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MOVEMENT AND SITE FIDELITY

From the Antarctic Peninsula to eastern Australia: the longest migration of a humpback whale through the South Pacific Ocean

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Abstract

Humpback whales (*Megaptera novaeangliae*) seasonally migrate between their corresponding breeding and feeding grounds; however, some individual whales deviate from this pattern migrating to different breeding or feeding grounds. Here, we report the first recorded movement of a humpback whale between the Antarctic Peninsula and the east coast of Australia. The individual whale, a known female, was identified by natural markings in the Antarctic Peninsula feeding area, and then photographed 15 years later in Byron Bay, on the eastern coast of Australia. This constitutes the longest migration for any humpback whale documented to date in the South Pacific Ocean and in the Southern Hemisphere (143° of longitude). Although the route is uncertain and the cues may be environmental, social or demographic, or some combinations thereof, this exceptional movement between two distant Breeding Stocks in the South Pacific Ocean demonstrates that longitudinal long-distance migrations among humpback whale populations do take place, at least occasionally, and perhaps may not be as atypical as it has been thought.

Keywords Antarctic Peninsula · Eastern Australia · Humpback whales · Migration · Photo ID

Humpback whales (*Megaptera novaeangliae*) undertake latitudinal seasonal migration, wintering in breeding grounds in tropical and subtropical latitudes and spending the summer foraging in productive feeding grounds at high latitudes (Mackintosh 1965; Clapham and Mead 1999). This migratory connectivity between low- and high-latitude areas is predominantly regular, seasonally predictable, and in a north–south direction. In the Southern Hemisphere, the International Whaling Commission (IWC) recognizes seven different breeding populations of humpback whales, assigned as "Breeding Stocks", numbered with the letters A to G (IWC 1998). Photo identification and genetic studies largely support this separation, although a certain level of gene flow between the different populations exists (Rosenbaum et al. 2017).

Three distinct breeding populations or Breeding Stocks of humpback whales located in the western, central and eastern South Pacific Ocean are currently recognized (IWC 2015). The humpback whale population in the western South Pacific is known as Breeding Stock E (BSE), and comprises three main breeding grounds or Sub-Stocks: those that reproduce in Australia's Great Barrier Reef (BSE-1), in the eastern coast of Australia; in New Caledonia (BSE-2); and the group of Tonga, Fiji and American Samoa Islands (BSE-3) (Smith et al. 2012; Steel et al. 2018). The population located in the central South Pacific is known as Breeding Stock F (BSF), and comprises those that breed around the Cook Islands (BSF-1) and French Polynesia (BSF-2) (IWC 2004). The humpback whale population from the eastern South

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Pacific is recognized as a single Breeding Stock (BSG), and reproduces in a continuous range from northern Peru to southern Nicaragua off the western coast of South and Central America (Pacheco et al. 2009; Acevedo et al. 2017; De Weerdt et al. 2020).

Historically, feeding and breeding ground connections in the Southern Hemisphere were established through seasonal distribution information derived from whaling records and from Discovery mark recoveries (e.g., Dawbin 1964; Mackintosh 1965). Based on this description, individuals of each Breeding Stock were assumed to migrate more or less directly south to a corresponding Antarctic management feeding area, numbered from I to VI (Donovan 1991). No overlap among the humpback whale populations was assumed between the different Antarctic management areas (Donovan 1991) despite what appears to be a more or less continuous distribution on those feeding grounds (Rosenbaum et al. 2017). The migratory relationships between the respective breeding grounds and Antarctic management feeding areas in the South Pacific Ocean are known with varying degrees of certainty for the BSE-1 to waters north of the western Ross Sea (Antarctic feeding Area V) (Constantine et al. 2014; Andrews-Goff et al. 2018), and for the BSG, which migrate to the Antarctic Peninsula waters (Antarctic feeding Area I) (Stevick et al. 2004; Acevedo et al. 2017), and to the inland fjord of southern Chile (Acevedo et al. 2013), South America. Less known is the feeding migratory connection of the BSF, being assumed that it should be the waters north of the Amundsen Sea (Antarctic feeding Area VI).

However, some whales deviate from this dominant north–south pattern. Fewer migratory movements involving longitudinal displacements between different breeding and feeding grounds have been documented for some individual humpback whales from Tonga and American Samoa Islands (BSE-3) to Antarctic feeding Area I (Dawbin 1964; Mikhalev and Tormosov 1997; Robbins et al. 2011; Riekkola et al. 2018; Steel et al. 2018) (Fig. 1). Here we report the first known movement for a humpback whale from Antarctic feeding Area I (Antarctic Peninsula) to eastern Australia breeding ground (BSE-1), involving the longest longitudinal migration for one humpback whale.

Whales were identified by photographs of the individually distinctive markings on the ventral fluke surface using standard procedures (Katona et al. 1979). The match was made possible through the Happywhale repository, an international collaborative effort of multiple research groups and public citizens sharing their fluke photographs for a better understanding of migratory movements of the species (Cheeseman et al. 2017). Happywhale's web-based platform contains records of 40,590 individual humpback whales identified by fluke photographs, including 13,685 whales from the breeding and feeding ground of the South Pacific Ocean. The Chilean Antarctic Institute (INACH) Catalogue from INACH-08-93 and INACH-163 projects consists of 276 identified humpback whales in the Antarctic Peninsula, with records spanning 1994–1999 and 2006–2008, respectively. Photographs judged to be of insufficient quality for a positive identification were discarded ($n = 49$), and a total of 227 unique humpback whales were used. This catalogue was submitted to Happywhale in 2020. The East Australian Whale Watch Catalogue (ECWWC) consists of 1308 individually identified humpback whales (2005–2019) along the Australian east coast, including Byron Bay. The study of humpback whale movements used opportunistically acquired ventral fluke photographs taken onboard whale watch vessels. In 2017 the ECWWC catalogue was submitted to Happywhale.

The INACH catalog was compared with all previously identified South Pacific humpback whales in the collection contained in the Happywhale web-based platform, regardless of the time or area of any prior encounter, using an automated image recognition algorithm hosted in Happywhale (Cheeseman et al. 2022). Molecular sex determination and mtDNA haplotype of the matched individual were determined from skin biopsy samples collected in Antarctic Peninsula as described in Olavarría et al. (2007). Two distances between both locations were calculated along a great circle route (Vincenty 1975). The first distance assumed a direct northwesterly route through the South Pacific Ocean on a similar trajectory for some movements of whales that have been reported from Tonga and American Samoa Islands to Antarctic Peninsula in a southeast direction (e.g., Robbins et al. 2011; Riekkola et al. 2018; Steel et al. 2018). The second distance assumed a route to the west following the contour of the Antarctic continent. Unlike the assumed northwest route, an Antarctic route would have the benefit that the whale can feed while covering that distance.

An individual humpback whale (with ID code INACH#0107 in the Chilean Antarctic Institute Catalogue, INACH) was first sighted in the Gerlache Strait, Antarctic Peninsula (64°32′ S, 62°33′ W), on 28 January 1997 (Fig. 2a). It was observed in a pair of adult whales without calves, and was photo-identified and biopsy-sampled. Both whales in the group were identified as females by genetic markers. Neither of the two whales have been sighted again on the Antarctic Peninsula or across the BSG, despite extensive photo identification matching with other catalogs in the BSG ($n = 5667$ identified whales). The mtDNA haplotype of INACH#0107 was characterized as SP90 (following Olavarría et al. 2007 nomenclature).

This same whale (with ID code ECWWC-BB12021 in the East Australian Whale Watch Catalogue, ECWWC) was photographed 15 years later on 18 July 2012 from a commercial whale watch tour vessel (Fig. 2b). It was a member of a pair of adult whales without calves in Byron Bay

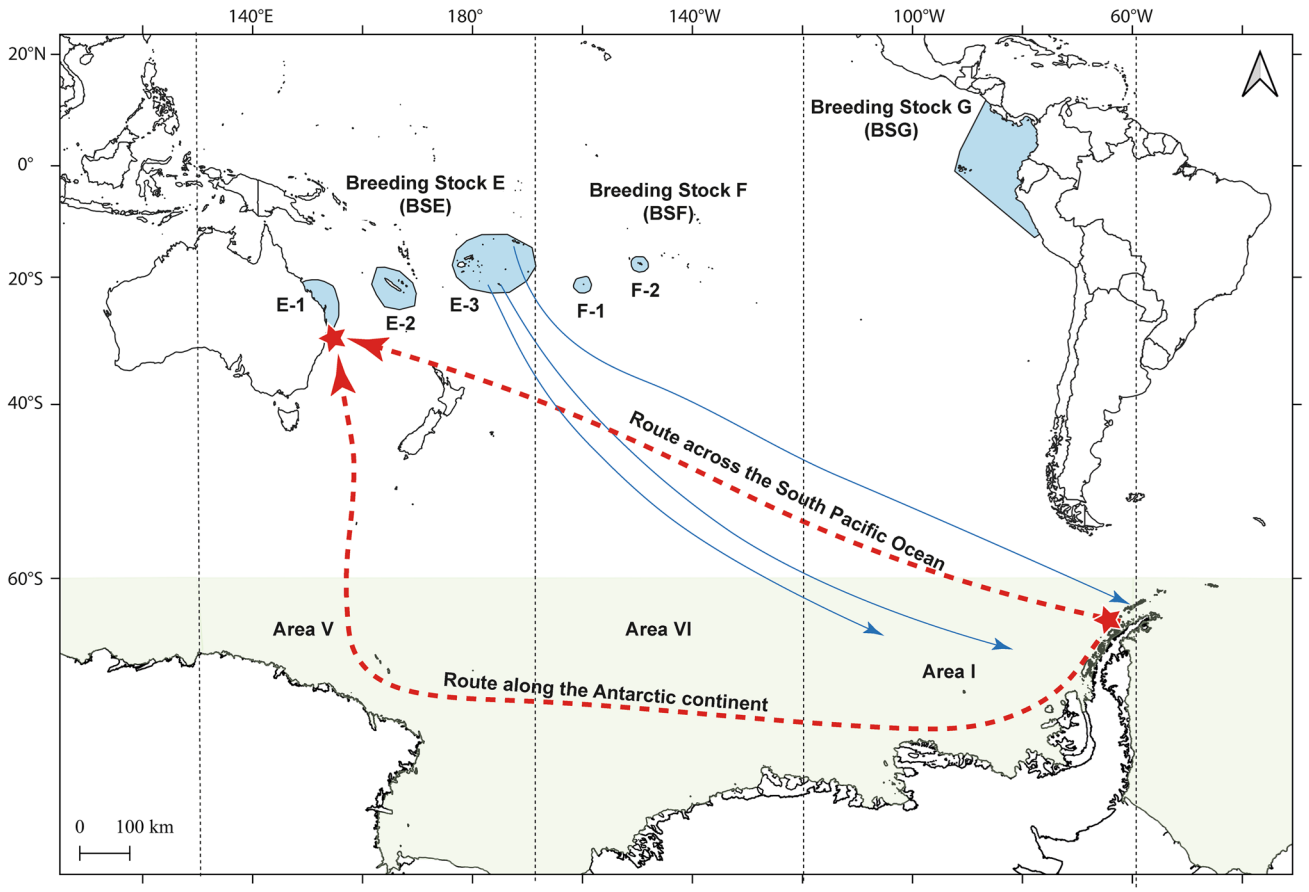

Fig. 1 Breeding (light blue areas) and feeding grounds (International Whaling Commission management areas; light green areas) of South Pacific Ocean humpback whales. Breeding Stock E comprises breeding Sub-Stocks E1, E2, and E3; Breeding Stock F comprises breeding Sub-Stocks F1 and F2; and Breeding Stock G is recognized as a single stock. Note that only feeding grounds V, VI and I are shown. Red stars denote the locations where the female humpback whale INACH#0107/ECWWC-BB12021 was seen in the feeding ground of Antarctic management Area I in 1997 and the Breeding Sub-Stock BSE-1 in 2012. Dashed red arrows denote the distance of two plausible direct migratory routes assumed in this study. Thin blue solid arrows denote the other known longitudinal movements of 13 humpback whales from the Breeding Sub-Stock BSE-3 (Tonga and American Samoa Islands) to the Antarctic management Area I. Vertical dashed lines denote the approximate boundaries of the respective Antarctic management feeding ground V, VI and I

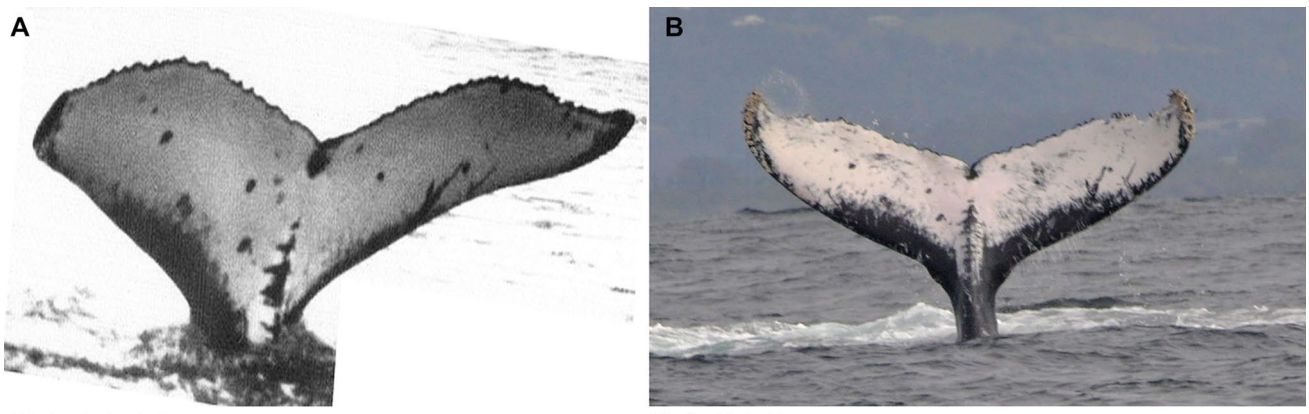

Fig. 2 Humpback whale INACH#0107/ECWWC-BB12021 photographed in Antarctic Peninsula waters in 1997 **A** and then in Byron Bay, eastern Australia in 2012 **B**

(approximately 28°37′ S, 153°37′ W), New South Wales, eastern coast of Australia. The pod engaged in active behaviors (e.g., breaching, pectoral slapping but not agonistic/competitive) as they migrated north.

The difference between the two encounter locations spans over 143.84° of longitude. Direct one-way distance of 9331 km was estimated if the whale migrated in a northwesterly direction through the South Pacific Ocean, or 9807 km if the whale migrated to the west along the contour of the Antarctic continent, potentially feeding while migrating (see Fig. 1).

In the Southern Hemisphere, it is unexpected to find exceptional long-distance movements between different humpback whale populations (e.g., Pomilla et al. 2005; Stevick et al. 2011, 2013). Previous published reports of exceptionally long longitudinal movements between the South Pacific humpback whale populations have all been from BSE-3 to Antarctic Area I (Dawbin 1964; Mikhalev and Tormosov 1997; Robbins et al. 2011; Riekkola et al. 2018; Steel et al. 2018), a well-established feeding ground used by whales of the Breeding Stock G (Stevick et al. 2004; Acevedo et al. 2017). Our documented encounters represent the first known movement of a humpback whale migrating from the Antarctic feeding Area I to the BSE-1, covering a distance of approximately 9331 km in a northwesterly direct route across the South Pacific Ocean, or 9807 km if the whale migrated to the west following the contour of the Antarctic continent, how the whale could benefit by feeding while migrating.

While we do not know the route taken by this whale from the Antarctic Peninsula to Byron Bay on the east coast of Australia, the distance of the first plausible route is similar to the range of 9000–9426 km (108° to 111° in longitude) reported for the few humpback whales moving from Tonga or American Samoa Islands (BSE-3) to Antarctic feeding Area I; while the second plausible route is close to the currently longest-known inter-ocean exchange record (9800–10,000 km) for an humpback whale from Madagascar (Breeding Stock C-3, BSC-3) in the western Indian Ocean to Brazil (Breeding Stock A, BSA) in the western South Atlantic Ocean (Stevick et al. 2011). However, the match reported here represents the greatest longitudinal movement by a humpback whale (143°), about 32 degrees farther than any previously reported exchange between humpback whale populations to date (111° in longitude).

Genetic studies have shown significant geographic differentiation in mtDNA across the South Pacific humpback whale populations (Olavarría et al. 2007). The greatest geographic differentiation was between BSG and BSE (Olavarría et al. 2007), probably as a result of strong maternally directed fidelity to breeding grounds, feeding areas and migratory routes (Baker et al. 2013). Mitochondrial DNA haplotype SP90 is a dominant maternal lineage in the BSG (Olavarría et al. 2007; Félix et al. 2012), but appears to be absent in the BSE (Olavarría et al. 2007). Therefore, this exceptional migration might increase genetic diversity within the BSE-1 in the future.

Because of the scarcity of records, we cannot determine what ecological factors may influence these instances of unprecedented longitudinal movement. Humpback whales may make long movements while feeding at high latitudes (e.g., Dalla-Rosa et al. 2012), and such movements have been suggested to occur through tracking prey or exploring potential foraging sites in the Southern Ocean (Stevick et al. 2011). Moreover, since little is known about the mechanisms that humpback whales use for navigation or for locating reproductively active conspecifics, it is not clear how they would locate or select a different breeding ground after moving to a feeding location at a very different longitude (Stevick et al. 2011). Such long-distance movement could also be influenced by environmental perturbations in the Antarctic ecosystem such as El Niño Southern Oscillation (ENSO) events (e.g., Aguayo-Lobo et al. 1998), which affect the availability of food and prey distribution for whales in their traditional feeding areas of the Antarctic, leading whales to move more widely in search of prey in response to ecological change (e.g., Dalla-Rosa et al. 2012).

The scarce inter-oceanic movements between breeding grounds distributed on both coasts of South America (BSG and BSA) have been suggested as consequence of large-scale phenomenon caused by warm ENSO years (Stevick et al. 2013; Félix et al. 2020). Given this, it may be interesting to note that the whale INACH#0107/ECWWC-BB12021 was once encountered in Antarctic Peninsula during the strong ENSO event of 1997/98 and never again sighted in the Bransfield or Gerlache Straits, Antarctic Peninsula in later years. However, a potential link of an extensive migration with the ENSO effect should be considered with caution, given that the whale could have migrated at any time within the period of 15 years elapsed until the encounter in Byron Bay, Australia.

It is not possible to do more than speculate on the reasons for these longitudinal migrations in this species, but as noted by Stevick et al. (2013), the documentation of multiple such events suggests that they may not be as unusual in the Southern Hemisphere as has been assumed. Future large-scale comparison of genotype matching, photographic catalogues, and satellite tagging may reveal a pattern of low level but consistent interchanges between distant humpback whale populations.

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Code availability Not applicable.

Declarations

Conflict of interest On behalf of all authors, the corresponding author states that there is no conflict of interest.

Ethical approval The whale studies at Antarctic Peninsula were carried out under the Permission of the Chilean Antarctic Institute. Whale research in Byron Bay was conducted under NSW National Parks and Wildlife Scientific License #S10403 (2008-2011) and #SL100446 (2011-2015).

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