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ABSTRACT

Since 1970, blue whales have been regularly seen feeding in the waters off southern Chile during the austral summer and autumn and regularly in this region since the early 2000s. Here we report the results of nine years of photo-identification surveys of this unique population feeding in the waters off Isla de Chiloé, southern Chile and Isla Chañaral, northern Chile. Over this time, 1070 blue whales were encountered yielding, after photo-quality control, 318 and 267 unique photographs of the left and right side of the flank respectively. High annual return rates suggest a degree of site-fidelity of individuals to Isla de Chiloé. Mark recapture analysis of left and right side photographs collected from Isla de Chiloé (2006-2011) using open population models suggest abundance in this region is small. Model-average POPAN super-population abundance estimates for the feeding ground in 2011 are 711 (95% CI = 574-848) and 549 (95% CI 442-656) for left and right side datasets respectively, similar to results from closed population models. Pradel and POPAN trend estimates reveal strong variation in abundance, peaking in 2009 and suggesting fluctuating use of this feeding area over time. Inter-annual fluctuations in abundance are also seen in the dataset when a 2012 survey at Isla Chañaral is included, with larger POPAN super-population abundances estimated overall (N=1353, SE=453 and N=1060, SE=283 for left and right side datasets respectively). This indicates that Isla de Chiloé feeding ground is part of a larger Chilean blue whale population feeding along the coast, with abundance estimates derived from surveys off Isla de Chiloé reflecting local abundance on this feeding ground.

INTRODUCTION

Two subspecies of blue whales currently are accepted in the Southern Hemisphere: the pygmy blue whale (*Balaenoptera musculus brevicauda)* in the Subantarctic zone; and the Antarctic or true blue whale (*B. m. intermedia*) that summers in the Antarctic Zone (Rice, 1998). Branch *et al*. (2007a) has proposed that blue whales off Chile belong to a unique population and are likely an unnamed subspecies.

Since 1970, blue whales are often seen feeding during the austral summer and autumn in southern Chilean waters spanning the northern Los Lagos region, south to the outer coast of Isla Grande de Chiloé (Isla de Chiloé), around Isla Guafo and eastward into the Golfo de Corcovado around the northern islands of the Chonos Archipelago (Figure 1b, Gilmore, 1971; Cummings and Thompson, 1971a, b; Findlay *et al*., 1998; Hucke-Gaete *et al*., 2004; Cabrera *et al*., 2005; Galletti Vernazzani *et al.,* 2012a). Recently, additional sightings have been reported during autumn and early winter in the inlet waters east of Isla de Chiloé near the mainland (Abramson and Gibbons, 2010; Försterra and Häussermann, 2012). In northern Chile, an additional feeding aggregation of blue whales off Isla Chañaral, northern Chile was reported in 2012 (Galletti Vernazzani *et al.,* 2012b).

Based on surveys conducted from the IWC-SOWER 1997/98 blue whale cruise off central Chile (Findlay *et al*., 1998), Branch *et al*. (2007b) used line-transect methods to estimate a population abundance of 452 (CV = 0.56, 95% CI: 160–1300) individuals. However, the survey was designed primarily to maximize blue whale encounters and thus did not have an equal coverage probability design. Williams *et al*. (2011) reanalyzed these data using spatial modeling methods and obtained a new abundance estimate of 303 (95% CI: 176–625) whales. Both estimates represent the number of whales present in the sampled area (Figure 2) but do not represent the abundance of Chilean blue whales nor the abundance of the whole southern Chile feeding ground, since a total of 363 individual blue whales have been photo-identified between 2004-2010 off Isla de Chiloé, southern Chile (Galletti Vernazzani *et al.,* 2012a).

Blue whales are individually identifiable from the unique pattern of mottling on both sides of the body near the dorsal fin (Sears *et al.*, 1990) and in some cases permanent scars can be used to identify or confirm individuals (Galletti Vernazzani *et al.*, 2012a). Centro de Conservacion Cetacea (CCC) has been conducting the Alfaguara (blue whale) Project since 2004. Individual photo-identifications of blue whales have been systematically collected using photographs of body sides and a photographic catalogue compiled (Galletti Vernazzani *et al.,* 2012a). Here we provide abundance estimates of blue whales feeding in the waters off Isla de Chiloé, using mark-recapture models and photo-identification data obtained by the Alfaguara Project off Isla de Chiloé in southern Chile from 2004 to 2012 and off Isla Chañaral in northern Chile during 2012.

METHODS

Study area

Surveys took place from 2004 to 2012. The primary/main survey area was off northwestern Isla de Chiloé, between Chacao Channel (41º45'S) and south of Isla Metalqui (42º 12'S) within 12nm from the coastline, on board the 7m *Alfaguara* research vessel. One marine survey was conducted off northern Los Lagos in 2008 and one around the Corcovado Gulf in 2004 on board a 30m Chilean Navy surveillance vessel (Galletti Vernazzani *et al.*, 2012a). In 2012, Isla Chañaral, located at 29ºS, 73ºW in northern Chile also was surveyed on board a small tourist boat from 24 to 27 February (Galletti Vernazzani *et al.*, 2012b, Figure 1).

Photo-identification

Clear, well-focused photographs of individual blue whales were compared within season to determine the number of individuals sighted and resighting matches. All individual whales then were compared to the master CCC catalogue to determine if they were new or known individuals. The catalogue consists of separate photographic collections for the left and right sides of the head region, dorsal fin, flank and caudal peduncles. Photographs of low quality or whales only partially photographed were not included in the catalogue. Overall consistency in research design, data collection techniques and data analysis allowed for between-year comparisons (Cabrera *et al.*, 2006; Galletti Vernazzani *et al*., 2012a). Photo-quality control was then applied to select the best left and right datasets to use in mark-recapture analyzes.

Since there were very few encounters during 2004-2005 (n=4, n=11 respectively) we pooled the data from these years. As these 2004-2005 data are sparse, and some of the photo-identifications collected in 2012 were from Isla Chañaral to the north, we primarily analysed two 'core' left and right side datasets spanning 2006-2011, and also analysed the full 2004-2012 dataset (including Isla de Chiloé and Isla Chañaral) for comparative purposes.

To determine the goodness of fit of the data to standard Cormack Jolly Seber models, we tested the goodness-of-fit of these data using single-state tests 3.SR, 3.SM, 2.CT and 2.CL in the program U-CARE V2.3.2 (Choquet *et al*., 2005), which tests for transience (individuals with unequal re-sight probabilities) and trap dependence (*i.e.* initial sightings of some whales are followed by lower or higher than expected probability of resights).

Mark-recapture analysis of abundance

Closed and open population models were explored on the basis that closed models can better account for capture heterogeneity within the data, but the long time period of the survey may make open population models (which include a emigration/mortality component) more appropriate for these data. Closed populations models were investigated using CAPTURE software. The fit of alternative models of capture heterogeneity was also investigated and models were discriminated using a model selection algorithm developed by Otis (1978).

For open population abundance estimation we chose the POPAN model implemented in MARK (Schwarz and Arnason, 1996), an extension of the Jolly Seber model which assumes that whales encountered over the survey period are a component of a larger 'super-population' using Chilean coastal waters to feed. The super-population size is interpreted as the total number of animals ever present during the study period and does not represent the number present at any particular point in time.

POPAN models can be used to calculate apparent survival (φ), probability of capture (p_t), probability of entry into the population (β) and the total super-population size (N_P). Since a number of parameters are unidentifiable when using the fully time dependent POPAN model (φ_t p_t β_t) we only explored POPAN models with constant apparent survival and always constrained two capture probabilities to be equal when capture probabilities were not fully identifiable (e.g., $p_1=p_2$ or $p_1=p_8$). To account for time between sampling occasions with the 2004/ 2005 pooled data, the first time interval was set to 1.5 in the open population model. Models were fitted using a logit link function for survival φ and capture probabilities p, a log link for N_p, and the multinomial logit link function to constrain entry probabilities β to sum to ≤ 1 for the POPAN model (Table S3).

In order to estimate trend in abundance from the data, the Pradel model (Pradel, 1996) was applied. This model can be used to estimate realized growth rates from the population (λ) as well as apparent survival (φ) and probability of capture (p_P). As with the POPAN model, all Pradel models were constrained to have constant apparent survival through time (Table S4). Estimates of annual abundance and their associated confidence intervals were derived from the capture probabilities of the best-fitting model under AIC criteria, by dividing the numbers of captures in each season by their associated probabilities. For both POPAN and Pradel models, the best fitting models were determined according to Akaike Information Criterion (AIC) scores of goodness of fit.

RESULTS

During 109 marine surveys totalling 591hr conducted off Isla de Chiloé from February to April 2004-2012, 710 groups of blue whales containing a total of 1070 individuals were encountered. In February 2012, during four marine surveys, totalling 26 hr, conducted off Isla de Chañaral, 17 groups of 22 blue whales were encountered (Table S1).

A total of 406 individual blue whales have been photo-identified from left side and 419 from right side. One hundred-and-one and 95 individuals were sighted in multiple years from left and right side respectively, including 21 left and 19 right sides sighted over three years and 4 individuals sighted in four years. During the 2012 field season, no matches were found between the individuals off Isla de Chañaral (n=14) and those catalogued off Isla de Chiloé. By contrast, four out of eleven individuals photographed off Isla de Chiloé were catalogued whales.

After photo-quality control and dataset selection, 22% of catalogued individuals were discarded from the left side and 36% from the right side. One of the individuals removed was observed in four different years, four in three years, 19 and 15 seen twice for left and right side respectively and 64 and 132 seen only once for left and right side respectively. A total of 318 sighting histories from left side and 267 from right side were used to perform the analyses.

Abundance estimates

Goodness of fit tests revealed a significant transience signal in the left side dataset ($p<0.05$) both with a two-sided test, one-sided test, and with standardized log-odds ratios. This was not significant for the right side dataset. Annual transience estimates reveal that the significant signal comes from 2009, with significantly less 2009 whales photo-identified in the following years than expected for both left and right side datasets. This result is also mirrored in the 2004-2012 dataset. A significant result was also found for test 2.CL for the right side dataset in 2008, violating the null hypothesis that whales sighted in 2009 had similar probabilities of being sighted and not sighted in 2007.

Model selection of closed models in CAPTURE supported time-varying models for both left and right side photographs, with the time and heterogeneity models most strongly supported both left and right datasets (Table S2). The Mth Chao model yielded an overall abundance estimate of 742 (595-961) and 540 (439-696) for left and right side datasets respectively over 2006-2011. Closed population estimates from the 2004-2012 datasets contrasted more strongly, with the left side dataset yielding very similar estimates over the two timeframes (2006-2011 and 2004-2012) but the right side dataset providing a lower estimate of 425 (368-506) for the 2004-2012 time-frame. If whales have seasonal feeding ground fidelity to different geographic areas along the Chilean coast, inclusion of whales from Isla Chañaral in 2012 violates assumptions of population closure.

Closed population models assume no births and deaths over the survey period but may be biased in this case due to the long period of survey (nine years). Animals recruiting to the population each year are all unmarked, so the proportion of marked animals in the population decreases over time, leading to fewer recaptures than expected under closed model assumption and overestimation of abundance. Closed models also assume no immigration or emigration over time, assumptions which are violated for this population if whales vary in their use of the feeding ground between years. The 2006-2011 POPAN and Pradel models compared for analysis are shown in Tables 2 and 3, sorted by AIC scores. Only models with constant survival and fully identifiable capture probabilities were compared.

The best fitting POPAN models were $\varphi_{(.)}p_{(1=2=5,t)}\mathrm{PENT}_{(t)}N_{(.)}$ and $\varphi_{(.)}p_{(1=2=5,t)}\mathrm{PENT}_{(2=4=5,t)}N_{(.)}$ respectively for left and right side photographs, though alternate models provided very similar fit (Table S3). Estimates of apparent survival and super-population abundance were congruent between the two datasets. Model averaged super-population abundance estimates were N= 711 (SD=70, $\mathrm{CI}_{95\%}$=[573; 849]) for left side and N = 549 (SD=55, $\mathrm{CI}_{95\%}$=[441; 657]) for right side photographs respectively (Table 2), while apparent survival was estimated at $\varphi = 0.85$ (SE 0.06) and $\varphi = 0.86$ (SE 0.06) for left and right side photographs respectively. The best fitting POPAN models for the 2004-2012 dataset were $\varphi_{(.)}p_{(1=2,t)}\mathrm{PENT}_{(t)}N_{(.)}$ and $\varphi_{(.)}p_{(1=8,t)}\mathrm{PENT}_{(1=2,t)}N_{(.)}$ respectively for the left and right side photographs, though alternate models provided very similar fit, with AIC scores <2 between the top two models. Model averaged estimates of super-population abundance were double those estimated to 2011, with N=1354 individuals (SD=463, $\mathrm{CI}_{95\%}$=[446; 2262]) for left side and N=1060 individuals (SD= 283, $\mathrm{CI}_{95\%}$=[505; 1615]) for right side photographs. The model averaged estimate of apparent survival was also higher, and nearly identical for left and right side photographs, with $\varphi = 0.91$ (SE 0.06).

All Pradel models with constant apparent growth (λ) were more poorly fitting to the data than models with variable growth (AIC differences were >8 in all cases). This was consistent over all datasets. For the 2006-2011 dataset, the best fitting Pradel models were identical for both left and right sides ($\varphi_{(.)}p_{(1=2=5=6,t)}\lambda_{(2=4=5)}$) suggesting that the features of this model were due to factors affecting left and right side sampling similarly. Apparent survival estimates were similar to those derived from the POPAN model, with $\varphi = 0.87$ (SE 0.06) and $\varphi = 0.89$ (SE 0.06) for left and right sides respectively. Estimates of capture probability and annual λ were also consistent across left and right side datasets (Table 3). When λ was constrained to be constant, estimated apparent growth was λ= 1.07 $\mathrm{CI}_{95\%}$=[0.91-1.25] and λ= 1.03 $\mathrm{CI}_{95\%}$=[0.88-1.21] respectively. This suggests there may be slow growth over the study period, but the wide confidence intervals on both estimates do not exclude the possibility of a constant-size population.

This was not the case for the 2004-2012 dataset, where the best fitting Pradel models were ($\varphi_{(.)}p_{(1=8,t)}\lambda_{(1=2=3=5=6,4=7)}$ and $\varphi_{(.)}p_{(1=3=6=7,t)}\lambda_{(1=4=8,t)}$ for left and right sides respectively. Estimates of apparent survival for these models were very similar at $\varphi = 0.92$ (SE 0.05) and 0.93 (SE 0.06) for left and right sides respectively.

Annual abundance estimates derived from the best fitting POPAN and Pradel models are shown in Figure 3. All models show a peak in feeding ground abundance in 2009 and a decline thereafter. Both left and right side models estimated a slight population decline from 2007-2008, 2009-2010 and 2010-2011 but with an enormous apparent population increase of >200% in 2009, suggesting an influx of whales into this feeding ground during the 2009 season. This pattern was also observed when the 2004-2012 dataset was analysed (data not shown). Strong apparent growth in 2012 is due to the inclusion of whales from Isla Chañaral in the 2012 dataset. Estimated population sizes between 2004-2006 are inconsistent among models, probably because data from 2004-2005 are sparse. In 2004/2005 the Pradel left and right side models produced very different initial abundance estimates (N=798 and 79 respectively). The opposite was true for POPAN estimates of abundance in 2004/2005, which were more congruent with each other (N=136 and 419 respectively). This inconsistency is likely to be the result of the small sample sizes collected in these two years, violating the assumptions inherent in both models regarding constant sample collection conditions in each year.

Overall both photo-ID datasets suggest that while blue whales show good fidelity to this feeding ground, (with resight rates over 10% in all years but 2009, Table 1), use of this feeding ground fluctuates between years, and overall abundance is low. There is no evidence for an increase in the size of the population using this feeding ground. It is likely that factors related to annual habitat quality influence the observed abundances.

DISCUSSION

Blue whales feeding in the waters off Isla de Chiloé are estimated to number 550-750 whales, with no discernable population growth over the period 2004-2012, but evidence for inter-annual fluctuation in use of the area. This type of inter-annual shift in distribution to find the highest density of prey is well known in other baleen whale populations. Although we are aware of continuous summer sightings of blue whales along the southern Chilean coast, high re-sight rates in Isla de Chiloé (modal capture probabilities of 14-16% annually) and the low numbers of matches made between this region and Isla Chañaral suggest that our population estimates from 2004-2011 are representative of the Isla de Chiloé local feeding ground rather than the entire Chilean coast. Previous IDCR/SOWER surveys along the central Chilean coast estimate similar numbers of blue whales using the broader continental shelf (Branch *et al*. 2007b; Williams et al. 2011). Our abundance estimates when including Isla Chañaral were much higher (>1000 whales) and likely more representative of the broader population feeding in the waters off southern Chile. Further dedicated sightings surveys along the coast will be required to investigate overall Chilean population abundance. Genetic and satellite telemetry studies will also be very useful to understand whether local feeding grounds are genetically distinct (possibly reflecting shared migratory routes from breeding grounds) and to identify the blue whale breeding and calving areas associated with this unique feeding ground.

These abundance estimates indicate that Chilean blue whales occur at low population levels in the environment of Isla de Chiloé. Furthermore, the southern Chile feeding ground is a critical habitat for this population, with strong site fidelity highlighting the importance of protecting the species and its critical habitats in Chilean waters.

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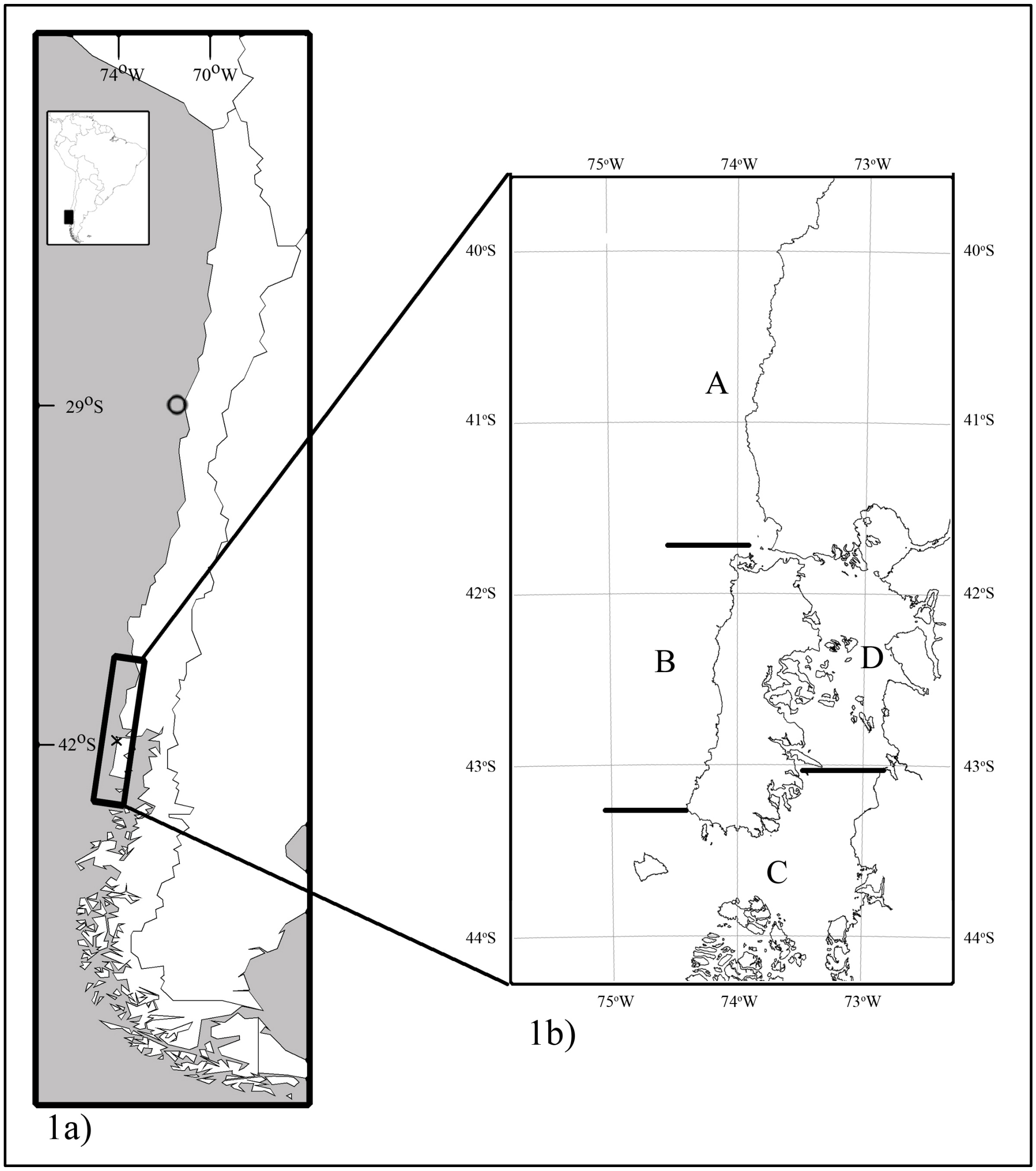

Figure 1 – a) Blue whale study areas in northern and southern Chile. Circle: waters around Isla Chañaral, northern Chile; Rectangle: southern Chile feeding area in the region of Isla Grande de Chiloé; b) Detail of southern Chile feeding area. A: off northern Los Lagos, B: off west Isla Grande de Chiloé, C: Golfo Corcovado, D: inlet waters east of Isla Grande de Chiloé.

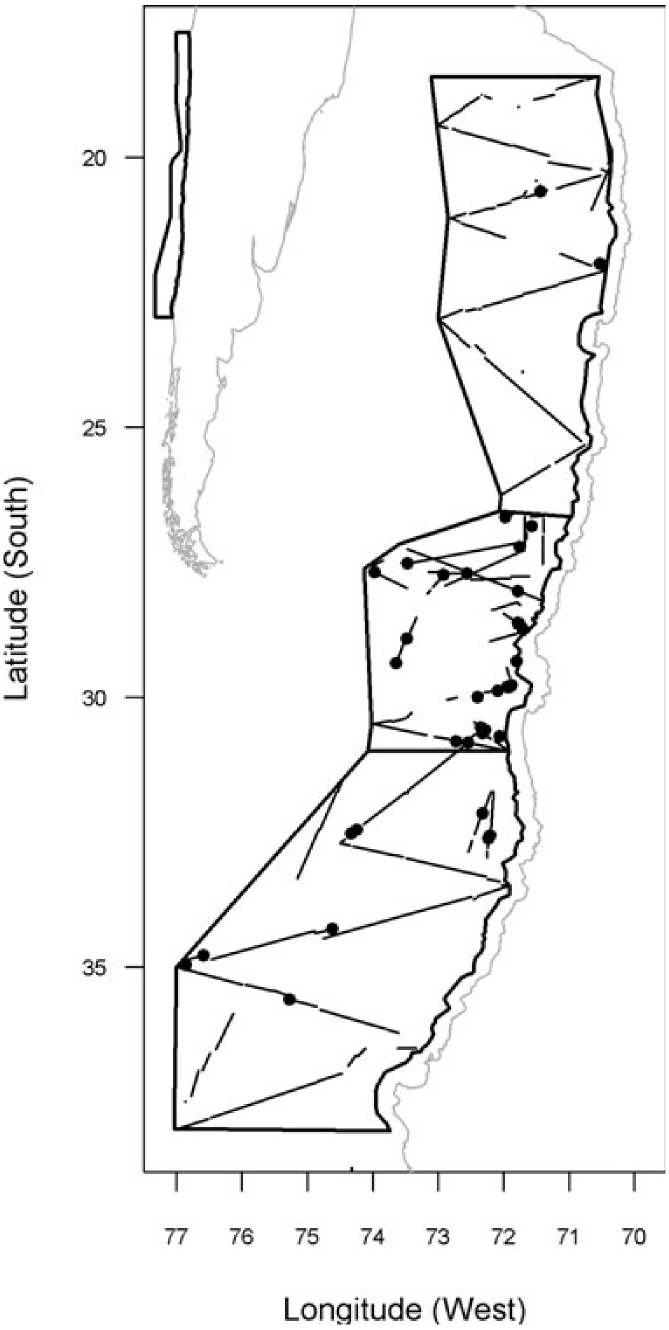

Figure 2 – Sightings of blue whales (filled circles) and survey track lines (lines within the polygon) made by IWC-SOWER vessels surveying in Chilean waters (inset shows South America south of 15°S) for blue whales from December 1997 through January 1998. Polygon outline marks the boundary of the survey region (Williams *et al*. 2011).

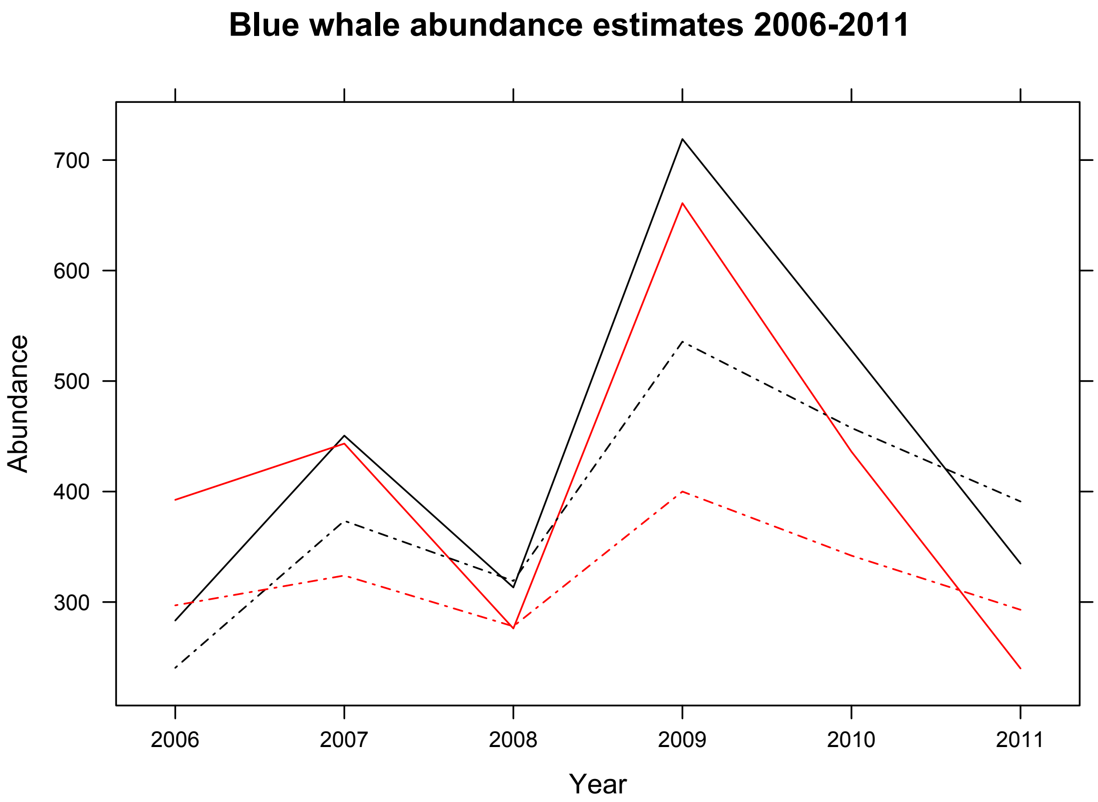

Figure 3. Estimates of abundance from 2006-2011 derived from best fitting POPAN (dashed lines) and Pradel (solid lines) models. Left side estimates are shown in black, right side estimates in red.

Table 1. Summary of photo-identified blue whales identified by photographs, shown by year of capture and recapture

	Year								
Left side	**2004**	**2005**	**2006**	**2007**	**2008**	**2009**	**2010**	**2011**	**2012**
Ind captured	4	11	44	70	85	50	82	52	20
Cumulative ind. captured	4	15	58	120	177	217	274	302	318
Year of	**Year of recapture**								
initial capture	**2004**	**2005**	**2006**	**2007**	**2008**	**2009**	**2010**	**2011**	**2012**
2004		0	0	1	1	0	0	0	0
2005			1	1	3	0	1	1	0
2006				6	9	4	7	1	0
2007					18	3	8	7	1
2008						5	11	12	1
2009							8	7	2
2010								6	0
2011									0

	Year								
Right side	**2004**	**2005**	**2006**	**2007**	**2008**	**2009**	**2010**	**2011**	**2012**
Ind captured	1	8	54	61	92	39	60	33	15
Cumulative ind. captured	1	9	62	116	174	203	242	255	267
Year of	**Year of recapture**								
initial capture	**2004**	**2005**	**2006**	**2007**	**2008**	**2009**	**2010**	**2011**	**2012**
2004		0	0	0	1	0	0	0	0
2005			1	1	3	0	0	1	0
2006				6	13	4	7	1	0
2007					21	4	6	8	0
2008						5	11	9	1
2009							7	4	2
2010								4	0
2011									0

Table 2. Estimates of apparent survival (ϕ), super-population size ($\widehat{N}$) and annual population abundance (N_t) for left side and right side 2006-2011 photo-ID datasets from the best-fitting POPAN mark-recapture models

	Left side		**Right side**	
ϕ	0.85 (0.85)		0.86 (0.86)	
SE	0.06 (0.06)		0.06 (0.06)	
$\widehat{N}$	706 (711)		548 (549)	
	584-854 (574-848)		452-663 (442-656)	
SE	69 (70)		54 (55)	
Year	**N_t**	**CI**	**N_t**	**CI**
2006	241	161-360	297	202-438
2007	374	285-489	324	252-417
2008	319	224-454	278	198-389
2009	536	435-659	400	320-501
2010	458	341-614	342	250-470
2011	391	261-586	293	191-450

Shown in parentheses are the estimates of survival (ϕ) and standard error (SE) derived from model averaging over all POPAN mark recapture models explored in MARK.

Table 3. Estimates of apparent survival (ϕ) and apparent population growth (λ) for 2006-2011 left side and right side photo-ID datasets from the best-fitting PRADEL mark-recapture model.

		Left side			**Right side**	
		$\phi(.)\ p(1=2=5=6,t)\ \lambda(2=4=5,t)$			$\phi(.)\ p(1=2=5=6,t)\ \lambda(2=4=5,t)$	
ϕ		0.87			0.89	
SE (CI)		0.06 (0.69-0.95)			0.06 (0.70-0.97)	
λ (constrained to $\lambda(.)$)		1.07			1.03	
SE (CI)		0.09 (0.91-1.25)			0.08 (0.88-1.21)	
Year	**p_t**	**λ**	**N_t**	**p_t**	**Λ**	**N_t**
2006	0.16	N/A	283 (201-408)	0.14	N/A	393 (276-570)
2007	0.16	1.56	451 (320-649)	0.14	1.10	443 (312-644)
2008	0.27	0.71	313 (220-472)	0.33	0.67	276 (200-407)
2009	0.07	2.29	719 (428-1235)	0.06	2.39	661 (378-1181)
2010	0.16	0.71	528 (375-760)	0.14	0.64	436 (307-633)
2011	0.16	0.71	335 (238-482)	0.14	0.64	240 (169-348)

Supplementary Tables

Table S1 – Summary of sightings and photo-identification after photo-quality control

Year	**Sampling Period (mo/d)**	**Number of surveys**	**Hours of observation (hrs)**	**Groups of blue whales encountered**	**Number of blue whales encountered**	**Left side photo-id after quality control**		**Right side photo-id after quality control**	
						New individuals	Individuals sighted previously	New individuals	Individuals sighted previously
2004	02/25 – 03/15	2	17:35	2	3	4	0	1	0
2005*	02/01 – 03/15	8	29:13	25	58	11	0	8	0
2006	02/04 – 04/15	12	67:15	70	112	43	1	53	1
2007*	02/01 – 04/29	17	94:54	142	188	62	8	54	7
2008	02/01 – 04/30	17	93:33	171	270	57	28	58	34
2009	02/01 – 04/30	12	68:55	82	124	40	10	29	10
2010*	01/25 – 04/30	17	81:39	129	182	57	25	39	21
2011	02/01 – 05/01	15	89:59	77	115	28	24	13	20
2012 – Chiloé	01/26 – 04/30	9	47:57	12	18	2	4	4	3
TOTAL Southern Chile		**109**	**591:00**	**710**	**1070**	**304**	**100**	**259**	**96**
2012 – Chañaral	02/24 – 02/27	4	26:05	17	22	14	0	8	0
	TOTAL	**113**	**617:05**	**727**	**1092**	**318**	**100**	**267**	**96**

Table S2. Abundance estimates from closed mark recapture models calculated in CAPTURE for 2006-2011

Test	Left side		Right side	
	N	Model selection	N	Model selection
M(0)	594 (512-704)	0.17	462 (400-544)	0.17
M(t)	588 (507-696)	0.48	453 (394-533)	0.62
M(b)	843 (481-1914)	0.00	359 (307-479)	0.18
M(h)	752 (671-851)	0.19	598 (526-689)	0.00
M(h) Chao	781 (626-1008)	0.19	563 (460-720)	0.00
M(bh)	511 (396-954)	0.23	288 (266-344)	0.18
M(th) Chao	**742 (595-961)**	**1.00**	**540 (439-696)**	**1.00**
M(tb)	676 (343-3288)	0.12	362 (288-975)	0.69
M(t) Chao	686 (562-870)	0.48	500 (417-626)	0.62
M(tbh)	NA	0.57	NA	0.49

Table S3. Summary of top p/ϕ-identifiable POPAN models explored in MARK

Model	# Parameters	AIC	ΔAIC	AIC_c weight	Model Likelihood
Left side					
ϕ(.) p(1=2=5,t) PENT(2=4=5,t) N(.)	8	586.17	0.00	0.22	1.00
ϕ(.) p(1=2=5,t) PENT(4=5,t) N(.)	9	586.17	0.00	0.22	1.00
ϕ(.) p(1=2=5,t) PENT(t) N(.)	10	586.17	0.00	0.22	1.00
ϕ(.) p(1=2=5=6,t) PENT(2=4=5,t) N(.)	9	587.30	1.13	0.12	0.57
ϕ(.) p(1=2,t) PENT(t) N(.)	11	587.98	1.80	0.09	0.41
ϕ(.) p(t) PENT(1=2,t) N(.)	11	588.00	1.83	0.09	0.40
ϕ(.) p(1=2,t) PENT(1=2,t) N(.)	10	591.01	4.84	0.02	0.09
ϕ(.) p(1=2=5,t) PENT(.) N(.)	7	593.29	7.12	0.01	0.03
ϕ(.) p(t) PENT(.) N(.)	9	594.57	8.40	0.00	0.02
ϕ(.) p(.) PENT(t) N(.)	6	599.87	13.70	0.00	0.00
Right side					
ϕ(.) p(1=2=5,t) PENT(2=4=5,t) N(.)	8	564.48	0.00	0.27	1.00
ϕ(.) p(1=2=5,t) PENT(t) N(.)	10	564.48	0.00	0.27	1.00
ϕ(.) p(1=2,t) PENT(2=4=5,t) N(.)	9	566.08	1.60	0.12	0.45
ϕ(.) p(1=2,t) PENT(t) N(.)	11	566.08	1.60	0.12	0.45
ϕ(.) p(t) PENT(1=2,t) N(.)	11	566.09	1.61	0.12	0.45
ϕ(.) p(1=2=5=6,t) PENT(t) N(.)	9	567.57	3.09	0.06	0.21
ϕ(.) p(t) PENT(.) N(.)	9	573.02	8.54	0.00	0.01
ϕ(.) p(4=5,t) PENT(t) N(.)	11	573.05	8.57	0.00	0.01
ϕ(.) p(5=6,t) PENT(t) N(.)	11	573.05	8.57	0.00	0.01
ϕ(.) p(1=2=4=5=6,t) PENT(t) N(.)	8	573.52	9.04	0.00	0.01

Table S4. Summary of top identifiable Pradel models explored in MARK

Model	# Parameters	AIC	ΔAIC	AIC_c weight	Model Likelihood
Left side					
ϕ(.) p(1=2=5=6,t) λ(2=4=5,t)	7	1585.67	0.00	0.76	1.00
ϕ(.) p(1=2=5=6,t) λ(t)	9	1588.45	3.78	0.12	0.15
ϕ(.) p(1=2=6,t) λ(t)	10	1589.72	5.05	0.06	0.08
ϕ(.) p(1=6,t) λ(t)	11	1591.57	6.90	0.02	0.03
ϕ(.) p(t) λ(.)	8	1592.99	8.32	0.01	0.02
ϕ(.) p(1=2=6,t) λ(.)	6	1596.56	11.89	0.002	0.003
ϕ(.) p(1=2=5=6,t) λ(.)	5	1601.66	16.99	0.001	0.000
Right side					
ϕ(.) p(1=2=5=6,t) λ(2=4=5,t)	7	1383.02	0.00	0.43	1.00
ϕ(.) p(1=2=5,t) λ(2=4=5,t)	8	1384.05	1.03	0.26	0.60
ϕ(.) p(t) λ(2=4=5,1=3)	9	1385.98	2.96	0.10	0.23
ϕ(.) p(1=2,t) λ(2=4=5,t)	9	1385.98	2.96	0.10	0.23
ϕ(.) p(t) λ(2=4=5,t)	10	1385.98	2.96	0.10	0.23
ϕ(.) p(t) λ(.)	8	1394.67	11.66	0.00	0.00
ϕ(.) p(1=2=4=5,t) λ(.)	5	1395.51	12.50	0.00	0.00
ϕ(.) p(1=2=5=6,t) λ(.)	5	1397.99	14.97	0.00	0.00