Investigating migratory patterns and interchange between breeding grounds by humpback whales (*Megaptera novaeangliae*) visiting Hervey Bay

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Abstract

Previous photo-identification and genetic studies have documented low levels of interchange by humpback whales in the South Pacific between east Australia, New Caledonia, east Oceania and Western Australia. Using an online photo-identification platform, this study matched 7791 unique whales sighted in Hervey Bay with the catalogues of the Great Barrier Reef (n = 672), Western Australia (n = 948), New Caledonia (n = 38), Tonga (n = 1466), the Samoan islands (n = 400), Niue (n = 145), Raoul Island (n = 225) and New Zealand (n = 181) to determine the level of interchange between Hervey Bay and the different breeding grounds. The degree to which New Zealand is used as a migratory corridor by whales sighted in Hervey Bay was also investigated. The interchange index between Hervey Bay and the Great Barrier Reef was the highest, followed by New Caledonia, New Zealand, Niue, Tonga, Western Australia and then Samoa. The most significant finding is the addition of 30 individual matches between Hervey Bay and east Oceania, a marked increase to numbers found in previous studies. Adding to a previous single published photo-identification match, seven Hervey Bay individuals were also connected to sightings off Western Australia. Out of the 50 whales matched in New Zealand, eight were sighted there and in Hervey Bay in the same year. The results show that there is more interchange to east Oceania breeding grounds by E1 whales than previously thought, and that New Zealand is occasionally used as a migration hub by whales that visit Hervey Bay.

Keywords: Humpback whale, Hervey Bay, interchange, breeding grounds, east Oceania, Western Australia, New Zealand, Happywhale

1 Introduction

Humpback whales (*Megaptera novaeangliae*) are found in all oceans of the world (Beeman 2017) and undertake yearly migrations between their warm water breeding areas in the low latitudes and their colder feeding areas in the high latitudes (Beeman 2017; Franklin et al. 2011), except the Arabian Sea humpback whales that remain in tropical waters throughout the year (Mikhalev 1997). There are reported to be 14 distinct populations worldwide (National Oceanic and Atmospheric Administration 2016). The International Whaling Commission (IWC) currently recognizes seven breeding populations in the Southern Hemisphere, designated A to G (Schmitt et al. 2014). Much study has been undertaken on the whales of Breeding Stock E.

The humpback whales of the E population spend the austral summer feeding in Antarctic waters between 130°E to 170°W, known as Antarctic Area V (Paton & Kniest 2011). Recent photo-identification, genetic and satellite-tagging studies suggested that this population is comprised of three distinct subpopulations: E1 migrating along the east Australian coast to the Great Barrier Reef, E2 journeying to the New Caledonia region and E3 travelling to Tonga (Olavarría et al. 2007; Paton & Kniest 2011); E1 is considered to be the largest of the three (Paton & Kniest 2011), the latest estimate (from 2015) being 24,545 whales (95% CI 21,631-27,851) (Noad, Kniest & Dunlop 2019).

The western and central South Pacific harbours thousands of islands and reefs at around 20°S. The result is a region of suitable wintering habitat that encompasses about 70˚ of longitude from the Great Barrier Reef to French Polynesia (Garrigue et al. 2000; Valsecchi et al. 2010), including the three above-mentioned breeding grounds among other locations. This would allow the migratory behaviour of humpback whales to not be restricted by substantial geographic boundaries. 'Discovery' tagging in the 1950's and 1960's and more recent photo-identification, genetic and satellite-tagging studies revealed a degree of interchange between east Australia, Western Australia, New Caledonia, Tonga, the Cook Islands and French Polynesia (Garrigue et al. 2007; Garrigue et al. 2000; Garrigue et al. 2011; Kaufman et al. 2011; Valsecchi et al. 2010), with New Zealand functioning as a migratory corridor to some of these destinations (Franklin et al. 2014) (Figure 1). Previous photo-identification-based research has reported on whales of the east Australian population travelling to other adjacent breeding regions such as Western Australia and New Caledonia, though observations of these interchanges are limited (Franklin et al. 2014; Garrigue et al. 2011; Kaufman et al. 2011). Beyond New Caledonia, no photo-identification match has been made between east Australia and other Oceania breeding grounds such as Tonga, Niue and Samoa (Franklin et al. 2014; Garrigue et al. 2011).

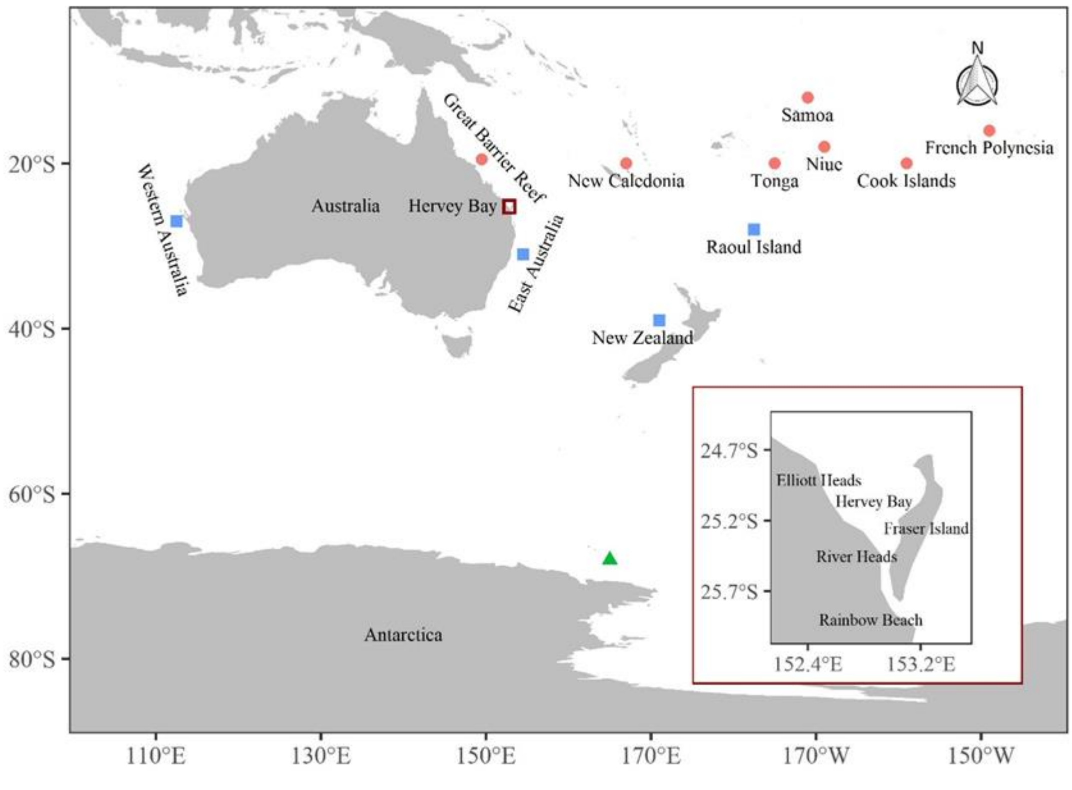


Figure 1. Map of breeding grounds, feeding regions and migratory corridors/stops, with map of Hervey Bay inset. Red circle = breeding ground, blue square = migratory corridor/stop, green triangle = feeding region.

During the southward migration along the east Australian coast, many E1 humpback whales deviate from the main route and enter Hervey Bay (Franklin et al. 2018; Martinez et al. 2015; Paton 2016). Hervey Bay (25˚S, 153˚E) is a large, sheltered bay with an area of 4000 km^2, located around 175 nautical miles north of the Gold Coast (Franklin 2014; Stack et al. 2020). It has an average depth of 20 m (18 m deep in most areas, with the deepest being more than 40 m going northwards) (Vang 2002, cited in Franklin et al. 2018; Franklin 2014; Stack et al. 2020).

Hervey Bay has been the subject of much study regarding its visiting humpback whales, one of the most notable examples being the Oceania Project. The Oceania Project is a non-profit research and education organisation founded by Drs Trish and Wally Franklin in 1988. Its main focus is research on humpback whales in Hervey Bay, which began with a six-week pilot study in 1989 to judge whether a long-term study of humpback whales in the bay would be possible. Prior research failed to ascertain what particular classes of humpback whales use Hervey Bay (Franklin et al. 2018). To address this question, the Oceania Project initiated a long-term systematic vessel-based photo-identification study from 1992 to 2017. Subsequently, Dr Trish Franklin compiled 3339 unique individuals' fluke photos into a photo-ID catalogue for Hervey Bay (Franklin et al. 2018; Franklin et al. 2011; Franklin et al. 2020; Franklin et al. 2021), which became a major component of this present study.

During the Oceania Project's study, it was found that Hervey Bay's purpose is as a stopover destination for E1 humpback whales early in their southern migration (Franklin 2013; Franklin et al. 2011). Chaloupka, Osmond and Kaufman (1999) found that around 30% to 50% of the southward-migrating whales use Hervey Bay, concentrating mainly on the eastern side of the bay along Fraser Island (Franklin 2013; Franklin et al. 2011). During August, non-lactating, resting and early pregnant females occur alongside immature males and females with peak density in late August, while the abundance of lactating females peaks in late September

(Franklin et al. 2018). Immature whales engage in social interactions with each other and the mature females (Franklin 2013). Unescorted mother-calf pods are rarely seen during the first four weeks of the season and arrive in larger numbers during September and October (Franklin et al. 2011; Franklin et al. 2021). Males are relatively rare in all three months; females outnumber males in Hervey Bay 2.9 to 1. This has led to Hervey being termed a "social and ecological niche for mature females" (Franklin et al. 2018).

The main use of photography in studying whale biology is to identify unique individuals. Individual humpback whales are distinguished by variations in pigmentation patterns, scarring on the ventral surface of their flukes and serration patterns on their flukes' trailing edges. Other identifiers are the overall fluke shapes, the shape of the v-notch between the flukes, and unique shapes and pigmentations of their dorsal fins. In 1990, the IWC reviewed the validity of photo identification as a tool for studying cetacean biology. It has proven to be useful in the field, as in experiments using genetic work and high-quality photographs, almost 100% of individual humpback whales could be identified (Calambokidis et al. 2008; Franklin et al. 2020; Garrigue et al. 2011). Due to this, photo identification work has been instrumental in significant findings such as interchange of individual humpback whales among different breeding locations in the south-west Pacific (Garrigue et al. 2000) and discovering the first feeding site (the Antarctic Peninsula) for whales breeding at American Samoa (Robbins et al. 2011).

As the use of photography in cetacean study increased, and as image catalogues grew, so did the difficulty of matching images across increasingly expansive databases, as this had to be done manually. One milestone humpback whale study was the Structure of Populations, Levels of Abundance and Status of Humpbacks (SPLASH) (Calambokidis et al. 2008), which ultimately recorded 18,469 encounters of 7,971 individuals (Cheeseman et al. 2021). The effort it takes to pairwise match increases immensely; in the case of SPLASH, this would have led to

170 million pairwise matches to be dealt with manually. In another example, it takes about an average 51.5 minutes for two experienced photo-ID technicians to compare a new individual against 10,314 known whales in the North Atlantic Humpback Whale Catalogue (Cheeseman et al. 2021). Therefore, there was a need to develop a system that would improve efficiency in image management and recognition.

Happywhale.com is one such answer, an online photo-identification matching system for citizen science and research collaboration. It employs algorithm-based automatic photo-matching for humpback whale flukes and has achieved a high rate of accuracy and success in matching photos (97%-99% with good to high quality images, >90% with poor to moderate quality flukes) (Olson et al. 2020). It was originally intended for just the South Pacific but expanded its coverage to humpback whale populations worldwide.

Up until recently, studies on humpback whales visiting Hervey Bay have been focused mainly on population characteristics and behaviours within Hervey Bay (Franklin 2013; Franklin et al. 2018; Franklin et al. 2011; Franklin et al. 2021; Franklin 2014). There has yet to be a study on whether these specific whales migrate to other breeding grounds besides the Great Barrier Reef, given that studies have shown that this is a female-dominated population (Franklin et al. 2018; Franklin et al. 2021). Generally, breeding dispersal is a behaviour predominantly observed in males of most mammal species (Greenwood 1980). Keeping this concept in mind, it would be easy to assume that a minority of whales in the Hervey Bay catalogue would be sighted in other breeding grounds.

This study would be the first attempt to match sightings of humpback whales collected in Hervey Bay with those recorded around the world using Happywhale after uploading the Oceania Project's catalogue. The aim was to determine the migration patterns and destinations of humpback whales visiting Hervey Bay (Figure 1). Special focus was in determining the degree of interchange between Hervey Bay and visited breeding grounds, whether these whales show bias towards one sex in breeding dispersal and the degree of use of New Zealand as a migratory corridor by these whales.

2 Methods

2.1 Photo-identification matching

The Oceania Project's Hervey Bay whale fluke catalogue (n = 3339) was uploaded to the Happywhale system to be added to this database or matched to known individuals. Prior to the upload, the photos were processed through Adobe Photoshop 2021 (version 23.1.0) to increase Happywhale's ability to successfully match fluke images with known individuals in the worldwide database. They were rotated until the flukes were horizontal, then cropped reasonably tightly around the flukes. Exposure adjustment was also performed upon the photos to improve chances of match confirmation; "shadows" were set to 35% and "highlights" to 0%. These cropped versions were saved with the original photos' names with '-cr' added to the end to distinguish them. They were saved in jpeg format and set to the highest resolution to retain quality.

Both the original photos and their cropped versions were uploaded in batches of around 50 to 70 originals to allow for a total of around 100 files per batch. In total, 54 batches containing 5053 original and cropped photos were uploaded. ID quality scores were added to each photo. A 0 score was awarded if no fluke was visible. Otherwise, a score of 1 to 5 was given. A score of 1 meant that the photo was of bad quality where the fluke was only just distinct or if the photo showed a partial fluke, and no ID was given if no match was made. 2 meant the pigment category or some distinguishing features could be identified; for this score too, no ID was given if no match was made. 3 meant a passable, matchable photo where most distinguishing features were visible even if not perfectly clear, and the photo was distinct enough to expect a match. It would be given a new ID if not matched. 4 was given to photos that were of good quality despite imperfections such as slight blurriness. 5 was a top-quality photo that was sharp, high-resolution and showed the full fluke oriented towards the camera with no rotation away. Tags were applied via keystroke letter shortcuts (Table 1).

Table 1. Photo tags and meanings.

Tag	Meaning
C	uncropped
P	partial fluke (for photos with less than 60% of the fluke/flukes' trailing visible, and if the V-notch was not visible)
U	scar of unknown origins (probable human-induced scarring)
S	scar from ship strikes
N	scar from entanglement
K	scar from killer whale bites
E	active entanglement
L	left dorsal
R	right dorsal
D	dorsal surface (along with a score of 0)

The photos were then sent through Happywhale's automated image recognition algorithm to attempt matching. The algorithm selected the five most likely matches across the entire database. The five potential matches received a score varying from zero to one, with scores near or below 0.38 suggesting an incorrect match. All the five suggested matches were manually compared against the uploaded fluke, looking closely for similar pigment patterns and fluke trailing edge patterns, taking the match score into account. The identical or closest possible match was selected ("closest possible" refers to when a proposed match is the actual correct match but may show differences in fluke features such as barnacle scarring or trailing edge serration patterns as these may change slightly over time). If none of the proposals seemed to be a good match, the fluke was left unmatched to be entered into the database as a new entry later and given a new Happywhale ID (by which individuals will be referred to in this study).

After the batch's photos were matched, a csv file of this batch's sighting records was downloaded. Each record was compared against the Oceania Project catalogue and the relevant information was entered (encounter date, encounter longitude and latitude, encounter location, location precision, the individual's nickname given by the Oceania Project, sex, the individual's bio, species, the Oceania Project's organization number, the research vessel the encounter was recorded on and comments about the encounter). If an individual record in the Oceania Project catalogue was not matched to a known individual in the Happywhale database, the Oceania Project ID number was entered instead. After all edits were satisfied, the csv was sent to Happywhale to add the encounters to the database (and make a new profile for previously unknown individuals). Once this step was finished, further edits to the Oceania Project-related whale profiles were implemented: adding the Oceania Project's alternate ID for an individual, as well as their nickname, sex, bio if applicable and pigment category (Figure 2).

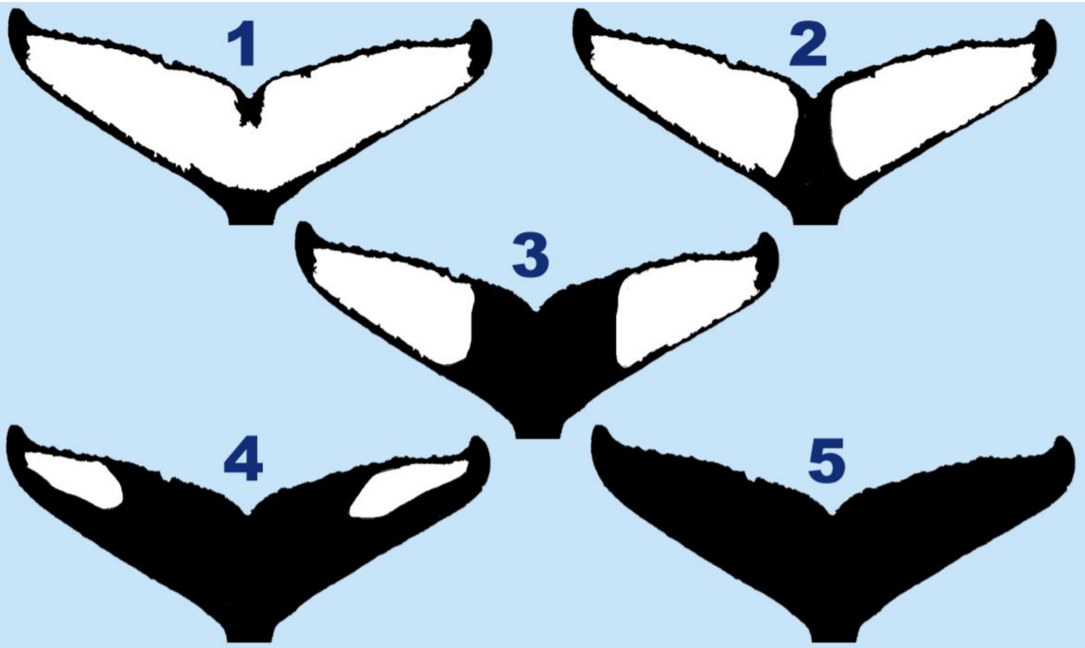


Figure 2. Pigment categories. Source: National Oceanic and Atmospheric Administration.

The resulting Hervey Bay fluke database in Happywhale contained 7795 individuals with 18735 sightings. After completing the required data-sharing agreement with relevant agencies, the dataset for this study was reduced to 7791 individuals with 18720 sightings.

2.2 Data validation

The Happywhale Hervey Bay dataset used in this study contained records from 24/06/1984 until 20/11/2021 and was validated and analysed in RStudio (version 4.1.2). Records without an individual ID or an encounter ID were removed if found. Duplicate records from the same day and year in a location were removed. Records without a value in the encounter location accuracy field were set to “General”. Individuals without a value in the individual sex field were called “Unknown”. Following these steps, the total number of sightings became 14754.

Currently, Happywhale relies on manual entry of location data when uploading new records and there is no automated validation between GPS coordinates and manual entries. Therefore, there were some records whose entered location names did not match their coordinates. To eliminate these data entry errors, a new region field was introduced into the dataset and populated automatically by matching the records’ coordinates against the defined regions (Table 2).

Table 2. Regions and their assigned boundaries (north, west, south, east).

Region	Boundaries
Hervey Bay	N: 24.7˚S, W: 152.4˚E, S: 25.45˚S, E: 153.3˚E
Great Barrier Reef	N: 10˚S, W: 140˚E, S: 24.49˚S, E: 154˚E
Western Australia	N: 10˚S, W: 100˚E, S: 40˚S, E: 120˚E
New Caledonia	N: 15˚S, W: 155˚E, S: 30˚S, E: 170˚E
Tonga	N: 17.5˚S, W: 177˚E, S: 22.8˚S, E: 173˚W
Samoa	N: 14˚S, W: 171.1˚W, S: 14.6˚S, E: 170.3˚W
Niue	N: 18.5˚S, W: 170˚E, S: 19.5˚S, E: 169.4˚W
New Zealand	N: 34˚S, W: 165˚E, S: 50˚S, E: 180˚E
Raoul Island	N: 25˚S, W: 180˚W, S: 35˚S, E: 168˚W
Antarctica	N: 50˚S, W: 180˚W, S: 80˚S, E: 180˚E

2.3 Sighting locations and periods

The full catalogue of Hervey Bay sightings and associated matches in the Happywhale database consisted of records from ten regions (Hervey Bay, Great Barrier Reef, Western Australia, New Caledonia, Tonga, Samoa, Niue, New Zealand, Raoul Island and Antarctica). Six of these regions were breeding grounds, and the other three were migratory corridors and stops (Table 3). Antarctica and Raoul Island were ignored for statistical analysis, as Antarctica is a feeding ground and Raoul Island is simply part of the migratory corridor of southbound humpback whales travelling from islands in Oceania such as New Caledonia and Tonga (Constantine, Garrigue & Baird 2010; Duffy, Baker & Constantine 2015; Steel et al. 2014), and were not within the scope of this project.

Table 3. Total number of individuals and sighting years of humpback whales in breeding regions and migratory stops/corridors as per the Happywhale database.

Region	Years	Total no. of individuals
Breeding regions		
Great Barrier Reef	1985-2020	672
Western Australia	1990-2021	948
New Caledonia	2016-2020	38
Tonga	1985-2019	1466
Samoa	1994-2016	400
Niue	2007-2020	145
Migratory stops and corridors		
New Zealand	1994-2018	181
Raoul Island	2015-2017	225
Hervey Bay	1985-2021	7791

A total of 7791 individuals was identified in Hervey Bay between 1985 and 2021 (Table 3, Figure 3). Between 1985 and 2021, 672 individuals were identified in the Great Barrier Reef. A total of 948 individuals was sighted between 1990 and 2021 off Western Australia between Camden Sound and Flinders Bay. The Happywhale database contained sightings of 38 whales sighted between 2016 and 2020 in New Caledonia, the majority being around the Chesterfield-Bellona archipelago and the rest near the main island Grande Terre. Photographs of 1466 whales were taken in the Tongan group of islands from Niuafo'ou in the north, down to Tongatapu and 'Eua from 1985 to 2019. A total of 400 individuals was photographed off the Samoan islands between 1994 and 2016. Between 2007 and 2020, 145 whales were sighted in the waters around Niue. In New Zealand, 181 unique whales were sighted around the mainland from 1994 to 2018. The majority of New Zealand sightings were recorded in the Cook Strait separating the North and South Islands, secondly from the bottom of the South Island and the remaining few from the northern coast of the country. A total of 225 individuals were recorded around Raoul Island between 2015 and 2017.

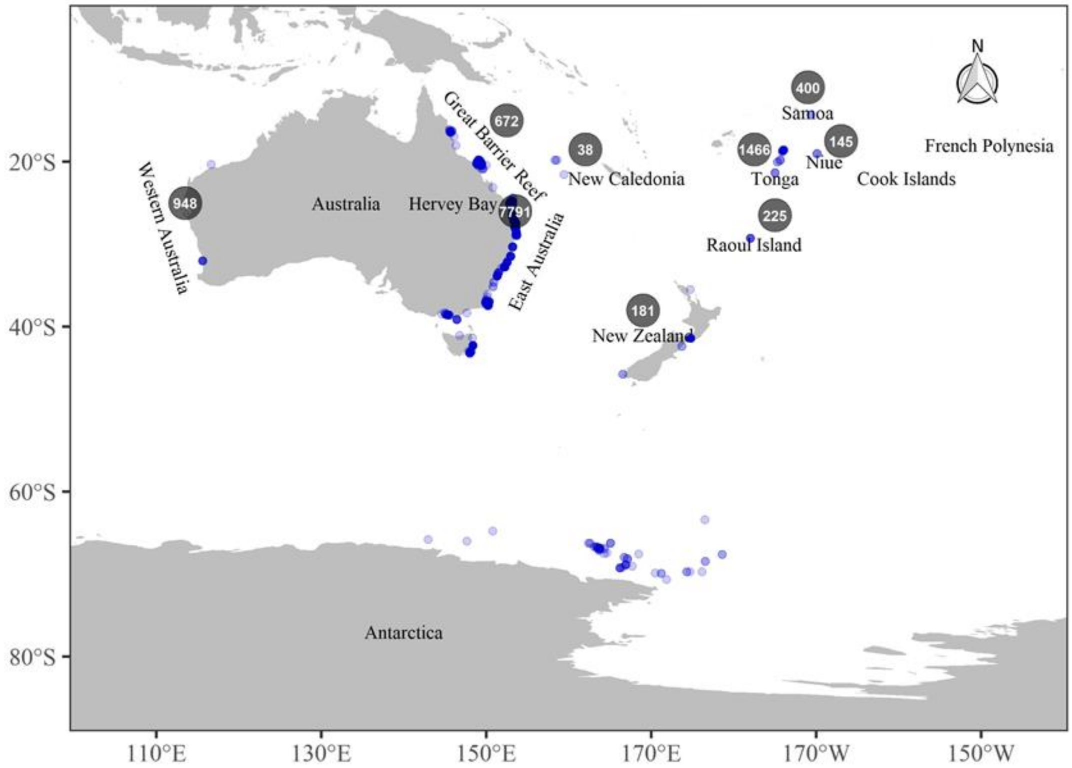


Figure 3. Total number of individuals in the Happywhale database in each region except Antarctica. Blue dots = matched sightings (n = 14754).

2.4 Interchange between Hervey Bay and breeding grounds

An interchange index was calculated to provide a relative degree of movement between Hervey Bay and the recorded breeding sites between 1985 and 2021 (New Zealand was included in this calculation). This was accomplished via the equation:

$$Interchange\ index = (m_{12}/(n_1 * n_2)) * 1000$$

where n_1 is the number of whales identified in Hervey Bay, n_2 is the number of whales identified in a specified breeding area and m_{12} is the number of whales matched between Hervey Bay and the breeding site. A higher value in this index suggests that there is a high probability of resighting the same individual between two distinct areas, while a lower value suggests that an interchange of whales between the two areas is unlikely (Acebes et al. 2021; Urbán R et al. 2000).

A goodness of fit chi-squared analysis was performed to test if humpback whales were uniformly distributed across all the breeding regions. The analysis was carried out using Microsoft Excel for Microsoft 365 (Version 2112). The goodness of fit analysis was used to compare observed versus expected matches between Hervey Bay and the visited breeding regions. The expected number of matches for each breeding region was calculated by dividing the observed number of matches in all breeding regions by the total number of whales seen in all breeding regions, then multiplying this proportion by the number of whales seen at each breeding region. This method was adapted from Urbán R et al. (2000).

3 Results

3.1 Migratory destinations

Matching of individual humpback whales identified in Hervey Bay with those identified in other regions resulted in 343 matches with the Great Barrier Reef, seven matches with Western Australia, four matches with New Caledonia, 25 matches with Tonga, two matches with Samoa, three matches with Niue, 50 matches with New Zealand, five matches with Raoul Island and 62 matches with Antarctica (Figure 4). A total of 489 individuals were matched between Hervey Bay and the other visited regions. Out of these 489 whales, 12 were identified in two or more regions apart from Hervey Bay in different years; six were identified in the Great Barrier Reef and Antarctica, two in the Great Barrier Reef and New Zealand, one in the Great

Barrier Reef and Western Australia, one at Niue and Raoul Island, one at Tonga and New Zealand, and one at Tonga and Samoa.

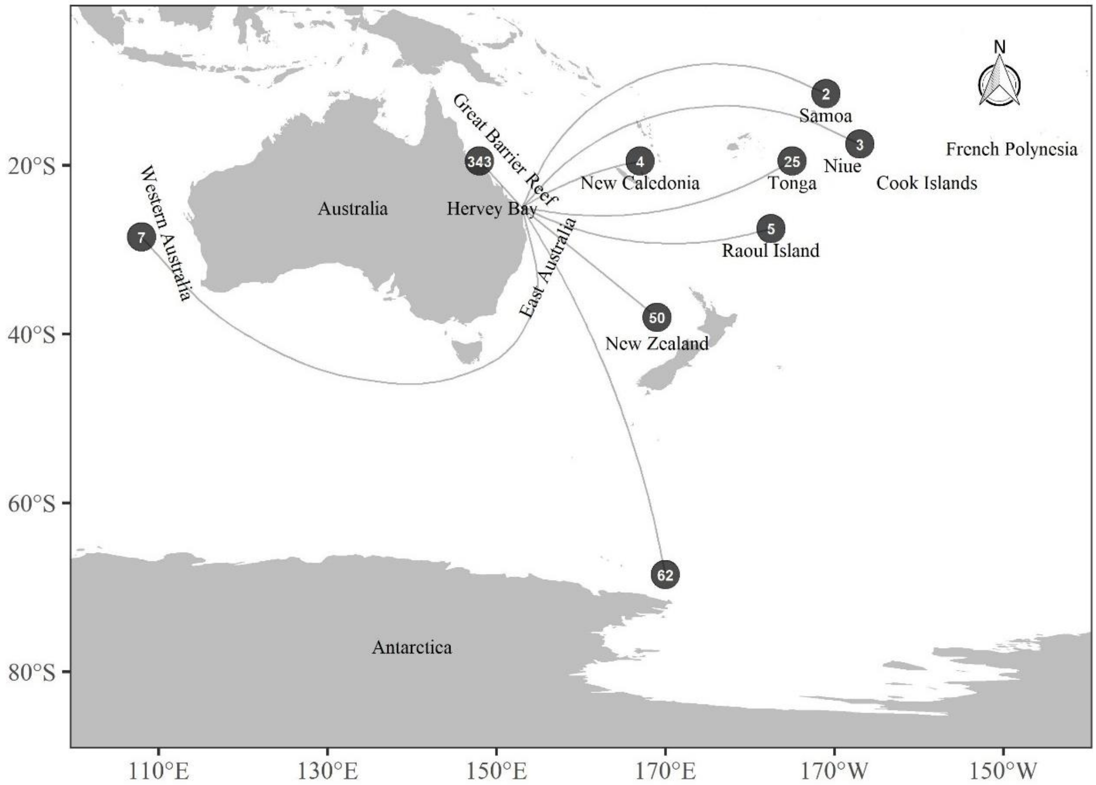


Figure 4. Number of matches with Hervey Bay for each region between 1985 and 2021.

3.2 Migrations past New Zealand

Out of the 50 whales matched in New Zealand, eight individuals were sighted passing through the Cook Strait and subsequently in Hervey Bay at least a month later the same year (Figure 5). Of the individuals sighted in New Zealand, 43 were part of the northward migration, being recorded between May and the end of July, while four were recorded between October and November during the southward migration. The remaining three were sighted in January, February and April each during the period of no distinct migration (Gibbs & Childerhouse 2000). Between January and October, 45 individuals were sighted in the Cook Strait (one in January, one in May, 18 in June, 24 in July and one in October) (Table 4). During November, two were reported off Dusky Sound, Fiordland. During April, one was spotted off Tawhiti Rahi Island, Northland Region. Between February and October, two were recorded near Kaikoura.

Table 4. Number of individuals sighted in New Zealand in all months between 1998 and 2021.

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Cook Strait	1	-	-	-	1	18	24	-	-	1	-	-
Fiordland	-	-	-	-	-	-	-	-	-	-	2	-
Northland Region	-	-	-	1	-	-	-	-	-	-	-	-
Kaikoura	-	1	-	-	-	-	-	-	-	1	-	-

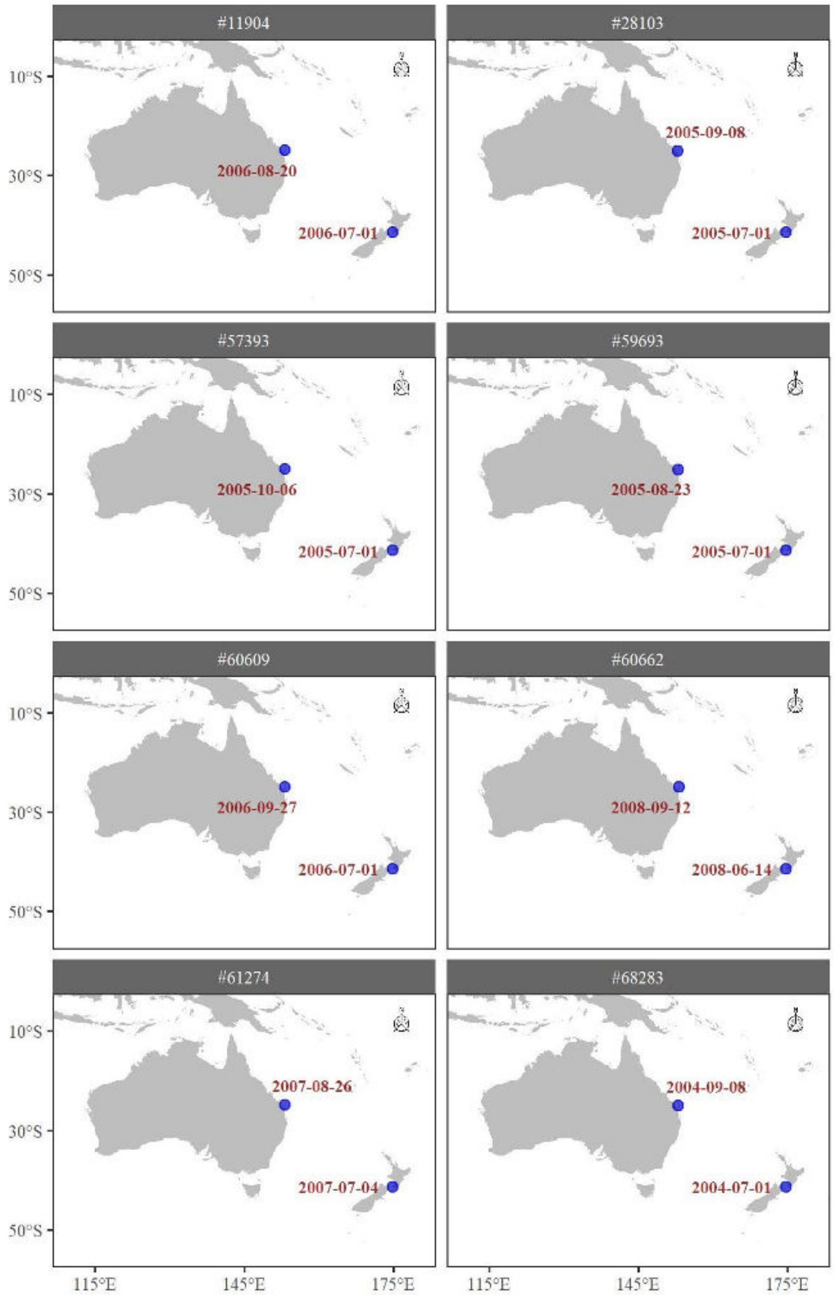


Figure 5. Sighting maps of whales seen in New Zealand and Hervey Bay in the same year.

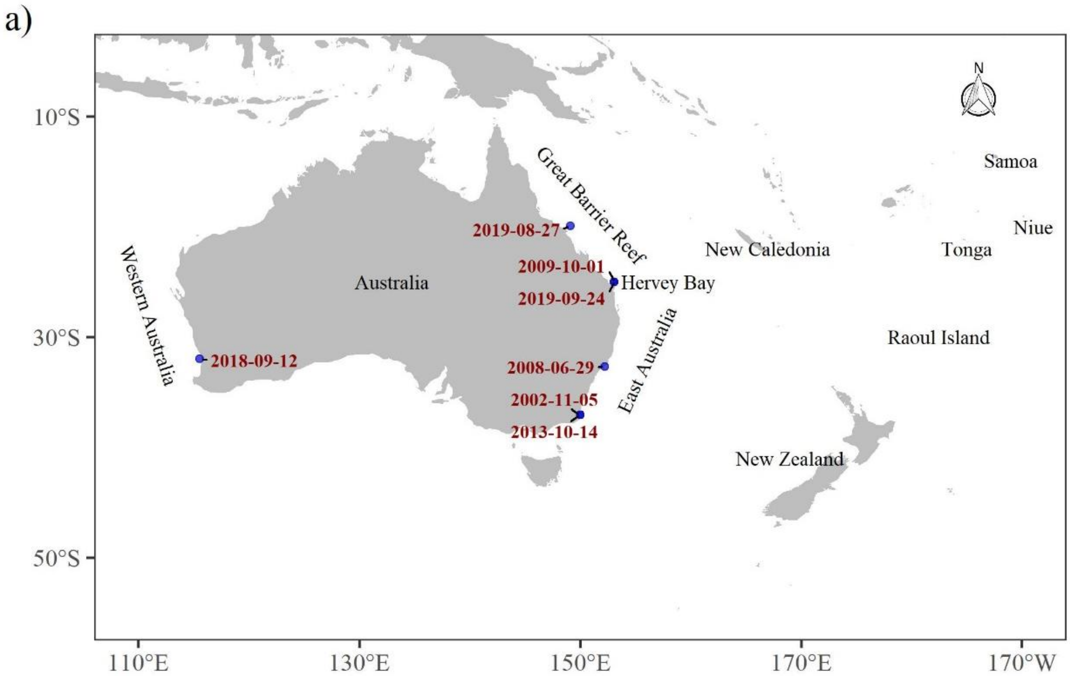
3.3 Breakdown of sex in sightings

In all regions, individuals of unknown sex were the majority, with a minimum of 57% of individuals per site for which the sex was not assigned (Table 5). Numbers of humpback whales with sex identified as male were in larger proportion than females in Western Australia (29%), Tonga (12%) and Raoul Island (20%) (Table 5). On the other hand, more females than males were identified in the Great Barrier Reef (20%), New Zealand (8%) and Antarctica (18%) (Table 5).

Table 5. Breakdown of sex and percentage breakdown in all regions from 1985 to 2021.

Region	Female	Male	Unknown	Total	Female %	Male %	Unknown %
Hervey Bay	852	389	6550	7791	11	5	84
Great Barrier Reef	67	39	237	343	20	11	69
Western Australia	1	2	4	7	14	29	57
New Caledonia	-	-	4	4	-	-	100
Tonga	2	3	20	25	8	12	80
Samoa	-	-	2	2	-	-	100
Niue	-	-	3	3	-	-	100
New Zealand	4	2	44	50	8	4	88
Raoul Island	-	1	4	5	-	20	80
Antarctica	11	2	49	62	18	3	79

Out of the whales with sexes identified, only two females showed significant sighting patterns in which they mostly followed the east Australian migration route, with detours to other breeding areas (Figure 6). #13984 was reported travelling to east Australia (with sightings in the Great Barrier Reef) between 2002 and 2019, with a deviation to Western Australia in 2018. #27856 was sighted in east Australia between 1988 and 2015, with one sighting in Tonga in 1991.



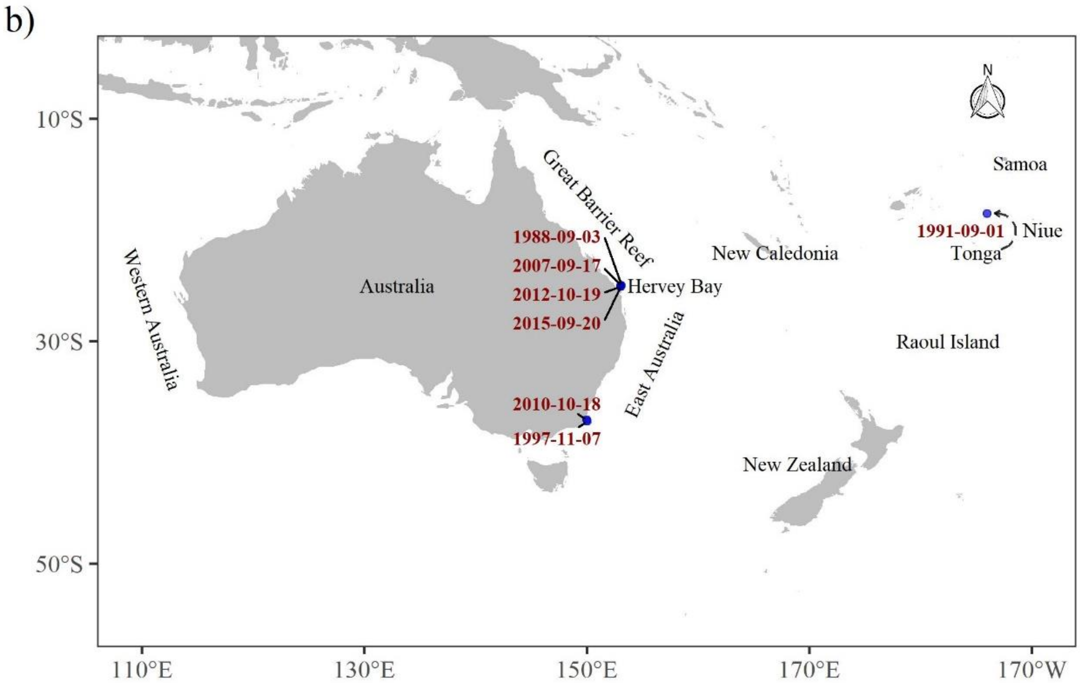


Figure 6. Sighting maps of a) #13984 and b) #27856.

3.4 Sightings of whales in regions in multiple seasons

Aside from Hervey Bay and the Great Barrier Reef, most of the other regions did not report resightings of individual whales in multiple seasons. The only region to do so was Tonga, reporting three unique whales returning in multiple years (Table 6). One animal, #42631, was seen around Tonga in three different years during the breeding season: 1994, 1996 and 1999. The other two, #42664 and #43449, were seen in 1991 and 2006, and 1996 and 2009 respectively (Figure 7).

Table 6. Proportion of identified whales resighted in multiple years in ten regions.

	No. of unique whales identified	No. of unique whales observed in multiple years	Proportion of whales resighted in multiple years (%)
Hervey Bay	7791	2983	38.29
Great Barrier Reef	343	25	7.29
Western Australia	7	-	-
New Caledonia	4	-	-
Tonga	25	3	12
Samoa	2	-	-
Niue	3	-	-
New Zealand	50	-	-
Raoul Island	5	-	-
Antarctica	62	-	-

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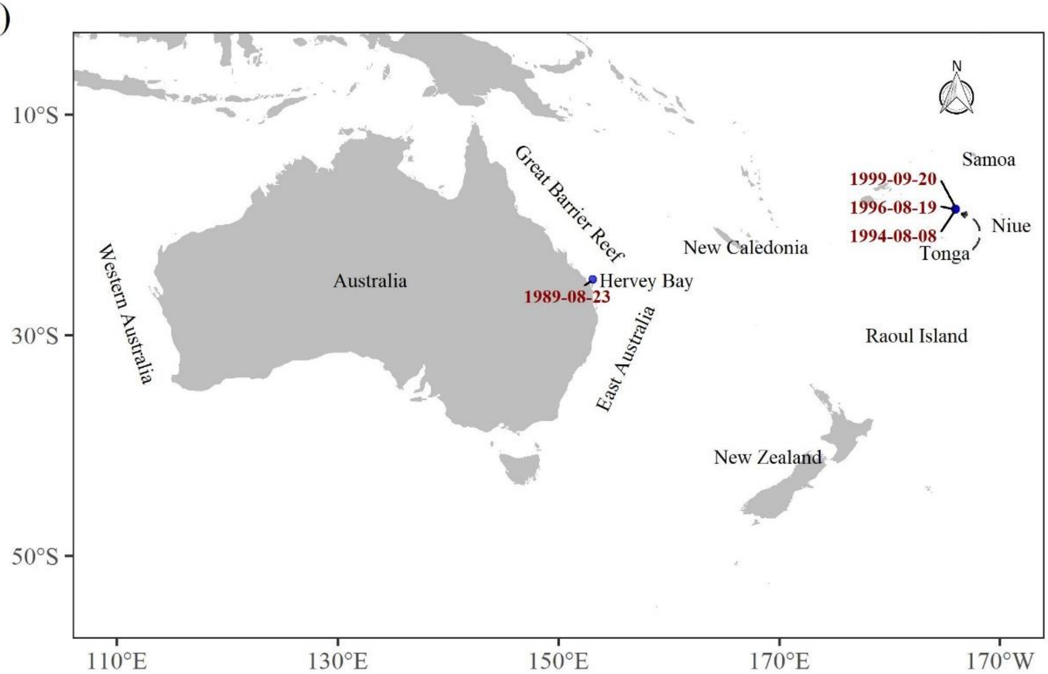

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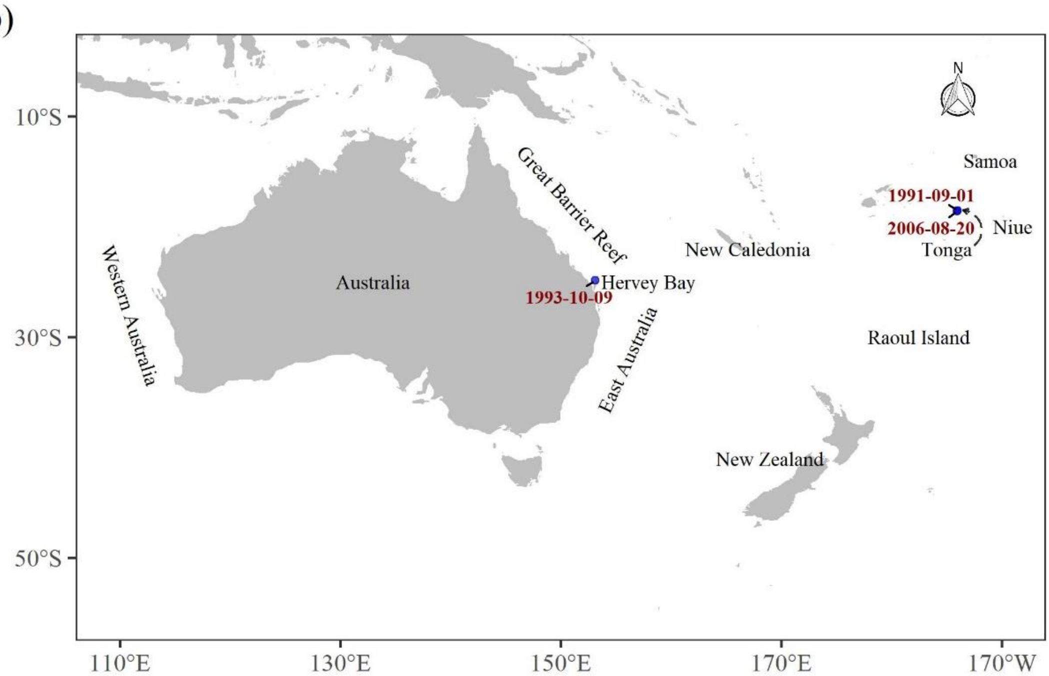

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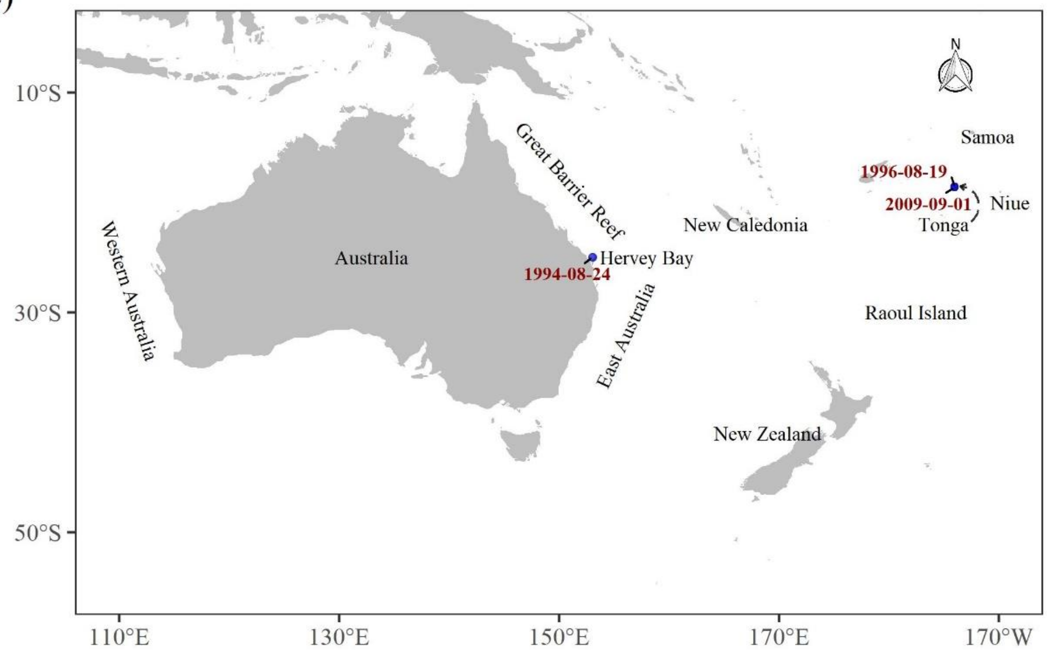
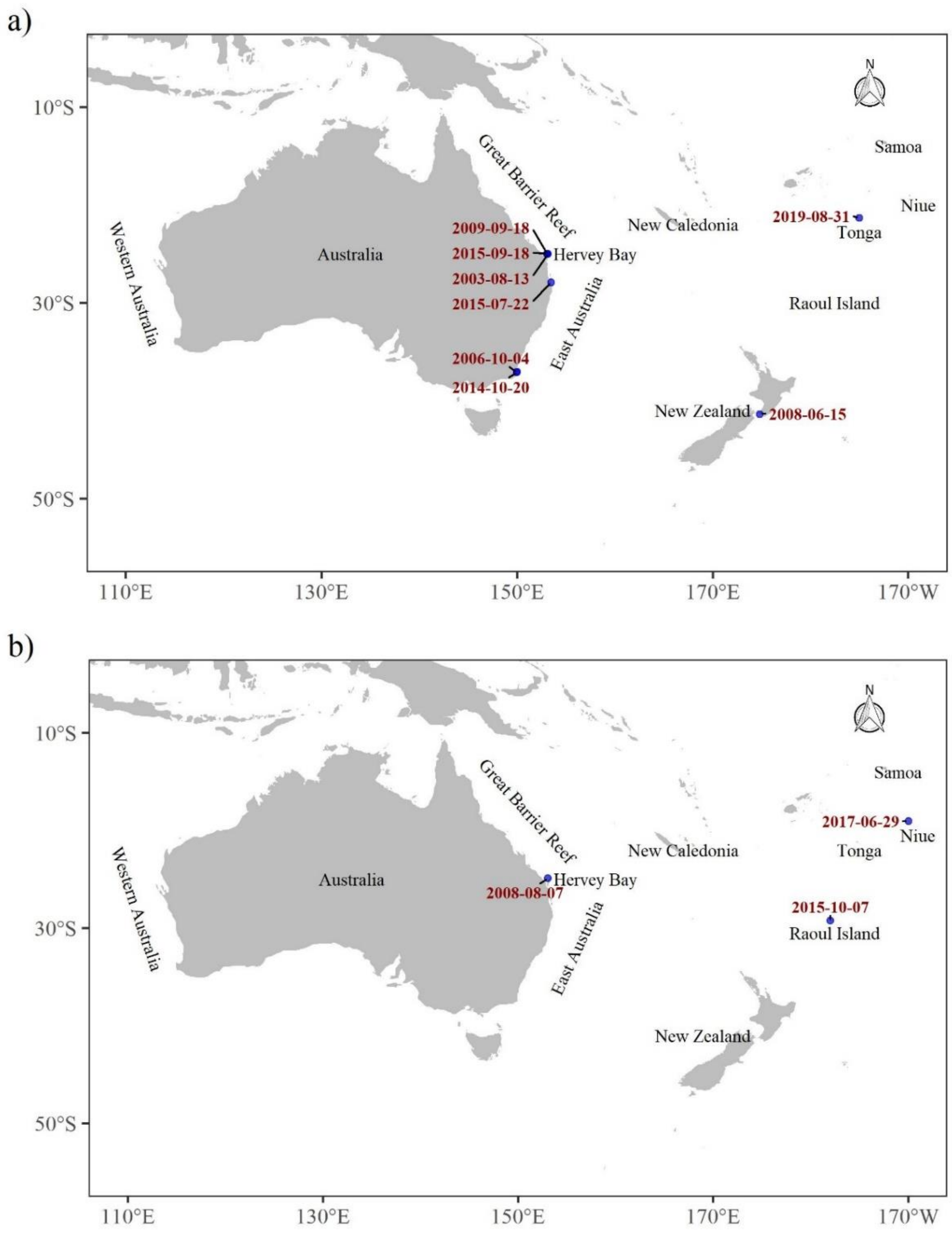


Figure 7. Sighting maps of a) #42631, b) #42664 and c) #43449.

3.5 Sightings of whales in multiple regions

Out of the 7791 identified whales, only three were sighted in two or more different regions apart from Hervey Bay (Figure 8). #39118 was sighted in New Zealand travelling northwards in 2008 and in Tonga in 2019. #39443 was spotted travelling past Raoul Island in 2015 and in Niue in 2017. #43745 was recorded in Tonga in 1996 and around the Samoan islands in 2009.



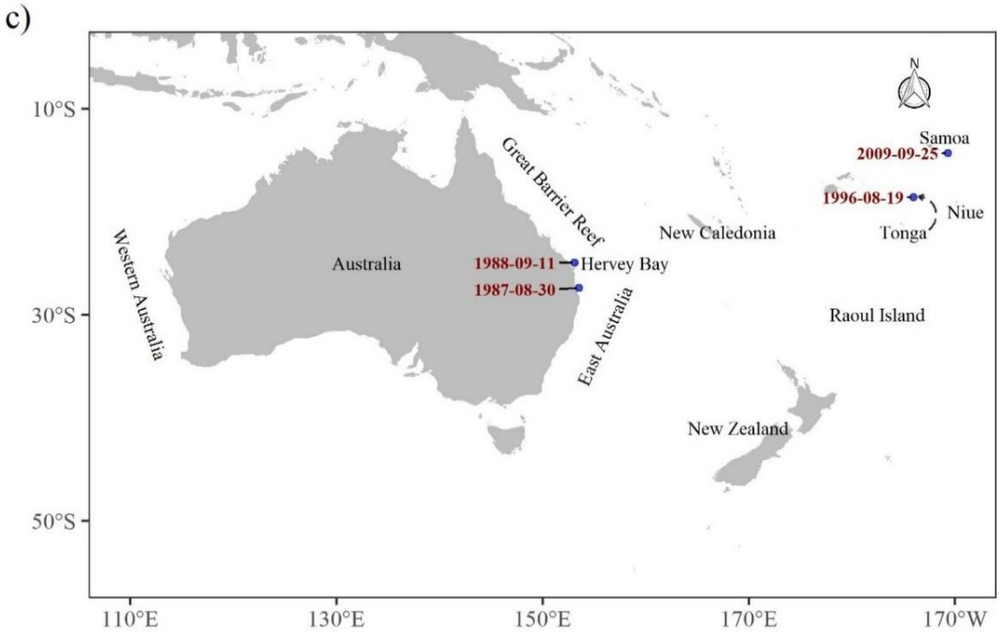


Figure 8. Sighting maps of a) #39118, b) #39443 and c) #43745

3.6 Interchange with other breeding grounds

Out of 489 individuals, 60 were not considered for the interchange calculation as they were sighted at either Antarctica (n = 56) or Raoul Island (n = 4). A total of 429 unique humpback whales from Hervey Bay matched to the reported breeding grounds and New Zealand, and showed an overall interchange index of 0.0143. The Great Barrier Reef had the highest interchange index with Hervey Bay at 0.0655, followed by New Zealand at 0.0355, and New Caledonia at 0.0135. Samoa and Western Australia had the lowest interchange indices of 0.0009 and 0.0006 respectively (Table 7, Figure 9).

Table 7. Number of matches observed and expected, and interchange index between Hervey Bay and breeding grounds (and New Zealand).

	Great Barrier Reef (n=672)	Western Australia (n=948)	New Caledonia (n=38)	Tonga (n=1466)	Samoa (n=400)	Niue (n=145)	New Zealand (n=181)	All breeding regions (n=3669)
Hervey Bay (n=7791)								
Observed	343	7	4	25	2	3	50	429
Expected	75	106	4	163	45	16	20	429
Index	0.0655	0.0009	0.0135	0.0022	0.0006	0.0027	0.0355	0.0143

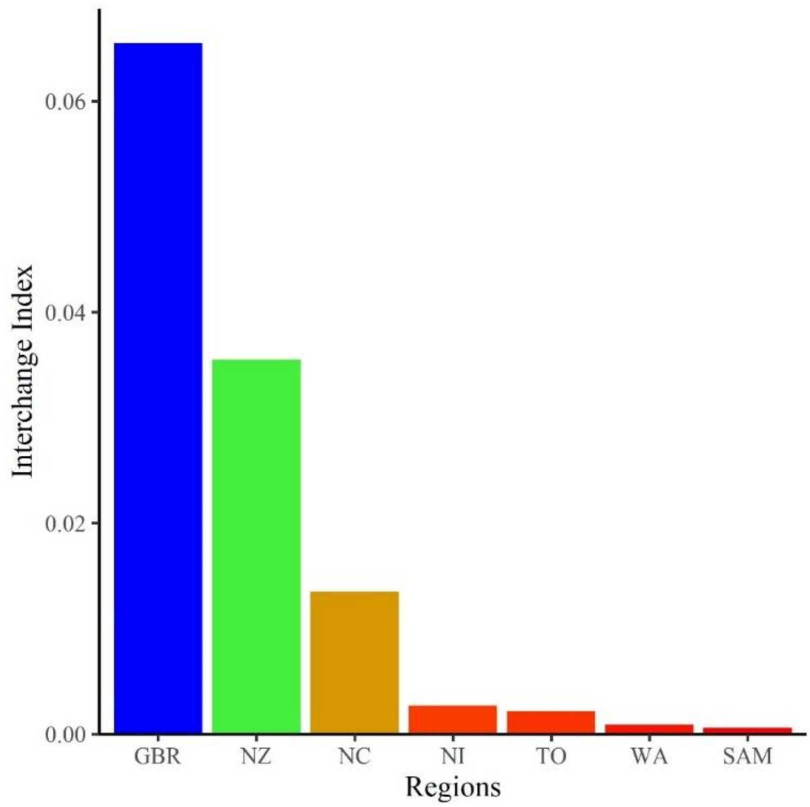


Figure 9. Interchange index between Hervey Bay and the six breeding regions (and New Zealand).

GBR = Great Barrier Reef, NZ = New Zealand, NC = New Caledonia, NI = Niue, TO = Tonga, WA = Western Australia, SAM = Samoa.

3.7 Statistical analysis of interchange

The goodness of fit analysis showed that the observed number of matches between Hervey Bay and each of the breeding areas significantly differed from the expected number of matches under the null hypothesis ($\chi^2 = 1264$, df = 5, $p < 0.05$). Whales visiting Hervey Bay did not distribute equally across the breeding grounds, but rather showed preferences for specific breeding sites. Therefore, aside from the indication that the Great Barrier Reef would be the main breeding ground, the interchange results show that Hervey Bay humpback whales may be more likely to preferentially divert to New Caledonia and to a lesser extent, move to east Oceania and Western Australia (Table 7).

4 Discussion

4.1 Interchange with east Oceania

The most significant finding of this study was the number of matches found between Hervey Bay and east Oceania breeding grounds (Tonga, Niue and Samoa). To date, reported connections between the E1 population and Oceania breeding grounds were very minimal. Kaufman et al. (1993, cited in Garrigue et al. 2002) found just one photo-ID match between the two regions. More recently, Garrigue et al. (2011) found no connections between the E1 population and any Oceania breeding grounds east of New Caledonia through photo-identification between 1999 and 2004, and one match was made to Tonga via genotype matching (Steel et al. 2018). Regarding the E1 population and east Oceania breeding grounds, this study makes what could be a significant change in current knowledge of interchange between the east Australian coast and east Oceania, using just a specific subset of the E1 population. Here, Tonga held the largest share of matches (n = 25) out of the three recorded east Oceania regions, while further away from Tonga, three whales were matched to Niue and two to the Samoan islands (Table 8).

Interestingly, out of the 25 individuals matched in Tonga, three (#42631, #42664 and #43449) were each sighted around Tonga in multiple years and only once in Hervey Bay. This raises the question whether these specific whales may actually be part of the E3 (Tonga) population rather than the E1 population. #42631 especially could be a case of this, as its sighting history consists of Hervey Bay in 1989, then Tonga in three nearby years: 1994, 1996 and 1999. Alternatively, it could simply be a matter of the irregularity of sighting some individuals. It could possibly be true for all three individuals to be E1 whales, more so for #42664 and #43449, given their relatively sparser sighting histories compared to #42631 (Table 8).

Table 8. Sighting history of individuals sighted in east Oceania breeding grounds.

Happywhale ID	Sex	Year First Sighted	Region first sighted	Years sighted			
				Hervey Bay	Tonga	Samoa	Niue
#5786	Female	2000	Hervey Bay	2000	2014	-	-
#5822	Unknown	2006	Hervey Bay	2006	2014	-	-
#7442	Unknown	1993	Hervey Bay	1993	2000	-	-
#11400	Unknown	2000	Hervey Bay	2000	2003	-	-
#13848	Male	1991	Tonga	2000, 2004, 2008	1991	-	-
#14272	Unknown	2008	Tonga	2021	2008	-	-
#27856	Female	1988	Hervey Bay	1988, 2007, 2012, 2015	1991	-	-
#39068	Unknown	2018	Tonga	2020	2018	-	-
#39118	Unknown	2003	Hervey Bay	2003, 2009, 2015	2019	-	-
#39131	Unknown	2018	Niue	2020	-	-	2018
#39443	Unknown	2008	Hervey Bay	2008	-	-	2017
#39534	Unknown	2005	Hervey Bay	2005	-	-	2018
#42587	Unknown	2002	Tonga	2007, 2008	2002	-	-
#42631	Unknown	1989	Hervey Bay	1989	1994, 1996, 1999	-	-
#42657	Male	1988	Hervey Bay	1988, 1998, 2002	2006	-	-
#42664	Unknown	1991	Tonga	1993	1991, 2006	-	-
#43449	Unknown	1994	Hervey Bay	1994	1996, 2009	-	-
#43745	Unknown	1988	Hervey Bay	1988	1996	2009	-
#43760	Unknown	1991	Hervey Bay	1991, 1994, 1998,2006	1996	-	-
#43834	Unknown	1989	Hervey Bay	1989	2001	-	-
#43969	Male	2006	Tonga	2015	2006	-	-
#43990	Unknown	1997	Hervey Bay	1997	2009	-	-
#44237	Unknown	2000	Tonga	2010	2000	-	-
#44249	Unknown	2005	Tonga	2008	2005	-	-
#46243	Unknown	2008	Hervey Bay	2008	2017	-	-
#50884	Unknown	1989	Hervey Bay	1989, 1997	-	2006	-
#58545	Unknown	1998	Hervey Bay	1998	2007	-	-
#59245	Unknown	2005	Hervey Bay	2005	2018	-	-
#59665	Unknown	2005	Hervey Bay	2005	2019	-	-

Despite these east Oceania findings, the interchange indices for these three breeding regions calculated in this study were quite low (0.0027 for Niue, 0.0022 for Tonga and 0.0006 for Samoa) compared to some of the other tested regions. The number of individuals in the Happywhale Hervey Bay database (n = 7791) far outnumber the Tonga, Niue and Samoa databases combined (n = 2011). Furthermore, the number of recorded matches between Hervey Bay and the three east Oceania breeding grounds were significantly lower than those between Hervey Bay and the Great Barrier Reef, giving low interchange indices and suggesting that there is low exchange of whales between Hervey Bay and east Oceania.

4.2 Interchange with the Great Barrier Reef

The Great Barrier Reef's interchange index with Hervey Bay was the highest (0.0655), followed by New Caledonia (0.0135) and Western Australia (0.0009). This result was expected, with the Great Barrier Reef being the main breeding ground of the E1 population. In this study, the majority of Hervey Bay humpback whales sighted in the Great Barrier Reef (305 sightings of 288 individuals, all of which were recorded by research organizations: the Pacific Whale Foundation, Blue Planet Marine and the East Coast Whale Watch Catalogue) were recorded from around 19˚S down to around 21˚S (Figure 10). This seems to corroborate the findings of Chaloupka and Osmond (1999), who recorded the majority of their limited sightings in the southern Great Barrier Reef, suggesting that the main breeding grounds of the E1 population is around the Whitsundays Islands and the Pompey/Swains reef complex. This is further supported by Smith et al. (2012) who identified this area as a major wintering ground based on habitat modelling and satellite tag data.

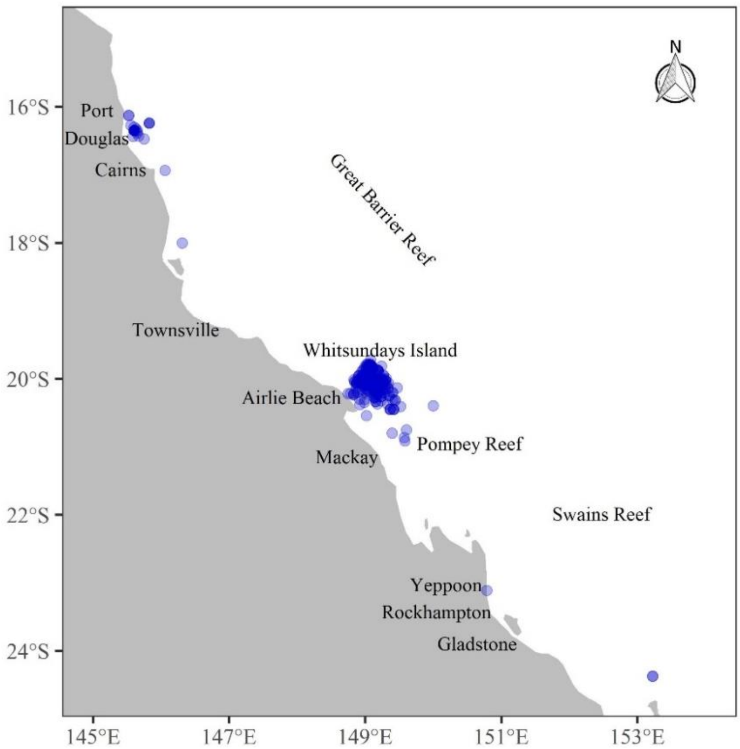


Figure 10. Sightings of Hervey Bay humpback whales in the Great Barrier Reef.

Blue dots = matched sightings (n = 373).

4.3 Interchange with New Caledonia

Next to the Great Barrier Reef, the nearby breeding ground of New Caledonia had the highest interchange index outside of the east Australia migration corridor, though the number of matches between Hervey Bay and New Caledonia was markedly small compared to other breeding regions (namely Tonga and Western Australia). None of these matches were sighted between New Caledonia and Hervey Bay in the same year. New Caledonia is the closest adjacent breeding ground to the Great Barrier Reef (~800 km from the Chesterfield-Bellona archipelago to Hervey Bay, ~1400 km from Grande Terre), and it would therefore be reasonable to hypothesize that at least some whales migrate from New Caledonian waters along the east Australian coast down to Antarctic Area V (Garrigue et al. 2010). However, previous photo-identification studies have only found four matches between these two breeding areas after a comparison between the east Australian catalogue and the New Caledonia catalogue (Franklin et al. 2014; Garrigue et al. 2000; Garrigue et al. 2011). A New Caledonian satellite-monitoring study by Garrigue et al. (2010) did not manage to find definite evidence of whales travelling between New Caledonia and the east Australian coast (though it should be noted that one tagged whale, a mother with a calf, was tracked going westwards in the direction of the east Australian coast until transmissions ceased 260 km east of the Chesterfield Reefs). The more recent but limited number of New Caledonian matches found by this study (one in 2016, three in 2017) support previous conclusions that the level of interchange between New Caledonia and the east Australian population is low, and same-year movements between the two regions are yet to successfully recorded.

4.4 Interchange with Western Australia

In this study, Western Australia had the second lowest interchange index (0.0009). Out of 948 whales currently recorded off Western Australia in the Happywhale database, six sighted in Hervey Bay were matched with sightings off Rottnest Island and one near the Dampier Marine Park (Table 9). Before these matches, there was only one published photographic record showing an interchange between the breeding stock D in Western Australia and E1 in eastern Australia. A single individual was first identified off North Stradbroke Island, Queensland in September 1987 and resighted in October 1995 off Fremantle, Western Australia (Kaufman et al. 2011). Additional evidence is provided by satellite tracking data, which reported humpback whales tagged off the east Australian coast swimming towards the western edge of Antarctic Area IV (70˚E-130˚E), said to be the main feeding grounds of stock D (Andrews-Goff et al. 2018; Franklin et al. 2017a; Franklin et al. 2017b). With the addition of the seven Hervey Bay-Western Australia matches in this study, it further supports the conclusion that some interchange occurs between the east Australian population and the Western Australian population.

Table 9. Sighting history of individuals sighted in Western Australian breeding ground.

Happywhale ID	Sex	Year first sighted	Region first sighted	Years sighted	
				Hervey Bay	Western Australia
13984	Female	2009	Hervey Bay	2009, 2019	2018
27710	Unknown	2012	Hervey Bay	2012, 2019	2017
46111	Male	1991	Western Australia	2012	1991
51343	Male	2004	Hervey Bay	2004, 2009	2020
60959	Unknown	2007	Hervey Bay	2007	2017
64455	Unknown	2015	Hervey Bay	2015	2020
66794	Unknown	2011	Hervey Bay	2011	2018

4.5 Migrations past New Zealand

New Zealand, a migratory corridor, had the second highest interchange index with Hervey Bay (0.0355), after the Great Barrier Reef, suggesting that a considerable number of humpback whales pass through New Zealand on their way to the east Australian corridor. Prior to this study, three whales out of the 13 in the New Zealand catalogue at the time were matched to east Australia (Franklin et al. 2014; Garrigue et al. 2011). All three whales were resighted in Hervey Bay, two of them in the same season as their corresponding sightings in New Zealand. Therefore, despite the small sample size, it was suggested that that E1 whales travel through New Zealand between east Australia and Antarctic feeding areas (Franklin et al. 2014). This study further supports this conclusion with a larger sample size of 50 matches to Hervey Bay out of 181 whales in the Happywhale database, with eight whales sighted in the Cook Strait and Hervey Bay in the same year.

Franklin et al. (2014) hypothesized on possible routes to different breeding grounds and feeding grounds that humpback whales may take passing northwards and southwards through New Zealand (Figure 11). Using this as a guide, it can be speculated that apart from the eight same-year Hervey Bay-New Zealand connections, the majority of sightings that were seen in the Cook Strait from May to October were heading to/from east Australia or New Caledonia. The two spotted near Fiordland at the south-western tip of New Zealand in November were likely to be swimming from eastern Australia. The single individual recorded at Kaikoura in October probably came from Tonga. Satellite-tagging work by Andrews-Goff et al. (2018) features tracks of southbound E1 whales diverting eastwards from the Bass Strait to the west coast of the South Island of New Zealand, rounding Fiordland and going south towards Area V. Perhaps satellite-tagging work on northbound whales passing New Zealand can provide more concrete answers about their northern destinations. Regardless, what is clear from this study and previous work is that New Zealand is a hub for different populations including whales that use Hervey Bay.

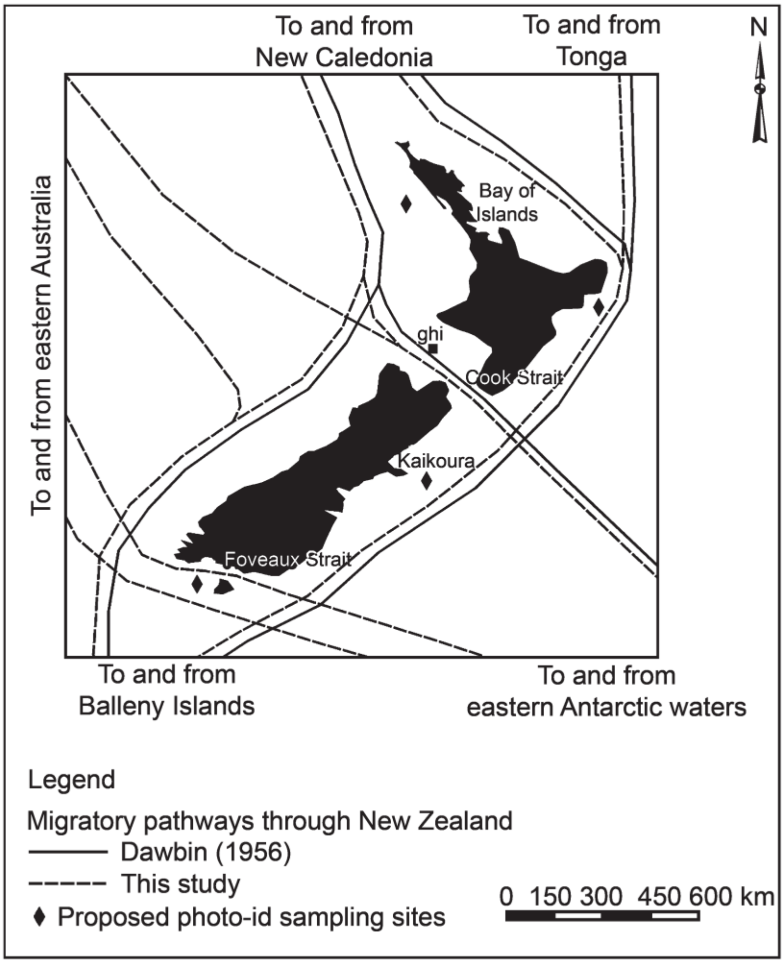


Figure 11. Migratory pathways and migratory destinations described in (Dawbin, 1956) and hypothesised migratory pathways and migratory destinations. Source: Franklin et al. (2014).

4.6 Sex bias in interchange

This study did not prove that there was bias in interchange towards a particular sex. This is considering that the sample of sightings used in this study is connected to a subset of the E1 population that visits Hervey Bay and is mainly female (Chaloupka, Osmond & Kaufman 1999; Franklin et al. 2011; Franklin et al. 2021; Franklin 2014). Therefore, it can be assumed that the findings of this study would be biased towards females. However, as seen from the results, in all breeding regions or migratory corridors/stops, the majority of matched individuals were of unidentified sex and there were too few sexed whales for a proper analysis to prove whether there would be a bias towards one sex in interchange to breeding grounds outside of the Great Barrier Reef. In future studies, this could be addressed to an extent by combining photo-identification and a greater use of genetic sampling.

5 Conclusion

This study has enhanced knowledge of humpback whales visiting Hervey Bay regarding their migrations to breeding grounds besides the Great Barrier Reef. Current knowledge of interchange between the eastern Australia migratory corridor and breeding grounds east of New Caledonia has been changed with the substantial addition of matches between Hervey Bay and east Oceania (Tonga, Samoa and Niue) compared to previous studies. Also, though based on a small sample, it is confirmed that Hervey Bay whales use New Zealand occasionally as a migratory hub to the Great Barrier Reef and other breeding regions.

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