ROYAL SOCIETY
OPEN SCIENCE

R. Soc. open sci.
doi:10.1098/not yet assigned

Humpback whale song revolutions continue to spread from the central into the eastern South Pacific

Josephine N. Schulze[1], Judith Denkinger[2,3], Javier Oña[2,3], M. Michael Poole[4], Ellen C. Garland[1,5,*]

[1]Sea Mammal Research Unit (SMRU), Scottish Oceans Institute, School of Biology, University of St Andrews, St Andrews, Fife KY16 8LB, United Kingdom
[2]Colegio464 de Ciencias Biológicas y Ambientales (Cociba), Universidad San Francisco de Quito, Quito EC170157, Ecuador
[3]Acoustic Ecology Program, CETACEA Ecuador Project, Quito, EC17015, Ecuador
[4]Marine Mammal Research Program, BP 698, Maharepa, 98728, Moorea, French Polynesia
[5]Centre for Social Learning and Cognitive Evolution, School of Biology, University of St Andrews, St Andrews, KY16 9TH, UK

ORCID: JNS, 0000-0002-2294-9685; JD,0000-0002-1343-7514; JO,0000-0001-9667-738X; ECG, 0000-0002-8240-1267

Keywords: Cultural transmission, song, vocal learning, cultural evolution, humpback whale, South Pacific

Electronic Supplementary Material 1

1. Supplementary Materials and Methods

1.1 Song recordings

Song recordings of 30 minutes in length were analysed when possible, but ranged from 9:51 to 35 minutes in length (table 1). Recording quality was qualitatively assessed following methods outlined by Oña et al. [1]; a song was deemed as having 'very good' signal-to-noise ratio (SNR) when the song of one individual was clearly distinguishable from background noise and singers, and when all units were identifiable and the theme patterns were easily followed. The recordings from French Polynesia were generally of good quality (one singer was easily followed), while recordings from Ecuador tended to have more background singers. For each year, one recording was selected from each of the beginning, middle and end of the season (July-September for Ecuador, and September-November for French Polynesia) to reduce the chance of encountering the same singer.

1.2 Acoustic parameters and random forest classification

Song transcription was conducted at the unit level by a human classifier (J.N.S.) with each unit classified based on its aural and visual characteristics, following previous studies [2–4]. To ensure unit classifications were consistent and repeatable, a subset of units was measured for 11 acoustic parameters following previous humpback unit classification analyses ([4–6]). The parameters included [5]: start, end, maximum, minimum and peak frequency (Hz); bandwidth (Hz), frequency trend (start/end frequency), frequency range (maximum/minimum frequency); duration (s); inflections (# reversals in slope); and pulse repetition rate (/s).

The subset of units selected for measurement (n=859) comprised all units from one high-quality example of each phrase type present for each location and year, plus any rare unit type not included in those selected phrases [6]. Thus, all unit types included in the analysis had at least one set of measurements included. All selected units were measured for the 11 parameters. As some unit types were composed of two (or three) humpback units (e.g., groan-ascending moan, ascending groan-whoop) to form a compound unit, each subunit of these compound units was measured separately as they were labelled based on this base level categorisation (i.e., a whoop is a whoop regardless of it being sung alone, or it being sung directly after an

*Author for correspondence: Ellen C. Garland (ecg5@st-andrews.ac.uk).

ascending groan where, to the human ear, there was no silence). Such subdivision (into sub-units) allows tracing of both unit types in compound sounds as they can lengthen and spilt apart during song evolution.

The random forest analysis was run in R (v3.5.3) [7] using the *randomForest* package [8] (mtry=6, 1,000 trees) which resulted in an out-of-bag (OOB) error rate of 27.47% indicating an adequate level of agreement between quantitative and qualitative classification of unit types. The importance of each parameter based on the mean decrease in Gini Index indicated that duration was the most important parameter (178.46), followed by frequency trend (98.73), peak frequency (97.62) and inflections (75.73) in classifying units. The inclusion of rare units which had sample sizes of two or less (42/116, table S2), increased the OOB but provided a fuller and more robust accounting of all unit types included in the analysis.

1.3 Similarity analyses

1.3.1 Levenshtein distance (LD)

The LD calculates a score based on the minimum number of changes (substitutions (s), deletions (d) or insertions (i)) required to turn string 'a' into string 'b' [3,4,9–12]:

$$LD(a,b)=\min(i+d+s)$$

The standardised version of the LD that accounts for different string lengths (*len*) is called the Levenshtein Distance Similarity Index (LSI), and allows for a more meaningful and direct comparisons between sequences of differing lengths [4,10]. LSI calculates a similarity proportion (from 0 to 1) as follows:

$$LSI(a,b)=1-LD(a,b)/\max(len(a),len(b)).$$

This calculation creates a matrix of LSI similarity for all strings. All calculations were run in R using custom-written code (package *leven*, available at http://github.com/ellengarland/leven). Results can then be visualised through hierarchical clustering and dendrograms.

1.3.2 Dice's similarity index (DSI)

A second similarity index, Dice's Similarity Index (DSI), was also created. This calculates the similarity between any two singers based on theme presence and sharing [6,13,14] as follows :

$$SI = 2A/(B + C)$$

where SI is the similarity in song phrases between pairs, A is the number of shared phrase types, B is the total number of phrase types present in singer 1, and C is the total number of phrase types present in singer 2 [13]. The DSI analysis was run in R using custom-written code (https://github.com/ellengarland/dice_si). The DSI similarity matrix was then hierarchically clustered and bootstrapped as per LSI analyses.

2. Supplementary Results

2.1 Song types

2.1.1 Song type 1 (Blue)

Song type 1 (figures S2-4, S7) was first identified in French Polynesia in 2016 (3/3 singers) and was also present in French Polynesia in 2017 (1/3 singers) and 2018 (2/3 singers, both hybrid (#7 and #8)), as well as in Ecuador in 2018 (3/3 singers). Song type 1 contained the following themes: Theme 1, 2a, 2b, 3, 4, 5, 6, 7a, 7b, 7c, 23*, 39a, 39b, 40a, 40b, 40c, 41 (table 1, table S1). Three themes in song type 1 matched between French Polynesia and Ecuador (Themes 1, 5 and 7a; figure 3, table S1). Themes 1-7 were commonly sung in French Polynesia, while three further themes were found solely in Ecuador 2018 as the song evolved. Theme 23 was not specifically assigned to any song type as it was sung solely by hybrid singer 7 (FP 2018) who sang predominantly song type 1, but also included theme 22 (from song type 3).

2.1.2 Song type 2 (Green)

Song type 2 (figures S3-4) was described in French Polynesia in 2017 (2/3 singers) and 2018 (1/3 singers, part of hybrid singer 8). This song type contained the following themes: Theme 9a, 9b, 10, 11, 12, 13, 14, 15, 16, 24* (table 1, table S1). Themes 9-16 were common in French Polynesia 2017, while Themes 10 and 24 were found in 2018 (hybrid singer). The most common themes of this song type were Themes 10 and 11, while the rarest were themes 9a, 9b, 15 and 16. Theme 24 (which was not considered part of any particular song type given it was solely heard in a hybrid song) was sung by hybrid singer 8 (FP 2018) along with theme 10 (song type 2), and both themes were spliced in the middle of the predominant song type 1 (table 1).

2.1.3 Song type 3 (Orange)

Song type 3 (figure S4) was sung by one singer (singer 9) in French Polynesia 2018. It contained themes 17, 18, 19, 20, 21, 22 (table 1, table S1). Theme 22 was also sung by hybrid singer 7 (see song type 1 above). The most common themes in song type 3 were themes 17 and 18, while the rarest was theme 22.

2.1.4 Song type 4 (Grey)

Song type 4 (figures S5-6) was sung in Ecuador in both 2016 (3/3 singers) and 2017 (4/4 singers). The song type consisted of the following themes: 25, 26, 27, 28, 29, 30, 31, 32, 33, 34, 35, 36a, 36b, 37, 38a, 38b (table 1, table S1). Themes 33, 34, 35, 37 and 38a were sung in both years. Additionally, themes 25-31 were commonly sung in 2016 but were not identified in 2017, and themes 36a, 36b and 38b were added.

3. Supplementary Figures

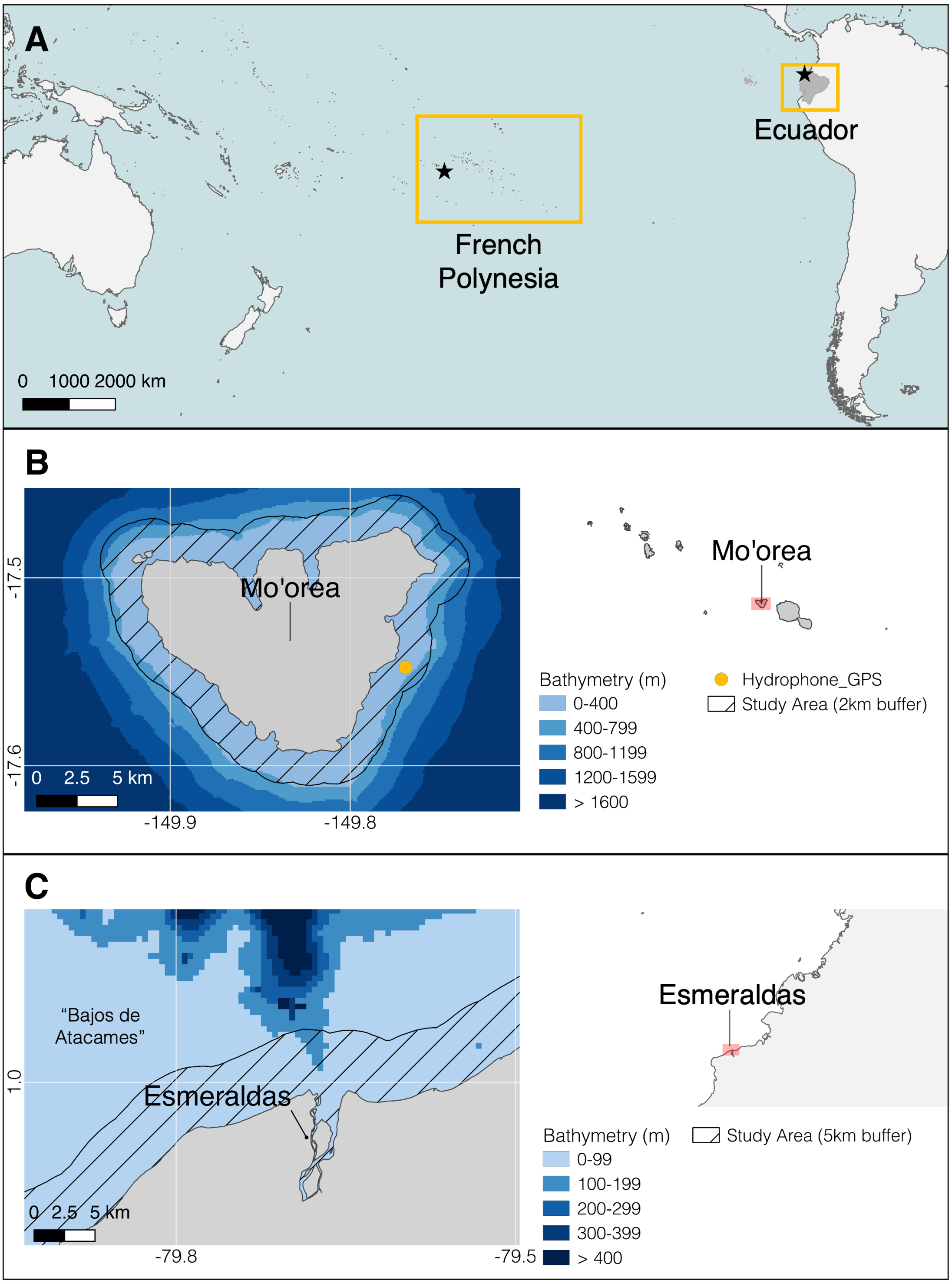

Figure S1. Study locations in French Polynesia (Mo'orea; star) and Ecuador (Esmeraldas; star), spanning a distance of roughly 8,000 km between them. A) Map of the wider South Pacific with general study locations. B) Song recording location off the island of Mo'orea (French Polynesia). Boat-based surveys took place within 2 km of the island (hashed buffer); the moored hydrophone was located at S17°32.860 and W149°46.148 (yellow dot). C) Song recording location for Esmeraldas (Ecuador). Boat-based recordings were typically made within 5 km of shore (hashed buffer).

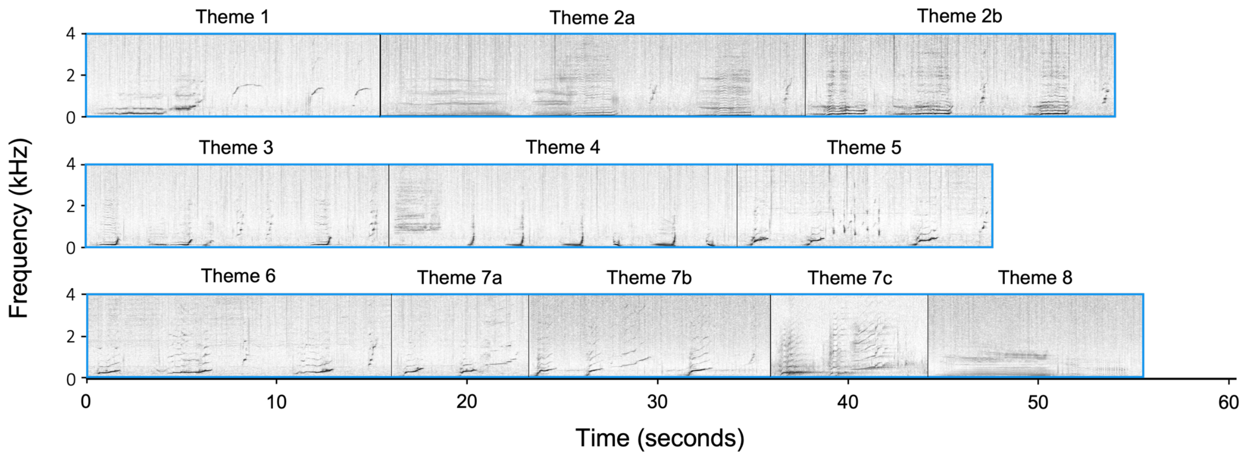

Figure S2. Spectrograms of themes (and phrase types) from French Polynesia 2016. Colour boarders correspond to song type(s). Spectrograms were produced in Raven Pro 1.6 (Fast Fourier Transform (FFT) 2048; Hann window, 50% overlap).

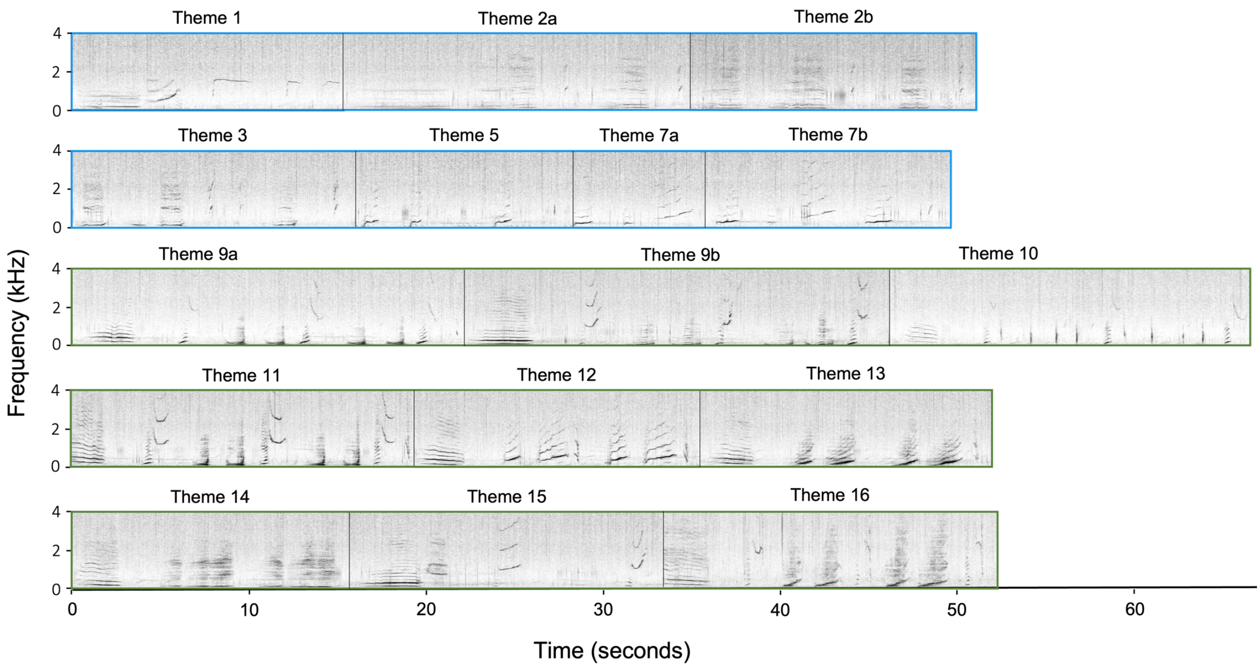

Figure S3. Spectrograms of themes and phrase types from French Polynesia 2017. Colour boarders correspond to song type(s). Spectrograms were produced as per figure S2.

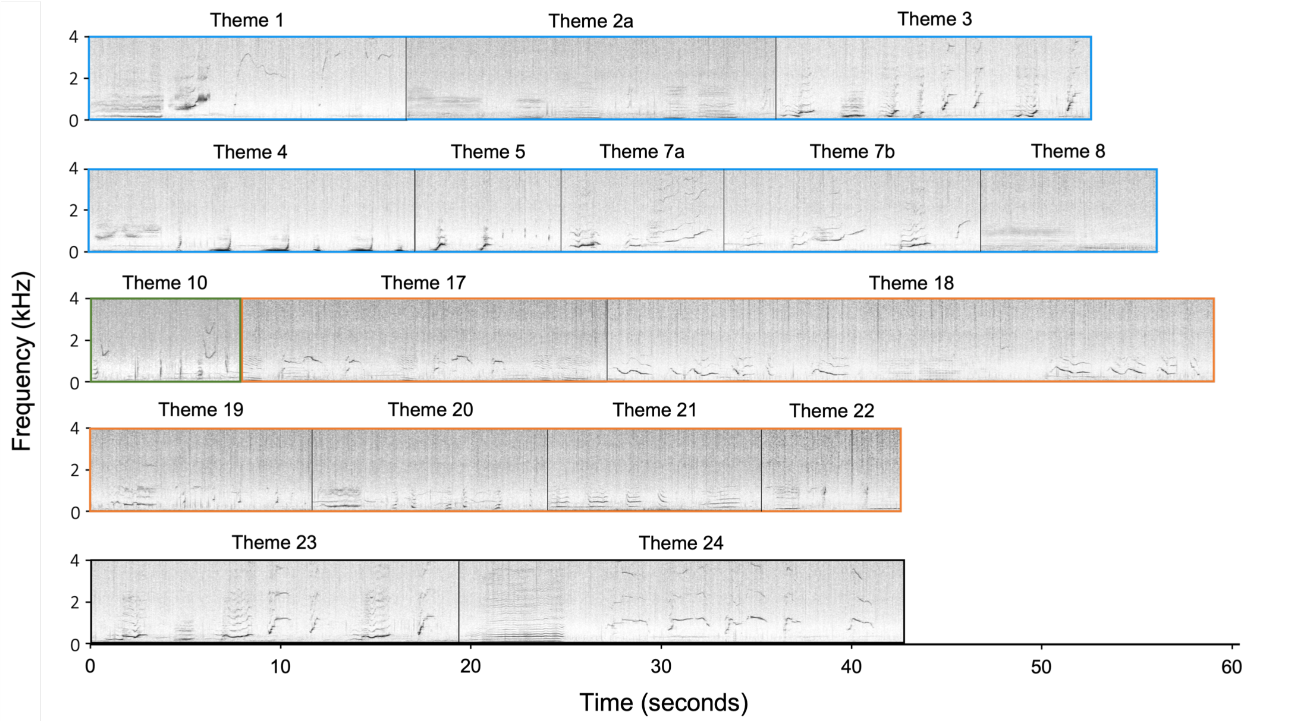

Figure S4. Spectrograms of themes and phrase types from French Polynesia 2018. Colour boarders correspond to song type(s). Spectrograms were produced as per figure S2.

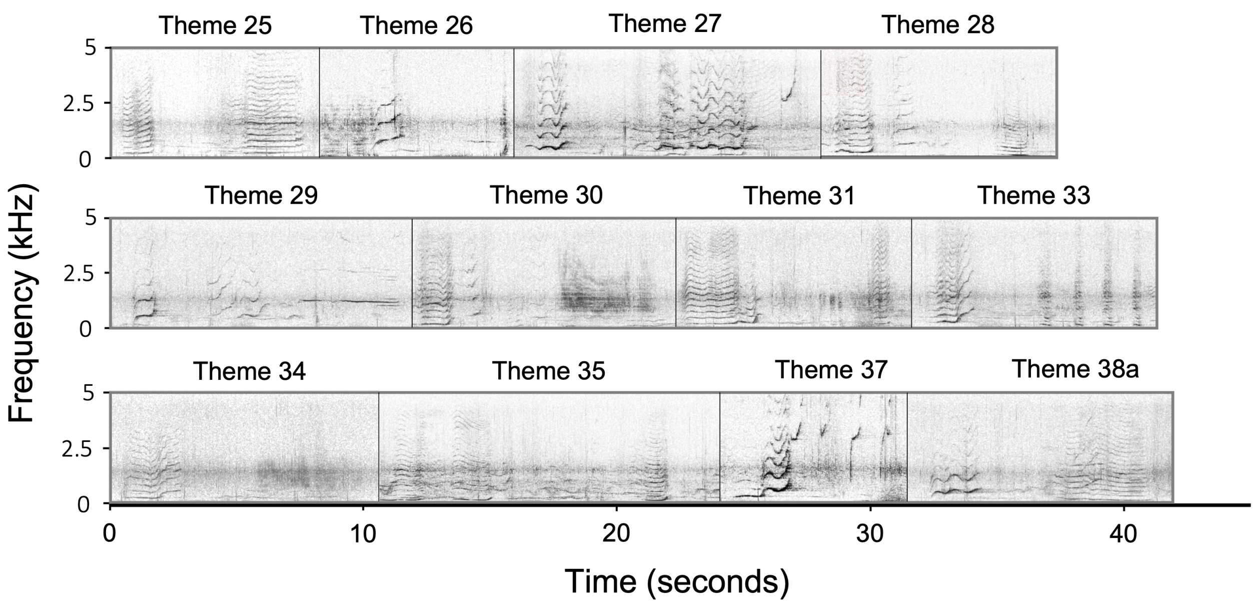

Figure S5. Spectrograms of themes and phrase types from Ecuador 2016. Colour boarders correspond to song type(s). Spectrograms were produced as per figure S2.

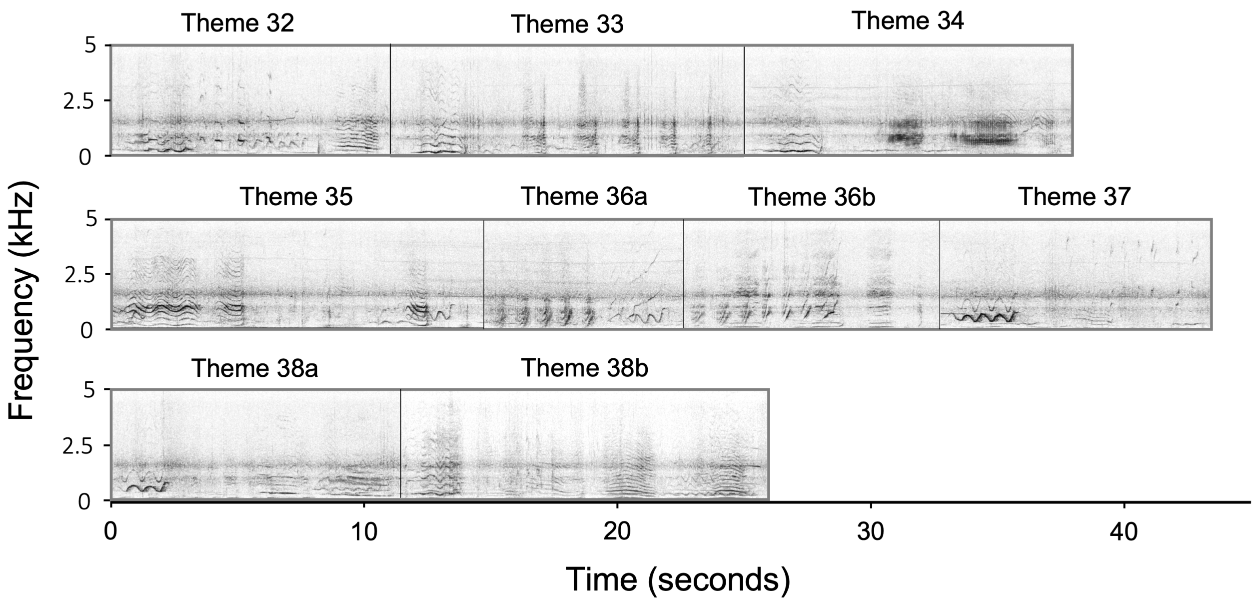

Figure S6. Spectrograms of themes and phrase types from Ecuador 2017. Colour boarders correspond to song type(s). Spectrograms were produced as per figure S2.

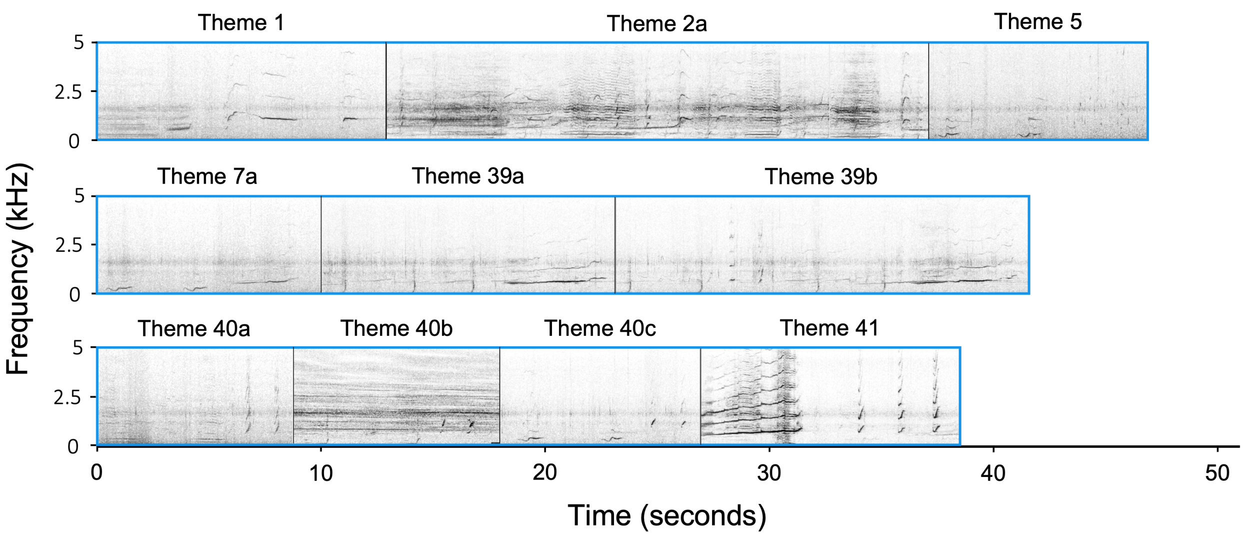

Figure S7. Spectrograms of themes and phrase types from Ecuador 2018. Colour boarders correspond to song type(s). Spectrograms were produced as per figure S2.

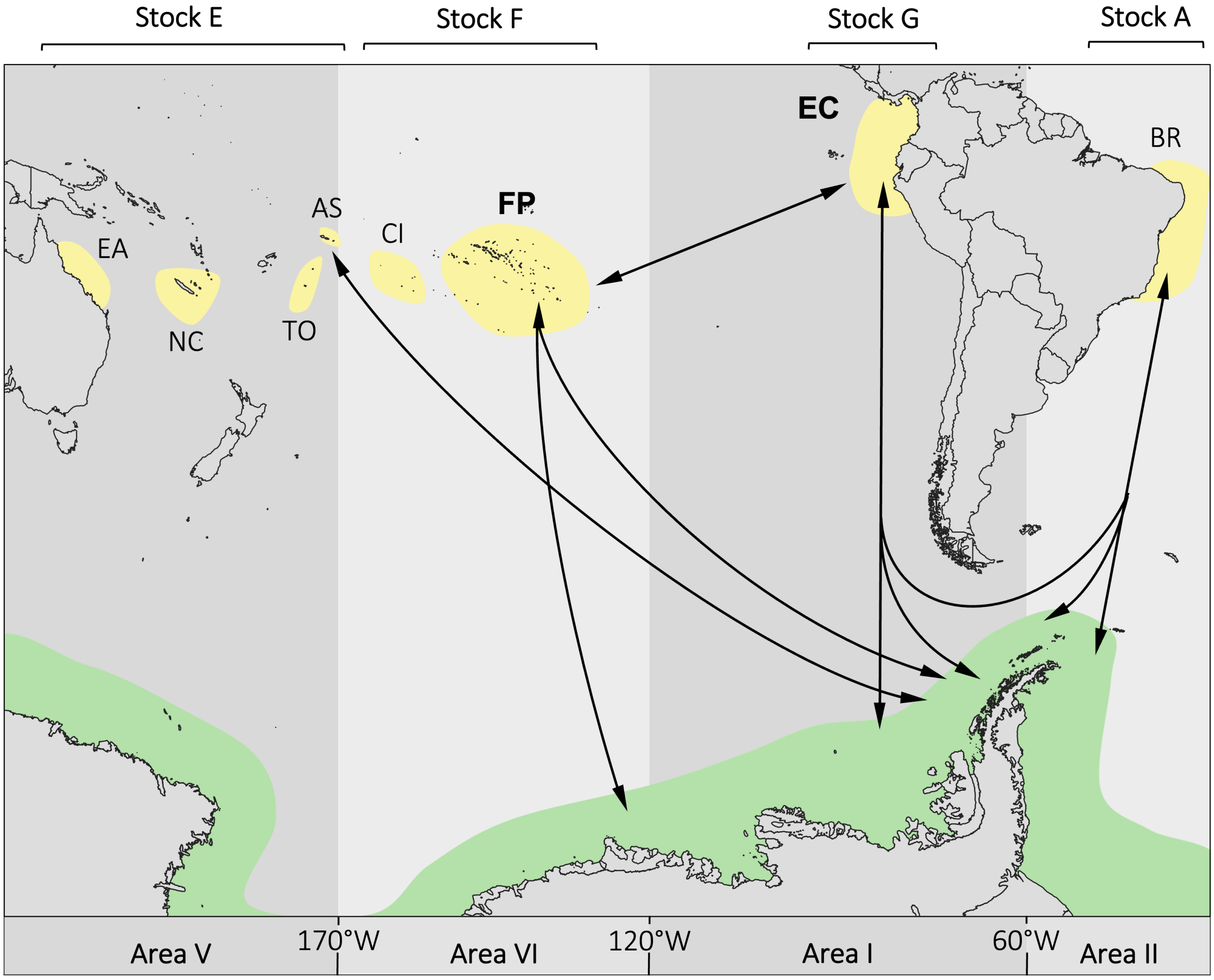

Figure S8. Map showing the core winter breeding grounds and summer feeding Areas. Connections discussed in the text are depicted by arrows and may not represent the exact migratory routes (see [15–19] for further information on matches). Most overlaps among populations have occurred on the West Antarctic Peninsula in Area I. Group E: eastern Australia (EA), New Caledonia (NC), Tonga (TO), with suggested feeding Area V; American Samoa (AS; boundary of Groups E & F); Group F: the Cook Islands (CI), French Polynesia (FP), with suggested feeding Area VI; Group G: Ecuador (EC), Colombia, Costa Rica, Panama, with suggested feeding Area 1; and Group A: Brazil (BR), with suggested feeding Area II [20].

4. Supplementary Tables

Table S1. Set medians (most representative sequence of units) for every phrase type for all song types per location and year. FP=French Polynesia, EC=Ecuador. Sample size (number of phrases) is included for each set median. *Unit code names can be found in table S2 and each letter or combination of letters represents the unit type (separated by a comma).

Song type	Theme	Location	Year	#Phrases	Set median unit sequence*
1	1	FP	2016	33	lm-as, aws, aws(s), aws
		FP	2017	15	lm, as, nws, nws(s), ws
		FP	2018	15	lm, as, nws, nws, nws
		EC	2018	77	lm-ti(a), nws(l), nws(s)
	2a	FP	2016	14	gw(l), gw-agr, asq, agr, asq
		FP	2017	4	gw(l), gw-gr, ahq, agr, ahq
		FP	2018	5	gw(l), gw-gr, ahq, gw-gr, ahq
	2b	FP	2016	15	agr, agr, asq, agr, asq
		FP	2017	2	ngr, gw(s)-agr, ahq, ahq, gr-w, ahq
		FP	2018	3	gr, gr-agr, aws(s), ahq, gr-w, aws(s)
	3	FP	2016	57	gr-w, gu, gr-w, sn, asq, asq, gr-w, asq

		FP	2017	36	gr-w, gu, gr-w, sn, ahq, asq, gr-w, asq
		FP	2018	79	ngr-w, gu, ngr-w, sn, as(s), asq, ngr-w, as(s)
	4	FP	2016	46	hs, ba, lb, lb, gt, lb, gt
		FP	2018	11	hs(l), ba, lb, lb, gt, lb
	5	FP	2016	42	am(s), am(s), hq, sq, hq, sq, hq, sq, hq, sq, hq, sq
		FP	2017	18	am(s), am(s), hq, hq, hq, hq, hq, sq
		FP	2018	14	am, am, hq, sq, sq, sq, sq, sq, am, sq,
		EC	2018	20	mm, mm, hq, hq, hq, hq, hq, hq, hq, hq, sq
	6	FP	2016	12	am, pe-am, asq, am, as(s)
	7a	FP	2016	39	am, am(s), as
		FP	2017	14	am, am(s), ac
		FP	2018	5	am, am(s), as
		EC	2018	33	mm, mm, as
	7b	FP	2016	6	am, pe-am, ac(s), am, ac(s)
		FP	2017	18	am, am(s), ac, am, asq
		FP	2018	4	am, am(s), as(l), am, ahq
	7c	FP	2016	6	am, am(s), as, hq, sq
	8	FP	2016	7	gw(l)-be
		FP	2018	2	gw(l)-be
	39a	EC	2018	5	ba, ba, ba, ac(l)
	39b	EC	2018	2	ba, ba, asq, asq, ba, ba, as(l)
	40a	EC	2018	2	m, m, ahq, asq
	40b	EC	2018	45	gr-ba, gr-ba, ahq, ahq
	40c	EC	2018	3	mm, mm, ahq, ahq
	41	EC	2018	17	as(l), asq, asq, ahq
2	9a	FP	2017	7	dm, agr(s)-uws(s), ngr, ngr, agr(s)-uws(s), ngr, ngr, agr(s)-dws(s), sq
	9b	FP	2017	2	lm, hs(s), gr(s)-aws(s), agr-ba, agr-ba, ngr(s)-aws(s), agr-ba, agr-ba, ngr(s)-hq
	10	FP	2017	21	dm, agr(s)-dws(s), sq, sq, sq, sq, agr(s)-dws(s), sq, sq, sq, sq, agr(s)-dws(s)
		FP	2018	2	agr(s)-uws(s), sq, sq, sq, uws(s)
	11	FP	2017	48	dm, agr(s)-uws(s), ba, ba, agr(s)-uws(s), ba, ba, agr(s)-uws(s)
	12	FP	2017	17	dm, ac, ac, dsq, ac, ac, dsq
	13	FP	2017	10	dm, ti(a), ti(a), ti(a), ti(a)
	14	FP	2017	3	dm, sc(l), sc(l)
	15	FP	2017	18	lm, hs, gr(s)-uws, gr(s)-aws
	16	FP	2017	18	dm, agr(s), dhq, ti(a), ti(a), agr(s), dhq, ti(a), ti(a), agr(s), dhq
3	17	FP	2018	22	dgr, nws, nws(s), dgr, nws, nws(s), dgr, dgr
	18	FP	2018	5	dc, modhc, dc(s), dc, sr, sr, dc, nm(s), nm, dc(s),
	19	FP	2018	14	nm, hq, sq, hq, sq, hq, sq, hq, sq
	20	FP	2018	19	nm, am(s), am(s), agr(s), gr(s), agr(s), sq
	21	FP	2018	7	m, dm(s), dm(s), dsq, m, gu
	22	FP	2018	8	gr, aws(s), asq
	23	FP	2018	16	gr(s)-um, ti, gr(s)-am, as, ns(s), gr-am, as
	24	FP	2018	3	gr(l), nws, nws, aws, nws
4	25	EC	2016	6	agr(s), sn, agr(l), sn
	26	EC	2016	13	aws, sq
	27	EC	2016	4	modhc, modhc
	28	EC	2016	53	m-hc, sq, dgr
	29	EC	2016	9	ac(s), modhc, nws(l)
	30	EC	2016	1	m-ac, sr
	31	EC	2016	11	mbd, abd(s)
	32	EC	2017	31	mm, sq, sq, hq, sq, sq, dsq, hq, dgr
	33	EC	2016	43	m-w, gr(s), gr(s), gr(s), gr(s)
		EC	2017	51	mm-w, gr, gr, gr, gr(s), gr(s)
	34	EC	2016	53	m-w, gw, sr(l)
		EC	2017	58	m, gw, sr

	35	EC	2016	17	mbd(l), ubd(s)
		EC	2017	63	mbd(l), mbd, sn, sn, sn
	36a	EC	2017	13	ti(a), ti(a), ti(a), ti(a), ti(a), aws, sq
	36b	EC	2017	4	ti(a), ti(a), sq, asq, sq, sq, sq, sq, nws(s)-aws, aws,
	37	EC	2016	6	modhc-ahq, ahq, ahq, ahq, ahq
		EC	2017	17	modhc, ahq, ahq, ahq, ahq, ahq, hq, ahq
	38a	EC	2016	15	modhc, dm(l)
		EC	2017	19	modhc, dm, dm
	38b	EC	2017	4	mm, dgr
Total				1,457	

Table S2. Unit names for all abbreviations in table S1. Note units can be combined to make compound units (e.g., lm-as, represents a 'long moan' connected to (-) an 'ascending shriek'). (l)= long, (s)= short. Sample sizes (N) provided for units included in random forest analysis.

Unit code	N	Unit name	Unit code	N	Unit name
abd	2	Ascending balloon deflate	mgr	5	Modulated groan
abd(s)	3	Short ascending balloon deflate	mgr(l)	1	Long modulated groan
ac	9	Ascending cry	mgr(s)	2	Short modulated groan
ac(l)	3	Long ascending cry	mm	30	Modulated moan
ac(s)	13	Short ascending cry	mm(l)	3	Long modulated moan
agr	19	Ascending groan	mm(s)	15	Short modulated moan
agr(l)	2	Long ascending groan	modhc	21	Modulated high cry
agr(s)	33	Short ascending groan	modhc(l)	2	Long modulated high cry
ahq	38	Ascending high squeak	modhc(s)	3	Short modulated high cry
am	26	Ascending moan	modhs	1	Modulated high shriek
am(l)	2	Long ascending moan	modws	2	Modulated whistle
am(s)	25	Short ascending moan	modws(l)	9	Long modulated whistle
as	11	Ascending shriek	modws(s)	1	Short modulated whistle
as(l)	3	Long ascending shriek	nbd	2	N-shaped balloon deflate
as(s)	2	Short ascending shriek	nbd(s)	2	N-shaped balloon deflate short
asq	26	Ascending squeak	nc	4	N-shaped cry
aws	6	Ascending whistle	nc(s)	8	Short n-shaped cry
aws(l)	3	Long ascending whistle	ngr	19	N-shaped groan
aws(s)	17	Short ascending whistle	ngr(l)	2	Long n-shaped groan
ba	24	Bark	ngr(s)	14	Short n-shaped groan
bd(s)	2	Short balloon deflate	nm	15	N-shaped moan
be	3	Bellows	nm(l)	5	Long n-shaped moan
bt	2	Bird trill	nm(s)	4	Short n-shaped moan
dbd	2	Descending balloon deflate	ns	1	N-shaped shriek
dbd(s)	3	Short descending balloon deflate	ns(s)	1	Short n-shaped shriek
dc	2	Descending cry	nws	8	N-shaped whistle
dc(l)	2	Long descending cry	nws(l)	3	Long n-shaped whistle
dc(s)	2	Short descending cry	nws(s)	5	Short n-shaped whistle
dgr	15	Descending groan	p	8	Purr
dgr(l)	1	Long descending groan	pe	5	Pulsative element
dgr(s)	12	Short descending groan	sc(l)	2	Long screech
dhq	5	Descending high squeak	sn	5	Snort
dm	4	Descending moan	sq	52	Squeak
dm(l)	3	Long descending moan	sr	8	Surface ratchet
dm(s)	3	Short descending moan	sr(l)	5	Long surface ratchet
dsq	7	Descending squeak	ti	2	Trill
dws	3	Descending whistle	ti(a)	9	Ascending trill
dws(s)	2	Short descending whistle	ti(a)(s)	9	Short ascending trill
gr	12	Groan	ti(d)	1	Descending trill
gr(l)	4	Long groan	ti(m)	2	Modulated trill
gr(s)	24	Short groan	ti(n)	2	N-shaped trill
gt	4	Grunt	ti(n)(s)	2	Short n-shaped trill
gu	19	Grumble	ti(s)	1	Short trill
gw	12	Growl	ubd	4	U-shaped balloon deflate
gw(l)	8	Long growl	ubd(s)	3	Short u-shaped balloon deflate
gw(s)	5	Short growl	uc	2	U-shaped cry
hc	2	High cry	uc(s)	1	Short u-shaped cry
hc(s)	4	Short high cry	ugr	2	U-shaped groan
hq	14	High squeak	ugr(s)	3	Short u-shaped groan
hs	3	High shriek	um	6	U-shaped moan
hs(l)	2	Long high shriek	um(s)	2	Short u-shaped moan
hs(s)	1	Short high shriek	uws	7	U-shaped whistle
lb	6	Long bark	uws(s)	13	Short u-shaped whistle
lm	4	Long moan	w	31	Whoop
m	4	moan	ws	2	Whistle
mbd	1	Modulated balloon deflate	ws(l)	1	Long whistle
mbd(l)	3	Long modulated balloon deflate	ws(s)	2	Short whistle
mbd(s)	2	Short modulated balloon deflate	**Total**	**859**	**116 unit types**

Table S3. Summary of song types and themes present in each location and year. Song type 1=blue, song type 2=green, song type 3=orange, song type 4=grey. *indicates theme was sung in a hybrid song (singers 7 and 8, French Polynesia 2018; see table 1).

Year	French Polynesia	Ecuador
2016	1,2a,2b,3,4,5,6,7a,7b,7c,8	25,26,27,28,29,30,31,33,34,35,37,38a
2017	1,2a,2b,3,5,7a,7b 9a,9b,10,11,12,13,14,15,16	25,26,27,28,29,30,31,32,33,34,35,36a,36b,37,38a,38b
2018	1,2a,2b,3,4,5,7a,7b,8 [10*,22*,23*,24*] 17,18,19,20,21,22	1,5,7a,7b,39a,39b,40a,40b,40c,41

Table S4. Connections between French Polynesia and Ecuador (2016-2018) song themes and previously known song themes across the western and central South Pacific including theme label, song type, year of recording and site/location. Matching themes (and thus song types) are shown from Owen et al. [21](Fig 1 and Supplementary Audio Files) and Warren et al. [6](Supplementary Info S5 and Supplementary Audio Files). Study site/locations listed are French Polynesia (FP), Ecuador (EC), Cook Islands (CI), Tonga (TO), New Caledonia (NC) and eastern Australia (EA).

Current study				Owen et al. [21]				Warren et al. [6]			
Song	Theme	Year	Site	Song	Theme	Year	Site	Song	Theme	Year	Site
1	1	2016-18, 2018	FP, EC	1a	7	2015	TO, CI, FP	-	-	-	-
1	3	2016-18	FP	1a	10	2015	TO, CI, FP	-	-	-	-
1	4	2016-18	FP	1a	11	2015	TO, CI, FP	-	-	-	-
1	5	2016-18, 2018	FP, EC	1a	8	2015	TO, CI, FP	-	-	-	-
1	8	2016	FP	1a	9	2015	TO, CI, FP	-	-	-	-
2	10	2017	FP	2	2	2015	NC, TO, CI	-	-	-	-
2	11	2017	FP	3	17	2015	EA	B	5	2015-16	EA(north), NC
2	13	2017	FP	2	1	2015	NC, TO, CI	-	-	-	-
2	14	2017	FP	2	3	2015	NC, TO, CI	B	8	2015	EA(north)

References

1. Oña J, Garland EC, Denkinger J. 2017 Southeastern Pacific humpback whales (Megaptera novaeangliae) and their breeding grounds: Distribution and habitat preference of singers and social groups off the coast of Ecuador. *Mar. Mammal Sci.* **33**, 219–235. (doi:10.1111/mms.12365)
2. Garland EC, Goldizen AW, Rekdahl ML, Constantine R, Garrigue C, Hauser ND, Poole MM, Robbins J, Noad MJ. 2011 Dynamic horizontal cultural transmission of humpback whale song at the ocean basin scale. *Curr. Biol.* **21**, 687–691. (doi:10.1016/j.cub.2011.03.019)
3. Garland EC *et al.* 2013 Quantifying humpback whale song sequences to understand the dynamics of song exchange at the ocean basin scale. *J. Acoust. Soc. Am.* **133**, 560–9. (doi:10.1121/1.4770232)
4. Garland EC, Rendell L, Lilley MS, Poole MM, Allen J, Noad MJ. 2017 The devil is in the detail: quantifying vocal variation in a complex, multi-levelled, and rapidly evolving display. *J. Acoust. Soc. Am.* **142**, 460–472. (doi:10.1121/1.4991320)
5. Dunlop RA, Noad MJ, Cato DH, Stokes DM. 2007 The social vocalization repertoire of east Australian migrating humpback whales (*Megaptera novaeangliae*). *J. Acoust. Soc. Am.* **122**, 2893–2905. (doi:10.1121/1.2783115)
6. Warren VE, Constantine R, Noad M, Garrigue C, Garland EC. 2020 Migratory insights from singing humpback whales recorded around central New Zealand: Humpback whale song, central New Zealand. *R. Soc. Open Sci.* **7**, 201084. (doi:10.1098/rsos.201084rsos201084)
7. 2019 The R Foundation for Statistical Computing. , R version 3.5.3.
8. Liaw a, Wiener M. 2002 Classification and Regression by randomForest. *R news* **2**, 18–22. (doi:10.1177/154405910408300516)
9. Eriksen N, Tougaard J. 2006 Analysing differences among animal songs quantitatively by means of the Levenshtein distance measure. *Behaviour* **143**, 239–252. (doi:10.1163/156853906775900685)
10. Garland EC, Lilley MS, Goldizen AW, Rekdahl ML, Garrigue C, Noad MJ. 2012 Improved versions of the Levenshtein distance method for comparing sequence information in animals' vocalisations: Tests using humpback whale song. *Behaviour* **149**, 1413–1441. (doi:10.1163/1568539X-00003032)
11. Kohonen T. 1985 Median strings. *Pattern Recognit. Lett.* **3**, 309–313. (doi:10.1016/0167-8655(85)90061-3)
12. Helweg DA, Cato DH, Jenkins PF, Garrigue C, McCauley RD. 1998 Geographic variation in South Pacific humpback whale songs. *Behaviour* **135**, 1–27. (doi:10.2307/4535507)
13. Garland EC *et al.* 2015 Population structure of humpback whales in the western and central South Pacific Ocean as determined by vocal exchange among populations. *Conserv. Biol.* **29**,

1198–1207. (doi:10.1111/cobi.12492)

14. Dice LR. 1945 Measures of the amount of ecologic association between species. *J. Chem. Inf. Model.* **53**, 297–302. (doi:10.1017/CBO9781107415324.004)
15. Felix F, Abras DR, Cheeseman T, Haase B, Figueiredo Santos JD, Milton MC, Southerland K, Acevedo J. 2020 A New Case of Interoceanic Movement of a Humpback Whale in the Southern Hemisphere: The El Niño Link. *Aquat. Mamm.* **46**, 578–583. (doi:10.1578/AM.46.6.2020.578)
16. Schmitt NT *et al.* 2014 Mixed-stock analysis of humpback whales (Megaptera novaeangliae) on Antarctic feeding grounds. *J. Cetacean Res. Manag.* **14**, 141–157.
17. Albertson GR *et al.* 2018 Temporal stability and mixed-stock analyses of humpback whales (Megaptera novaeangliae) in the nearshore waters of the Western Antarctic Peninsula. *Polar Biol.* **41**, 323–340. (doi:10.1007/s00300-017-2193-1)
18. Robbins J, Rosa LD, Allen JM, Mattila DK, Secchi ER, Friedlaender AS, Stevick PT, Nowacek DP, Steel D. 2011 Return movement of a humpback whale between the Antarctic Peninsula and American Samoa: A seasonal migration record. *Endanger. Species Res.* **13**, 117–121. (doi:10.3354/esr00328)
19. Steel D *et al.* 2017 Migratory interchange of humpback whales (Megaptera novaeangliae) among breeding grounds of Oceania and connections to Antarctic feeding areas based on genotype matching. *Polar Biol.* **3**. (doi:10.1007/s00300-017-2226-9)
20. Jackson JA *et al.* 2015 Southern Hemisphere Humpback Whale Comprehensive Assessment - A synthesis and summary: 2005-2015. *Rep. to Sci. Comm. Int. Whal. Comm.* **SC/66a/SH3**, 1–38.
21. Owen C *et al.* 2019 Migratory convergence facilitates cultural transmission of humpback whale song. *R. Soc. Open Sci.* **6**, 190337. (doi:10.1098/rsos.190337)