Note



Short-Term Recovery of Humpback Whales After Percutaneous Satellite Tagging

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ABSTRACT Long-term re-sightings of individuals used in satellite telemetry research are important for determining the effects of tagging on large whales. We evaluated the initial behavioral response, healing process, and short-term reproductive behavior and success of 7 percutaneous-tagged humpback whales (4 M, 3 F) monitored for 4-10 years in the feeding ground of the Magellan Strait, Chile. We took post-tagging photographs incidentally every year during re-sighting expeditions. We did not observe an initial reaction to tagging or sudden change in behavior or direction of movement. Two of the females had 3 and 2 calves before tagging, and one of them had 2 calves every 3 years after tagging. Post-tagging annual site fidelity remained nearly 100%. We did not observe initial tag protrusion in any individual. Four whales (57%) showed no signs of initial tissue damage shortly after tagging; we observed tissue shedding in 2 individuals, and traces of blood on 1 whale. Complete wound healing apparently occurred in all individuals within the first 2 years after tagging, and 5 of them showed no scars 3–6 years later. Four individuals showed small to medium (<5 cm) tumor-like lumps for several years after tagging, but some were undistinguishable from other natural lumps (e.g., barnacles) observed near the tag injury. Overall, tagging did not seem to affect reproductive success or the behavior of individuals during and immediately after tagging. The development of new technologies always can pose a risk to animal welfare, thus studies such as this one are important for carefully evaluating the effects of tagging on whales. © 2017 The Wildlife Society.

KEY WORDS animal welfare, humpback whale, IACUC, Megaptera novaeangliae, movement behavior, satellite tracking, Magellan Strait, Chile.

The behavior of the humpback whale (*Megaptera novaean-gliae*) and its interactions with human activities along coastal habitats have been the target of research for decades. Satellite tracking of individual whales has increased our understanding of the animal's migratory routes of thousands of kilometers and its home range and seasonal habitat use across several ocean regions, resulting in valuable information for protection and conservation of the species (Mate et al. 1998, Dalla-Rosa et al. 2008, Garrigue et al. 2010, Hauser et al. 2010, Kennedy et al. 2013).

At the more regional level in the eastern Pacific, 2 populations of humpback whales migrate seasonally from high-latitude feeding areas in the northern and southern hemispheres to low-latitude tropical breeding areas along coastal and insular habitats (Clapham and Mead 1999). Both wintering populations overlap in Central America (Acevedo and Smultea 1995, Flórez-González et al. 1998, Rasmussen et al. 2011). To date, few studies of humpback whales in this region have used satellite telemetry (Mate et al. 1998,

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Lagerquist et al. 2008, Guzman et al. 2012, Félix and Guzman 2014), but tagging is anticipated to increase.

Walker et al. (2011) made a convincing argument about the potential short-term physiological effects of tagging and its effects on behavior and the survival rates of small marine mammals, but data for large whales are limited (but see Gendron et al. 2015). Therefore, researchers and research institutions should comply with the minimum requirements for improving animal welfare when conducting studies of marine mammals and implement the guidelines of the Institutional Animal Care and Use Committees (IACUC). Reporting changes in animal behavior and health during and after tagging is ethical and critical (Bekoff 2002, Wilson and McMahon 2006, Walker et al. 2011, Moore et al. 2013) to developing new technological devices and deployment tools (Mate et al. 2007, Balmer et al. 2013, Robbins et al. 2013). In addition, Gendron et al. (2015) pointed out the importance of long-term sighting history of individuals coupled with satellite tracking data to evaluate the effects of tagging on large whales.

One goal of our tagging project in the Magellan Strait in Chile initiated in 2009 and elsewhere in the region (Costa Rica, Panama, Colombia, and Ecuador) was to determine whether our methods comply with the Smithsonian IACUC. We evaluated the initial behavioral response, healing process, survival rates, and short-term reproductive behavior and success of 7 percutaneous-tagged whales incidentally monitored for 4–10 years. We obtained nearly 2 decades of sighting records from each individual's annual visits to the feeding ground in the Magellan Strait (Capella et al. 2012), which provided a unique opportunity for the assessment of animal welfare.

STUDY AREA

The eastern South Pacific humpback whale population or breeding Stock G (International Whaling Commission 1998) is distributed along neritic waters from northern Peru ($\sim 4^{\circ}$ S) to Costa Rica ($\sim 12^{\circ}$ N) with known breeding sites of concentration in northern Peru (Guidino et al. 2014), Ecuador (Scheidat et al. 2000, Félix et al. 2011), Colombia (Flórez-González 1991), Panama (Rasmussen et al. 2007, Guzman et al. 2015), and southeastern Costa Rica (Rasmussen et al. 2007). The stock has ≥ 3 summer destinations for feeding, particularly in the Patagonia Fjords, the Magellan Strait, the Corcovado Gulf in Chile, and the Gerlache Strait (64°30'S, 62°20'W) in western Antarctic Peninsula (Gibbons et al. 2003, Stevick et al. 2004, Acevedo et al. 2007, Hucke-Gaete et al. 2013). The entire population uses nearly 9,000 km of coastline and is estimated at approximately 6,000-7,000 animals (Félix et al. 2011).

We tagged whales at the Francisco Coloane Marine Protected Area, which encompasses the areas of Whale Sound, Magellan Strait, and Charles Islands off Carlos III Island (53°37'S, 72°21'W). The feeding concentration of humpback whales in the Strait of Magellan can be considered a seasonal subpopulation of the Stock G. Humpbacks have been systematically studied for 18 consecutive feeding seasons from 1999 to 2016 in the strait, with approximately 85% site fidelity (Gibbons et al. 2003; Capella et al. 2008, 2012). Presently, 177 individuals have been identified from photographs of their unique natural marks and pigmentation and scars on the ventral fluke and dorsal fin (Katona and Whitehead 1981), and a seasonal abundance of about 120 individuals is estimated (Capella et al. 2012), representing about 2.5% and 1.7%, respectively, of estimated population for Stock G (Félix et al. 2011). Previous research efforts have sexed 105 individuals using DNA techniques. Every year 4 to 8 new individuals enter to this subpopulation.

METHODS

Tagging Procedures

We used satellite tags (SPOT tag model AM-S193; Wildlife Computers, Redmond, WA, USA) deployed with a modified pneumatic line-thrower (model ARTS; Restech, Bodø, Norway) in 2009 and 2013. Transmitter life is estimated to be 550 days, but deployment length is limited by tag retention rather than battery capacity. Factory transmitters consisted of a 2-cm-diameter stainless steel tube case coupled to a custom-made stainless steel spear with a 3-cm triangular double-edged blade tip containing 1 to 3 pairs of 5-cm barbs placed at 90° to each other for a length of 17.5– 22 cm. Tag weight (transmitter and spear) was approximately 380 g. We tagged whales from rigid-hulled inflatable boats at a maximum distance of 2–3 m from the whale, nearly perpendicular to dorsal fin. When necessary we adjusted air pressure in the pneumatic launcher, which ranged from 10 to 15 bars (10.2–15.3 kg/cm²). We attached the transmitters to the whales about 10–25 cm below the dorsal fin on the right or left side to minimize potential injury to the animals and changes in behavior, as standardized and previously suggested in different studies (Zerbini et al. 2006, Gales et al. 2009, Guzman et al. 2012, Robbins et al. 2013). Our tag was not designed to penetrate deep and anchor in muscle and connective tissue (Robbins et al. 2013). A detailed description of tag configuration and tagging procedures is provided by Guzman et al. (2012).

Tags were chemically sterilized and plastic wrapped in the laboratory. In the field, we sprayed the tag and spear with neomycin sulfate-clostebol acetate (Neobol[®]) before deployment. The Animal Care and Use Committee of the Smithsonian Tropical Research Institute reviewed and approved the tagging procedures. The Smithsonian directives ensure the humane care and use of all animals involved in research, as required by the United States Animal Welfare Act; United States Government Principles for the Utilization and Care of Vertebrates Animals Used in Testing, Research, and Training; and other policies. The research was conducted in accordance with the Guide for the Care and Use of Laboratory Animals (National Research Council 2011). We conducted this study under research permits issued by the Government of Chile's Sub-Secretaria de Pesca to Universidad de Magallanes, Punta Arenas (940-07).

Behavioral Observations

We took photographs incidentally every year during sighting expeditions as part of a long-term monitoring program of humpback whales feeding in the Magellan Strait, following standard protocols described elsewhere (Capella et al. 2008, 2012). Briefly, the same researcher made behavioral observations between January and April-May of each year for over a decade (1999-2016), developing a baseline behavior for nearly all animals visiting the area. The researcher made observations from an inflatable boat for >500 vessel-days at random schedules and weather permitting. In addition, researchers made land-based observations using 10×40 binoculars and a theodolite (model NE-205; Nikon, Tokyo, Japan) located <1 km from the subject and at 50 m above sea level. Sighting information included date, location, photo identification number for fluke and dorsal fins, group size, and behavior (e.g., movement, changes in speed, feeding, napping, harassment by predator, spyhopping [holding vertical position out of the water showing head], lobtailing [lifting fluke up and down out of the water], flippering [slapping flippers against water]). When individuals were new to the area, researchers obtained a skin biopsy with a crossbow for obtaining sex and genetic information.

Recording pre- and post-tagging behavioral response of whales followed a regular protocol (years before, immediately before and after tagging, and years after), which included characterization of baseline behavior for 4 aspects:

Table 1. Life-history summary (1999–2016) and short-term post-tagging (2009–2016) summary of 7 humpback whales satellite tagged in the Magellan Strait, Chile.

Tag no.	Whale catalog no.	First year reported	Sex	Overall site fidelity (yr)	Calving pre-tagging (yr)	Tagging date	Post-tagging sightings (yr)	Calving post-tagging (yr)
68547	007	1999	F	17	2003	4 Mar 2009	2010-2016	2012
					2005			2015
					2008			
87728	060	2005	Μ	11		6 Mar 2009	2010-2016	
87733	085	2007	F	7	None	6 Mar 2009	2010-2011	None
							2013	
							2015-2016	
87729	043	2003	Μ	11		8 Mar 2009	2010-2016	
68545	074	2006	Μ	11		11 Mar 2009	2010-2016	
129270	005	2003	F	13	2009	10 May 2013	2014-2016	None
					2013	,		
129277	081	1999	Μ	10		10 May 2013	2014-2016	

swimming speed (slow [<5 km/hr], medium [5–12 km/hr], fast [>12 km/h]) measured by boat speed; direction of movement (or erratic in a delimited sector of 0.5-km radius); immersion and on surface time; and occurrence of indifferent or evasive behavior to the boat. In addition, we recorded any sudden behavior (e.g., feeding, breaching, flipper slap). The amount of time to collect information was weather- and whale-dependent but regularly fluctuated among 30-60 minutes for pre-tagging observations and 20-120 minutes for post-tagging observations. We collected similar behavioral records during sighting of individuals at any time logistically possible in the next days and seasons. We considered a wound to be totally cured when no necrotic cutaneous tissue, blood, shredded tissue, or subcutaneous blubber (collagen fibers) was visible on the tagged area.

RESULTS

We tagged 7 adult whales (>14 m long) cataloged previously in the area: 3 males and 2 females in 2009 and 1 female and 1 male in 2013. We did not observe any initial reactions (jumping, fluke slapping, body bending) to tagging or sudden changes in direction aside from the normal increase in speed when the whales sensed an approaching boat (Mate et al. 2007). We followed whales for several minutes after tagging and did not observe changes in social behavior patterns (e.g., breaching, spyhopping, lobtailing, flippering) even for solitary individuals, a mother-calf pair, or whales inside a social group with several other individuals.

Overall site fidelity for all individuals averaged 11.4 years (range = 7–17 yr; Table 1), with an average of 5.9 years (range = 2–10 yr) for the pre-tagging period. Two of the females had 3 and 2 calves before tagging, and one of them (no. 007) had 2 calves every 3 years after tagging (Table 1). Nearly all individual whales returned to the area each year after tagging for the duration of the study, with the exception of 1 female (no. 085) that missed 2 years after tagging (Table 1). The 4 males returned yearly after tagging. Subsequently, post-tagging survivorship for all 7 whales was 100%, and annual site fidelity remained nearly 100%. None of the re-sighted tagged whales had the satellite tag attached to the body.

Yearly detailed photographic records of tagged whales were not possible because of logistical conditions, and in all cases the best quality photos analyzed were taken a few years after tagging. Therefore, the availability of yearly photographs varied considerably among the individuals (Table 2). We did not observe initial tag protrusion in any individual. Four whales (57%) showed no signs of initial tissue damage (bleeding, tissue shredding) immediately after tagging; we observed tissue shedding in 2 individuals, and saw traces of blood on 1 whale. Complete wound healing apparently occurred in all individuals within the first 2 years of tagging, and 5 of them showed no scars 3-6 years later (Table 2). Only 4 individuals showed small to medium (<5 cm) tumor-like lumps for several years after tagging; some of these lumps were indistinguishable from other natural lumps (e.g., barnacles) observed near the tag injury, and they disappeared completely in 3 of the whales (75%) between 3 and 6 years (Table 2).

In addition, 5 whales showed body depressions or divots in the injury area 2–3 years after tagging, and only 2 continued showing the sign through the end of the study (Table 2). The only female sighted with 2 calves after tagging (no. 007) had a medium size swelling in 2012 with the first calf, and no swelling or depression with the second calf in 2015 (Fig. 1).

Remarkably, the swelling in 1 male (no. 074) tagged in 2009 was present for 2 consecutive years, was not visible in the third year (2012), and then became visible again from the fourth year through 2016 (Fig. 1). We observed a similar scar pattern, suggesting a secondary injury or re-opening of the initial wound years later. This individual was the only whale with a tag that penetrated slightly beyond the stopper (because of higher air pressure used in the launcher), possibly affecting deeper connective tissue; the tag may have detached from the body of the whale, leaving some broken 5-cm barbs to produce fibrosis.

DISCUSSION

Weather conditions often affected logistics and precluded continuous monitoring of tagged individuals across different seasons. Sighting of tagged individuals was always possible, but the whales often showed only flukes or the untagged side, making it impossible to obtain a precise and continuous photographic record for all years. Consequently, external

Table 2. Short-term response (presence [P] or absence [A]) of skin tissue and wound healing time (monitored year) of 7 humpback whales tagged in 2009 and 2013 in the Magellan Strait, Chile. We also indicate whether wound was a small swell <5 cm (S) or a medium swell 5-15 cm (M).

Whale catalog no.	Tagged year	Post-tagging photography record (yr)	Skin or blood trace	Swelling (lumps)	Depression (divot)	Wound healing (%)	Scar
007	2009	2012	P (2009)	PS (2012)	PS (2012)	100 (2012)	A (2012)
		2013		PS (2013)	PS (2013)		
		2015		A (2015)	A (2015)		
		2016					
060	2009	2011	P (2009)	A (2011)	PS (2011)	100 (2011)	PS (2011)
		2013		A (2013)	PS (2013)		PS (2013)
		2015		A (2015)	PS (2015)		PS (2015)
		2016		A (2016)	PS (2016)		PS (2016)
085	2009	2015	P (2009)	A (2015)	A (2015)	100 (2015)	A (2015)
		2016		A (2016)	A (2016)		A (2015)
043	2009	2015	A (2009)	PS (2015)	PS (2015)	100 (2015)	A (2015)
		2016		A (2016)	A (2016)		A (2016)
074	2009	2010	A (2009)	PS (2010)	A (2010)	100 (2010)	PS (2010)
		2011		PS (2011)	A (2011)		PS (2011)
		2012		A (2012)	PS (2012)		A (2012)
		2015		PM (2015)	A (2015)		PS (2015)
		2016		PM (2016)	A (2016)		A (2016)
005	2013	2015	A (2013)	PS (2015)	PS (2015)	100 (2015)	PS (2015)
		2016		A (2016)	PS (2016)		A (2016)
081	2013	2015	A (2013)	PS (2013)	A (2015)	100 (2015)	PS (2015)
				PM (2015)			

wound healing could have occurred in a shorter time than the couple of years observed here. However, the internal injury inflicted on the whales, evident as a small swelling, remained visible for a number of years, only receding after a few years in 5 of the 7 tagged animals. As mentioned by Mate et al. (2007),

veterinarians are not sure if an infection or a foreign encapsulated object causes the observed swelling. However, Moore et al. (2013) reported that implanted rigid devices in the blubber-muscle interface "could have secondary health impacts."

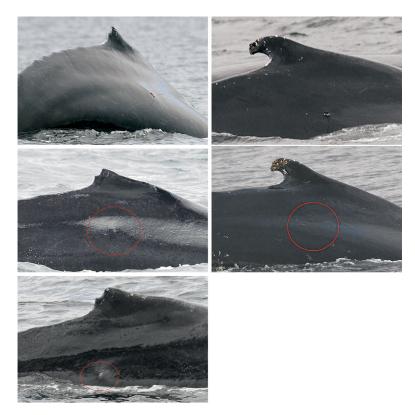


Figure 1. Recovery time series of humpback whales tagged on March 2009 in the Magellan Strait, Chile. Tag implanted on male (no. 074) slightly beyond stopper (upper left column), healing with swelling by 2011 (mid-left column), and wound opened by 2015 (lower left column); tag implanted on female (no. 007) with 2 calves post-tagging (upper right column) with full wound recovery by 2016 (bottom right column).

Walker et al. (2011) pointed out the lack of information on the whale's natural behavior (movement, feeding, growth, health) after tagging. Even though follow-up observations were possible for only a small amount of time (30–60 min), tagging did not appear to affect the immediate behavior of individuals during and after tagging or any demographic parameter of the population, including survivorship. All 3 females returned nearly every year, showing normal feeding behavior and never in poor health. Our results suggest that the tag does not impair reproductive behavior, as shown by the female that returned with a new calf every 3 years after tagging. Lack of reproduction in 2 of our whales does not indicate reproductive failure, at least for this population, considering that of 51 adult females monitored within 2-17 years in the Magellan Strait, 31.4% were never observed with a calf (Capella et al. 2012). However, we recognize the potential impacts of tagging on whale health and breeding success as previously suggested (Gendron et al. 2015).

This study is not intended to be a compressive evaluation of the effects of tagging on the welfare of large whales, and we recognize the limitations imposed by the small number of whales observed. Nevertheless, we add new results from a new region in the Southeast Pacific that can be compared to other long-term studies of humpback whales (Robbins et al. 2013, Best et al. 2014) in support of the importance of satellite telemetry research and innovation to improve animal welfare. However, Moore et al. (2013) cautioned on the invasive nature of larger tags penetrating below the connective tissue sheath. New tags have been designed to penetrate nearly 30 cm beneath the skin to anchor in muscle and connective tissue. Tags also have been implanted at some distance behind the head (Best et al. 2014), and in humpback whales ahead of the anterior insertion of the dorsal fin (Mate et al. 2007, Gales et al. 2009), a few centimeters below the base of the dorsal fin (Guzman et al. 2012, Robbins et al. 2013), and in other suboptimal areas (Robbins et al. 2013). Therefore, detailed anatomical and pathological studies are required to complement and advance tagging of cetaceans (sensu Lockyer et al. 1985, Pfeiffer and Jones 1993, Clapham and Mead 1999, Hof and Van Der Gucht 2007, Moore et al. 2013).

The development of new technologies always can pose a risk to animal welfare, and this issue only recently began to be carefully evaluated and communicated to the scientific community (Mate et al. 2007, Walker et al. 2011, Robbins et al. 2013, Best et al. 2014, Gendron et al. 2015). Long-term monitoring of tagged whales as this study and others (Mate et al. 2007, Gendron et al. 2015, Szesciorka et al. 2016) is important to be considered under different ocean conditions and populations. Mate et al. (2007) clearly stated that effective management measures are nearly impossible to implement without basic information about several aspects of the life history of humpback whales (and other species), including population structure, migratory routes, and seasonal distribution. Therefore, assessment of any population must involve large temporal and spatial scales and myriad potential human interventions. Satellite telemetry has increased our understanding of several behavioral aspects of whales at the right scale and between feeding and breeding

areas, and in many cases it has produced the data required to inform policy on important local and regional management problems (e.g., Guzman et al. 2012).

Future studies need to include individuals without a thick blubber layer where the recovery of wounds may be different to the one described here. The low fidelity rate observed in breeding areas, usually reported at <25% (Flórez-González 1991, Capella et al. 2008, Félix et al. 2011, Guzman et al. 2015), is one difficulty affecting monitoring of individual whales. Nonetheless, a mother tagged in Salinas (Ecuador) in 2013 returned in 2015 with a new calf and with the tag wound completely healed (Guzman and Félix 2017).

MANAGEMENT IMPLICATIONS

Tagged whales recovered relatively fast and with no changes in animal behavior in our study area. The sizes of our tags were small enough to expect such results and should be compared with the new generation of larger tags. We recommend conducting detailed anatomical and pathological studies of the different whale species to define the most suitable upper body areas (e.g., relative to blubber thickness and underlying muscle tissue) for tagging that are consistent with maintaining animal welfare.

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LITERATURE CITED

- Acevedo, A., and M. A. Smultea. 1995. First records of humpback whales including calves at Golfo Dulce and Isla del Coco, Costa Rica, suggesting geographical overlap of northern and southern hemisphere populations. Marine Mammal Science 11:554–560.
- Acevedo, J., K. Rasmussen, F. Félix, C. Castro, M. Llano, E. Secchi, M. Saborío, A. Aguayo-Lobo, B. Haase, M. Scheidat, L. Dalla-Rosa, C. Olavarría, P. Forestell, P. Acuña, G. Kaufman and L. A. Pastene. 2007. Migratory destinations of humpback whales from the Magellan Strait feeding ground, Southeast Pacific. Marine Mammal Science 23:453–463.
- Balmer, B. C., R. S. Wells, L. E. Howle, A. A. Barleycorn, W. A. McLellan, and D. A. Pabst. 2013. Advances in cetacean telemetry: a review of single-pin transmitter attachment techniques on small cetaceans and development of a new satellite-linked transmitter design. Marine Mammal Science 30:656–673.
- Bekoff, M. 2002. Ethics and marine mammals. Pages 398–404 in W. F. Perrin, B. Würsig, and J. G. M. Thewissen, editors. Encyclopedia of marine mammals. Academic Press, San Diego, California, USA.
- Best, P. B., B. Mate, and B. Lagerquist. 2014. Tag retention, wound healing, and subsequent reproductive history of southern right whales following satellite-tagging. Marine Mammal Science 31:520–536.
- Capella, J., J. Gibbons, L. Flórez-González, M. Llano, C. Valladares, V. Sabaj, and Y. Vilina. 2008. Migratory round-trip of individually identified humpback whales of the Strait of Magellan: clues on transit times and philopatry to destinations. Revista Chilena de Historia Natural 81:547–560.

- Capella, J. J., J. Gibbons, Y. A. Vilina, L. Florez-Gonzalez, V. Sabaj, and C. Valladares. 2012. Abundance population structure and fidelity of humpback whales in the Strait of Magellan, Chile. Report SHWP22. Scientific Committee of the 64th Annual Meeting of the International Whaling Commission. International Whaling Commission, 11 June–6 July 2012, Panama City, Panama.
- Clapham, P. J., and J. G. Mead. 1999. *Megaptera novaeangliae*. Mammalian Species 604:1–9.
- Dalla-Rosa, L., E. R. Secchi, Y. G. Maia, A. N. Zerbini, and M. P. Heide-Jøergensen. 2008. Movements of satellite-monitored humpback whales on their feeding ground along the Antarctic Peninsula. Polar Biology 31:771–781.
- Félix, F., C. Castro, J. Laake, B. Haase, and M. Scheidat. 2011. Abundance and survival estimates of the southeastern Pacific humpback whale stock from 1991–2006 photoidentification surveys in Ecuador. Journal of Cetacean Research and Management 3:301–308.
- Félix, F., and H. M. Guzman. 2014. Satellite tracking and sighting data analyses of southeast Pacific humpback whales (*Megaptera novaeangliae*): Is the migratory route coastal or oceanic? Aquatic Mammals 40:329–340.
- Flórez-González, L. 1991. Humpback whales, Megaptera novaeangliae, in the Gorgona Island, Colombian Pacific breeding waters: population and pod characteristics. Memoires of the Queensland Museum 20:291–295.
- Flórez-González, L., J. J. Capella, B. Haase, G. A. Bravo, F. Félix, and T. Gerrodette. 1998. Changes in winter destinations and the northernmost record of southeastern Pacific humpback whales. Marine Mammal Science 14:189–196.
- Gales, N. I., M. C. Double, S. A. Robinson, C. U. Jenner, M. I. Jenner, E. R. King, J. A. Gedamke, D. A. Paton, and B. Raymond. 2009. Satellite tracking of southbound East Australian humpback whales (*Megaptera novaeangliae*): challenging the feast or famine model for migrating whales. Scientific Committee of the 61st Annual Meeting of the International Whaling Commission. International Whaling Commission, 22–26 June 2009, Madeira, Portugal.
- Garrigue, C., A. N. Zerbini, Y. Geyer, M. P. Heide-Jøergensen, W. Hanaoka, and P. Clapham. 2010. Movement of satellite-monitored humpback whales from New Caledonia. Journal of Mammalogy 91:109–115.
- Gendron, D., I. Martinez-Serrano, A. Ugalde de la Cruz, J. Calambokidis, and B. Mate. 2015. Long-term individual sighting history database: an effective tool to monitor satellite tag effects on cetaceans. Endangered Species Research 26:235–241.
- Gibbons, J., J. J. Capella, and C. Valladares. 2003. Rediscovery of a humpback whale, *Megaptera novaeangliae*, summering ground in the Strait of Magellan, Chile. Journal of Cetacean Research and Management 5:203–208.
- Guidino, C., M. A. Llapapasca, S. Silva, B. Alcorta, and A. S. Pacheco. 2014. Patterns of spatial and temporal distribution of humpback whales at the southern limit of the Southeast Pacific breeding area. PLoS ONE 9(11):e112627.
- Guzman, H. M., R. Condit, B. Pérez-Örtega, J. J. Capella, and P. Stevick. 2015. Population size and migratory connectivity of humpback whales wintering in Las Perlas Archipelago, Panama. Marine Mammal Science 31:90–105.
- Guzman, H. M., and F. Félix. 2017. Movements and habitat use by southeast Pacific humpback whales satellite tracked at two breeding sites. Aquatic Mammals 43:139–155.
- Guzman, H. M., C. G. Gómez, and C. A. Guevara. 2012. Potential vessel collisions with Southern Hemisphere humpback whales wintering off Pacific Panama. Marine Mammal Science 29:629–642.
- Hauser, N., A. N. Zerbini, Y. Geyer, M. P. Heide-Jogensen, and P. Clapham. 2010. Movement of satellite-monitored humpback whales, *Megaptera* novaeangliae, from the Cook Islands. Marine Mammal Science 26:679–685.
- Hof, P. R., and E. Van Der Gucht. 2007. Structure of the cerebral cortex of the humpback whale, *Megaptera novaeangliae* (Cetacea, Mysticeti, Balaenopteridae). The Anatomical Record 290:1–31.
- Hucke-Gaete, R., D. Haro, J. P. Torres-Florez, Y. Montecinos, F. Viddi, L. Bedriñana-Romano, M. F. Nery, and J. Ruiz. 2013. A historical feeding ground for humpback whales in the eastern South Pacific revisited: the case of northern Patagonia, Chile. Aquatic Conservation of Marine and Freshwater Ecosystem 23:858–867.
- International Whaling Commission. 1998. Report of the scientific committee, annex G. Report of the sub-committee on the comprehensive assessment of southern hemisphere humpback whales. Report of the International Whaling Commission 48:170–182.
- Katona, S., and H. Whitehead. 1981. Identifying humpback whales using their natural markings. Polar Record 20:439–444.

- Kennedy, A. S., A. N. Zerbini, O. V. Vázquez, N. Gandilhon, P. J. Clapham, and O. Adam. 2013. Local and migratory movements of humpback whales (*Megaptera novaeangliae*) satellite-tracked in the North Atlantic Ocean. Canadian Journal of Zoology 92:8–17.
- Lagerquist, B. A., B. R. Mate, J. G. Ortega-Ortiz, and M. Winsor. 2008. Migratory movements and surfacing rates of humpback whales (*Megaptera novaeangliae*) satellite tagged at Socorro Island, Mexico. Marine Mammal Science 24:815–830.
- Lockyer, C. H., L. C. McConnell, and T. D. Waters. 1985. Body condition in terms of anatomical and biochemical assessment of body fat in North Atlantic fin and sei whales. Canadian Journal of Zoology 63:2328–2338.
- Mate, B. R., R. Gisiner, and J. Mobley. 1998. Local and migratory movements of Hawaiian humpback whales tracked by satellite telemetry. Canadian Journal of Zoology 76:863–868.
- Mate, B. R., R. Mesecar, and B. A. Lagerquist. 2007. The evolution of satellite-monitored radio tags for large whales: one laboratory's experience. Deep-Sea Research Part II 54:224–247.
- Moore, M., R. Andrews, T. Austin, J. Bailey, A. Costidis, C. George, K. Jackson, T. Pitchford, S. Landry, A. Ligon, W. McLellan, D. Morin, J. Smith, D. Rotstein, T. Rowles, C. Slay, and M. Walsh. 2013. Rope trauma, sedation, disentanglement, and monitoring-tag associated lesions in a terminally entangled North Atlantic right whale (*Eubalaena glacialis*). Marine Mammal Science 29:E98–E113.
- National Research Council. 2011. Guide for the care and use of laboratory animals. Eighth edition. National Academies Press, Washington, D.C., USA.
- Pfeiffer, C. J., and F. M. Jones. 1993. Epidermal lipid in several cetacean species: ultrastructural observations. Anatomy and Embryology 188:209–218.
- Rasmussen, K., J. Calambokidis, and G. H. Steiger. 2011. Distribution and migratory destinations of humpback whales off the Pacific coast of Central America during the boreal winters of 1996–2003. Marine Mammal Science 28:E267–E279.
- Rasmussen, K., D. Palacios, J. Calambokidis, M. T. Saborío, L. Dalla-Rosa, E. R. Secchi, G. H. Steiger, J. M. Allen, and G. S. Stone. 2007. Southern Hemisphere humpback whales wintering off Central America: insights from water temperature into the longest mammalian migration. Biology Letters 3:302–305.
- Robbins, J., A. N. Zerbini, N. Gales, F. M. D. Gulland, M. Double, P. J. Clapham, V. Andrews-Goff, A. S. Kennedy, S. Landry, D. K. Mattila, and J. Tackaberry. 2013. Satellite tag effectiveness and impacts on large whales: preliminary results of a case study with Gulf of Maine humpback whales. Report SC/65a/SH05. Scientific Committee of the 65th Annual Meeting of the International Whaling Commission. International Whaling Commission, 3–15 June 2013, Jeju, South Korea.
- Scheidat, M., C. Castro, J. Denkinger, J. González, and D. Adelung. 2000. A breeding area for humpback whales (*Megaptera novaeangliae*) off Ecuador. Journal of Cetacean Research and Management 2:165–172.
- Stevick, P. T., A. Aguayo, J. Allen, I. C. Avila, J. Capella, C. Castro, K. Chater, M. H. Engel, F. Félix, L. Flórez-González, A. Freitas, B. Haase, M. Llano, L. Lodi, E. Munoz, C. Olavarría, E. Secchi, M. Scheidat, and S. Siciliano. 2004. A note on the migrations of individually identified humpback whales between the Antarctic Peninsula and South America. Journal of Cetacean Research and Management 6:109–113.
- Szesciorka, A. R., J. Calambokidis, and J. T. Harvey. 2016. Testing tag attachments to increase the attachment duration of archival tags on baleen whales. Animal Biotelemetry 4:1–18.
- Walker, K. A., A. W. Trites, M. Haulena, and D. M. Weary. 2011. A review of the effects of different marking and tagging techniques on marine mammals. Wildlife Research 39:15–30.
- Wilson, R. P., and C. R. McMahon. 2006. Measuring devices on wild animals: What constitutes acceptable practice? Frontiers in Ecology and the Environment 4:147–154.
- Zerbini, A. N., A. Andriolo, M. P. Heide-Jørgensen, J. L. Pizzorno, Y. G. Maia, G. R. Douglas, P. DeMaster, P. C. Simões-Lopes, S. Moreira, and C. Bethlem. 2006. Satellite-monitored movements of humpback whales *Megaptera novaeangliae* in the Southwest Atlantic Ocean. Marine Ecology Progress Series 313:295–304.

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