



Population size and migratory connectivity of humpback whales wintering in Las Perlas Archipelago, Panama

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ABSTRACT

From 2003 to 2009, we surveyed Las Perlas Archipelago off the Pacific coast of Panama 53 times between the months of August and October to estimate abundance of humpback whales and to test for a migratory connection with populations from the southern hemisphere. We identified 295 individuals using photo-identification of dorsal fins, including 58 calves, and the population estimate for a single season was 100–300 solitary adults plus 25–50 mothers with calves; the estimated population of animals across all seasons using a mark and recapture model was over 1,000. Eight of the 139 fluke identifications were matched to whales in photograph catalogues from the Antarctic Peninsula and a ninth was matched to a whale sighted in Chilean waters; four of these nine individuals have also been sighted in Colombia. We conclude that Panama (Las Perlas Archipelago in particular) is an important calving area for humpback whales in the Southern Hemisphere. These data should provide a foundation for monitoring of population change and to increase awareness in Panama about the need to manage vessel traffic and tourism related to the whales at Las Perlas.

Key words: humpback whale, *Megaptera novaeangliae*, nursery area, population size, satellite tracking, Las Perlas Archipelago, Panama, Antarctic Peninsula, southeastern Pacific stock.

The Gulf of Panama has been known as a breeding area for humpback whales (*Megaptera noveangliae*) since the 19th century, when commercial whalers used the area during the austral winter (Best 2008). More recently, studies have demonstrated that humpback whale populations from both the Northern and Southern Hemispheres visit the Pacific coast of Panama and Central America during their respective breeding seasons (Calambokidis *et al.* 2000; Rasmussen *et al.* 2007, 2011). Northern animals are found in Panama between December and April, and southern animals are present between June and December. Temporal overlap of the populations between Panama and Costa Rica is likely (Stone *et al.* 1990, Acevedo and Smultea 1995, Flórez-González *et al.* 1998, Rasmussen *et al.* 2007).

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Other than the summaries of old whaling records provided by Townsend (1935) and Best (2008), the only published reports of humpback whales in Panama are as follows: a characterization of their vocalizations in Las Perlas Archipelago, Gulf of Panama (Oviedo *et al.* 2008); a photo-identification study in the northwestern part of the Gulf of Chiriquí, located about 350 km west of Las Perlas Archipelago, looking at feeding area-breeding area connectivity (Rasmussen *et al.* 2007, 2011); and an analysis of the frequency of vessels en route to the Panama Canal that could potentially collide with whales (Guzman *et al.* 2012).

The main goals of this study were to estimate the size of the humpback whale population at Las Perlas Archipelago in Pacific Panama and to gain a better understanding of the migratory connections between the whales from the Southern Hemisphere. Photo-identification of individual animals allowed us to achieve both goals. Between 2003 and 2009, we conducted surveys during the austral winter to determine whether animals from southern feeding locations (the Antarctic and southern Chile) were breeding in Panama (see Flórez-González *et al.* 1998, Rasmussen *et al.* 2007) and, most importantly, to obtain the first preliminary estimate of the population size in Panama. The ultimate goal of this research is to acquire the knowledge needed to determine if protection is warranted for the species in Panama from the effects of increasing coastal development, maritime traffic, and tourism.

METHODS

Study Area and Photo-identification

Las Perlas Archipelago includes over 200 islands and islets 60 km southeast of Panama City in the Gulf of Panama, Pacific Ocean (8°25'N, 7°91'W). The archipelago encompasses an area of 168,771 ha, of which 135,618 ha are marine environments, and it was declared a Marine Protected Area in 2007. The entire area is shallow, averaging 15 m depth and all <50 m. It is a breeding subarea for humpback whales from the Southern Hemisphere, and it likely was an area where whales were hunted in the past (Best 2008). Breeding lasts from June to December, with peaks in August and September.

A preliminary evaluation of site preference and whale distribution within the archipelago was carried out with monthly aerial surveys from July to December 2005. Information from aerial surveys was not used in any population analyses (Fig. 1). Photo-identification of whales in the archipelago started in 2003 (only 3 d) and the systematic boat surveys to estimate abundance were completed only from 2004 to 2009 (2008 was not surveyed), all between August and October. Abundance surveys were made using a 5 m Avon inflatable boat with two observers for 10 consecutive days, for about 8 h (0730–1630 with a 60 min break), during each of the five seasons encompassing daily the entire area of the archipelago and following predetermined routes that included all islands.

In total we conducted 53 one-day boat surveys over six seasons, including about 312 h of observations, supported from the Smithsonian's R/V *Urraca*. Whales were photographed for later identification using ventral fluke and dorsal fin marks (Katona *et al.* 1979, Barlow *et al.* 2011). Using the software IMatch3, we edited and catalogued the best picture of each animal photographed. The flukes and dorsal fins were

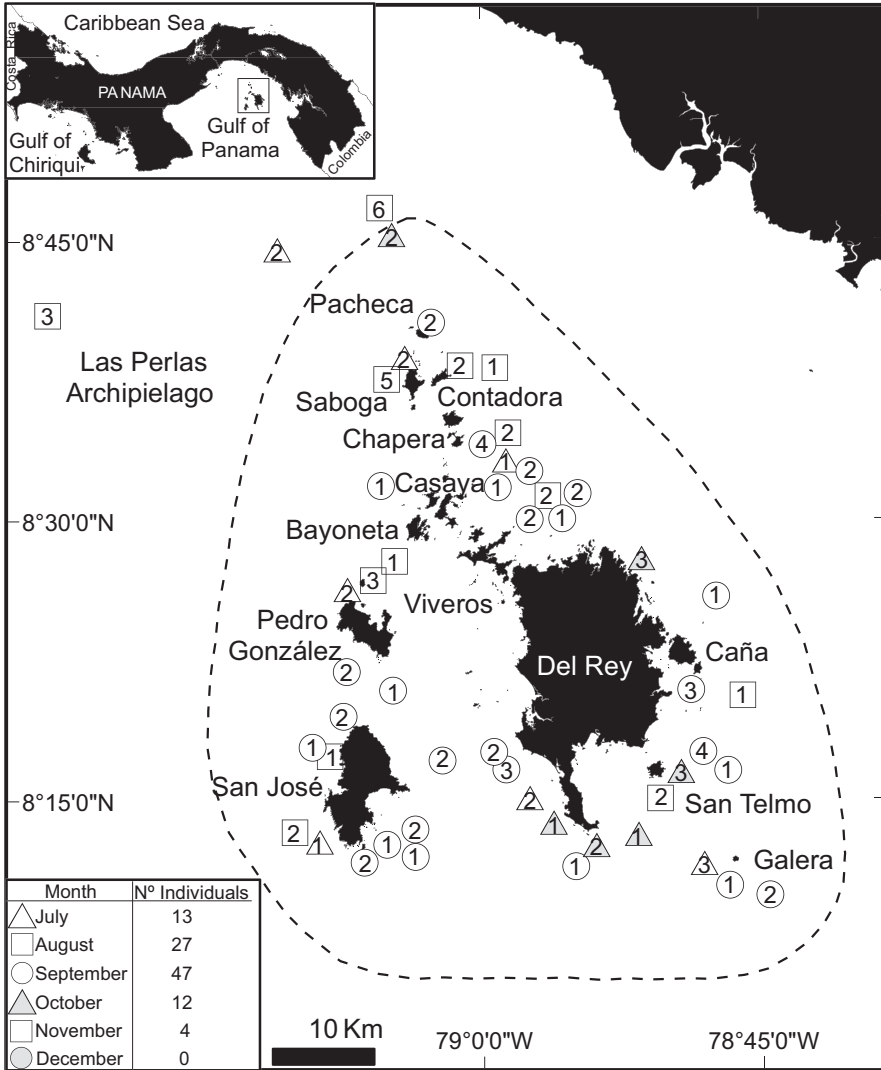


Figure 1. Distribution of humpback whales (*Megaptera novaeangliae*) sighted during the 2005 aerial surveys in Las Perlas Archipelago, Pacific Panama. Outer dash-line indicates the arbitrarily defined 10 km border of the core breeding subarea. Numbers inside symbols represent sighted whales.

first compared internally for each year, but only the flukes ($n = 139$) were used for the purpose of comparison against the Antarctic Humpback Whale Catalogue (AHWC, $n = 2,857$; Allen *et al.* 2011) and the Magellan Strait, Chile (EMa, $n = 126$) catalogue from the Southern Hemisphere. All matches (flukes and dorsal fins) were verified by a second person at the College of the Atlantic, Bar Harbor, Maine, where the Antarctic catalogue is maintained.

Whale Satellite Tracking

Humpback whales were tagged between 23 and 27 August 2009 to track movements within the archipelago and to estimate seasonal residence. Real-time satellite transmitters were employed (Wildlife Computers, SPOT5 host version 5.02.1007, model AM-S193C with two AA lithium batteries). A transmitter consisted of a 2 cm diameter stainless steel tube case, 7.5 cm in length, coupled to a custom-made stainless steel spear with a 3 cm triangular double-edged blade tip containing two pairs of 5 cm barbs placed at 90° to each other (modified from Zerbini *et al.* 2006). We tagged nineteen whales 2–5 m from the inflatable boat, but four tags never transmitted signals. Tags were deployed using a modified pneumatic line-thrower (model ARTS, Restech Inc., Norway) fitted with a ZOS Universal waterproof and fog-proof 1 × 40 riflescope. In order to reduce infections, spears and tags were soaked with oxytetracycline-polylyxin topical ointment (Terramycin) before deployment.

The transmitters were set for constant transmission. We used tag-derived positions from Argos location classes 3, 2, 1, 0, A, and B, providing positional errors of 150 m to 5 km radius (Zerbini *et al.* 2006, Hammerschlag *et al.* 2011). A detailed description of the tags, satellite transmissions, and tagging procedure are available elsewhere (Guzman *et al.* 2012). Whale transmission data were processed using the Satellite Tracking and Analysis Tool (STAT), which allows data filtering and editing Argos location classes and the integration of environmental data layers of interest (*i.e.*, bathymetry, transmission quality, speed, and distances) with animal tracking (see Coyne and Godley 2005).

Capture-recapture Methods

Resightings with photos—Based on the photo-identifications from systematic boat surveys, we assembled a sample of 295 individuals whose dorsal fin was recognizable. Daily sighting histories were constructed for those animals, covering all 50 observation days over the 5 yr (all years except 2003, which was a trial only). There were 14 d on which we photographed no animals at all, leaving 36 d that contributed data. The resighting history for each animal is a vector of length 36, set equal to 1 on days it was photographed and 0 on days it was not. Animals known by flukes alone were excluded because they might overlap with those known by dorsal fin alone. The sighting histories formed the basis of an analysis of population size and residency using the Cormack-Jolly-Seber mark-recapture method (Williams *et al.* 2002).

As a preliminary assessment of residency, we examined resighting frequency as a function of lag (in days) since an animal's initial sighting. For example, consider the 216 sightings made of adults on all but the last day of each season. On the day following each of those sightings, 18 of the 216 animals were resighted, and a similar tally was made after two, three, *etc.* days. This was used principally to justify use of an open population model for analysis, though the open analysis is routinely assumed for humpback whales (Flórez-González 1991, Scheidat *et al.* 2000, Barlow *et al.* 2011, Felix *et al.* 2011).

The open-population mark-recapture model—Estimating population size in the Cormack-Jolly-Seber method requires estimating first two key parameters: the probability δ_t of detecting (*i.e.*, in a photograph) an animal in the study area on day t , and the probability ε_t that an animal in the study area on day t departs (so it can no longer be detected) before day $t + 1$. These two probabilities lead to estimates of population size on day t , N_t , and the number of animals leaving the study area after day t , L_t . The

standard method is to find parameters which best account for observations (sighting histories) based on maximum likelihood, including a separate estimate for each parameter on every day. We used a Bayesian method, based on the same likelihood formulations but producing also 95% credible intervals for every parameter, and we employed a multilevel, hierarchical model, in which daily variation in the parameters was permitted but constrained to follow overarching hyperdistributions. This improves statistical power relative to unconstrained day-to-day variation (Clark *et al.* 2005, Gelman and Hill 2007). Daily N_t and L_t were both assumed to follow normal hyperdistributions with mean μ_N (μ_L) and SD σ_N (σ_L); ε_t was assumed to follow a logit-normal hyperdistribution with mean μ_ε and SD σ_ε . For calves, in which the number of sightings was low, daily estimates collapsed to a constant, so we reverted to the model in which ε and N were the same each day. Detection probability δ was held constant across all days in all years (but different for adults and calves) since it is based on our ability to photograph, which we thought was reasonably consistent. (Since we omitted days on which no animals were seen, δ is the probability of detection conditioned on successful sightings that day, thus slightly higher than an overall daily detection probability; this does not affect abundance estimates.)

Likelihood formulation—The estimates of detection δ and departure ε were based on the likelihood of individual sighting histories, as given in Williams *et al.* (2002, p. 421). To estimate population size N and departures L , binomial likelihood was used. The probability that N_t animals were present on day t is

$$P(N_t) = \text{Binom}(S_t, N_t, \delta) \times \text{Norm}(N_t, \mu_N, \sigma_N) \quad (1)$$

The first part of P is the binomial probability of S successes (S = number of animals seen on day t) in N trials given probability δ of success (detection) for each of the N animals. The second part is the hierarchical feature, the probability of N animals being present given the Gaussian hyperdistribution. A similar likelihood gives the probability that L_t animals departed after t , since the expected number departing is a binomial distribution around $\varepsilon_t N_t$. There must also be likelihood equations governing the hyperparameters, so $P(\mu_N) = \text{Norm}(N, \mu_N, \sigma_N)$, where N means the vector of N_t across all t , and similarly for σ_N , μ_ε , and σ_ε . Two additional parameters were derived from N and L : the number of recruits R_t prior to day t was calculated as $R_t = N_t - N_{t-1} + L_{t-1}$, and the total number of animals using the study site during the observation period as $M = N_1 + \sum R_t$, which is the number present on day 1 plus all that recruited since (the sum starts at $t = 2$).

The accounting of the number of departures and recruits adds a component to the likelihood formulation for population size N_t , whose probability $P(N_t)$ must also depend on other N and L . If the value of N_t forced either $R_{t-1} < 0$ or $R_t < 0$, then $P(N_t) = 0$. The same held for each L_t .

Besides the estimates made in individual years, based on daily population, detection, and departure, we also ran the model across all years. The model was identical, but population N_t , detection δ_t , and all other parameters refer to season t instead of day t . All adults, mothers plus solitary, were combined, producing an estimate for the total number of adults using the study area across all seasons.

Prior likelihood on parameters—Prior probability distributions for population sizes N , departures L , and their hypermeans μ_N and μ_L were improper: uniform on $(0, \infty)$. Priors for probabilities of detection, δ , and departure, ε , were uniform on $(0, 1)$ and thus proper. These flat priors had no influence on the resulting posterior

distributions, which were consistent across repeated estimates, well-defined, and distinct from priors; there were no hidden priors, because all parameters are direct measures of desired statistics. For the hyper-standard deviations σ_N , σ_L , and σ_ε , we tested models with prior probability either (1) uniform on the variance over $(0, \infty)$ or (2) inversely proportional to the variance. The latter is the standard conjugate prior based on the inverse-gamma distribution. Results from the two sets of priors were indistinguishable, and we present only those from the conjugate.

Parameter estimation—All model parameters, $\theta = (\delta, \varepsilon, N, L, \mu_N, \sigma_N, \mu_L, \sigma_L, \mu_\varepsilon, \sigma_\varepsilon)$, were estimated simultaneously with Monte-Carlo Markov chains (MCMC), using a Gibbs sampler and the Metropolis algorithm based on the likelihoods defined above. Each parameter was updated in turn based on the likelihood of all observations across years as well as the value of all other parameters. A single step of the chain included an update for every parameter. The number of daily recruits R_t and the total population M were updated at each step by algebra. Details of the procedure are given in Condit *et al.* (2007), and Gelman and Hill (2007) give many examples. The chains of estimates for every parameter converged quickly and were well-mixed, with low autocorrelation and no sign of variation in estimates after 2,000 steps (Gelman and Rubin 1992). A full model was run 10,000 steps, and posterior distributions for every parameter taken as the final 8,000; the mean was used as the best estimate and the central 95% quantiles as credible intervals for every parameter. All models were run using the programming language R (R Development Core Team 2013)

RESULTS

Distribution and Movements

Humpback whales were distributed in the entire archipelago, generally in shallow waters, with a peak in abundance in August and September (Fig. 1). The shortest and longest transmission times from the satellite data were 1 and 24 d, respectively. Whales stayed consecutively without leaving the defined core area for an average of 2.3 d (range 1–8 d); only six individuals returned and four of those for four consecutive times (Fig. 2A, B). Whales that returned stayed outside only for 1 or 2 d, showing the openness of the visiting population; for example, whale No. 1 stayed for 8 d inside the core area, left for 1 d, returned 1 d, left for 2 d, returned for 3 d, left 1 d, and returned for 2 d (Table 1). Maximum distance travelled was 2,023 km in 24 d; this whale (No. 12) stayed only 2 d inside the core area and nearly 20 d in the Gulf of Panama and reached latitude 4°N near Malpelo Island (Colombia) within 2 d (Fig. 2C). Three other humpback whales traveled as far as Gorgona Island, Colombia (latitude 3°N) visiting other known breeding subareas within days, while staying within an mean maximum distance of 63.5 km (range 11–199 km) from the mainland: Individual No. 4 traveled 1,228 km in 7 d, No. 8 traveled 823 km in 8 d, and No. 10 traveled 1,180 km in 11 d (Fig 2C).

Sightings and Resightings

We identified 295 distinct animals based on dorsal fin markings, including 185 solitary adults, 52 mothers (with a calf), and 58 calves (with a mother). The six extra calves relative to mothers were due to three cases where calves were identified but the nearby mother was not, and three females who had calves in two different years.

Table 1. Movement of 15 humpback whales (*Megaptera novaeangliae*) tagged during August 2009 in Las Perlas Archipelago, Panama, showing number of consecutive and returning days inside and outside of the core area. Asterisk indicates whales that traveled to other breeding subareas (as Fig. 2C).

No.	PTT	Tagged date	Transmission days	Distance traveled (km)	Inside	Outside
1	87721	27	22	1,039	8/1/3/2	1/2/1
2	87722	25	1	17	1	
3	87723	25	11	2,001	1/4/2/1	1/1/1
4	87725*	26	7	1,228	1	
5	87726	25	2	326	1	
6	87727	25	1	36	1	
7	87731	25	1	71	1	
8	87734*	26	8	823	1	
9	87736	26	8	471	1/5	2
10	87738*	25	11	1,180	1	
11	87739	23	6	184	6	
12	87740	26	24	2,023	2	
13	87741	27	17	680	6/4/3/1	2/1/1
14	87742	23	7	271	2/4	1
15	87743	23	13	740	2/5/1/3	0/1/2

There were 51 other adults whose flukes we could identify, but whose dorsal fin we did not photo-identify; those 51 might overlap with the group of 295 identified by dorsal fin.

Of the 295 animals known by dorsal fin, 243 were never resighted, either in the same year or in later years, and 40 were resighted just once; only 12 animals were seen on three or more days. One animal was seen in three different years, a solitary adult seen in 2006, 2007, and 2009, and 11 solitary adults plus 7 mothers were seen in two years; the remaining 218 adults were seen in only one year. Three females were seen with calves in two different years, including two with calves in consecutive years.

Within a single season, no solitary whale was resighted ≥ 5 d after its initial sighting, out of 278 d on which it could have happened. Calves, on the other hand, were seen up to 7 d apart (just 1 of 22 opportunities ≥ 6 d).

Population Size

The total population of solitary adults using the study area was over 200 in the 3 yr with most observations (Table 2). The minimum 95% credible estimate was >100 in 4 of 5 yr (Table 2). Since this population was open, the total is quite a bit higher than the number present on any one day, which averaged 45–55, with no difference between years. There was, however, substantial daily variation in the number of solitary adults present, with the SD across days $\sigma_N = 13$.

The estimated number of calves was 25–50 in each year, with 18 present on any single day (Table 2). Credible intervals were wide, however, owing to limited sample sizes, and the minimum number identified each year is nearly as informative as the model estimates.

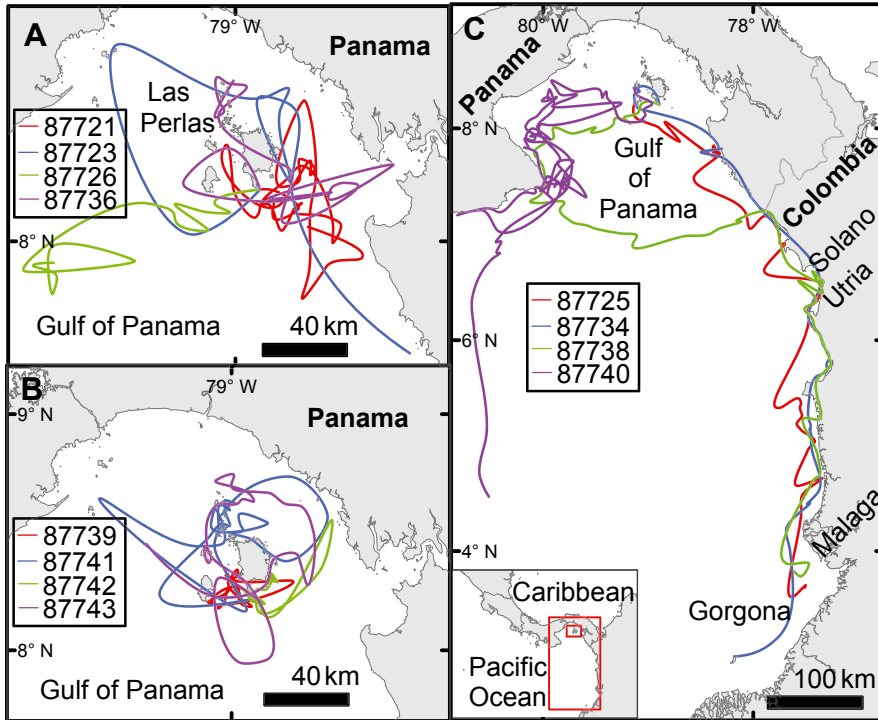


Figure 2. Satellite tracks of 15 individual humpback whales (*Megaptera novaeangliae*) tagged between 21 and 26 August 2009 in Las Perlas Archipelago, Pacific Panama, showing movements inside and outside of core breeding area and to areas in Colombia (see Table 1 for details).

Table 2. Observed and estimated number of solitary adults and calves at the Perlas Archipelago, 2004–2009. Days = number of days on which whales were observed (out of 10 total days observing). Observed/d = mean number of animals observed per day. Observed season = total number identified in all observations during one season. Estimated abundance season = estimated number of animals using the study area during the observation period in each season, with 95% confidence limits.

Year	Days	Observed/d		Observed season		Estimated abundance season	
		Solitary	Calves	Solitary	Calves	Solitary	Calves
2004	3	1.3	0.7	12	6	95.0 (63,134)	25.2 (11,49)
2005	6	2.7	0.2	24	2	164.0 (120,222)	36.4 (14,73)
2006	9	5.9	2.7	56	25	243.9 (186,320)	47.7 (25,97)
2007	10	6.6	2.8	57	17	283.9 (224,368)	51.4 (18,105)
2009	8	4.7	0.7	46	8	221.3 (170,290)	43.9 (16,89)

Departure and Detection Probabilities

In solitary animals, the estimated daily probability of detection was 0.12, and of departure 0.48, indicating nearly half the animals present on one day were gone by

the next. In calves, detection was slightly higher at 0.15 but departure much lower, at 0.25. Credible intervals for the two groups were wide and overlapping, however. Further details of model results for solitary animals and calves, including all daily parameter estimates, are presented in Appendices S1–S3.

Population Estimate Across Seasons

Across all years, including 2003, the estimated number of adults using the study area, including solitary as well as mothers, was 1,041 (credible interval 664–1,546). The estimated departure probability, indicating the proportion of animals present in one year but not returning the next, was 0.49, but with very wide credible intervals (0.17–0.74).

Migratory Connectivity

A total of 139 flukes were used for catalogue comparisons. Eight of the animals identified in Panama were matched to animals seen in Area I (120°W–60°W) in the Southern Hemisphere, which stretches from the Antarctic Peninsula to the western Bellingshausen Sea (IWC 1998). These animals were sighted mainly between the coast of the Antarctic Peninsula and South Shetland Island and eastward toward Elephant Island (~55°W) (Allen *et al.* 2011), with the exception of one animal photographed west of the Antarctic Peninsula (80°W–60°W, Ensor *et al.* 2000). In addition, one animal identified in Panama was sighted in the Magellan Strait off southern Chile for almost 10 consecutive years, for a total of nine sightings in feeding areas (Table 3). Four of these nine individuals also were commonly sighted in Colombia in different years and one in Ecuador (Table 3).

DISCUSSION

Migratory Connections

Humpback whales have a wide distribution along the coasts of Central and South America during the austral winter, including the coasts of Costa Rica, Panama, Colombia, Ecuador, and Peru (Stone *et al.* 1990, Acevedo and Smultea 1995, Flórez-González *et al.* 1998, Stevick *et al.* 2004, Rasmussen *et al.* 2007). In Panama, Las Perlas Archipelago is an important area for breeding and calving, and our data indicate that at least some whales come to Panama from feeding areas in the Antarctic Peninsula (Area I) in the Southern Hemisphere.

Our results include a second resighting for a whale migrating between Panama and the Magellan Strait for several consecutive years. The first sighting evidenced that Panama is an important breeding area for some whales feeding in Chile (Acevedo *et al.* 2007). This connectivity was previously confirmed between the feeding areas of the Magellan Strait, a high fidelity area, with breeding areas in Colombia (Capella *et al.* 2008). Many whales in our study were not resighted in any other part of the feeding areas, suggesting that many animals feeding near the Antarctic Peninsula have yet to be identified. The Antarctic Peninsula and the Magellan Strait are considered two separate feeding areas in Area I of the Southern Hemisphere (Olavarría *et al.* 2005), and it is possible that humpback whales visit Las Perlas from both sites.

Table 3. Sighting history of the whales that were matched between Panama (STRI) and other breeding and feeding areas from the Antarctic Humpback Whale Catalogue (AHWC) and the Magellan Strait, Chile (EMa) catalogue*.

STRI #	AHWC #	Date	Breeding	Summer
LP-013	0069	1999	–	Antarctic Peninsula
		2000	Colombia	–
		2004	Panama	–
LP-159	0207	1991	–	Gerlache Strait, Antarctic Peninsula
		1992	–	Antarctic Peninsula
		2007	Panama	–
LP-038	0453	1994	–	Yalour Islands, Antarctic Peninsula
		2000	Colombia	–
		2005	Panama	–
		2006	Panama	–
		2007	Panama	–
LP-011	1989	2002	Colombia	–
		2003	Panama	–
Gr1210805-1	2000	2002	Colombia	–
		2002	–	Antarctic Peninsula
		2005	Panama	–
LP-197	2692	2003	–	Antarctic Peninsula
		2007	Panama	–
LP-129	3102	2000	–	Biscoe Islands, Antarctic Peninsula
		2006	Panama	–
LP-083	3320	2007	–	Cierva Cove, Antarctic Peninsula
		2006	Panama	–
LP-024	EMa-033*	1995, 1996, 2003	Panama	–
		2004	Colombia	–
		2001, 2003, 2004, 2005, 2006, 2008, 2009, 2010, 2011, 2012	Panama	–
			–	Magellan Strait, Chile
			–	–
LP-104	0117	1988	Ecuador	–
		1999	–	Gerlache Strait, Antarctic Peninsula

Some animals recaptured in Las Perlas were also resighted off Colombia, but none of them were resighted in the same year. Within season and between-year recaptures were uncommon in Las Perlas and Colombia. There are three possible explanations for this result: (1) Las Perlas is the final destination during short periods for most whales that winter in Central America and use the coasts of Colombia and Ecuador as a migratory route (but see Rasmussen *et al.* 2007); (2) humpback whales can move between breeding areas (Flórez-González *et al.* 1998), and Panama may be an extension of their primary breeding areas (*i.e.*, the coasts of Colombia and Ecuador) (Rasmussen *et al.* 2007); and (3) resighting is generally low due to low site fidelity in breeding areas (Flórez-González 1991, Capella *et al.* 2008, Felix and Botero-Acosta 2011, Fleming and Jackson 2011). Further satellite tagging could help clarify these intra-annual connections; preliminary satellite tracking (details in Guzman *et al.*

2012) has shown that three whales tagged in Las Perlas in Panama followed the Colombia coastal contour to known breeding areas in Solano, Utria, Malaga, and Gorgona (Caballero *et al.* 2001) and traveled as far as 600 km within 3–11 d in the middle of the breeding season (Fig. 2).

In this study, dorsal fin identification was a valuable tool for local identification of whales, but it was not useful for comparisons with other catalogues. Identification by fluke has long been considered more reliable than dorsal fin identification (Katona and Whitehead 1981). However, Blackmer *et al.* (2000) recently reported that the dorsal fin tends to change less over time, and they concluded that the dorsal fin provides the best way to identify humpback whales, especially calves. Dorsal fin shape and markings have been used successfully to identify other large cetaceans, including gray whales (*Eschrichtius robustus*) (Jones 1990), fin whales (*Balaenoptera physalus*) (Aglar *et al.* 1990), and small cetaceans (Würsig and Jefferson 1990).

Capture-recapture Estimate

In the southeastern Pacific, the mark-recapture method has been used to estimate population sizes of humpback whales in Colombia and Ecuador (Flórez-González 1991, Scheidat *et al.* 2000, Felix *et al.* 2011) but not in Central America. The results presented here are the first preliminary estimates for a breeding area in Central America, specifically Las Perlas Archipelago, Pacific Panama, during the austral winter. We found annual population sizes of 200–300 solitary adults and another 25–50 calves, plus their mothers over our 10 d observation periods. The populations were conspicuously open, particularly the solitary animals, with a high fraction departing each day; we never saw the same animal >5 d apart. The population is in rapid flux, meaning that longer observation periods lead to more animals; this is the main reason the 2004 population estimate is much lower than those in other years. Credible intervals for population sizes were broad, though, reflecting the low resighting frequency, nevertheless, these results are similar to those found at Gorgona Island, Colombia (170–450) (Flórez-González 1991) and Ecuador (405, 95% CI 221–531) (Scheidat *et al.* 2000).

By pooling our data across seasons, we estimated that the population size at Las Perlas is just over 1,000 animals. This number represents one-seventh of the total population recently estimated by capture-recapture for the stock G breeding area (ca. 6,000–7,000) (Felix *et al.* 2011) and of the 6,991 humpback whales (CV = 0.32) estimated based on a visual line transect for Area I (western Antarctic Peninsula) carried out by CCAMLR (Fleming and Jackson 2011). If the Las Perlas population is solely a subset of those two groups, a high proportion of the population used Las Perlas during the five-year period. All of these data suggest that Las Perlas is visited by a significant number of animals.

We estimated 25–50 calves present around Las Perlas each year, though calves were not resighted often suggesting low fidelity, and estimates are poorly constrained. Nevertheless, we identified 58 different calves over 5 yr, and 25 in 2006 alone. Calves made up 15%–25% of the population each year, comparable to results from Gorgona Island in Colombia (Flórez-González 1991) and Ecuador (Felix and Botero-Acosta 2011). The presence of a high number of calves indicates that Las Perlas is an important area for females and their calves, similarly to other areas to the south.

Since our photo-resighting observations covered only 10 d each year out of a season lasting about 4 mo, with an open population from which many animals are coming

and going, estimates of population size must be considered biased downward. Additional distinct animals were likely to arrive after our observations ended. We estimated 50 solitary adults present per day, with nearly half of those departing, replaced by a similar number. Had this continued many more weeks, clearly the total number of animals visiting is much higher than our estimates of 200–300. The pooled estimate across seasons, just over 1,000 solitary animals, may reflect this higher number. Had our observations continued for longer, we very likely would start detecting animals returning to the study area, and the nature of the model assumptions would change.

We anticipated that calf populations would turnover less than solitary animals, and this was supported by a lower daily departure rate. The seasonal estimate of calves is still an underestimate, but perhaps not by much. Statistical confidence in all calf results was weak and results should be considered as rough estimates.

Satellite Tracks

The individuals we were able to track with satellite tags support the conclusion of mark-recapture analysis that the population around Las Perlas is fluid. Moreover, three whales we identified in Panama were seen near Colombia in the Gulf of Tribugá, Malaga Bay, and Gorgona Island, approximately 320, 520, and 600 km away from Las Perlas, respectively. It is thus clear that animals move quickly over areas much larger than the Perlas study site. According to Flórez-González *et al.* (1998), there is a regular interchange of animals between breeding areas in the southeastern Pacific, similar to the observed with the three animals tagged in Panama (see Fig. 1). Ideally, population estimates should include this wide area (Cerchio *et al.* 1998).

Tagged animals also returned after departing, though in all cases within 2 d, which from a model perspective is barely different from remaining in the study area throughout. In contrast to photo-identified solitary animals, which were never seen >5 d apart, four of the tracked whales were within the study area for most of the time over >10 d. However, our photo records were restricted to 10 d intervals, and several of the tracked animals did indeed depart immediately and never return. Mother-calf pairs seemed less mobile, with fewer departing the study area during our observations, but data were insufficient to confirm this. Satellite tracking should be used to inform estimates on population fluidity, defined by the daily departure probability in the open population model. Considering the 11 animals tracked for at least 6 d, four departed after 2 d and did not return, a fraction roughly consistent with the mark-recapture estimate that 48% depart each day. The other seven individuals moved in and out, and observations (transmissions) ended with them inside the study area; in the mark-recapture model, these animals effectively never left. With considerably more satellite tracking, the mark-recapture estimates could be informed by direct knowledge about movements. We plan future photo-identification efforts spread over longer periods in order to better detect movements, particularly of calves, using simultaneous satellite and photo records to inform estimates of residency and movement.

Humpback whales in Pacific Panama appear to concentrate their activities in two areas: Las Perlas Archipelago (present study) and the Gulf of Chiriquí (Rasmussen *et al.* 2007), and our estimates at Las Perlas may reflect only a fraction of the entire whale population that winters off the coast of Panama. Further collaborative studies are needed to provide better estimates of population size in Pacific Panama, and

long-term monitoring is essential in order to detect and understand changes and potential risks to the population, particularly calf production. Our current study provides an antecedent to such monitoring.

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SUPPORTING INFORMATION

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Appendix S1. Daily parameter estimates from mark-recapture analysis of solitary humpback whales, Perlas Islands, Panama. The model used was the open-population Cormack-Jolly-Seber, allowing animals to depart the study area each day with probability ϵ ; the number of animals present in the study area each day (N), departing prior to the next day (L), and ϵ all were allowed to vary following Gaussian (N , L) or logit-Gaussian (ϵ) hyperdistributions. The number entering the study area prior to each day (R), was calculated by subtraction and was not modeled with a hyperdistribution. Daily variation in ϵ was scant, that is, the model almost collapsed to a constant ϵ . Observed = number of distinct animals photographed each day. CI = 95% credible intervals. Hyperparameters and the estimated detection probability δ , which was modeled as constant every day, are given in Appendix S2. Gaps in the sequence (e.g.,

16 August 2005) are days animals were not observed, so on those days L , R , and ε refer to two-day totals; since the model allowed daily variation in all three parameters, this violates no assumptions.

Appendix S2. Hyperparameters for daily population size N , departures L , detection probability δ , and departure probability ε from the mark-recapture model for solitary humpback whales, Perlas Islands, Panama. Credible intervals are given in parentheses. Since no annual term was included, there is only one hypermean (μ) and hyperstandard deviation (σ) per variable. Since daily arrivals were calculated by subtraction, no hyperdistribution was used for R . In the case of departure probability, the hyperparameters were estimated for a Gaussian distribution of $\text{logit}(\varepsilon)$, but the values presented here have been back-transformed (inverse-logit) to probabilities. In the case of $\text{SD}(\varepsilon)$, this meant adding the mean of the logit to the SD of the logit then back-transforming and subtracting the back-transformed mean. There was no hyperdistribution for δ : it was assumed constant every day, and the value under μ is thus not a hypermean but simply the best estimate.

Appendix S3. Daily parameter estimates from mark-recapture analysis of humpback whale calves, Perlas Islands, Panama. The model used was the open-population Cormack-Jolly-Seber, allowing animals to depart the study area each day with probability ε . As for solitary animals, a model was attempted allowing daily variation in the number of animals present in the study area each day (N), departing prior to the next day (L), and ε , but for calves, all hyperdistributions collapsed to point estimates, meaning the data were insufficient to detect daily variation. Without hyperdistributions, the estimates presented are simply the best point estimates of daily numbers.