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HUMPBACK WHALE BREEDING STOCK G: UPDATED POPULATION ESTIMATE BASED ON PHOTO-ID MATCHES BETWEEN BREEDING AND FEEDING AREAS

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ABSTRACT

We report a new mark-recapture-based population estimate for the humpback whale Breeding Stock G (BSG), defined by breeding grounds on the northwestern coast of South America and southwestern Central America and feeding grounds around the Antarctic Peninsula and southern Chile. Photographic fluke catalogs from 23 research groups working in both breeding and feeding areas were compiled in the largest photo-ID matching effort ever made for this stock. A total of 6,354 unique individuals including 1,698 (26.7%) from feeding areas and 4,656 (73.3%) from breeding areas covering the period 1991-2018 were used for this purpose. The dataset was fitted to closed

population models to estimate population size and Jolly-Seber models to estimate apparent survival, both implemented in the software Mark. Mixture models with two different data types, full likelihood and conditional likelihood, produced similar results of 11,784 and 11,786 (SE = 266 for both estimates) whales, respectively. In both cases, a model with two mixtures {M_{th2}} provided the best fit. Two Cormack-Jolly-Seber with Pledger mixtures models produced apparent survival estimates for the two mixtures (0.924 and 0.959, SE = 0.003 and 0.008; respectively). The new population estimate is 181% higher than a previously obtained in 2006. The annual rate of increase in the 27-year study period was 5.07%. Sources of bias were associated with effort heterogeneity, population stratification and the time scale. These and other sources of bias should be considered in future modeling estimates.

KEYWORDS: humpback whale, breeding grounds, feeding grounds, abundance estimate, apparent survival, Southeast Pacific, Antarctic Peninsula.

INTRODUCTION

The humpback whale (*Megaptera novaeangliae*) Breeding Stock G (BSG) also referred to as the Southeast Pacific Stock, is one of the seven stocks of this species in the Southern Hemisphere recognized by the International Whaling Commission (IWC, 2006). BSG whales breeding off the northwestern coast of South America between northern Peru and southern Nicaragua in Central America (Flórez-González, 1991, Félix et al., 2001a, Rasmussen et al., 2007, Pacheco et al., 2009, DeWeerdt et al., 2020) are connected to three discrete feeding areas (Acevedo et al., 2013) located around the Antarctic Peninsula (e.g., Stevick et al., 2004, Acevedo et al., 2017, Rasmussen et al., 2007) and central and southern Chile (e.g., Acevedo et al., 2007, 2017; Hucke-Gaete et al. 2013). The BSG is the most genetically differentiated stock in the Southern Hemisphere (Olavarría et al., 2007; Amaral et al., 2016), despite some connections found through photo-ID and genetic studies with other stocks breeding off Brazil and Oceania (Stevick et al., 2013; Steel et al., 2017; Félix et al., 2020), suggesting complex migratory and connectivity dynamics among the southern stocks.

The first attempts to estimate the size of the BSG with mark-recapture models date from studies in the mid-1990s, based on local studies on the central coast of Colombia (Capella et al., 1998; N =1,120-2,190), Ecuador (Scheidat et al. 2000; Felix and Haase, 2001b; N = 405, 95% CI 221-531, and N = 2,683 (95% CI = 397-4,969), respectively), Panamá (Guzmán et al., 2015; N = 221, 95% CI = 170-290) and around the Antarctic Peninsula (Stevick et al., 2006; N = 3,851, 95% CI 3,666-4,036). Efforts continued in Ecuador, where most of the research effort of this whale population has been concentrated for many years. Off Ecuador, based on a 16 years dataset, the population of the BSG was estimated at 6,504 individuals (95% CI 4,270-9,907) in 2006 with the Petersen model modified by Chapman (Félix et al., 2011a). During that time, an attempt was also made to estimate the survival rate using the Jolly-Seber model for open populations, obtaining lower than expected values due to different sources of heterogeneity in the dataset. Such heterogeneity would be related not only to an irregular effort between years but also to aspects associated with the whales´ migratory behavior and repeated monitoring in the same area (Félix et al., 2011a).

Recent satellite tagging studies in Ecuador and Panama showed that the BSG is highly spatially structured on the breeding grounds (Guzmán and Félix, 2017), supporting previous findings through genetic studies (Félix et al., 2012) and photo-ID (Acevedo et al., 2007, 2013, 2017, Valdivia et al., 2017). This structure is also consistent with lower population estimates from central and northern sites of the breeding grounds, from Colombia north (e.g. Flórez-González, 1991, Guzmán et al., 2015) compared to those obtained in Ecuador, which is both a breeding ground and migratory corridor. A

more reliable population estimate of the BSG should integrate information from multiple sites, both in the breeding and feeding areas, to deal with spatial structure.

IWC-SC 66 recommended a collaborative photo-ID approach to humpback whales in the Southeast Pacific, integrating data from multiple research programs across the full range of the BSG (Jackson et al., 2016). This is now possible through the integration of datasets gathered over the last 25 years – some based on whale-watching tourism – along the west coast of Central and South America and around the Antarctic Peninsula. During the biennial meeting of the Latin American Society of Aquatic Mammals, SOLAMAC, in December 2016, a workshop on a collaborative approach to carrying out a new abundance estimate on the BSG was convened (IWC, 2017a, b). In this context, we report preliminary BSG abundance and survival estimates resulting from these efforts.

MATERIALS AND METHODS

Data sources

Humpback whale monitoring programs have been established in all countries throughout the Southeast Pacific region since 1990, comprising from 11°N to 65°S (Figure 1). Throughout 2017 and 2018, we compiled, reconciled, and compared photo-ID catalogs and capture-recapture histories from 23 research groups (see Appendix 1). A total of 8,451 fluke images taken between 1991 and 2018 were collated, of which 1,961 (23.2%) came from the three feeding areas and southern migratory corridor off central Chile and 6,490 (76.8%) from breeding areas. The number of images of unique whales received per year from each research group is shown in Table 1.

Image selection

Images were graded as a high-, medium- or low-quality for the analysis based on five criteria: 1) exposure/contrast/illumination; 2) angle of the fluke in relation to the surface of the water; 3) lateral angle of the fluke with respect to the photographer; 4) focus and sharpness; and 5) visible proportion of the flukes. Both high- and medium-quality images were included in the analysis. After selection, 6,474 images (76.6% of the total compiled photographs) were selected. Each photograph was pre-treated (lighting and contrast) and trimmed, leaving only the fluke.

Matching process

The process of image matching within and among the photo-identification catalogs started with the post-treatment images by the use of the HotSpotter recognition software version 1.0 (Crall et al., 2013), scoring the likelihood of potential matches based on a combination of the SIFT algorithms of Wild-ID (Lowe 2004) and a "local naïve Bayes nearest-neighbor algorithm". To reduce bias, both the selection and the matching process were carried out by the same person, who was experienced in matching humpback whale photographs (JA). First, the photographs within each catalog were compared internally to eliminate potential duplicate whales (N = 120 individuals). Then, the catalogs were compared to each other, allowing us to build capture-recapture histories. A second comparison process was carried out later using the automated image recognition algorithm hosted at the Happywhale web-based platform (https://happywhale.com/home, Cheeseman et al., in press), which allowed the detection of additional matches not found in the first comparison process.
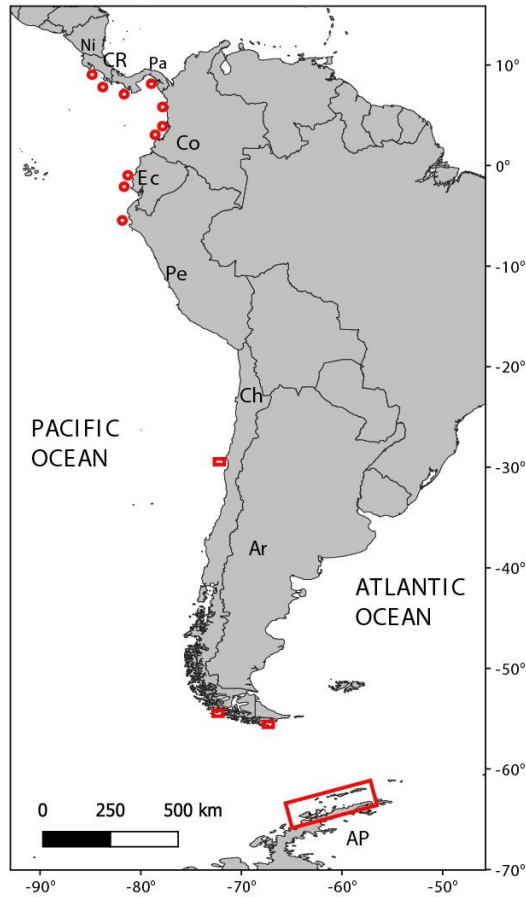
Figure 1. Area of distribution of the Breeding Stock G and sampling sites. Red circles are breeding sites and red squares feeding areas.

Recapture rates

Recapture rates for each sampling area in both breeding and feeding grounds were calculated for those datasets with more than 100 individuals by dividing the number of different recaptured individuals by the total number of individuals identified. Individuals with low-quality images were excluded.

Population abundance

Two different modeling approaches to estimate abundance open and closed populations are commonly used with data from mark-recapture studies. Open population models allow gains from immigration and births and losses from emigration and mortality, while closed population models consider the population to be constant during the study period (Seber and Schwarz, 1999). Both approaches assume conditions of equal and consistent capture probability across all sampling periods, such as unique, permanent correctly recorded marks that do not affect catchability (Hammond, 2010). The violation of such assumptions may lead to biased estimates.

For the analyses, capture-recapture histories of the 5,197 individuals were constructed using the binary sequence "1" and "0", where "1" indicates that the individual was observed during that sampling period and "0" indicates that the individual was not observed in that sampling period (Cooch and White, 2009). The complete dataset corresponds to 28 sampling periods (1991-2018). Individuals

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recorded at breeding and feeding grounds in the same year were included in the same sampling period to achieve a larger sample. Because of the small effort with few identified individuals in the first five years (1991-1995), data were pooled in one single period. Thus, 24 annual periods were used for the analysis. Open and closed population models were fitted to estimate abundance using program Mark 9.0 (White and Burnham, 1999).

The fourteen models for closed populations implemented in Mark are divided into two main data types "full likelihood" (Otis et al, 1978) and "conditional likelihood" (Huggins, 1989). Full likelihood models take into account the probability of an individual not being observed or captured, that is, the scenario "000" is given, while the conditional likelihood models eliminate this scenario from their calculations. Full likelihood models are based on the parameterization of three types of parameters: 1) p = the probability that an animal in the population is captured and marked for the first time; 2) c = the probability that an individual has been captured at least once before; and 3) f_0 = the number of individuals in the population that have not been counted. Conditional likelihood models are restricted to the number of animals detected; therefore, f_0 is not taken into consideration and only includes the parameters p and c. An advantage of the conditional likelihood approach is that covariates can be used to model the encounter process.

Four of the fourteen models belonged to a group called heterogeneity models, which contain an additional parameter to p and c called mixture parameter pi (π), which calculates the heterogeneity that exists between individuals at the time of capture. The following six models incorporated another parameter that considers the probability of identifying an individual correctly in its first observation "α". Finally, there were the four Huggins models with parameters "p" and "c" with random effects that use numerical integrations to add individual differences in the match probabilities.

Closed population models in Mark used the following notations:

M_0: probability that an animal is captured and marked for the first time (p) remains constant.
M_t: probability that an animal is captured and marked for the first time (p) varies with time.
M_b: response of the behavior of individuals.
M_h: probability that an animal is captured and marked for the first time (p) is heterogeneous.
M_{h2}: probability that an animal is captured and marked for the first time (p) is heterogeneous, and the population comprises a mixture of two types of animals.

Mark chooses the most parsimonious model based on the Akaike information criterion (AIC), where the model with the lowest value (AICc or AICweight) is the one that best fits the data (Freitas and Marino 2012). Since AICc values between full likelihood and conditional likelihood models are not comparable, the analyses were conducted separately.

Apparent survival

Apparent survival Phi (φ) was estimated using Jolly-Seber models for open populations implemented in Mark. We fitted 105 different models to the data using the different formulations implemented in Mark: *POPAN*, Link-Barker, Pradel-recruitment, Burnham JS, and Pradel-λ. The difference among such formulations is the way they parameterize new entrants to the population.

Table 1. Information compiled in this study of the different research groups in the Southeast Pacific and Antarctic Peninsula, number of fluke images per site and sampling period (year), for the period 1991-2018. Numbers in the table indicate new individuals discovered in the season by each research group.

Contributor	Site	Total	91	92	93	94	95	96	97	98	99	00	01	02	03	04	05	06	07	08	09	10	11	12	13	14	15	16	17	18
Feeding ground																														
INACH	Antarctic Peninsula	276					23	40	46	19	38							55	10	45										
PROANTAR	Antarctic Peninsula	766				2				53	60	21	65	106	51	17	22	13	21	1	53	18	26		57	54	51	75		
AF	Antarctic Peninsula	256																			21	33		10	38	69	85			
CEQUA_ANT	Antarctic Peninsula	38																			38									
MHNRS	Antarctic Peninsula	17																										6	11	
OTROS_ANT	Antarctic Peninsula	105																2	7	28	11				55			2		
MBS_ANT	Antarctic Peninsula	9		1																							8			
ACMA	Antarctic Peninsula	35																											35	
CHAC	Chañaral - Chile	10																					2		1	5	1		1	
EUTROPIA	Chañaral - Chile	15													1		2	3	1							4	2		2	
CBA	Corcovado Gulf - Chile	41													2	1	2	15	3	2	4	4	1	7						
CEQUA	Magellan St. - Chile	177													11	27	29	16	10		3	8	10	24		2	21	16		
EMA	Magellan St. - Chile	178								18	3	6	7	12	10	7	12	17	10	8	10	7	11	9	5	14	12			
CADICCB	Beagle Ch.- Argentina	37																							3		2	3	8	21
Breeding ground																														
KETO	Osa Pen.- Costa Rica	130															2	11	13	1	7	19	9	9	37	22				
PAN	Costa Rica	41			1		1			3		10	9	1	1				15											
CEIC	Dulce G.- Costa Rica	30																			8	1	2	13	1	1	4			
PAN	Chiriqui G.- Panama	552												5	8	4		4	34	28	34	12	35	79	106	126	77			
PMA-LP	Las Perlas Arch.- Panama	173													12	8	22	51	31		2		4	8	6	2	7	9		11
PAN-CONT	Panama	18																					18							
ICA	Solano and Malaga Ba.- Colombia	42															6	11		4	3	8	4	3	3					

Code	Location	Total																												
BGT	Tribuga G.- Colombia	543																		16				127	98	66	236		
SENTIR	Tribuga G.- Colombia	36											7	3	26														
EC	North/Central Ecuador	628						24		7	8	14	82	96	65	143	57	4		10	7	3	4	26	4	12	39	23		
PWF	Machalilla- Ecuador	1468						20	12	26	23	13	60	88	111	237	258	159	178	283										
MBS	Salinas- Ecuador	2157	8	13	1	15	29	79	70			3		69	88	132	183	266	284	252	158	229	37	48	65	56	38	34		
MBS	Perú	2																2												
MBS	Panama	2																								2				
PAO	Los Órganos - Perú	650																			13	34	16	96	111	84	131	165		
CEPEC	Sechura - Perú	18																1			13	4								
TOTAL		**8451**	**8**	**14**	**2**	**17**	**53**	**163**	**128**	**105**	**150**	**54**	**223**	**387**	**364**	**606**	**589**	**620**	**620**	**646**	**355**	**455**	**174**	**323**	**637**	**540**	**543**	**585**	**57**	**32**

RESULTS

Recapture rates

Recapture rates were highly variable within the dataset in both feeding and breeding areas (Table 2). Major datasets from Antarctic Peninsula (n=3) ranged between 0.025 to 0.048 and the number of recaptures per individual between 1.0 and 1.16, but in the continental feeding area (Magellan Strait), the recapture rate was six times higher on average (0.645 and 0.765, CEQUA and Whalesound, respectively). High variability was also found in the breeding grounds datasets where the recapture rate ranged between 0.026 to 0.194 and the number of recaptures per individual between 1 and 1.38.

The overall comparison process resulted in 5,197 unique individuals. A total of 2,329 recaptures of 1,176 whales across catalogs were found. The overall recapture rate was 0.226 and the number of recaptures per individual was 1.98 (range 1-16) on average.

Table 2. Calculated recapture rates of individual datasets from feeding and breeding areas containing more than 100 individuals.

Research group	No. Individuals	No. Recaptured individual	Recapture rate	No recaptures/ individual
Feeding areas				
INACH	227	6	0.026	1.00
Proantar-Furg	608	29	0.048	1.07
Institute of Marine Science UCSC	255	6	0.025	1.16
Fundación CEQUA-Magallanes	169	109	0.645	4.09
Whalesound	161	121	0.765	6.22
Breeding areas				
Panacetacea	485	80	0.165	1.33
KETO	112	3	0.026	1.33
MBS	1541	173	0.112	1.21
Macuático	425	15	0.035	1
Pacific Adventure	551	26	0.047	1.07
UFSQ	257	50	0.194	1.38
Héctor Guzmán	135	4	0.029	1.25
Pacific Whale Foundation	1045	86	0.082	1.24

Population abundance estimates

Abundance estimates obtained with open population models did not reach numerical convergence or produced unrealistic estimates due to the spatial and temporal structure of the data and high heterogeneity resulting from uneven sampling effort along a large geographic region. Estimates obtained with closed population models were considered more suitable with the current data structure. Results obtained with two different closed population data types are shown in Table 3. In both cases, the model that best fitted the data allowed capture probability to vary by time with heterogeneity in capture probability with two mixtures (M_{th2}). The population size obtained with both models was similar (11,784 and 11,786, respectively; SE= 266 in both cases).

Table 3. Population abundance estimates for the BSG obtained with the two data types using information from breeding and feeding areas of the period 1991-2018, fitted using closed population models in program Mark 9.0.

Data type	Model	N-hat	SE	Lower	Upper
Full likelihood	$\{M_{th2}\}$	11,784	266	11,282	12,326
Conditional likelihood	$\{M_{th2})\}$	11,786	266	11,284	12,328

Apparent survival estimates

Two CJS models with heterogeneous capture probabilities (Cormack-Jolly-Seber model with Pledger mixtures) resulted in the same AICc value and model likelihood best fitted the data: 1) constant survival and heterogeneity and time-dependent capture probability; and 2) constant survival and time-dependent heterogeneity and capture probability. These models incorporate a mixture parameter (pi) to model heterogeneity in both phi and *p*. Thus, two *g*roups with different variation in both parameters are reported for each model. Both models produced the same values of survival in the two mixtures 0.924 and 0.959, with marginal differences in the standard errors (Table 4).

Table 4. Survival estimates obtained with the Cormack-Jolly-Seber with Pledger mixtures models.

Model	Mixture	Estimate	Standard error	Lower	Upper
$\{pi(.) \ Phi(.) \ p(t)\}$	1	0.924	0.003	0.916	0.978
	2	0.959	0.008	0.938	0.973
$\{pi(t) \ Phi(.) \ p(t)\}$	1	0.924	0.006	0.911	0.936
	2	0.959	0.008	0.937	0.973

DISCUSSION

These updated abundance estimates of the BSG resulted from the collaborative effort of research groups working throughout the entire distribution range (~11°N to 65°S), allowing the integration of data from breeding and feeding areas for the first time. However, it is recognized that different sources of bias persist, particularly those associated with the effort heterogeneity and the time scale that models most probably were unable to depict completely (see Table 1). Likewise, the low rate of recaptures, despite the enormous research effort, precluded the use of models for open populations. In such a long-term data series, closed population models could introduce an important downward bias affecting the estimate, and therefore our estimates should be considered conservative. The enormous extent of the distribution range, its high level of population structure in the breeding (Guzmán and Félix, 2017) and feeding areas (Acevedo et al., 2013), and even during migration (Félix and Guzmán, 2014) are aspects difficult to quantify but should be considered in future population modeling attempts.

In both abundance and apparent survival estimates, mixture models fitted the data best, which confirms the heterogeneity within datasets. An example of such heterogeneity can be found in the two subsets from Magellan Strait (CEQUA and EMA). These two datasets include 15 years of sampling from small population units with a high level of annual philopatry and therefore with a different capture probability when compared to the full range of BSG breeding, feeding and transit

areas. Recent estimates for Magellan Strait using a robust design Bayesian framework estimated humpback whale abundance at 204 (95% CI 199-210) for the period 2004-2016 (Monnahan et al., 2019), which presents the highest confidence estimate for any population unit in the full dataset. By contrast, some datasets accounted for once or few years of effort with low recapture probabilities. Furthermore, breeding areas were disproportionately more frequently sampled than feeding areas (3.3:1; see Figure 1 and Table 1).

These new abundance estimates show a population increase of 181% with respect to a previous estimate made with information only from the breeding area off Ecuador in 2006 (Felix et al., 2011a), yielding an annual average growth rate of 5.07% in 12 years (2006-2018). This annual growth rate is low compared with other southern hemisphere humpback whale populations, ~ 10% in the Western Australian population (Bannister and Hedley, 2001) and 7.4% in the Southwestern Atlantic population (Ward et al., 2011). The maximum plausible rate of increase (ROI) for this species is estimated at 11.8% (Zerbini et al., 2010). Differences between estimates with data from one breeding area and the estimate obtained in this study including a combined dataset of breeding and feeding areas could be caused, among other factors, by the following: 1) a previous overestimation; 2) the dataset from the feeding areas included whales from an area not sampled in the breeding zone; and 3) the datasets from the feeding areas included whales sampled in Antarctica that do not belong to the BSG. In the first case, the estimate made in 2006 has a wide range of confidence (95% CI 4,270-9,907) (Félix et al., 2011a), so in a strict sense, the new estimate could be considered consistent with such calculation. In the second case, unmonitored areas may persist in the Southeast Pacific such as the Galapagos Islands, where one female was identified to belong to the BSG through molecular studies (Felix et al., 2011b) but no fluke images were available, as well as in other oceanic islands such as Malpelo in Colombia (Herrera et al., 2011, Palacios et al. 2012) and perhaps Cocos Island in Costa Rica (Acevedo-Gutierrez and Smultea, 1995). Lastly, in the third factor above, a certain degree of mixing exists between humpback whales from different Southern Hemisphere stocks in Antarctic waters (Dawbin, 1964, Amaral et al., 2016; Steel et al., 2017), so it cannot be ruled out that some whales photographed in the Antarctic Peninsula and included in the new dataset do not belong to the BSG.

The current analyses also showed an improvement regarding apparent survival estimates. The former average survival estimated at 0.919 (Félix et al., 2011a) is lower than the value obtained for the mixture with the lowest value (0.924). The apparent survival values are also higher than the recent estimate in the Magellan Strait feeding aggregation (0.892, CI: 0.871–0.910) which also showed an annual increasing rate of 55% lower than the whole BSG (2.3%: CI 2.1%-3.1%) (Monnahan et al., 2019). The mixture with the highest apparent survival value (0.959) is within the range reported in other humpback whale populations (Zerbini et al. 2010).

The population increase rate of the BSG could be influenced by anthropogenic factors such as the high rate of whale entanglement in fishing gear reported in waters of Ecuador and Colombia (e.g., Capella et al. 2001, Félix et al., 2011c) and ecological factors such as the increase in the predation rate, suggested by an increase of scars from killer whale *Orcinus orca* in the flukes of BSG individuals over time (Capella et al., 2018; Testino et al., 2019). Other threats of anthropogenic origin include vessel collision (Van Waerebeek et al., 2007) and vessel disturbance (Scheidat et al., 2004; Ávila et al., 2015), as well as emergent issues with a potential effect on cetaceans such as marine litter (Panti et al., 2019) and climate change (Askin et al., 2017), particularly, changes in the extent of sea coverage/pack mass influencing food availability in Antarctic (Ávila et al., 2020).

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Appendix 1.

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