

**Population structure of humpback whales in the western and central South Pacific
Ocean as determined by vocal exchange among populations**

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Abstract

For cetaceans population structure is traditionally determined by molecular genetics or photographically identified individuals. Acoustic data, however, has provided information on movement and population structure with less effort and cost than traditional methods in an array of taxa. Male humpback whales (*Megaptera novaeangliae*) produce a continually evolving vocal sexual display, or song, that is similar among all males in a population. The rapid cultural transmission (the transfer of information/behaviour between conspecifics through social learning) of different versions of this display between distinct but interconnected populations in the western and central South Pacific region presents a unique way to investigate population structure based on the movement dynamics of a song (acoustic) display. Using 11 years of data, we investigated an acoustically based population structure for the region by comparing stereotyped song sequences among populations and years using the Levenshtein distance technique, to group previously defined populations into (vocally based) clusters using the overall similarity of their song display in space and time. We identified the following distinct vocal clusters: western cluster, 1 population off eastern Australia; central cluster, populations around New Caledonia, Tonga, and American Samoa; and eastern region, either a single cluster or two clusters, one around the Cook Islands and the other off French Polynesia. These results are consistent with the hypothesis that each breeding aggregation represents a distinct population (each occupied a single, terminal node) in a metapopulation, similar to the current understanding of population structure based on genetic and photo-identification studies. However, the central vocal cluster had higher levels of song-sharing among populations than the other clusters, indicating that levels of vocal connectivity varied within the region. Our results demonstrate the utility and value of using culturally transmitted vocal patterns as a way of defining connectivity to infer population structure. We suggest

vocal patterns be incorporated by the International Whaling Commission in conjunction with traditional methods in the assessment of structure.

Introduction

Effective management and conservation measures depend on an understanding of populations and their connectivity. A population is typically defined as a group of individuals in a species that occur in a defined geographic area and share a common gene pool (are interbreeding) (also called demes or subpopulations [Hanski & Simberloff 1997]). However, due largely to methodological constraints, it can be difficult to accurately group individuals into meaningful populations and to assess mixing between them. Mitochondrial DNA (mtDNA) and nuclear DNA (e.g., microsatellite) studies have traditionally been undertaken to investigate gene flow and connectivity. As with all methods, limitations exist. For example, mtDNA studies only examine historical movements by females (Wright & Wilkinson 2001). Another method for investigating connectivity is tracking individuals' movements within and between populations using photo-identification, marked animals, or satellite tracking of tagged animals. Indices of within-area and between-area resightings (mark-recapture) can be used to assess the strength of fidelity of individuals to particular locations and the relative interchange among locations. However, photo-identification and satellite tagging studies usually result in a small sample size from a high level of effort and cost to collect the data.

Endangered South Pacific humpback whale (*Megaptera novaeangliae*) populations are still recovering from historical declines caused by whaling (e.g., Childerhouse et al. 2008; Clapham et al. 2009; Constantine et al. 2012); understanding population structure is thus of critical importance to the assessment and management of this recovery. Current understanding of the population structure of these whales is based on traditional methods (mtDNA and mark-recapture) and is therefore limited, yet it forms the basis for management by the International Whaling Commission (IWC). Mark-recapture studies (photo-

identification and Discovery marking) and genetic analyses with mtDNA suggest that each breeding aggregation (winter breeding location) within the western and central South Pacific region (eastern Australia, New Caledonia, Tonga, the Cook Islands, and French Polynesia) represents a demographically distinct population, with rare but identifiable movements of individuals among them (e.g., Dawbin 1964; Olavarria et al. 2007; Garrigue et al. 2011a; Supporting Information). The IWC divides these populations into 2 different breeding Groups (E & F), which are thought to migrate to two corresponding feeding regions in Antarctica (Areas V & VI) (IWC 2006). Humpback whales undertake long-distance migrations each year between seasonal breeding and feeding grounds (e.g., Chittleborough 1965; Dawbin 1966; Baker et al. 1990). Group E has three populations, eastern Australia (E1), New Caledonia (E2) and Tonga (E3), and Group F has two populations, the Cook Islands (F1) and French Polynesia (F2) (Fig. 1).

The population structure within the region resembles a complex metapopulation due to the likely differential extinction probabilities of these populations and the small but identifiable levels of interchange among populations (Levins 1969; Supporting Information). Recovery from whaling within the region has been uneven because populations within Oceania (the region containing New Caledonia, Tonga, the Cook Islands, and French Polynesia) are recovering very slowly (Constantine et al. 2012), while the eastern Australian population is recovering strongly with a high rate of population growth (Noad et al. 2011; Supporting Information). This further complicates the management and assessment of recovery for this region; additional lines of evidence are necessary in combination with existing information (genetic, photo-identification, and satellite tagging) to provide a comprehensive understanding of population structure.

For an array of taxa, acoustic data can provide information on movement and population structure with less effort and cost than traditional methods. Acoustic data have been used to infer population and group separation in, for example, Mountain White-crowned Sparrows (*Zonotrichia leucophrys oriantha*) (MacDougall-Shackleton & MacDougall-Shackleton 2001), killer whales (*Orcinus orca*) (Ford 1991), sperm whales (*Physeter macrocephalus*) (Rendell et al. 2012), Yellow-naped Amazon Parrot (*Amazona auropalliata*) and Yellow-crowned Amazon Parrot (*A. ochrocephala*) (Wright & Wilkinson 2001), and fin whales (*Balaenoptera physalus*) (Delarue et al. 2009). Despite challenges introduced by the migratory life histories of large whales, consistent vocal differences have been successfully used to identify populations over large spatial scales (e.g., Delarue et al. 2009; Castellote et al. 2012). These species have stable vocal displays (i.e., songs) that do not change over short (monthly) time spans. In contrast, the songs of humpback whales change continuously, but the geographic patterns of these changes can also be examined to elucidate population structure.

The South Pacific humpback whale populations provide a model set of populations for examining the utility of acoustically derived models of connectivity, because multiple lines of evidence (mtDNA and photo-identification mark-recapture) already exist and can be compared to structures derived from vocal (acoustic) data. Song functions in sexual selection through mate attraction and/or male social sorting, behaviours that are most commonly observed on the winter breeding grounds and while whales migrate (Payne & McVay 1971; Darling et al. 2006; Noad & Cato 2007). Songs of male humpback whales constantly evolve and are shared among all conspecific males within a population through some form of social learning (e.g., Payne & McVay 1971; Payne et al. 1983; Payne & Payne 1985). Song variants or song types are culturally transmitted among individuals and populations within an ocean

basin (Garland et al. 2011, 2012, 2013b) and occasionally between ocean basins (Noad et al. 2000). Songs appear to undergo progressive evolution or complete revolution, but it remains unclear whether these two types of change are distinct or whether one is simply an extreme form of the other (Noad et al. 2000; Garland et al. 2013b). However, because most males in a population conform to the same song type at any given time, a song can serve as a vocal identifier for each population (Garland et al. 2011, 2012, 2013b). As with traditional methods, there are limitations to acoustic methods. Song analyses provide insights into the movements of or contact between males only, the collection of information about individuals or the movements of specific individuals is not usually possible, and complex acoustic movement patterns may not reflect mating patterns and thus gene flow.

Song transmission requires acoustic contact to allow whales to hear and learn each others' song. It has been suggested that individual humpback whales need to be within approximately 20 km (Payne & Guinee 1983; Cato 1991; Helweg et al. 1998) of each other for this to happen. Song transmission therefore involves acoustic contact between migrating whales or those on shared feeding grounds or movement of individuals between breeding grounds either between or within seasons (Payne & Guinee 1983). All of these mechanisms for song transmission are at least theoretically possible (e.g., Noad & Cato 2007; Garrigue et al. 2011a; Garland et al. 2013a). The acoustically isolated breeding grounds provide locations where songs should diverge among populations due to the absence of acoustic contact. This divergence, along with the strong conformity to the current song type within a population, means that song should serve as a vocal identifier for each population (Garland et al. 2011, 2012, 2013b). Song may be a very sensitive indicator of dispersal events; novel song types introduced at a very low prevalence can rapidly and completely replace (within 2-3 months) existing song types within a population (Noad et al. 2000). In the South Pacific, song sharing

occurs with a 1-2 year delay in transmission across the region from eastern Australia to French Polynesia, leading to within-year differences in song among areas (Garland et al. 2011, 2013a, b). Connectivity among populations can be shown by tracing the movement of novel song types and sections within existing song types from one population to the next. The inclusion of song analyses in the assessment of population structure is warranted because their results provide a sensitive indicator of current contact among males.

Song types and the directionality of song exchange across the South Pacific have been documented (Garland et al. 2011, 2012, 2013b). These authors used an initial human classification of songs followed by quantitative analyses (i.e., classification and regression tree analysis of individual sounds and song sequence analysis with the Levenshtein distance similarity index). The sequence of themes within the song was used to compare the song display among individuals and populations (Garland et al. 2012, 2013b). This work demonstrated that songs of the same type cluster together regardless of the years or populations from which the recordings were made (Garland et al. 2013b), indicating that similar versions of the display were grouped.

We used this baseline understanding of the direction of song transmission and quantitative methods that indicate the similarity of any two versions of the song display to assess the strength and yearly variability in the connections among whales from different areas in the South Pacific to investigate if the song type exhibited at each location was acoustically distinct and indicative of a distinct population. We hypothesized that songs from each breeding aggregation occupy a single, terminal node in the structure and thus represent a distinct vocal population and that there is some level of similarity among all breeding aggregations, indicating that the region's whales represent a metapopulation. We used the

strength of song similarity as an alternative to genetic or photo-identification data and as a proxy for connectivity among populations. Given the dynamics of the display in space and time (Garland et al. 2011), we investigated similarity on a yearly basis (a snapshot in time each year) to determine the strength and variability in song transmission and therefore to highlight when and where such transmission occurred.

Methods

Field sites

From 1998 to 2008 whale songs were recorded by multiple researchers on recorders and hydrophones suspended from boats (Supporting Information) at six primary migration or breeding sites in the western and central South Pacific. These were the southeastern Queensland coast in eastern Australia, the southern lagoon in New Caledonia, the Vava'u island group in Tonga, the island of Tutuila in American Samoa, the island of Rarotonga in the Cook Islands, and the island of Mo'orea in French Polynesia (Fig. 1).

Song transcription and classification

The arrangement of humpback whales' songs is highly stereotyped (Payne & McVay 1971), with units or sounds occurring in a stereotyped sequence called a phrase. Phrases are repeated multiple times to create a theme, and a series of themes, produced in a particular order, comprises a song. We defined a *song* as any complete cycle of themes with no repetition of a theme (Payne & Payne 1985). At a higher level of song classification, different versions of the display are grouped together into song types based on similarity (Garland et al. 2011, 2013b).

Each unit was transcribed by a person, based on the visual and aural qualities of the sound, and assigned a name. Both a discriminant function analysis with cross-validation and a non-parametric classification tree analysis with cross-validation were performed on a subset of units (400). Respectively, 80% and 88% of sounds were classified correctly (Garland et al. 2011, 2012). We also had 3 naive people classify phrases; they correctly matched over 94% of phrases with the primary human classifier (Garland et al. 2011).

Similarity analyses

The Levenshtein distance similarity index (LSI) is used to calculate the similarity of any two strings of data through a count of the minimum number of changes (insertions, deletions, or substitutions) required to change one string into another. The result is divided by the length of the longest string within the pair (e.g., Kohonen 1985; Tougaard & Eriksen 2006; Garland et al. 2012). The LSI is calculated as

$$\text{LSI}(a, b) = 1 - \frac{\min(I+D+S)}{\max[L(a),L(b)]} \quad (1)$$

where string a is converted into string b by the minimum number of insertions (I), deletions (D), and substitutions (S) and divided by the string with the maximum length (L). The LSI is used to calculate the proportion or percentage of similarity between every pair of strings after accounting for string length (Garland et al. 2012). Here, a string was the typical sequence of themes that made up the song of a population in a given year. The LSI was calculated between every pair of individuals, and a representative song string for each population and year was produced (presented in Garland et al. 2012, 2013b). We investigated the relationships among the representative songs from each population to gain an understanding

of the variability and strength of vocal sharing across the period to infer connectivity and derive a population structure.

To investigate structure with such a dynamic signal, a LSI score was produced each year for each population pair (Table 1, rows 3-13), and then these scores were averaged across these years (Table 1, row 14) to gain an overall measure of similarity for each pair of populations. Two song types were occasionally present within a single population in a single year. In such cases, each LSI score contributed one half to the LSI score between that particular pair of populations in that particular year. On the rare occasions when both populations being compared contained two different song types (resulting in four comparisons), each LSI score contributed one quarter to the LSI score for that particular year.

A second separate analysis was also conducted. This examined the presence and sharing of phrases in songs without considering the sequential information within the songs to test whether our results were robust to the index we used. Dice's coincidence index was originally designed as a measure of the amount of association between two species (Dice 1945). Here, we used it as a measure of phrase sharing:

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

where SI is the similarity in song phrases between population pairs, A is the number of shared phrases, B is the total number of phrases present in population 1, and C is the total number of phrases present in population 2. Ninety-three phrases were present across the region from 1998 to 2008 (Garland et al. [2011] provides a detailed description of each phrase). Phrase presence was compiled for each population in each year. Phrase sharing each year was

calculated between population pairs, and then the similarity scores were averaged (as with LSI) to produce a single measure of similarity per population pair (Table 2, \bar{x} SI). Given our uneven sample sizes (Supporting Information), the possible absence of phrases due to an absence of data, the constantly changing nature of humpback song, and the rapid integration of novel songs, we suggest examining song similarity on a yearly basis may be more representative of the song data.

Population Structure

The mean similarity scores from each similarity analysis (LSI and Dice's SI; Tables 1 & 2) produced two similarity matrices. Each matrix was converted to a dissimilarity matrix (by subtracting each score from one) and subjected to hierarchical clustering (using the `hclust` function) in the statistics program R (R Development Core Team 2012). Average (UPGMA) clustering was undertaken because this produces clusters based on all pair-wise similarities (Manning et al. 2009). The output of each analysis was displayed in a dendrogram. To investigate the stability of clusters, each cluster matrix was bootstrapped with multiscale bootstrap resampling (AU) and normal bootstrap probability (BP) 1,000 times in R (with `pvclust` and `pvrect` packages) to establish p values (significance for AU at $p > 95\%$ and for BP at $p > 70\%$) and SE for each split in the tree (Garland et al. 2012). An out-group with 0% similarity to all breeding aggregations was included in each matrix to establish the p value for the first split in the tree (not shown). We suggest the occupation of a single, terminal node (100% similarity) indicated a vocal population, whether this contained songs of whales from one or more breeding aggregations. Higher level associations were suggested by the dendrograms and reflected the hypothesized metapopulation structure. These broader-scale clusters may indicate a closer acoustic and potentially demographic relationship, but

examining average similarity scores smoothed the variability in song sharing over the study period.

Vocal similarity with distance

We investigated the relationship between song similarity and distance among populations. The LSI scores and Dice's SI were compared with the distances between populations to understand how vocal similarity correlated with geographic distance. The data were first checked for homogeneity of variance (Figner-Killeen) and normality (Shapiro-Wilk) in R. A linear regression analysis and Pearson's correlation coefficient were conducted to investigate whether distance was a good predictor of song sharing, as is common in avian songs.

Results

Levenshtein distance similarity index

The overall population structure from hierarchical clustering and bootstrapping of the LSI similarity matrix indicated each breeding aggregation represented a distinct population and that all aggregations were related, indicating whales in the region formed a metapopulation. There were four clusters (termed 'vocal clusters' from here on as they were based on acoustic data) within the metapopulation (Fig. 2a). Cluster one contained the population from eastern Australia, cluster two those from New Caledonia, Tonga and American Samoa, cluster three the population from the Cook Islands, and cluster four the French Polynesian population. We considered the third and fourth were separate based on the AU p value and 25% similarity score. Multiscale bootstrap resampling indicated that Oceania and eastern Australia represented significant clusters ($> 98\%$, $SE < 0.004$), and each split in the tree was significant and likely to be stable ($p > 98\%$). Normal bootstrap probability produced p values from 64-

97%, indicating that the tree represented stable subdivision of these populations, except potentially between the Cook Islands and French Polynesia (BP $p = 64\%$).

Dice's similarity index

Clustering and bootstrapping of Dice's SI (Fig., 2b) indicated that each breeding aggregation represented a single, distinct population and that whales in the region formed a metapopulation. Three vocal clusters (Fig., 2b) were apparent. French Polynesia and the Cook Islands formed a single cluster (56% similarity) in this analysis, while Oceania again formed a higher level cluster. Multiscale bootstrap resampling and normal bootstrap probability indicated that each split in the tree was significant and likely to be stable (AU: $p = 100\%$; BP: $p > 89\%$; Fig. 2b).

Vocal similarity with distance

The distance between populations appeared to be negatively correlated to the mean similarity in song sequences (LSI: Pearson's, $t = -3.247$, $df = 13$, $p = 0.006$, $r = -0.669$), or yearly phrase sharing (Dice's SI: Pearson's, $t = -3.936$, $df = 13$, $p = 0.002$, $r = -0.737$). As geographic distance between populations increased, song similarity within the region decreased. Linear regression indicated that 45% (LSI) and 54% (Dice's SI) of the variation in the amount of song sharing between populations was explained by distance (LSI: $F_{1-13} = 10.54$, $p = 0.006$, $R^2 = 0.448$, $n = 14$; Dice's SI: $F_{1-13} = 15.49$, $p = 0.002$, $R^2 = 0.544$, $n = 14$; Fig. 3).

Discussion

Metapopulation structure of South Pacific humpback whales

The complex metapopulation structure derived from song suggests that the humpback whale populations of the western and central South Pacific grouped together into three or four distinct vocal clusters during the years of our study. The western-most cluster contained a single population, off eastern Australia, and the central cluster consisted of populations around New Caledonia, Tonga and American Samoa. The eastern group, which formed a single cluster or was split into two clusters, depending on the analysis used, contained the populations of the Cook Islands and French Polynesia. These results provide insight into the movements or contact between males only. Despite this, the results are consistent with the hypothesis that each breeding aggregation represents a distinct population (each occupied a single, terminal node in the dendrogram) within a metapopulation, similar to the current understanding of population structure based on genetic and photo-identification studies (Olavarria et al. 2007; Garrigue et al. 2011a, b). Both LSI and Dice's SI indicated that the eastern Australian population represents an outlier or out-group to the rest of the Oceania populations.

Photo-identification mark-recapture studies and mtDNA analyses indicate that each breeding aggregation within the western and central South Pacific region represents a demographically distinct population, with rare but documented interchanges of individuals (Olavarria et al. 2007; Garrigue et al. 2011a, b). Clustering based on song similarity scores indicated that the populations in Oceania were more similar to each other than to the eastern Australian population. The eastern Australian population shared the same song type with New Caledonia 31% (LSI) and 38% (Dice's SI) of the time, agreeing with the low levels of interchange shown in a comparison of photographically identified individuals from eastern Australia and

Oceania (Garrigue et al. 2011b) and in the uneven rates of population recovery within the region (Noad et al. 2011; Constantine et al. 2012). Despite it representing an out-group within the region, there was still a connection between the eastern Australian population and others in the region, shown by the high levels of song sharing evident in some years (88-0%, LSI, Table 1; 95-0%, Dice's SI, Table 2). This indicates the western and central South Pacific breeding aggregations formed a metapopulation that can be subdivided into smaller clusters of populations. The population structure may take the form of a mainland-island or stepping stone model (Hartl & Clark 1988; Hanski & Gyllenberg 1993; Hanski & Simberloff 1997). Future analyses should further examine the underlying model driving the observed structure.

There appeared to be a hierarchy in the levels of similarity among populations. The New Caledonian, Tongan, and American Samoan populations had higher levels of song similarity with each other and represented a tighter cluster regardless of the analysis used. Previous quantitative song analyses show that New Caledonian and Tongan songs and Tongan and American Samoan songs are sometimes identical (100% similar) within a season (Garland et al. 2013b). Song from French Polynesia was sometimes identical to New Caledonian song from the previous year (Garland et al. 2013b). This time lag does not result in within-season similarity, but it does demonstrate the relationships within the metapopulation. The region is vocally connected at a general level, but these time lags inform the fine-scale interactions of populations each year, which were changeable. Averaging the LSI and Dice's SI scores across years allowed us to examine the strength and variability in song sharing between pairs of populations. The stepwise transmission of song across the region created a disjointed pattern of within-season transmission (see Garland et al.'s [2011] Fig. 1 for the pattern of transmission). Breaks in transmission regularly occurred between eastern Australia and New Caledonia (and the rest of Oceania) and between Tonga and American Samoa and the Cook

Islands. These breaks created within-season boundaries to transmission which we used as a proxy for connectivity (or lack thereof) among populations.

The decrease in song similarity as distance between populations increased also suggests that adjacent populations in the western and central South Pacific region, at least, are sometimes connected and thus form a metapopulation. It may alternatively represent an isolation-by-distance relationship. Although humpback whales are sighted in low numbers at other sites in the South Pacific (e.g., Pitcairn), there is currently no evidence of any other large aggregations analogous to those reported here. There is, however, significant maternal population structuring across Oceania (Olavarria et al. 2007), and recent population estimates indicate that most whales in the region are aggregated within the primary breeding grounds (i.e., those included in the current study) (Constantine et al. 2012). The evidence of isolation by distance we found, therefore, does not provide evidence of the presence or absence of population structure in this data set because this distance relationship can be confounded by population structure.

The groupings within the large Oceania cluster were consistent with the current IWC separation of populations into New Caledonia (E2), Tonga (E3), the Cook Islands (F1), and French Polynesia (F2) (IWC 2006) (American Samoa is not currently included in the IWC classification). Our placement of American Samoa in the central cluster should be viewed with caution given its small sample size (Supporting Information) and the potential for variability in song sharing. However, in view of the reduced connection of the eastern Australian (E1) population to those of Oceania, based on the dissimilarity among songs based on two different measures of vocal similarity, additional subdivision of the IWC groupings is suggested to incorporate this separation. This could take the form of a reassignment of

populations to reflect the three or four vocal clusters within the metapopulation: eastern Australia (E1), New Caledonia (F1a), Tonga (F1b), American Samoa (F1c), the Cook Islands (F2a), and French Polynesia (F2b).

Integration of multiple approaches to inform management decisions

Our use of acoustic data aided in the determination of population structure within the region. However, song does not usually allow the collection of information about individuals or the movements of specific individuals, and complex acoustic movement patterns may not reflect mating patterns and thus gene flow. Despite these weaknesses, the collection of song data can be less costly than other methods, and, importantly, it provides a sensitive indicator of male acoustic contact among populations and thus facilitates the investigation of movement dynamics. Song differences can aid in defining population boundaries to complement genetic differences, photo-identification, and satellite tracking studies.

To investigate the relationship between population genetic structure and regional differences in songs and to assess which one should be weighted most heavily when making management decisions, we suggest use of the approach used by MacDougall-Shackleton and MacDougall-Shackleton (2001) with White-crowned Sparrows, Wright and Wilkinson (2001) with Yellow-naped Amazon Parrots, and Rendell et al. (2012) with Sperm whales. Genetic, vocal, and geographic distance matrices are correlated using Mantel and partial Mantel tests to determine which variable provides the highest explanatory power for the observed structure (Rendell et al. 2012). For example, song differences act as a partial barrier to gene flow in the White-crowned Sparrow (MacDougall-Shackleton & MacDougall-Shackleton 2001), while vocal clan membership explains mtDNA haplotype distributions better than geographical area in Sperm whales (Rendell et al. 2012). We predict Humpback whales may display a structure

similar to the White-crowned Sparrow, where vocal differences act as a partial barrier to gene flow and are less likely to follow Sperm whales' structure. The integration of both lines of evidence (genetic and vocal) into the definition of management units should be undertaken. Further, we suggest a fourth matrix should be added to the analysis involving the use of interchange indices from photo-identification studies. This framework could be applied to any highly vocal species. It provides a broad understanding of which method provides the highest explanatory power in elucidating population structure and thus should be given the highest weighting when making decisions about management and subsequent conservation actions regarding structure.

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Supporting Information

Supplementary methods including demographic information and sample sizes (Appendix S1), and additional acknowledgments (Appendix S2) are available online. The authors are

solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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Table 1. Similarity, determined with the Levenshtein distance similarity index, in song sequences analysed at the theme level^a per year between pairs of South Pacific populations.

Year	EA vs.					NC vs.				TG vs.			AS vs.		CI vs.
	NC	TG	AS	CI	FP	TG	AS	CI	FP	AS	CI	FP	CI	FP	FP
1998	0.88	0.75		0	0	0.88		0	0		0	0			0.50
1999	0.88	0.60			0.63	0.70			0.63			0.70			
2000	0	0				0.50									
2001	0.71	0.30		0	0	0.36		0	0		0.25	0.04			0
2002	0.67	0.33				0.29									
2003	0	0	0	0		0.78	0.33	0.56		0.43	0.67		0.22		
2004	0.30		0	0	0		0.33	0.19	0.29				0.56	0.67	0.38
2005	0		0	0	0		0.67	0	0.30				0	0.42	0.22
2006	0	0	0	0	0	0.83	0.83	0.40	0	1	0.33	0	0.33	0	0
2007	0	0		0	0	1		0.38	0		0.38	0			0.05
2008	0	0		0	0	1		0	0		0	0			0.60
\bar{x} LSI	0.31	0.22	0 (0)	0 (0)	0.08	0.70	0.54	0.19	0.15	0.71	0.27	0.12	0.28	0.36	0.25
(SD)	(0.39)	(0.29)			(0.22)	(0.27)	(0.25)	(0.23)	(0.23)	(0.40)	(0.25)	(0.28)	(0.23)	(0.34)	(0.25)

^a Stereotyped sequence of sounds repeated multiple times. See Methods for further information.

^b Blank, no data available.

^c EA= eastern Australia, NC=New Caledonia, TG= Tonga, AS=American Samoa, CI=Cook Islands, FP=French Polynesia.

Table 2. Song phrase sharing per year between pairs of South Pacific populations of humpback whales calculated with Dice's similarity index .

Year	EA vs.					NC vs.				TG vs.			AS vs.		CI vs.
	NC	TG	AS	CI	FP	TG	AS	CI	FP	AS	CI	FP	CI	FP	FP
1998	0.94	0.94		0	0	1		0	0		0	0			0.83
1999	1	0.95			0.82	0.95			0.82			0.89			
2000	0	0				0.73									
2001	0.83	0.56		0	0	0.70		0	0		0.40	0.39			0.88
2002	0.76	0.80				0.84									
2003	0	0	0	0		0.78	0.63	0.50		0.57	0.78		0.50		
2004	0.64		0	0	0		0.61	0.35	0.50				0.67	0.84	0.74
2005	0	0	0	0	0		0.77	0	0.36				0	0.48	0.42
2006	0	0	0	0	0	0.91	0.67	0.55	0	0.62	0.50	0	0.77	0.27	0.19
2007	0	0		0	0	1		0.76	0		0.76	0			0.22
2008	0	0		0	0	1		0	0		0	0			0.67
\bar{x} LSI	0.38	0.32	0 (0)	0 (0)	0.10	0.88	0.67	0.27	0.21	0.59	0.41	0.21	0.49	0.53	0.56
(SD)	(0.45)	(0.43)			(0.29)	(0.12)	(0.07)	(0.31)	(0.32)	(0.03)	(0.35)	(0.37)	(0.34)	(0.29)	(0.27)

^a Blank, no data available.

^b EA= eastern Australia, NC=New Caledonia, TG= Tonga, AS=American Samoa, CI=Cook Islands, FP=French Polynesia.

Figure captions

Figure 1. Western and central South Pacific showing areas where groups of humpback whales breed, according to the International Whaling Commission (IWC). Groups E and F are thought to migrate to two corresponding feeding regions in Antarctica (Areas V and VI). Group E has 3 populations: eastern Australia (E1), New Caledonia (E2), and Tonga (E3), and Group F has 2 populations: the Cook Islands (F1) and French Polynesia (F2). American Samoa is not currently included in the IWC classification. Ovals represent breeding location of populations studied. Our song recordings from eastern Australia were taken while the whales were on migration off south-eastern Queensland (x).

Figure 2. Dendrograms representing vocal population structure of humpback whales in the South Pacific based on average (UPGMA) clustering and bootstrapping (1,000 times) determined by (a) Levenshtein distance similarity index (LSI) and (b) Dice's similarity index. Numbers represent multiscale bootstrap resampling (AU) (left) and normal bootstrap probability (BP) (right) p values (significance for AU $p > 95\%$ and for BP $p > 70\%$).

Figure 3. Mean (SE) similarity in song sequences (LSI) and yearly phrase sharing (Dice's SI) versus distance between population pairs.