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SHORT NOTE

First evidence of interchange of humpback whales (*Megaptera novaeangliae*) between the Magellan Strait and Antarctic Peninsula feeding grounds

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Abstract

Eastern South Pacific humpback whales (*Megaptera novaeangliae*) migrate to three distinct mid- to high-latitude feeding areas. While movements between local breeding sites have been reported, interchange among the feeding areas has not been documented and thus has assumed not to exist. Identifying photographs of 187 humpback whales in the Magellan Strait were compared with 2,553 whales from the Antarctic Peninsula feeding area, resulting in two matches. Additionally, 37 skin samples collected at the Magellan Strait were analyzed for carbon and nitrogen stable isotopes, resulting in evidence that two other individuals traveled to the Antarctic Peninsula. Our findings provide the first known evidence of interchange between two of these feeding areas in the eastern South Pacific. The data suggest a very limited interchange, but demonstrate that some whales may permanently leave the Magellan Strait, or perform short, round-trip movement between these areas. This previously undocumented interchanges do not necessarily change existing management recommendations that the Magellan Strait is a demographically independent feeding area, but does suggest that future abundance estimate models should assume low immigration rates. Further research to better understand the extent and frequency of interchange in the austral region of South America is needed, as this will further clarify the population structure of these whales leading to more accurate scientific knowledge supporting the conservation and management of the species.

Keywords Eastern South Pacific · Interchange · Humpback whale (*Megaptera novaeangliae)* · Magellan strait · Antarctic Peninsula

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Introduction

Effective management and conservation measures for population-based units depends on an understanding of population structure and their connectivity. Large baleen whale species were hunted by the hundreds of thousands during nineteenth and twentieth century, and currently many populations are still recovering from this exploitation (Childerhouse et al. 2008; Rocha et al. 2014). Consequently, understanding the current population structure –such as their distribution, degree of interbreeding and the relative interchange among locations– is an important step in the assessment and management of these recovering populations. Observed subpopulation structures include a unique breeding-feeding area, a shared breeding ground for multiple feeding areas, or a shared feeding ground for multiple breeding grounds (Katona and Beard 1990; Calambokidis et al. 2001; Stevick et al. 2006; Barlow et al. 2011). Determining the

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type of connectivity between feeding and breeding grounds is thus a key step to effective management for recovering whale populations.

Humpback whales (*Megaptera novaeangliae*) typically feed at higher latitudes during summer/fall and breed at lower latitudes during winter/spring seasons (Chittleborough 1965). For Southern Hemisphere humpback whales, seven breeding populations (or Breeding Stocks) are recognized (IWC 1998). Eastern South Pacific humpback whales (or breeding stock G) were known to breed and calve in Ecuadorian and Colombian waters and feed around the Antarctic Peninsula (Stone et al. 1990; Caballero et al. 2001; Stevick et al. 2004). More recently, the population connectivity was recognized as more complex, due to an expanded range in breeding grounds into northern Peru and Costa Rica (Rasmussen et al. 2007; Pacheco et al. 2009) and even reaching the waters of Nicaragua (De Weerdt et al. 2020). Likewise, a small part of the population does not reach Antarctic Peninsula waters, instead migrating to two feeding areas in the inland waters of the southern tip of Chile, in the northern Patagonian and Magellan Strait, respectively (Fig. 1).

Of particular interest are the humpback whales in the Magellan Strait, because of the risk posed by spatial overlap with a busy shipping lane, and inclusion of a Marine and Coastal Protected Area to protect a portion of their feeding area. Previous comprehensive assessments of identified humpback whales found no interchange among the feeding areas and thus have been widely assumed not to exist (Acevedo et al. 2013, 2017). Consequently, the Magellan Strait humpback whales have been assumed to be a distinct feeding subpopulation in statistical models used for abundance estimates. Mark-recapture methods have estimated 132 (95%

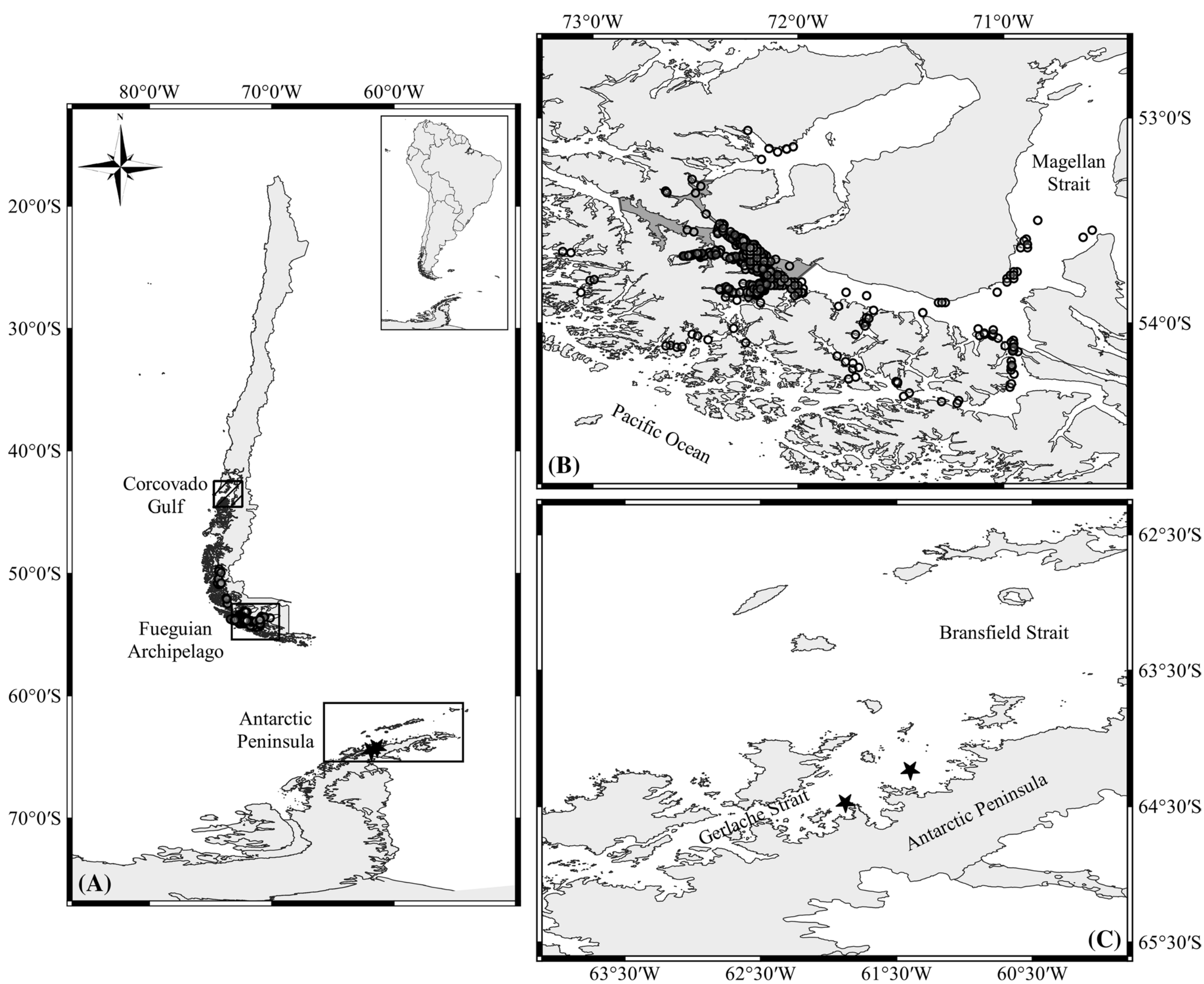

Fig. 1 **a** Current feeding areas for the eastern South Pacific humpback whale population. **b** Details of the distribution of humpback whales (open circle) in the Magellan Strait feeding area and Francisco Coloane Marine and Coastal Protected Area (gray shaded). **c** Local area of the two matches yielded through fluke photography at the Antarctic Peninsula feeding area

CI: 125–138) whales during 1999–2011 (Capella et al. 2012) and 204 (95% CI: 199–210) during 2004–2016 (Monnahan et al. 2019). Furthermore, estimated population growth is low relative to other populations, with current annual rates of 2.3% (CI: 2.1%–3.1%; Monnahan et al. 2019). Both abundance models were made assuming no interchange with the other feeding areas in addition to homogenous occurrence probabilities. However, if interchange among feeding areas does exist, the type and degree of bias in the estimates will depend on the rate of interchange, and individual movement patterns between feeding areas.

We use two approaches to investigate potential interchange of individually identified humpback whales between the Magellan Strait and the Antarctic Peninsula feeding areas. We then discuss the potential implications for the resilience of the Magellan Strait feeding subpopulation in the context of the abundance estimates.

Materials and methods

We compared individuals identified photographically by natural marks on the ventral side of their flukes (Katona et al. 1979) between both feeding areas. In the Magellan Strait, two catalogs are available and were previously compared to determine the number of unique individuals photographed. For the Antarctic Peninsula, we used the database of identified whales maintained by Happywhale, a web-based marine mammal photo ID crowd-sourcing platform (Cheeseman and Southerland 2016). Previous studies of photographic comparison between these feeding areas had not included the Happywhale database (e.g. Acevedo et al. 2013, 2017). Photographs judged to be of insufficient quality for a positive identification (see Friday et al. 2000) were discarded. We searched for matching individuals using the recently-developed fast, high-quality algorithm for automated image recognition of humpback whale flukes, implemented in the Happywhale platform.

We then looked at stable carbon (^{13}C) and nitrogen (15N) isotope ratios. Thirty-seven skin samples of identified humpback whales collected in the Magellan Strait between 2011 and 2013 were analyzed. Results of stable isotopes of the skin samples of 2011 and 2012 were previously published (see Haro et al. 2016 for details). For the skin samples collected in 2013 ($n = 4$), lipids were extracted and the samples analyzed with an elemental analyzer at the Stable Isotopes Facility Lab, University of California Davis, USA. Stable isotope ratios of individual humpback whales sampled twice in 2011 and 2012 ($n = 5$) were averaged to prevent double weighting animals in analyses. We used a lipid-free threshold value for humpback whale skin of 3.3 ± 0.17 (Ryan et al. 2012), and normalization model from Kiljunen et al. (2006) to correct arithmetically $\delta^{13}C$ values exceeding this threshold.

To explore geographic consistency, stable isotope of $\delta^{13}C$ and $\delta^{15}N$ in skin from Magellan Strait humpback whales were compared to samples collected in the Bransfield ($n = 20$) and Gerlache ($n = 49$) Straits, Antarctic Peninsula (Seyboth et al. 2018). We assume the stable isotopes signals in the diet of each feeding area remain relatively stable over the years (Born et al. 2003; Aurioles-Gamboa et al. 2013), and therefore we assigned the skin samples to the respective sampling locations. Quadratic discriminant function analysis (QDA) in the 'MASS' package (Venables and Ripley 2002) was used to explore regional differences in foraging due to lack of multivariate normality in some data groups (Zhong 2004). Test error rates of the QDA model were estimated with the predict() function of the MASS package and the visualization of the classifications was made using the partimat() function of the 'klaR' package (Roever et al. 2018). All analyses were performed using R software version 3.5.1 (R Core Team 2018).

Results

Photo identification

A total of 187 unique whales of the Magellan Strait feeding subpopulation were compared with 2,553 unique humpback whales photographed at Antarctic Peninsula, producing matches of two individuals. Both Magellan Strait whales were photographed on a single occasion in the Gerlache Strait in February 2th, 2018 (whale No 1) and February 11, 2018 (whale No 2) (Figs. 1 and 2). Both whales were sighted in the Magellan Strait feeding area seven and ten years before their sighting in Antarctica. Briefly, the first whale, an adult male, was initially photographed on February 14, 2006 and subsequently resighted throughout the feeding season during the next five years until January 3, 2011. The second whale, an adult female, was identified on February 11, 2001 and then resighted 4 years later with a calf. Two subsequent sightings were then made in 2007 (March) and 2008 (April). The last sighting in the Magellan Strait was on April 27, 2008.

Stable isotopes

Results indicated a lack of geographical consistency in the stable isotopes of two whales (No 3 and 4, see Fig. 2) collected in the Magellan Strait in May 22, 2013. Both samples had low values of $\delta^{13}C$ (-20.7 ‰ and -21.3 ‰) and $\delta^{15}N$ (11.3 ‰ and 11.7 ‰) relative to the average values for the Magellan humpback's of -16.2 ± 0.64 ‰ and 14.8 ± 1.02 ‰, respectively (Fig. 3a). As expected, QDA model

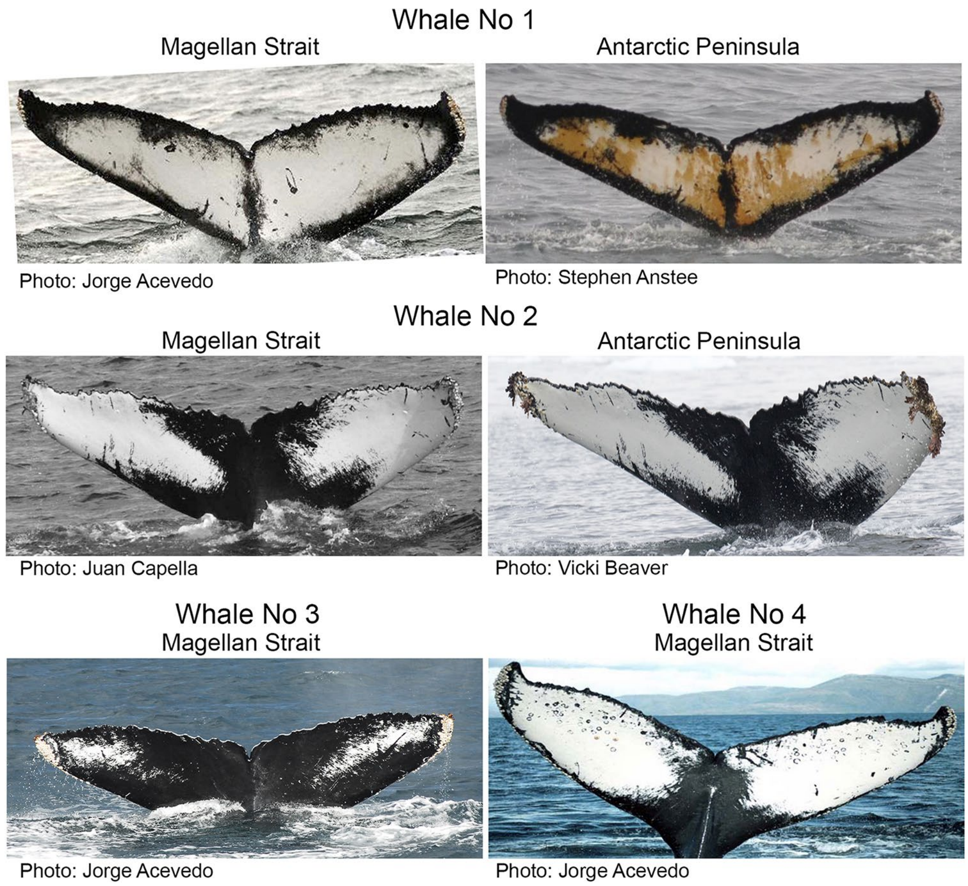

Fig. 2 Fluke photographs of humpback whales matched between Magellan Strait and Antarctic Peninsula (whales No 1 and 2), and flukes of the other two whales inferred by stable isotopes ratios (whales No 3 and 4)

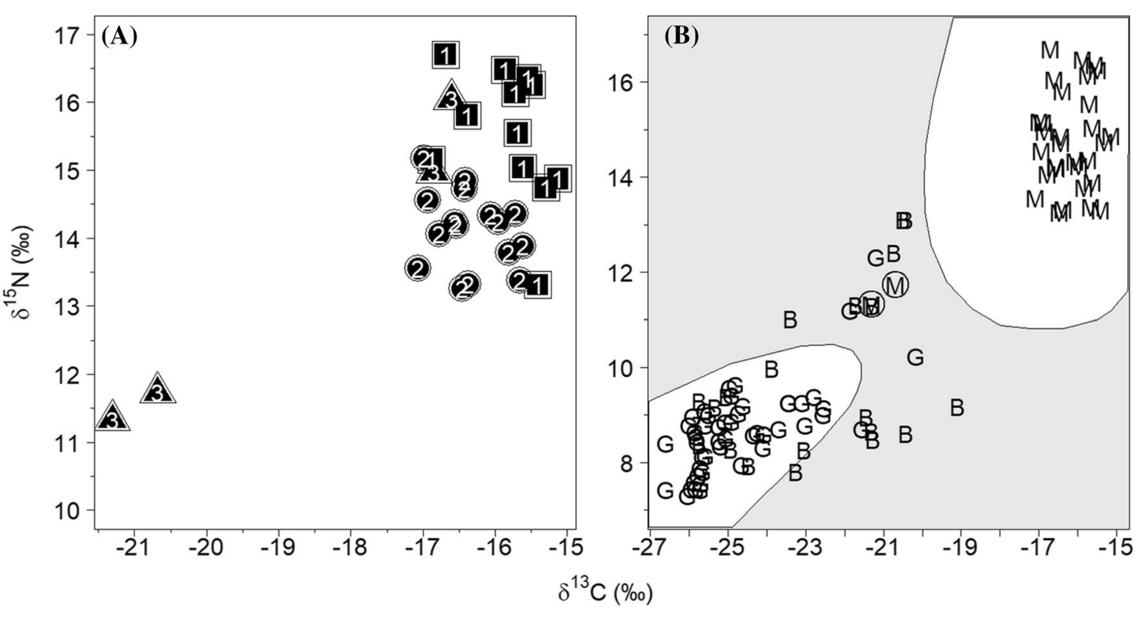

Fig. 3 **a** δ^{13}C and δ^{15}N ratios of skin samples of the Magellan Strait humpback whales in 2011 (square), 2012 (circle) and 2013 (triangle). **b** Display of the posterior classifications made by the QDA function. The gray area indicates the Bransfield stable isotope ratios. Letters represent Magellan (M), Bransfield (B) and Gerlache (G) Straits

predictions correctly classified 96.4% of the skin samples (30/32) collected in the Magellan Strait. When subregion assignment is considered (“Magellan Strait”, “Bransfield Strait”, “Gerlache Strait”), the QDA model assigned stable isotopes ratios of whales No 3 and 4 of the Magellan Strait to the Bransfield Strait subregion, with a probability of 81.7 and 89.4%, respectively (Fig. 3b). Unlike the two previous whales, both of these individuals have been sighted annually in the Magellan Strait throughout the complete feeding season from 1999 (whale No 3, an adult female) and 2001 (whale No 4, an adult male), until 2018 summer season. In the 2013 summer season, these last two whales were sighted subsequently in the Magellan Strait in February and March (2th and 24th) and missing in April. Then both whales were again sighted in the Magellan Strait 21 days apart, on the 1st (whale No 4) and 22 of May of 2013 (whale No 3), suggesting a short-round trip from the Magellan Strait to the Antarctica waters. The former also is suggested through the Bayesian stable isotope mixing model (results not shown here), as the prediction indicates an important contribution of Antarctic krill (*Euphausia superba*) over the typical diet in the Magellan Strait.

Discussion

Movements of humpback whales between feeding areas in the eastern South Pacific from previous photo-ID studies had not revealed any interchanges (Acevedo et al. 2013, 2017), and thus have been widely assumed not to exist. The documentation of at least two whales through photo identification, and other two individuals inferred through stable isotopes, provide the first evidence of interchange between the Magellan Strait and the Antarctic Peninsula feeding areas. Our findings show low rates of interchange between these two feeding areas, given the relatively large Antarctic Peninsula catalogues used in previous comparisons and in this study spanning several years. The Magellan Strait feeding area has been recognized as a demographically independent feeding subpopulation (Acevedo et al. 2013), and this very low contemporary rate of interchange does not necessarily challenge existing management strategies, nor how the feeding aggregations are viewed. This low interchange rate is consistent with the high levels of persistent site fidelity in the Magellan Strait feeding area (Capella et al. 2012; Acevedo et al. 2014), and with significant levels of differentiation observed in mtDNA from these regions (Félix et al. 2012), a pattern that has also been proposed to explain the limited demographic interchange between adjacent feeding sites in another population (Stevick et al. 2006). Furthermore, movement rates between areas depend on their proximity (Stevick et al. 2006), and although humpback whales can traverse large distances in a day (Mate et al. 1998), fidelity to successful foraging areas is likely a strong incentive to avoid moving to other feeding areas, even though occasional exploration at greater distances could be beneficial (Stevick et al. 2006).

The qualitative evidence presented here that some whales permanently leave the Magellan Strait, or perform round-trip movement to another feeding area, gives important new insight in the current understanding of the movement patterns of the Magellan Strait humpback whales, and into the implications of local and regional abundance estimates. It is well known that the eastern South Pacific humpback whale population migrates mainly to the Antarctic Peninsula to feed on the dense patches of Antarctic krill and obtain much of their energetic requirements for the subsequent fasting months (Chittleborough 1965). In the Magellan Strait, humpback whales feed on squat lobster (*Munida gregaria*), krill (*Euphausia* sp.), and Fueguian sprat (*Sprattus fueguensis*) (Acevedo et al. 2011; Haro et al. 2016). Even though we do not have data on biomass and/or seasonal fluctuations of these prey species in the Magellan Strait, the whales can disperse beyond the current reach of researchers in order to improve supplementary feeding and replenish blubber stores in response to low local abundance of prey species, seasonal changes in prey distribution or availability. This makes it likely that the whales assumed to feed permanently in the Magellan Strait might not be equally available for sampling, resulting in heterogeneous detection probabilities for the statistical model of abundance estimates.

On the other hand, this potential heterogeneity may also be a reflection of local sub-structure, with groups of whales exhibiting different rates of fidelity to specific sites inside and outside of the main feeding area of the Magellan Strait. Under this scenario, it is possible that low re-sighting rates of some individuals in the Magellan Strait –seen only once or twice in a few years with a low residence time in the study area– represent transient groups that allocate their time preferentially to other unknown feeding sites within the Fuegian Archipelago or even the Antarctic Peninsula feeding area. It is not possible at this time to differentiate the cause of heterogeneity between transient groups hypothesis vs. an artifact correlated to lack of survey effort, timing or extent. Transient whales could use the Magellan Strait as a migratory stopover, or simply pass-through during parts of the feeding season; however, it does not necessarily imply that hypothetical resident individuals never leave the area. Semi-geographical structuring, in which groups of individuals have different patterns of movement and site fidelity, occurs in some other migrants species and may apply here as well (Rappole 1995; Dingle 1996; Dinis et al. 2016). Even though for the moment we cannot evaluate the existence of a local substructure, there has been an increase in sightings of humpback whales in recent years as far away as the southernmost channels such as Beagle Channel (54°52′S), and therefore we cannot exclude the possibility that other less well-studied areas in the Fueguian Archipelago could be equally important.

The inability to accurately distinguish the presence (observed whale) from the apparent non-presence (present but not observed) from true absence could result in a biased estimates of some important population parameters (e.g., occurrence probability, survival, recruitment) and finally in the local population sizes. Specifically, the current local abundance estimate would be slightly overestimated if a portion of whales is transient. A rigorous exploration of the impact of heterogeneity on abundance estimates should be considered in the future to refine abundance estimates of the Magellan Strait feeding area, or abundance for the region as a whole.

Nevertheless, the evidence of interchange between the Magellan Strait and any another feeding area such as the Antarctic Peninsula appears considerably low, and is unlikely that the abundance estimates of the Magellan Strait subpopulation have an important bias caused by immigration effects. Expanded geographic coverage of fluke photographs across the austral region of South America combined with satellite tracking data will lead to a better understanding of the dynamic movements, and the frequency of dispersal events among the Magellan Strait and other emergent feeding sites within or outside of the southernmost tip of South America. Such work would build off our results here and improve understanding the structure and connectivity of this particular feeding subpopulation of humpback whales, and will bolster effective management and conservation measures.

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Author contributions TC and KS provided the photo-ID matches in Happywhale web-based platform. JA, AAL and TC conceived the short note. JA and JC provided the data of sightings for the Magellan Strait. JA and PA analyzed the data and created the figures. JA and CM wrote the manuscript. All authors read and approved the manuscript.

Compliance with ethical standards

Conflict of interest We declare we have no conflicts of interest.

Ethical approval The whale studies at Magellan Strait were carried out under Ethical Standards and the Permission No 2757 and 2527 of the Secretary of Fisheries and Aquaculture of Chile.

References

Acevedo J, Plana J, Aguayo-Lobo A, Pastene LA (2011) Surface feeding behaviors in the Magellan Strait humpback whales. Rev Biol Mar Oceanogr 46:483–490. https://doi.org/10.4067/S0718-19572011000300018

Acevedo J, Haro D, Dalla-Rosa L, Aguayo-Lobo A, Hucke-Gaete R, Secchi E et al (2013) Evidence of spatial structuring of eastern South Pacific humpback whale feeding grounds. Endanger Species Res 22:33–38. https://doi.org/10.3354/esr00536

Acevedo J, Mora C, Aguayo-Lobo A (2014) Sex-related site fidelity of humpback whales (*Megaptera novaeangliae*) to the Fueguian Archipelago feeding area, Chile. Mar Mamm Sci 30:433–444. https://doi.org/10.1111/mms.12048

Acevedo J, Aguayo-Lobo A, Allen J, Botero-Acosta N, Capella J, Castro C et al (2017) Migratory preferences of humpback whales between feeding and breeding grounds in the eastern South Pacific. Mar Mamm Sci 33:1035–1052. https://doi.org/10.1111/mms.12423

Aurioles-Gamboa D, Rodríguez-Pérez M, Sánchez-Velasco L, Lavín M (2013) Habitat, trophic level, and residence of marine mammals in the Gulf of California assessed by stable isotope analysis. Mar Ecol Prog Ser 488:275–290. https://doi.org/10.3354/meps10369

Barlow J, Calambokidis J, Falcone EA, Baker CS, Burdin AM, Clapham PJ et al (2011) Humpback whale abundance in the North Pacific estimated by photographic capture-recapture with bias correction from simulation studies. Mar Mamm Sci 27:793–818. https://doi.org/10.1111/j.1748-7692.2010.00444.x

Born EW, Outridge P, Riget FF, Hobson KA, Dietz R, Oien N et al (2003) Population substructure of North Atlantic minke whales (*Balaenoptera acutorostrata*) inferred from regional variation of elemental and stable isotopic signatures in tissues. J Mar Syst 43:1–17. https://doi.org/10.1016/S0924-7963(03)00085-X

Caballero S, Hamilton H, Jaramillo H, Capella J, Flórez-González L, Olavarría C et al (2001) Genetic characterisation of the Colombian Pacific Coast humpback whale population using RAPD and mitochondrial DNA sequences. Mem Queensl Mus 47:459–464

Calambokidis J, Steiger GH, Straley JM, Herman LM, Cerchio S, Salden DR et al (2001) Movements and population structure of humpback whales in the North Pacific. Mar Mamm Sci 17:769–794. https://doi.org/10.1111/j.1748-7692.2001.tb01298.x

Capella J, Gibbons J, Vilina Y, Flórez-González L, Sabaj V, Valladares C (2012) Abundance, population structure, and Fidelity of humpback whale in the Strait of Magellan, Chile. Working Paper SC/64/SH21. Scientific Committee of the International Whaling Commission. Panama City, Panama

Cheeseman T Southerland K (2016) Happywhale.com: A web-based citizen science marine mammal photoidentification platform. Working Paper SC/66b/SH06. Scientific Committee of the International Whaling Commission. Bled, Slovenia

Childerhouse S, Jackson J, Baker CS, Gales N, Clapham PJ, Brownell Jr RL (2008) *Megaptera novaeangliae* (Oceania subpopulation). In: IUCN (ed) IUCN Red List of Threatened Species. Version 2009.2. Available at www.iucnredlist.org

Chittleborough R (1965) Dynamics of two populations of the humpback whale, *Megaptera novaeangliae* (Borowski). Mar Freshwater Res 16:33–128

De Weerdt J, Ramos EA, Cheeseman T (2020) Northernmost records of Southern Hemisphere humpback whales (*Megaptera novaeangliae*) migrating from the Antarctic Peninsula to the Pacific coast of Nicaragua. Mar Mamm Sci 36(3):1015–1021. https://doi.org/10.1111/mms.12677

Dingle H (1996) Migration: the biology of life on the move. Oxford University Press, New York

Dinis A, Alves F, Nicolau C, Ribeiro C, Kaufmann M, Cañadas A et al (2016) Bottlenose dolphin *Tursiops truncatus* group dynamics, site fidelity, residency and movement patterns in the Madeira Archipelago (North-East Atlantic). Afr J Mar Sci 38(2):151–160. https://doi.org/10.2989/1814232X.2016.1167780

Félix F, Caballero S, Olavarría C (2012) Genetic diversity and population structure of humpback whales (*Megaptera novaeangliae*) from Ecuador based on mitocondrial DNA analyses. J Cetacean Res Manag 12:71–77

Friday N, Smith T, Stevick P, Allen J (2000) Measurement of photographic quality and whale distinctiveness for the photographic identification of humpback whales, *Megaptera novaeangliae*. Mar Mamm Sci 16:355–374. https://doi.org/10.1111/j.1748-7692.2000.tb00930.x

Haro D, Riccialdelli L, Acevedo J, Aguayo-Lobo A, Montiel A (2016) Trophic ecology of humpback whales (*Megaptera novaeangliae*) in the Magellan Strait using carbon and nitrogen stable isotopes. Aquatic Mamm 42:233–244. https://doi.org/10.1578/AM.42.2.2016.xxx

International Whaling Commission (1998) Report of the Scientific Committee. Rep Int Whal Commn 48:53–118

Katona SK, Beard JA (1990) Population size, migrations and feeding aggregations of the humpback whale (*Megaptera novaeangliae*) in the western North Atlantic Ocean. Rep Int Whal Commn (Special Issue) 12:295–305

Katona SK, Baxter B, Brazier O, Kraus S, Perkins J, Whitehead H (1979) Identification of humpback whales by fluke photo graphs. In: Winn HE, Olla BL (eds) Behavior of marine animals, vol 4. Plenum Press, New York, pp 33–34

Kiljunen M, Grey J, Sinisalo T, Harrod C, Immonen H, Jones RI (2006) A revised model for lipid normalizing ^{13}C values from aquatic organisms, with implications for isotope mixing models. J Appl Ecol 43:1213–1222. https://doi.org/10.1111/j.1365-2664.2006.01224.x

Mate BR, Gisiner R, Mobley J (1998) Local and migratory movements of Hawaiian humpback whales tracked by satellite telemetry. Can J Zool 76:863–868

Monnahan C, Acevedo J, Hendrix AN, Gende S, Aguayo-Lobo A, Martínez F (2019) Population trends for humpback whales (*Megaptera novaeangliae*) foraging in the Coastal-Marine Protected Area in Magellan Strait, Chile. Mar Mamm Sci 35:1212–1231. https://doi.org/10.1111/mms.12582

Pacheco AS, Silva S, Alcorta B (2009) Winter distribution and group composition of humpback whales (*Megaptera novaeangliae*) off northern Peru. Lat Am J Aquat Mamm 7(1–2):33–38

R Core Team (2018) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/

Rappole JH (1995) The ecology of migrant birds: a neotropical perspective. Smithsonian Institution Press, Washington DC

Rasmussen K, Palacios D, Calambokidis J, Saborío MT, Dalla-Rosa L, Secchi ER et al (2007) Southern Hemisphere humpback whales wintering off Central America: Insights from water temperature into the longest mammalian migration. Biol Lett 3:302–305. https://doi.org/10.1098/rsbl.2007.0067

Rocha CR, Clapham PJ, Ivashchenko YV (2014) Emptying the Oceans: A summary of industrial whaling catches in the 20th century. Mar Fish Rev 76:37–48. https://doi.org/10.7755/MFR.76.4.3

Roever C, Raabe N, Luebke K, Ligges U, Szepannek G, Zentgraf M (2018) Package 'klaR'. URL: http://www.statistik.tu-dortmund.de

Ryan C, McHugh B, Trueman CN, Harrod C, Berrow SD, O'Connor I (2012) Accounting for the effects of lipids in stable isotope (d^{13}C and d^{15}N) analysis of skin and blubber of balaenopterid whales. Rapid Commun Mass Spectrom 26:2745–2754. https://doi.org/10.1002/rcm.6394

Seyboth E, Botta S, Borges CR, Negrete J, Dalla-Rosa L, Secchi ER (2018) Isotopic evidence of the effect of warming on the northern Antarctic Peninsula ecosystem. Deep-Sea Res II 149:218–228. https://doi.org/10.1016/j.dsr2.2017.12.020

Stevick PT, Aguayo A, Allen J, Avila IC, Capella J, Castro C et al (2004) A note on the migrations of individually identified humpback whales between the Antarctic Peninsula and South America. J Cetacean Res Manag 6:109–113

Stevick PT, Allen J, Clapham PJ, Katona SK, Larsen F, Lien J et al (2006) Population spatial structuring on the feeding grounds in North Atlantic humpback whales (*Megaptera novaeangliae*). J Zool (Lond) 270:244–255. https://doi.org/10.1111/j.1469-7998.2006.00128.x

Stone G, Flórez-González L, Katona S (1990) Whale migration record. Nature 346:705

Venables WN, Ripley BD (2002) Modern Applied Statistics with S, 4th edn. Springer, New York

Zhong X (2004) A Study of several statistical methods for classification with application to microbial source tracking. Dissertation, Worcester Polytechnic Institute