	0.013	0.040	0.091

Supplementary Table 1. Parameter estimates for the left side photos with 90% assigned survival with standard errors and logarithmic lower and upper confidence intervals.

parameter years	estimate	se	lcl	ucl
p0 t2004	0.020	0.044	0.000	0.630
p1 t2005	0.020	0.021	0.003	0.139
p2 t2006	0.040	0.024	0.012	0.124
p3 t2007	0.063	0.026	0.027	0.139
p4 t2008	0.002	0.001	0.000	0.008
p5 t2009	0.006	0.003	0.003	0.016
p6 t2010	0.002	0.001	0.001	0.008
p9 t2013	0.014	0.006	0.006	0.032
p10 t2014	0.003	0.001	0.001	0.008
p11 t2015	0.010	0.004	0.004	0.023
p12 t2016	0.006	0.003	0.002	0.015
p13 t2017	0.001	0.001	0.000	0.005
p15 t2019	0.005	0.003	0.002	0.014
N t2004-t2019	4129.8	17167	1935.1	9121.5
pent t2005-2019	0.062	0.012	0.042	0.089

Supplementary Table 2. Parameter estimates for the left side photos with 96% assigned survival with standard errors and logarithmic lower and upper confidence intervals.

parameter years	estimate	se	lcl	ucl
p0 t2004	0.017	0.029	0.001	0.341
p1 t2005	0.010	0.010	0.001	0.073
p2 t2006	0.031	0.021	0.008	0.111
p3 t2007	0.062	0.030	0.023	0.153
p4 t2008	0.002	0.001	0.000	0.008
p5 t2009	0.006	0.003	0.002	0.016
p6 t2010	0.005	0.002	0.002	0.013
p9 t2013	0.018	0.008	0.008	0.043
p10 t2014	0.002	0.001	0.001	0.008
p11 t2015	0.015	0.007	0.006	0.038
p12 t2016	0.007	0.004	0.003	0.020
p13 t2017	0.001	0.001	0.000	0.005
p15 t2019	0.010	0.005	0.004	0.028
N t2004-t2019	4296.4	1681.3	2094.7	9085.1
pent t2005-2019	0.058	0.015	0.035	0.096

Supplementary Table 3. Parameter estimates for the right side photos with 90% assigned survival with standard errors and logarithmic lower and upper confidence intervals.

parameter years	estimate	se	lcl	ucl
p0 t2004	0.020	0.039	0.000	0.511
p1 t2005	0.010	0.011	0.001	0.080
p2 t2006	0.029	0.020	0.008	0.104
p3 t2007	0.055	0.026	0.021	0.135
p4 t2008	0.001	0.001	0.000	0.007
p5 t2009	0.005	0.002	0.002	0.013
p6 t2010	0.004	0.002	0.001	0.010
p9 t2013	0.013	0.006	0.006	0.030
p10 t2014	0.002	0.001	0.000	0.005
p11 t2015	0.010	0.005	0.004	0.025
p12 t2016	0.005	0.002	0.002	0.013
p13 t2017	0.001	0.001	0.000	0.003
p15 t2019	0.006	0.003	0.002	0.017
N t2004-t2019	4623.9	1994.9	2108.7	10490.5
pent t2005-t2019	0.060	0.014	0.038	0.095

Supplementary Table 4. Parameter estimates for the right side photos with 96% assigned survival with standard errors and logarithmic lower and upper confidence intervals.