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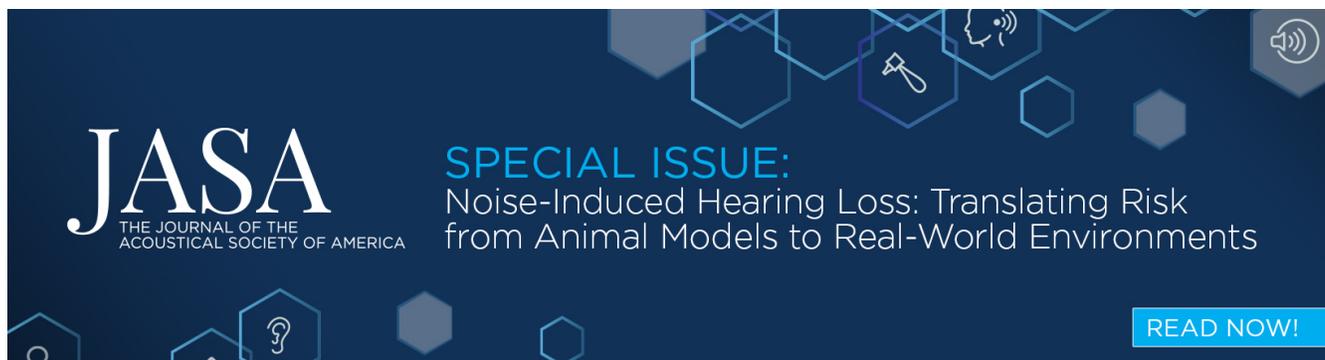
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Physical constraints of cultural evolution of dialects in killer whales

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Odontocete sounds are produced by two pairs of phonic lips situated in soft nares below the blowhole; the right pair is larger and is more likely to produce clicks, while the left pair is more likely to produce whistles. This has important implications for the cultural evolution of delphinid sounds: the greater the physical constraints, the greater the probability of random convergence. In this paper the authors examine the call structure of eight killer whale populations to identify structural constraints and to determine if they are consistent among all populations. Constraints were especially pronounced in two-voiced calls. In the calls of all eight populations, the lower component of two-voiced (biphonic) calls was typically centered below 4 kHz, while the upper component was typically above that value. The lower component of two-voiced calls had a narrower frequency range than single-voiced calls in all populations. This may be because some single-voiced calls are homologous to the lower component, while others are homologous to the higher component of two-voiced calls. Physical constraints on the call structure reduce the possible variation and increase the probability of random convergence, producing similar calls in different populations. © 2016 Acoustical Society of America.

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I. INTRODUCTION

Understanding the physical basis of sound production is essential to categorize vocal signals into natural categories. For the sounds of terrestrial mammals, the development of the source-filter theory has enabled researchers to describe the acoustic structure of sounds according to their mode of production and to predict acoustic variation caused by variation in the anatomical or physiological attributes of the caller (Taylor and Reby, 2010). Even finer resolution of phoneme classification in humans is based on the detailed knowledge

of their production: the position of tongue and lips, properties of the airflow, and other features of the vocal tract (Bickford, 2006).

Sounds of killer whales *Orcinus orca* have a complex structure (Ford, 1991; Yurk *et al.*, 2002), but their categorization is hindered by the lack of understanding of their production mechanisms. Odontocete sounds are not produced in the larynx, as in terrestrial mammals. Instead, their source is situated in a complex system of air sacs and tissues that surround the nasal passage (Norris, 1968; Cranford *et al.*, 1996; Cranford and Amundin, 2004). All toothed whales (except sperm whales *Physeter macrocephalus*) have two pairs of phonic lips situated in each of the soft nares on the ventral

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side of the vestibular air sacs, just below the blowhole; both pairs are used in sound production (Cranford *et al.*, 1996; Cranford and Amundin, 2004).

Dolphin sounds were traditionally divided into three classes: clicks, burst-pulse sounds, and whistles. However, some species (e.g., killer whales, pilot whales *Globicephala* sp., false killer whales *Pseudorca crassidens*) regularly produce calls intermediate in structure between whistles and burst-pulse sounds, suggesting that these classes are not discrete, but rather the two extremes of a perceptual continuum (Murray *et al.*, 1998; Sayigh *et al.*, 2013). Indeed, Madsen *et al.* (2012) showed that dolphin “whistles” are in fact not airborne, but produced by pneumatically induced vibrations of phonic lips analogous to the operation of vocal folds in terrestrial mammals. In most delphinoids the right pair of phonic lips is larger than the left (Cranford *et al.*, 1996). Madsen *et al.* (2013) examined the sound production of common bottlenose dolphin *Tursiops truncatus* and false killer whale and showed that in both species clicks were produced by the right pair while whistles (tonal calls) were mostly produced by the left pair of the phonic lips. This finding explains the long known observation that dolphins can simultaneously produce clicks and whistles (Murray *et al.*, 1998).

However, some delphinoids can simultaneously produce two tonal sounds, yielding “two-voiced” or “biphonic” calls (e.g., killer whales: Ford, 1991; Tyson *et al.*, 2007; short-finned pilot whales *Globicephala macrorhynchus*: Sayigh *et al.*, 2013; bottlenose dolphins: Papale *et al.*, 2015). Therefore, the “clicking” right pair of phonic lips is also capable of emitting tonal sounds. In addition, Cranford *et al.* (2011) found that bottlenose dolphins can produce clicks with both pairs of phonic lips working independently or simultaneously, though the right pair was used more often. So, the phonic lips are not strictly specialized, but differences in the size of the right and left phonic lips suggest that they may be most effective for producing vocalizations with different frequency characteristics.

This assumption has important implications for the cultural evolution of delphinid sounds. In some, vocalizations are learned rather than transmitted genetically (killer whales: Ford, 1991; Deecke *et al.*, 2000; Foote *et al.*, 2006; bottlenose dolphins: Tyack and Sayigh, 1997) and can indicate individuality (bottlenose dolphins: Janik and Sayigh, 2013) or group affiliation (killer whales: Ford, 1991). Killer whales have unique family dialects—sets of stereotyped sounds. Calves learn their dialect from their mother and other family members (Bowles *et al.*, 1988; Crance *et al.*, 2014). With time, these dialects slowly change through learning errors and innovations in a process called cultural evolution (Deecke *et al.*, 2000; Wieland *et al.*, 2010; Filatova *et al.*, 2015b). The recently diverged dialects are more similar than dialects that have passed a long process of independent evolution (Ford, 1991; Deecke *et al.*, 2010). However, in some cases, calls from distantly related dialects become more similar. Plausibly, this could happen by either horizontal transmission or random convergence (Filatova *et al.*, 2013). By horizontal transmission we mean here the transmission of calls and call features from one family to another. Random convergence occurs when calls of different families become

more similar by chance, without any influence on each other’s evolution. This is more likely to happen if the variety of possible states is limited. In this case the variation in the diverging calls soon reaches a limit and then the differences between them can no longer increase. This situation is analogous to the phenomenon called “mutational saturation” which occurs when many changes at a given locus eliminate phylogenetic signals (Delsuc *et al.*, 2005). This happens because variation in nucleotide sequences is restricted by the structure of deoxyribonucleic acid: there are only four nucleotides and four possible types of mutations (transitions, transversions, insertions, and deletions). Saturation can lead to homoplasy, i.e., convergence of traits in non-related taxa, which has been described not only in genetics, but also in morphology (e.g., Alvarez *et al.*, 1999; Mueller *et al.*, 2004).

In vocal repertoires, a similar situation can be caused by constraints imposed on call structure by the physical properties of the sound producing apparatus. Therefore, it is important to understand these constraints to interpret the importance of call similarity: the stricter the constraints, the higher the probability that calls can become similar at random. In this paper we examine the call structure of eight killer whale populations to identify the scope of the constraints and test whether they are consistent among all populations.

II. METHODS

A. Data collection

Acoustic recordings used for this study were collected over various field projects using a variety of equipment. All recordings were made at a sampling rate of 44.1 kHz or higher.

Recordings of the Northern resident (NR) and West Coast transient (WT) killer whale populations were made from 1988 to 1999 in the waters off northern Vancouver Island. Recordings of the Southern resident (SR) population were made from 1980 to 2009 in the waters of Salish Sea (northern Washington State and southern Vancouver Island). The Alaskan resident (AR) killer whale population was recorded from 1984 to 2008 in Prince William Sound and the Kenai Fjords area. Calls from Kamchatkan residents (KR) were obtained in 2000–2014 off the southeastern coast of Kamchatka peninsula. Eastern Aleutian transient (AT) killer whales were recorded in 2003–2008 in False Pass (between mainland Alaska and Unimak Island). Calls from Icelandic killer whales (Ice) were obtained between 2008 and 2014 using both digital acoustic recording tags (Dtags; Johnson and Tyack, 2003) and various other recording systems at two main locations: one near Grundarfjörður on the Snæfellsnes Peninsula (West Iceland), the other near Vestmannaeyjar off the southern coast of Iceland. Calls from Norwegian killer whales (Nrw) were obtained between 2005 and 2009 using Dtags in the northern Norwegian Vestfjord fjord system and off Vesterållen.

Calls from four North Pacific resident populations and the WT population were classified according to existing catalogues (Ford, 1987; Yurk *et al.*, 2002; Filatova *et al.*, 2004). For the False Pass transient population, call

categorisation was performed based on audible characteristics of calls and visual inspection of spectrographic features. For Icelandic and Norwegian killer whales, we have modified and updated existing catalogues (Strager, 1995; Shapiro, 2008; Duc, 2011).

Each killer whale population produces several tens of stereotyped call types recognized even by inexperienced observers (Yurk *et al.*, 2002; Shamir *et al.*, 2014); these call types retain stereotypy in varying circumstances (Ford, 1989) and over the years (Deecke *et al.*, 2000; Foote *et al.*, 2008). Call types have different degrees of structural variation: some types are very stereotyped while others demonstrate some variation that can be either discrete or gradual. Call types with a discrete variation are traditionally divided into a number of subtypes according to their structural characteristics; call types with a gradual variation are not divided into subtypes, and all variations are regarded as a single call type (Ford, 1991). To cover the full range of structural variation within a type, we selected two calls from each call type or subtype that were the least similar to each other. If a call type had no subtypes, two samples from that call type were used; for call types that comprised discrete subtypes, we used two samples from each subtype. For calls that did not fall into discrete subtypes but showed apparent variations, two calls from opposite extremes of the structural continuum were selected. When possible, the pairs of call samples from the same type/subtype were selected from different encounters and different years to cover the presumed variation in the call structure.

Norwegian killer whales are known to produce compound calls, which consist of combinations of other stereotyped calls produced in stable sequences (Strager, 1995; Shapiro *et al.*, 2011). Treating every stable sequence as a separate type would produce pseudo-replication through the increased presence of calls used as parts of stable sequences (as they will be measured twice—as a separate call and as a part of a stable sequence). Thus, we only measured those stable sequences that contained calls or syllables not observed occurring separately.

In total, 638 call samples were used for the analysis: 96 from ARs, 102 calls from KRs, 96 calls from NRs, 62 calls from SRs, 34 calls from ATs, 36 calls from WTs, 72 calls from Norway, and 140 calls from Iceland. Sample sizes of calls from the transient populations were lower because the overall repertoire size of stereotyped calls is typically lower in these populations (Ford, 1987; Saulitis *et al.*, 2005). The differences in sample sizes from different populations did not bias our results, because each sample size was selected to cover the full range of structural variation of stereotyped calls in the respective population.

B. Acoustic and statistical analysis

To capture the frequency parameters over the whole call duration, we extracted call contours following the method described in Filatova *et al.* (2012a). The extracted contours represented a set of frequency measurements of each call's fundamental frequency spaced 0.01 s apart. If the fundamental frequency was not visible, we measured one of the

harmonics and divided the measurements by the number of that harmonic to obtain the fundamental frequency values. For two-voiced (biphonic) calls, containing overlapping frequency components, we extracted the contours of both the lower-frequency component (LFC) and upper-frequency component (UFC).

In many two-voiced calls the start and end of the lower and upper components do not match, so that a call can be partly two-voiced and partly single-voiced (Fig. 1). Single-voiced segments can consist of either lower or upper components (Fig. 1). As we were interested in constraints imposed by the structure of both pairs of phonic lips, we analysed two- and single-voiced segments of the calls separately. For each point of a two-voiced segment of each two-voiced call we obtained two values: the frequency of the lower and upper components at that point. Single-voiced segments of two-voiced calls (both from the lower and upper components) were pooled together with single-voiced calls; for each point of these vocalizations we obtained a single frequency measurement.

We analyzed the distribution of frequency values of the lower and upper components of the two-voiced call segments and single-voiced calls and call segments using plots and descriptive statistics in R (R Core Team, 2014).

III. RESULTS

To identify the scope of the constraints of the sound producing apparatus in killer whales, we analyzed the frequency range of the two- and single-voiced calls and call segments in different populations. In the two-voiced segments of calls the frequency of the lower component was typically below 4 kHz (Fig. 2). Only in five calls did the frequency values of the lower component range above 4 kHz. The first call type with a frequency of the lower component ranging above 4 kHz was AKS16b from the AR population. The lower component of this call is a short up-sweep that sometimes can rise above 4 kHz at the end. In our sample, only one frequency point of one AKS16b call ranged above this value;

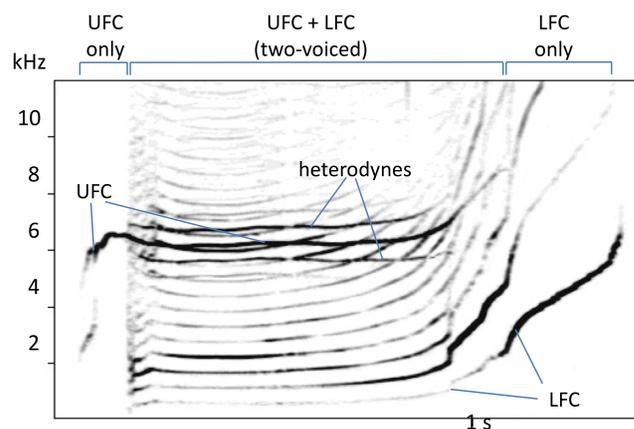


FIG. 1. (Color online) The start and end of the LFC and UFC in a two-voiced call do not match, so that only the middle segment of the call is two-voiced, while the beginning and end of the call are single-voiced. Heterodyne frequencies arise from the interaction of LFC and UFC; the lower heterodyne in each point is equal to $LFC - UFC$, and the higher heterodyne is equal to $LFC + HFC$.

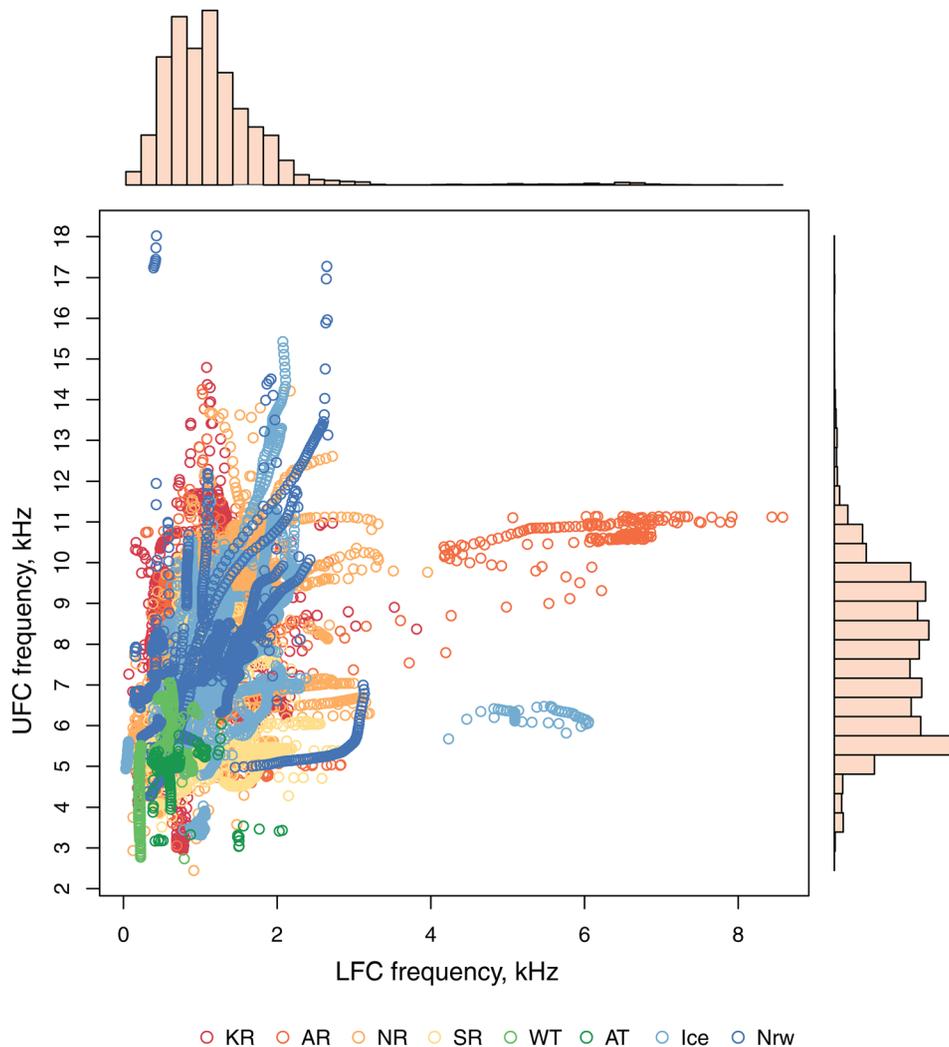


FIG. 2. (Color online) Scatterplot with marginal histograms showing the distribution of frequency points of the lower and upper components in two-voiced calls from all populations: KR, Kamchatkan residents; AR, Alaskan residents; NR, Northern residents; SR, Southern residents; WT, West Coast transients; AT, Eastern Aleutian transients; Ice, Iceland; Nr, Norway.

the second call of this type had the whole lower component below 4 kHz.

Four other calls with the frequency values of the lower component above 4 kHz belonged to two call types: the AKS18 call type from the AR population and the I84 call type from the Icelandic population (Fig. 3). Most of the lower component of both AKS18 calls and about half of the contour of the lower component of both I84 calls were centered above 4 kHz.

The frequency of the upper component was typically centered above 4 kHz, though in some calls the upper component ranged down to 3 kHz (Fig. 2). The upper component ranging below 4 kHz was found in 16 call types from all populations except Norwegian. Usually (in 11 of the 16

call types) it occurred in calls where the upper component started with an abrupt upsweep, and its section with a frequency below 4 kHz was rather short—10 to 30 ms. Only five call types included relatively long (>50 ms) sections of the upper component with a frequency below 4 kHz: K20 call type from KR, N18 call type from NR, T12ii call type from WT, FP4 call type from AT, and I41 call type from Ice.

The frequency of the lower component of two-voiced call segments had a narrower range than single-voiced calls and call segments in all populations (Fig. 4). The 5% quantile of single-voiced calls was lower than the 5% quantile of the lower component of two-voiced call segments in all populations except WTs, and the 95% quantile of single-voiced

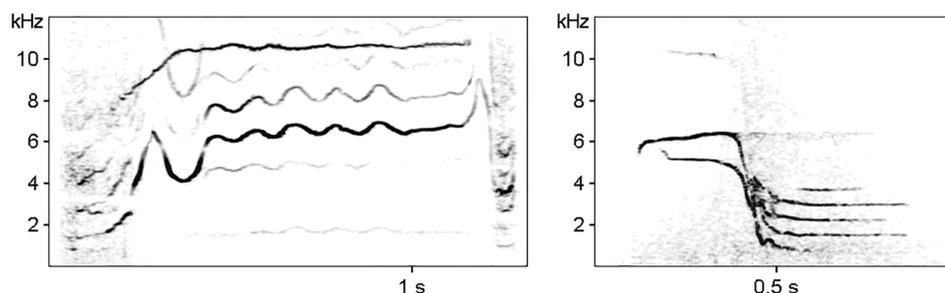


FIG. 3. Two call types with the lower component above 4 kHz: Alaskan call AKS18 (left) and Icelandic call I84 (right).

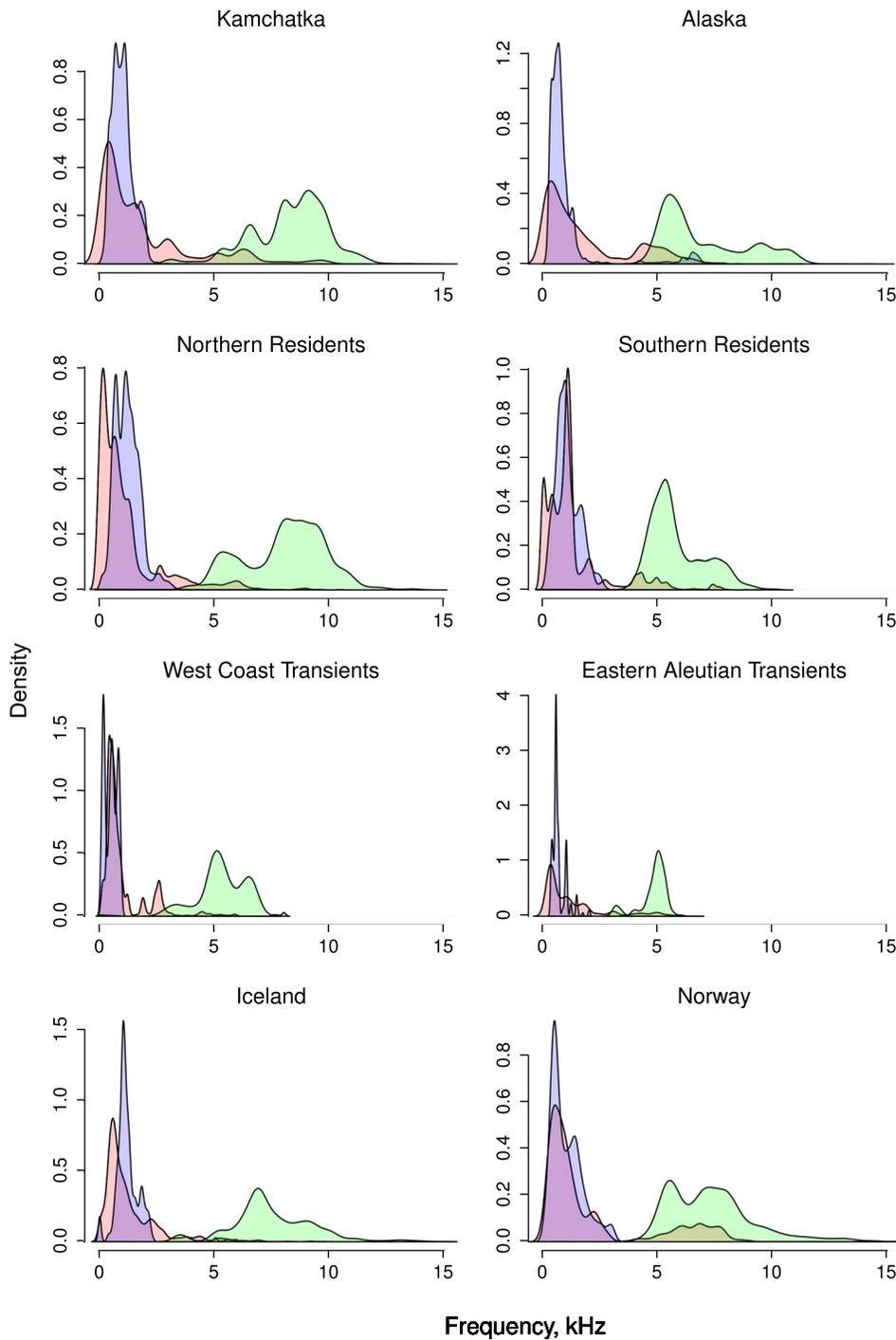


FIG. 4. (Color online) Density plots of the frequency values of the lower (blue) and upper (green) components of two-voiced call segments and of single-voiced calls and call segments (red) from all studied populations.

calls was higher than the 95% quantile of the lower component of two-voiced call segments in all populations except Alaska (Table I).

The 95% quantile of the lower component was very similar among all populations except transients, which had lower values, and ARs which had a much higher value due to the presence of a single call type (AKS18). The 5% quantile of the lower component was more variable, but in all populations except WTs it was above 300 Hz.

All populations had similar 5% and 95% quantiles for the upper frequency component, except for West Coast and ATs which had lower values. Nevertheless, in all populations the 95% quantile for single-voiced calls was lower than the

95% quantile of the upper component of two-voiced call segments (Table I).

IV. DISCUSSION

In the stereotyped calls of all eight killer whale populations, the frequency values of the lower component were mostly centered below 4 kHz, while the frequency values of the upper component were mostly above that value. It appears that 4 kHz is a natural boundary between lower and upper components. Killer whales are technically capable of producing lower components at frequencies above, and upper components at frequencies below this value, but such

TABLE I. Five percent and 95% quantiles of frequency values (in kHz) of single-voiced and both components (LFC: lower frequency component; UFC: upper frequency component) of two-voiced calls and call segments in eight studied populations.

	Single-voiced		LFC of two-voiced		UFC of two-voiced	
	5%	95%	5%	95%	5%	95%
Kamchatka	0.13	6.55	0.42	1.92	5.37	10.76
Alaska	0.10	5.63	0.34	5.71	5.04	10.64
NRs	0.05	4.63	0.54	2.17	5.12	10.66
SRs	0.04	4.80	0.36	2.02	4.51	8.12
WTs	0.23	2.99	0.20	0.90	3.32	6.71
ATs	0.25	4.73	0.40	1.49	3.28	5.42
Ice	0.25	4.33	0.66	2.14	5.01	10.47
Nrw	0.27	7.52	0.32	2.50	5.21	11.28

calls are rare, suggesting that there is a physical constraint. Despite the relatively small sample size (two calls per type/subtype, total of 638 calls from eight populations), the overall frequency values of two-voiced calls from different populations were mostly similar (Table I), suggesting that the sample size was enough to cover the full range of variation in stereotyped calls of the studied populations.

A. Implications for sound production

Many odontocete species have been reported to produce two overlapping sounds simultaneously (e.g., common bottlenose dolphins: Lilly and Miller, 1961; Risso’s dolphins *Grampus griseus*: Corkeron and Van Parijs, 2001; common dolphins *Delphinus* sp.: Moore and Ridgway, 1995; short-finned pilot whales: Sayigh *et al.*, 2013; long-finned pilot whales *Globicephala melas*: Nemiroff and Whitehead, 2009; false killer whales: Murray *et al.*, 1998; beluga whales *Delphinapterus leucas*: Belikov and Bel’kovich, 2006; Garland *et al.*, 2015), but the structure of these sounds varies across species. An upper component is typically a high-frequency tonal sound (“whistle”) in all species, but most dolphins (bottlenose dolphins, common dolphins, Risso’s dolphins) and beluga whales typically produce burst-pulse sounds or click trains as a lower component, and only killer whales, false killer whales, and both species of pilot whales have been reported to regularly produce calls as a lower component of two-voiced sounds.

Research on sound production in odontocetes has been so far mostly focused on bottlenose dolphins which typically produce click trains (echolocation clicks and burst pulse sounds) and high-frequency whistles, but rarely emit “calls”—the sound category intermediate between click trains and whistles (Murray *et al.*, 1998). Even in the study of sound production where a false killer whale was involved (Madsen *et al.*, 2013), the authors referred to the tonal vocalizations as whistles and did not provide any sonograms that could clarify the structure of these sounds. In many cases, the terminology used to classify sounds into categories is still poorly linked to sound production mechanisms, often due to a lack of knowledge on the mechanisms involved in producing different types of sound. In the future, advances in the understanding of delphinid sound production would

benefit from collaboration between morphologists and bioacousticians familiar with vocal repertoires.

The frequency of the lower component of two-voiced call segments had a narrower range than single-voiced calls and call segments in all populations: single-voiced calls had lower minimum and higher maximum frequency values. The higher maximum frequency values are easy to explain: we did not make a distinction between upper and lower components in single-voiced calls and call segments, so some single-voiced calls and call parts are homologous to the lower component while others are homologous to the upper component of two-voiced calls. This distinction is important to consider in future studies of killer whale acoustic behavior, because “upper” and “lower” single-voiced calls can potentially have different communicative functions.

It is less clear why single-voiced calls had lower minimum values than the lower component of two-voiced calls. In our dataset, the 5% quantile of the lower component in two-voiced calls was above 300 Hz in all populations except WTs. In WTs, the lower values of the lower component were due to the presence of WCT12 call type which has a two-voiced segment with the frequency of the lower component below 300 Hz (Fig. 5). However, the non-harmonic frequency modulation in this segment suggests that the sidebands are not true harmonics. In humans, a similar phenomenon occurs when both vocal folds vibrate at different frequencies (see Fig. 3 in Wilden *et al.*, 1998).

Therefore, our results indicate that killer whales rarely produce two-voiced calls with a lower component below 300 Hz, though they often produce sounds with a frequency below 300 Hz separately as single-voiced calls. One of the reasons can be that it is physically difficult to produce two sounds simultaneously with such a drastically different structure. However, dolphins and beluga whales routinely produce simultaneous whistles and burst pulse sounds (Lilly and Miller, 1961; Corkeron and Van Parijs, 2001; Moore and Ridgway, 1995; Garland *et al.*, 2015). Dolphin burst pulse sounds resemble low-frequency killer whale calls and likely result from a similar sound production mechanism (Murray *et al.*, 1998).

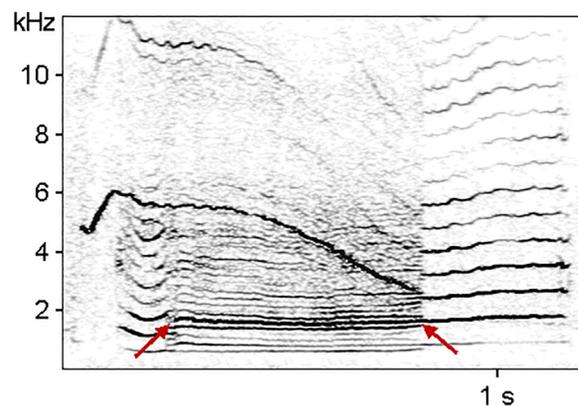


FIG. 5. (Color online) WCT12 call type showing the two-voiced segment with the frequency of the lower component below 300 Hz. Note the non-harmonic modulation in the beginning and end of the segment (marked by arrows) indicating that the sidebands are not true harmonics.

Dolphin sounds are produced by two pairs of phonic lips (Cranford *et al.*, 2011; Madsen *et al.*, 2013). Two-voiced calls most likely arise from both pairs of phonic lips oscillating simultaneously with different frequencies, one pair producing the upper and the other, the lower component. In this case, the lack of the upper component in calls below 300 Hz can indicate that both pairs of phonic lips are involved in their production (i.e., technically the low-frequency sounds are two-voiced, but both pairs of lips oscillate at low frequency).

It is also possible that sound sources other than phonic lips might exist. Most two-voiced calls of killer whales have heterodyne frequencies below and above the upper component (Fig. 1). Heterodyne frequencies arise from the interaction of the lower and upper components (Wilden *et al.*, 1998; Brown, 2008), confirming that these components are produced by coupled sound sources (most likely, two pairs of phonic lips). However, some call types lack heterodynes, suggesting either that the level of coupling between the right and left phonic lips pairs can vary across call types, or that an alternative sound production source can be involved. Production of two-voiced calls by baleen whales (Gedamke *et al.*, 2001; Tyson *et al.*, 2007; Tervo *et al.*, 2011) that lack the system of phonic lips also suggests that cetaceans can have other potential sources of sound production.

Terrestrial mammals can produce biphonic calls without specific anatomical adaptations of the sound-producing structures (Frey *et al.*, 2016). Humans can produce sounds with two independent, but similar frequencies by asynchronous vibration of the left and right vocal folds (Tigges *et al.*, 1997). Other proposed sources of biphonation in terrestrial mammals include air vortices at the narrowings of the vocal tract (Solomon *et al.*, 1995) and source-filter interaction when the vocal folds start oscillating at one of the resonance frequencies of the vocal tract (Titze *et al.*, 2008; Volodin *et al.*, 2013). Both of these mechanisms, however, are unlikely to occur in cetaceans because these mechanisms rely on air resonances which depend upon the air volume in the vocal tract. This would lead to a shift in the fundamental frequency when the whales dive and air cavities contract under pressure. However, both lower and upper components of stereotyped two-voiced calls in killer whales are produced with stable fundamental frequencies (Ford, 1991; Yurk *et al.*, 2002; Miller *et al.*, 2007). Miller *et al.* (2007) demonstrated the differences in the relative intensity of harmonics between male and female killer whales, suggesting that air volume in odontocete nasal sacs can act as a filter similar to the vocal tract in terrestrial mammals.

If a sound source besides right and left pairs of phonic lips exists, three-voiced sounds are theoretically possible. Such sounds have not been reported in killer whales, but Sayigh *et al.* (2013) provides a sonogram [Fig. 2(C) and Fig. 5 in Sayigh *et al.*, 2013] of a call of short-finned pilot whales which apparently contain three independently modulated components: an upsweep upper component, a down-sweep lower component, and a low-frequency buzz or squeak. The upper component has clear heterodynes, indicating that the upper and lower components are produced by coupled sources, most likely phonic lips, but the source

for the overlapping low-frequency buzz is unknown. Future studies are required to understand the sound production of two-voiced (and possibly three-voiced) calls in killer and pilot whales using experimental approaches similar to those tried in bottlenose dolphins.

We found that constraints were especially pronounced in two-voiced calls. Single-voiced calls ranged further down than the lower component of two-voiced calls. The upper component ranged higher than in single-voiced calls; however, in this study we have not considered so-called whistles which can occur at much higher frequencies (Samarra *et al.*, 2010; Filatova *et al.*, 2012b; Simonis *et al.*, 2012). Our study did not include whistles because we included only stereotyped calls that allow consistent sampling, while whistles are typically not stereotyped (Ford, 1991). Stereotyped whistles are reported in killer whales, but they are less common than calls and not specific to a particular pod or clan (Riesch *et al.*, 2006). This suggests that whistles have other communicative functions than stereotyped calls, probably due to the differences in their propagation range (Thomsen *et al.*, 2002; Miller, 2006).

Besides stereotyped calls and whistles, the killer whale acoustic repertoire includes variable calls that cannot be divided into discrete categories and so-called aberrant calls that represent highly distorted stereotyped calls. Analyzing the structure of these calls as well as whistles can provide important insights into sound production mechanisms in killer whales.

B. Implications for cultural evolution

Calls with either lower or upper component frequencies that go far beyond the assumed boundary of 4 kHz were rare in general and completely absent in some populations. Calls with the frequencies of the lower component above 4 kHz were found only in the Alaskan and Icelandic populations. Of note, the Alaskan AKS18 call has sidebands (Fig. 3) in some (but not all) samples, suggesting that the real fundamental frequency can be lower, and that the energy is being shifted to the upper harmonic due to filtering. The lower limit of the upper component is not as strict, but only in transient populations does the 5% quantile of the upper component go below 4 kHz, confirming that transients generally have lower call frequencies than residents and North Atlantic killer whales (Filatova *et al.*, 2015a). Besides, the lower component in two-voiced calls rarely goes below 300 Hz, though killer whales often produce such low-frequency sounds separately as single-voiced calls.

If some socially learned sounds are easier to produce than others, the morphology of the phonic lips plays a role in the formation of a cultural attractor. The idea of cultural attraction (Sperber, 1996) is based on two contradicting observations: (a) social learning is generally not a copying process and typically results in modifications of the transmitted information or behavior; but (b) cultural information/behavior is often relatively stable within whole populations and across generations. Cultural attractors are abstract “centers of gravity” in the space of possibilities; they exist because some factors affect the probability that individual

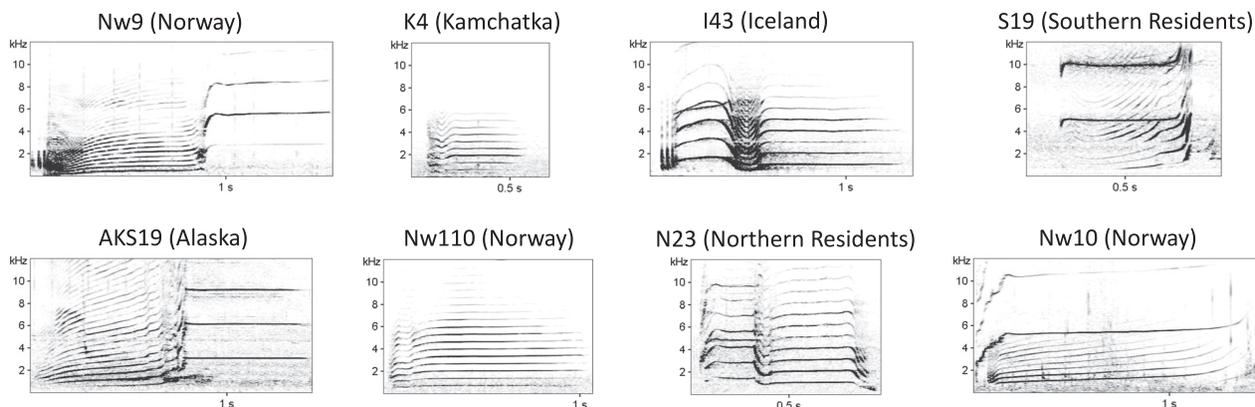


FIG. 6. Examples of convergence of call structure in different populations.

memes will depart from their models in one direction rather than in another. In the two-voiced calls of killer whales, it appears that such centers of gravity occur at frequencies around 1 kHz for the lower component and around 5–10 kHz for the upper component. This would define the most probable direction of call change, causing multiple convergences in different populations.

This finding is particularly important for the understanding of the cultural evolution of killer whale sounds. Physical constraints on call structure reduce the possible variation, so that calls more often become similar by random convergence. Indeed, very similar calls were found in different populations (Fig. 6). Since these populations are not in contact, and some of them are separated by thousands of kilometers, the most plausible explanation is random convergence.

Filatova *et al.* (2012a) found no correlation between the dynamic time warping similarity of calls and geographic distance in four North Pacific resident populations. One of the suggested explanations of this finding was that calls change too fast and populations soon reach the maximum possible divergence, and after that they can only converge, so the similarity of population repertoires is not phylogenetically meaningful (at least, at the level of the dynamic time warping comparison of call contours). The current study provides clear evidence in favor of this hypothesis. A similar situation exists in human languages: phonemes change faster than other language features (Labov, 2011), but due to the limited variation they often converge randomly in non-related languages (Moran *et al.*, 2014).

This phenomenon is especially important to understand when interpreting the similarities in calls of captive-born killer whales. For example, Kremers *et al.* (2012) found some vague similarities in calls of captive-born killer whales of Icelandic maternal origin compared to calls of Northern and SRs (even though none of them was related to NRs, and only two of the four whales had SR grandfathers). Kremers *et al.* (2012) explain this finding by multiple chain learning events among captive individuals, ignoring the arguably more plausible explanation of random call convergence.

Sounds of killer whales and other cetaceans are usually referred to as culturally transmitted, as opposed to the genetically inherited sounds of most other mammals. However, Laland and Janik (2006) emphasize that it is

counterproductive to interpret behavior as being either genetic or cultural, because every learned behavior has some genetic basis. This basis can include the tendency to learn specific behaviors as well as the physical ability to perform them. Our work illustrates the genetically inherited constraints of socially learned killer whale sounds that should be considered in further studies of their cultural evolution.

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- Alvarez, Y., Juste, J., Tabares, E., Garrido-Pertierra, A., Ibáñez, C., and Bautista, J. M. (1999). "Molecular phylogeny and morphological homoplasy in fruitbats," *Mol. Biol. Evol.* **16**, 1061–1067.
- Belikov, R. A., and Bel'kovich, V. M. (2006). "High-pitched tonal signals of beluga whales (*Delphinapterus leucas*) in a summer assemblage off Solovetskii Island in the White Sea," *Acoust. Phys.* **52**(2), 125–131.
- Bickford, A. (2006). *Articulatory Phonetics: Tools for Analyzing the World's Languages*, 4th ed. (Summer Institute of Linguistics, Dallas, TX).
- Bowles, A. E., Young, W. G., and Asper, E. D. (1988). "Ontogeny of stereotyped calling of a killer whale calf, *Orcinus orca*, during her first year," *Rit Fiskideildar* **11**, 251–275.
- Brown, J. C. (2008). "Mathematics of pulsed vocalizations with application to killer whale biphonation," *J. Acoust. Soc. Am.* **123**(5), 2875–2883.
- Corkeron, P. J., and Van Parijs, S. M. (2001). "Vocalizations of eastern Australian Risso's dolphins, *Grampus griseus*," *Can. J. Zool.* **79**(1), 160–164.
- Crance, J. L., Bowles, A. E., and Garver, A. (2014). "Evidence for vocal learning in juvenile male killer whales, *Orcinus orca*, from an adventitious cross-socializing experiment," *J. Exp. Biol.* **217**(8), 1229–1237.
- Cranford, T. W., and Amundin, M. (2004). "Biosonar pulse production in odontocetes: The state of our knowledge," in *Echolocation in Bats and Dolphins*, edited by J. A. Thomas, C. F. Moss, and M. Vater (The University of Chicago, Chicago), pp. 27–35.

- Cranford, T. W., Amundin, M., and Norris, K. S. (1996). "Functional morphology and homology in the odontocete nasal complex: Implications for sound generation," *J. Morphol.* **228**(3), 223–285.
- Cranford, T. W., Elsberry, W. R., Van Bonn, W. G., Jeffress, J. A., Chaplin, M. S., Blackwood, D. J., and Ridgway, S. H. (2011). "Observation and analysis of sonar signal generation in the bottlenose dolphin (*Tursiops truncatus*): Evidence for two sonar sources," *J. Exp. Mar. Biol. Ecol.* **407**(1), 81–96.
- Deecke, V. B., Barrett-Lennard, L. G., Spong, P., and Ford, J. K. B. (2010). "The structure of stereotyped calls reflects kinship and social affiliation in resident killer whales (*Orcinus orca*)," *Naturwissenschaften* **97**, 513–518.
- Deecke, V. B., Ford, J. K. B., and Spong, P. (2000). "Dialect change in resident killer whales: Implications for vocal learning and cultural transmission," *Anim. Behav.* **60**, 629–638.
- Delsuc, F., Brinkmann, H., and Philippe, H. (2005). "Phylogenomics and the reconstruction of the tree of life," *Nat. Rev. Genet.* **6**, 361–375.
- Duc, A. V. (2011). "A comparison of the discrete call repertoires of Northeast Atlantic killer whales (*Orcinus orca*)," M.S. dissertation, Uppsala University.
- Filatova, O. A., Burdin A. M., and Hoyt, E. (2013). "Is killer whale dialect evolution random?," *Behav. Proc.* **99**, 34–41.
- Filatova, O. A., Burdin, A. M., Hoyt, E., and Sato, H. (2004). "A catalogue of discrete calls of resident killer whales (*Orcinus orca*) from the Avacha Gulf of Kamchatka Peninsula," *Zoologicheskii J.* **83**, 1169–1180 (in Russian).
- Filatova, O. A., Deecke, V. B., Ford, J. K. B., Matkin, C. O., Barrett-Lennard, L. G., Guzev, M. A., Burdin, A. M., and Hoyt, E. (2012a). "Call diversity in the North Pacific killer whale populations: Implications for dialect evolution and population history," *Anim. Behav.* **83**, 595–603.
- Filatova, O. A., Ford, J. K., Matkin, C. O., Barrett-Lennard, L. G., Burdin, A. M., and Hoyt, E. (2012b). "Ultrasonic whistles of killer whales (*Orcinus orca*) recorded in the North Pacific (L)," *J. Acoust. Soc. Am.* **132**(6), 3618–3621.
- Filatova, O. A., Miller, P. J. O., Yurk, H., Samarra, F. I. P., Hoyt, E., Ford, J. K., and Barrett-Lennard, L. G. (2015a). "Killer whale call frequency is similar across the oceans, but varies across sympatric ecotypes," *J. Acoust. Soc. Am.* **138**(1), 251–257.
- Filatova, O. A., Samarra, F. I. P., Deecke, V. B., Ford, J. K., Miller, P. J. O., and Yurk, H. (2015b). "Cultural evolution of killer whale calls: Background, mechanisms and consequences," *Behaviour* **152**(15), 2001–2038.
- Foote, A. D., Griffin, R. M., Howitt, D., Larsson, L., Miller, P. J., and Hoelzel, A. R. (2006). "Killer whales are capable of vocal learning," *Biol. Lett.* **2**(4), 509–512.
- Foote, A. D., Osborne, R. W., and Hoelzel, A. R. (2008). "Temporal and contextual patterns of killer whale (*Orcinus orca*) call type production," *Ethol.* **114**, 599–606.
- Ford, J. K. B. (1987). "A catalogue of underwater calls produced by killer whales (*Orcinus orca*) in British Columbia," Canadian Data Report of Fisheries and Aquatic Sciences, 633 pp.
- Ford, J. K. B. (1989). "Acoustic behaviour of resident killer whales (*Orcinus orca*) off Vancouver Island, British Columbia," *Can. J. Zool.* **67**, 727–745.
- Ford, J. K. B. (1991). "Vocal traditions among resident killer whales (*Orcinus orca*) in coastal waters of British Columbia," *Can. J. Zool.* **69**, 1454–1483.
- Frey, R., Volodin, I. A., Fritsch, G., and Volodina, E. V. (2016). "Potential sources of high frequency and biphonic vocalization in the dhole (*Cuon alpinus*)," *PloS One* **11**(1), 1–26.
- Garland, E. C., Castellote, M., and Berchok, C. L. (2015). "Beluga whale (*Delphinapterus leucas*) vocalizations and call classification from the eastern Beaufort Sea population," *J. Acoust. Soc. Am.* **137**(6), 3054–3067.
- Gedamke, J., Costa, D. P., and Dustan, A. (2001). "Localization and visual verification of a complex minke whale vocalization," *J. Acoust. Soc. Am.* **109**, 3038–3047.
- Janik, V. M., and Sayigh, L. S. (2013). "Communication in bottlenose dolphins: 50 years of signature whistle research," *J. Comp. Physiol. A* **199**(6), 479–489.
- Johnson, M. P., and Tyack, P. L. (2003). "A digital acoustic recording tag for measuring the response of wild marine mammals to sound," *IEEE J. Ocean. Eng.* **28**, 3–12.
- Kremers, D., Lemasson, A., Almunia, J., and Wanker, R. (2012). "Vocal sharing and individual acoustic distinctiveness within a group of captive orcas (*Orcinus orca*)," *J. Compar. Psychol.* **126**(4), 433–445.
- Labov, W. (2011). *Principles of Linguistic Change, Cognitive and Cultural Factor* (John Wiley and Sons, New York), Vol. 3.
- Laland, K. N., and Janik, V. M. (2006). "The animal cultures debate," *Trends Ecol. Evol.* **21**(10), 542–547.
- Lilly, J. C., and Miller, A. M. (1961). "Vocal exchanges between dolphins," *Science* **134**(3493), 1873–1876.
- Madsen, P. T., Jensen, F. H., Carder, D., and Ridgway, S. (2012). "Dolphin whistles: A functional misnomer revealed by heliox breathing," *Biol. Lett.* **8**(2), 211–213.
- Madsen, P. T., Lammers, M., Wisniewska, D., and Beedholm, K. (2013). "Nasal sound production in echolocating delphinids (*Tursiops truncatus* and *Pseudorca crassidens*) is dynamic, but unilateral: Clicking on the right side and whistling on the left side," *J. Exp. Biol.* **216**(21), 4091–4102.
- Miller, P. J. O. (2006). "Diversity in sound pressure levels and estimated active space of resident killer whale vocalizations," *J. Comp. Physiol. A* **192**(5), 449–459.
- Miller, P. J. O., Samarra, F. I. P., and Perthuisson, A. D. (2007). "Caller sex and orientation influence spectral characteristics of 'two-voice' stereotyped calls produced by free-ranging killer whales," *J. Acoust. Soc. Am.* **121**(6), 3932–3937.
- Moore, S. E., and Ridgway, S. H. (1995). "Whistles produced by common dolphins from the Southern California Bight," *Aquat. Mamm.* **21**(1), 55–63.
- Moran, S., McCloy, D., and Wright, R. (eds.). (2014). "PHOIBLE Online," Leipzig: Max Planck Institute for Evolutionary Anthropology, available online at <http://phoible.org> (Last viewed 1 June 2016).
- Mueller, R. L., Macey, J. R., Jaekel, M., Wake, D. B., and Boore, J. L. (2004). "Morphological homoplasy, life history evolution, and historical biogeography of plethodontid salamanders inferred from complete mitochondrial genomes," *Proc. Nat. Acad. Sci. U.S.A.* **101**, 13820–13825.
- Murray, S. O., Mercado, E., and Roitblat, H. L. (1998). "Characterizing the graded structure of false killer whale (*Pseudorca crassidens*) vocalizations," *J. Acoust. Soc. Am.* **104**(3), 1679–1688.
- Nemiroff, L., and Whitehead, H. (2009). "Structural characteristics of pulsed calls of long-finned pilot whales *Globicephala melas*," *Bioacoustics* **19**(1–2), 67–92.
- Norris, K. S. (1968). "The evolution of acoustic mechanisms in odontocete cetaceans," in *Evolution and Environment*, edited by E. T. Drake (Yale University, New Haven, CT), pp. 298–323.
- Papale, E., Buffa, G., Filiciotto, F., Maccarrone, V., Mazzola, S., Ceraulo, M., and Buscaino, G. (2015). "Biphonic calls as signature whistles in a free-ranging bottlenose dolphin," *Bioacoustics* **24**(3), 223–231.
- R Core Team (2014). "R: A language and environment for statistical computing," R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org/> (Last viewed 1 June 2016).
- Riesch, R., Ford, J. K., and Thomsen, F. (2006). "Stability and group specificity of stereotyped whistles in resident killer whales, *Orcinus orca*, off British Columbia," *Anim. Behav.* **71**(1), 79–91.
- Samarra, F. I. P., Deecke, V. B., Vinding, K., Rasmussen, M. H., Swift, R. J., and Miller, P. J. O. (2010). "Killer whales (*Orcinus orca*) produce ultrasonic whistles," *J. Acoust. Soc. Am.* **128**(5), EL205–EL210.
- Saulitis, E. L., Matkin, C. O., and Fay, F. H. (2005). "Vocal repertoire and acoustic behavior of the isolated AT1 killer whale subpopulation in southern Alaska," *Can. J. Zool.* **83**(8), 1015–1029.
- Sayigh, L., Quick, N., Hastie, G., and Tyack, P. (2013). "Repeated call types in short-finned pilot whales, *Globicephala macrorhynchus*," *Mar. Mammal Sci.* **29**(2), 312–324.
- Shamir, L., Yerby, C., Simpson, R., von Benda-Beckmann, A. M., Tyack, P., Samarra, F., Miller, P. J. O., and Wallin, J. (2014). "Classification of large acoustic datasets using machine learning and crowdsourcing: Application to whale calls," *J. Acoust. Soc. Am.* **135**(2), 953–962.
- Shapiro, A. D. (2008). "Orchestration: The movement and vocal behavior of free-ranging Norwegian killer whales (*Orcinus orca*)," Doctoral dissertation, Massachusetts Institute of Technology and Woods Hole Oceanographic Institution.
- Shapiro, A. D., Tyack, P. L., and Seneff, S. (2011). "Comparing call-based versus subunit-based methods for categorizing Norwegian killer whale, *Orcinus orca*, vocalizations," *Anim. Behav.* **81**, 377–386.
- Simonis, A. E., Baumann-Pickering, S., Oleson, E., Melcón, M. L., Gassmann, M., Wiggins, S. M., and Hildebrand, J. A. (2012). "High-frequency modulated signals of killer whales (*Orcinus orca*) in the North Pacific," *J. Acoust. Soc. Am.* **131**(4), EL295–EL301.
- Solomon, N. P., Luschi, E., and Kang, L. (1995). "Fundamental frequency and tracheal pressure during three types of vocalizations elicited from anaesthetized dogs," *J. Voice.* **9**, 403–412.

- Sperber, D. (1996). *Explaining Culture: A Naturalistic Approach* (Blackwell, Oxford, UK).
- Strager, H. (1995). "Pod-specific call repertoires and compound calls of killer whales, *Orcinus orca* Linnaeus, 1758, in the waters of northern Norway," *Can. J. Zool.* **73**, 1037–1047.
- Taylor, A. M., and Reby, D. (2010). "The contribution of source-filter theory to mammal vocal communication research," *J. Zool.* **280**(3), 221–236.
- Tervo, O. M., Christoffersen, M. F., Parks, S. E., Kristensen, R. M., and Madsen, P. T. (2011). "Evidence for simultaneous sound production in the bowhead whale (*Balaena mysticetus*)," *J. Acoust. Soc. Am.* **130**(4), 2257–2262.
- Thomsen, F., Franck, D., and Ford, J. K. B. (2002). "On the communicative significance of whistles in wild killer whales (*Orcinus orca*)," *Naturwissenschaften* **89**, 404–407.
- Tigges, M., Mergell, P., Herzel, H., Wittenberg, T., and Eysholdt, U. (1997). "Observation and modelling of glottal biphonation," *Acta Acust. Acust.* **83**, 707–714.
- Titze, I. R., Riede, T., and Popollo, P. (2008). "Nonlinear source-filter coupling in phonation: Vocal exercises," *J. Acoust. Soc. Am.* **123**, 1902–1915.
- Tyack, P. L., and Sayigh, L. S. (1997). *Vocal Learning in Cetaceans. Social Influences on Vocal Development* (Cambridge University Press, Cambridge, UK).
- Tyson, R. B., Nowacek, D. P., and Miller, P. J. (2007). "Nonlinear phenomena in the vocalizations of North Atlantic right whales (*Eubalaena glacialis*) and killer whales (*Orcinus orca*)," *J. Acoust. Soc. Am.* **122**(3), 1365–1373.
- Volodin, I. A., Volodina, E. V., Frey, R., Carranza, J., and Torres-Porras, J. (2013). "Spectrographic analysis points to source-filter coupling in rutting roars of Iberian red deer," *Acta Ethol.* **16**, 57–63.
- Wieland, M., Jones, A., and Renn, S. C. (2010). "Changing durations of southern resident killer whale (*Orcinus orca*) discrete calls between two periods spanning 28 years," *Mar. Mammal Sci.* **26**, 195–201.
- Wilden, I., Herzel, H., Peters, G., and Tembrock, G. (1998). "Subharmonics, biphonation, and deterministic chaos in mammal vocalization," *Bioacoustics* **9**(3), 171–196.
- Yurk, H., Barrett-Lennard, L. G., Ford, J. K. B., and Matkin, C. O. (2002). "Cultural transmission within maternal lineages: Vocal clans in resident killer whales in southern Alaska," *Anim. Behav.* **63**, 1103–1119.