

1 **Physical constraints of cultural evolution of dialects in killer whales**

2 Running title: **Constraints of dialect evolution in killer whales**

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24 **Abstract** Odontocete sounds are produced by two pairs of phonic lips situated in soft nares  
25 below the blowhole; the right pair is larger and is more likely to produce clicks, while the left  
26 pair is more likely to produce whistles. This has important implications for the cultural  
27 evolution of delphinid sounds: the greater the physical constraints, the greater is the  
28 probability of random convergence. In this paper we examine the call structure of eight killer  
29 whale populations to identify structural constraints and to determine if they are consistent  
30 among all populations. Constraints were especially pronounced in two-voiced calls. In the  
31 calls of all eight populations, the lower component of two-voiced calls was typically centered  
32 below 4 kHz, while the upper component was typically above that value. The lower  
33 component of two-voiced calls had narrower frequency range than single-voiced calls in all  
34 populations. This may be because some single-voiced calls are homologous to the lower  
35 component, while others are homologous to the higher component of two-voiced calls.  
36 Physical constraints on call structure reduce the possible variation and increase the probability  
37 of random convergence, producing similar calls in different populations.

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## 40 I. INTRODUCTION

41 Understanding the physical basis of sound production is essential to categorize vocal signals  
42 into natural categories. For the sounds of terrestrial mammals, the development of the source-  
43 filter theory has enabled researchers to describe the acoustic structure of sounds according to  
44 their mode of production and to predict acoustic variation caused by variation in the  
45 anatomical or physiological attributes of the caller (Taylor and Reby, 2010). Even finer  
46 resolution of phoneme classification in humans is based on the detailed knowledge of their  
47 production: the position of tongue and lips, properties of the airflow and other features of the  
48 vocal tract (Bickford, 2006).

49 Sounds of killer whales *Orcinus orca* have a complex structure (Ford, 1991; Yurk et al.,  
50 2002), but their categorization is hindered by the lack of understanding of their production  
51 mechanisms. Odontocete sounds are not produced in the larynx, like in terrestrial mammals.  
52 Instead, their source is situated in a complex system of air sacs and tissues that surround the  
53 nasal passage (Norris, 1968; Cranford et al., 1996; Cranford and Amundin, 2003). All toothed  
54 whales (except sperm whales) have two pairs of phonic lips situated in each of the soft nares  
55 on the ventral side of the vestibular air sacs, just below the blowhole; both pairs are used in  
56 sound production (Cranford et al., 1996; Cranford and Amundin, 2003).

57 Dolphin sounds were traditionally divided into three classes: clicks, burst-pulse sounds and  
58 whistles. However, some species (e.g. killer whales, pilot whales *Globicephala sp.*, false  
59 killer whales *Pseudorca crassidens*) regularly produce calls intermediate in structure between  
60 whistles and burst-pulse sounds, suggesting that these classes are not discrete, but rather the  
61 two extremes of a perceptual continuum (Murray et al., 1998; Sayigh et al., 2013). Indeed,  
62 Madsen et al. (2012) showed that dolphin 'whistles' are in fact not air-born, but produced by  
63 pneumatically induced vibrations of phonic lips analogous to the operation of vocal folds in  
64 terrestrial mammals. In most delphinoids the right pair of phonic lips is larger than the left

65 (Cranford et al., 1996). Madsen et al. (2013) examined the sound production of bottlenose  
66 dolphin and false killer whale and showed that in both species clicks were produced by the  
67 right pair while 'whistles' (tonal calls) were mostly produced by the left pair of the phonic lips.  
68 This finding explains the long known observation that dolphins can simultaneously produce  
69 clicks and 'whistles' (Murray et al., 1998).

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

79 This assumption has important implications for the cultural evolution of delphinid sounds. In  
80 some, vocalizations are learned rather than transmitted genetically (killer whales: Ford, 1991;  
81 Deecke et al., 2000; Foote et al., 2006; bottlenose dolphins: Tyack and Sayigh, 1997) and can  
82 indicate individuality (bottlenose dolphins: Janik and Sayigh, 2013) or group affiliation (killer  
83 whales: Ford, 1991). Killer whales have unique family dialects – sets of stereotyped sounds.  
84 Calves learn their dialect from their mother and other family members (Bowles et al., 1988;  
85 Crance et al., 2014). With time, these dialects slowly change through learning errors and  
86 innovations in a process called cultural evolution (Deecke et al., 2000; Wieland et al., 2010;  
87 Filatova et al., 2015b). The recently diverged dialects are more similar than dialects that have  
88 passed a long process of independent evolution (Ford, 1991; Deecke et al., 2010). However,  
89 in some cases calls from distantly related dialects become more similar. Plausibly, this could

90 happen by either horizontal transmission or random convergence (Filatova et al., 2013). By  
91 horizontal transmission we mean here the transmission of calls and call features from one  
92 family to another. Random convergence occurs when calls of different families become more  
93 similar by chance, without any influence on each other's evolution. This is more likely to  
94 happen if the variety of possible states is limited. In this case the variation in the diverging  
95 calls soon reaches a limit and then the difference between them can no longer increase. This  
96 situation is analogous to the phenomenon called "mutational saturation" which occurs when  
97 many changes at a given locus eliminate phylogenetic signals (Delsuc et al., 2005). This  
98 happens because variation in nucleotide sequences is restricted by the structure of DNA: there  
99 are only four nucleotides and four possible types of mutations (transitions, transversions,  
100 insertions and deletions). Saturation can lead to homoplasy, i.e. convergence of traits in non-  
101 related taxa, which was described not only in genetics, but also in morphology (e.g. Alvarez et  
102 al., 1999; Mueller et al., 2004).

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

109

## 110 **II. METHODS**

### 111 **A. Data collection**

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

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

128 Calls from four North Pacific resident populations and the West Coast transient population  
129 were classified according to existing catalogues (Ford, 1987; Yurk et al., 2002; Filatova et al.,  
130 2004). For the False Pass transient population, call categorisation was performed based on  
131 audible characteristics of calls and visual inspection of spectrographic features. For Icelandic  
132 and Norwegian killer whales, we have modified and updated existing catalogues (Strager,  
133 1995; Shapiro, 2008; Duc, 2010).

134 Each killer whale population produces several tens of stereotyped call types recognized even  
135 by inexperienced observers (Yurk et al., 2002; Shamir et al., 2014); these call types retain  
136 stereotypy in different circumstances (Ford, 1989) and over the years (Deecke et al., 2000;  
137 Foote et al., 2008). Call types have different degrees of structural variation: some types are  
138 very stereotyped while others demonstrate some variation that can be either discrete or

139 gradual. Call types with a discrete variation are traditionally divided into a number of  
140 subtypes according to their structural characteristics; call types with a gradual variation are  
141 not divided into subtypes, and all variations are regarded as a single call type (Ford, 1991). To  
142 cover the full range of structural variation within a type, we selected two calls from each call  
143 type or subtype that were the least similar to each other. If a call type had no subtypes, two  
144 samples from that call type were used; for call types that comprised discrete subtypes, we  
145 used two samples from each subtype. For calls that did not fall into discrete subtypes but  
146 showed apparent variations, two calls from opposite extremes of the structural continuum  
147 were selected. When possible, the pairs of call samples from the same type/subtype were  
148 selected from different encounters and different years to cover the presumed variation in the  
149 call structure.

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

157 In total, 638 call samples were used for the analysis: 96 from Alaskan residents, 102 calls  
158 from Kamchatkan residents, 96 calls from Northern residents, 62 calls from Southern  
159 residents, 34 calls from Eastern Aleutian transients, 36 calls from West Coast transients, 72  
160 calls from Norway, and 140 calls from Iceland. Sample sizes of calls from the transient  
161 populations were lower because the overall repertoire size of stereotyped calls is typically  
162 lower in these populations (Ford, 1987; Saulitis et al., 2005). The differences in sample sizes

163 from different populations did not bias our results, because each sample size was selected to  
164 cover the full range of structural variation of stereotyped calls in the respective population.

## 165 **B. Acoustic and statistical analysis**

166 To capture the frequency parameters over the whole call duration, we extracted call contours  
167 following the method described in Filatova et al. (2012). The extracted contours represented a  
168 set of frequency measurements of each call's fundamental frequency spaced 0.01 s apart. If  
169 fundamental frequency was not visible, we measured one of the harmonics and divided the  
170 measurements by the number of that harmonic to obtain the fundamental frequency values.  
171 For two-voiced (biphonic) calls, containing overlapping frequency components, we extracted  
172 the contours of both the lower- and upper-frequency components.

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

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

185

## 186 **III. RESULTS**



187 To identify the scope of the constraints of the sound producing apparatus in killer whales, we  
188 analyzed the frequency range of two-voiced and single-voiced calls and call segments in  
189 different populations. In the two-voiced segments of calls the frequency of the lower  
190 component was typically below 4 kHz (Fig. 2). Only in five calls the frequency values of the  
191 lower component ranged above 4 kHz. The first call type with frequency of the lower  
192 component ranging above 4 kHz was AKS16b from the Alaskan resident population. The  
193 lower component of this call is a short upsweep that sometimes can rise above 4 kHz in the  
194 end. In our sample, only one frequency point of one AKS16b call ranged above this value; the  
195 second call of this type had the whole lower component below 4 kHz.

196 Four other calls with the frequency values of the lower component above 4 kHz belonged to  
197 two call types: the AKS18 call type from the Alaskan resident population and the I84 call type  
198 from the Icelandic population (Fig. 3). The most of the lower component of both AKS18 calls  
199 and about the half of the contour of the lower component of both I84 calls were centered  
200 above 4 kHz.

201 The frequency of the upper component was typically centered above 4 kHz, though in some  
202 calls the upper component ranged down to 3 kHz (Fig. 2). The upper component ranging  
203 below 4 kHz was found in sixteen call types from all populations except Norwegian. Usually  
204 (in eleven of the sixteen call types) it occurred in calls where the upper component started  
205 with an abrupt upsweep, and its section with frequency below 4 kHz was rather short – 10-30  
206 ms. Only five call types included relatively long (> 50 ms) sections of the upper component  
207 with frequency below 4 kHz: K20 call type from Kamchatkan residents, N18 call type from  
208 Northern residents, T12ii call type from West Coast transients, FP4 call type from Eastern  
209 Aleutian transients, and I41 call type from Iceland.

210 The frequency of the lower component of two-voiced call segments had narrower range than  
211 single-voiced calls and call segments in all populations (Fig. 4). The 5% quantile of single-

212 voiced calls was lower than the 5% quantile of the lower component of two-voiced call  
213 segments in all populations except West Coast transients, and the 95% quantile of single-  
214 voiced calls was higher than the 95% quantile of the lower component of two-voiced call  
215 segments in all populations, except Alaska (Table 1).

216 The 95% quantile of the lower component was very similar among all populations except  
217 transients (that had lower values) and Alaskan residents that had a much higher value due to  
218 the presence of a single call type (AKS18). The 5% quantile of the lower component was  
219 more variable, but in all populations except West Coast transients it was above 300 Hz.

220 All populations had similar 5% and 95% quantiles for the upper frequency component, except  
221 for West Coast and Eastern Aleutian transients that had lower values. Nevertheless, in all  
222 populations the 95% quantile for single-voiced calls was lower than the 95% quantile of the  
223 upper component of two-voiced call segments (Table 1).

224

#### 225 **IV. DISCUSSION**

226 In the stereotyped calls of all eight killer whale populations, the frequency values of the lower  
227 component were mostly centered below 4 kHz, while the frequency values of the upper  
228 component were mostly above that value. It appears that 4 kHz is a natural boundary between  
229 lower and upper components. Killer whales are technically capable of producing lower  
230 components at frequencies above, and upper components at frequencies below this value, but  
231 such calls are rare, suggesting that there is a physical constraint. Despite the relatively small  
232 sample size (two calls per type/subtype, total of 638 calls from eight populations), the overall  
233 frequency values of two-voiced calls from different populations were mostly similar (Table  
234 1), suggesting that the sample size was enough to cover the full range of variations in  
235 stereotyped calls of the studied populations.

236 **A. Implications for sound production**

237 Many odontocete species have been reported to produce two overlapping sounds  
238 simultaneously (e.g., bottlenose dolphin: Lilly and Miller, 1961; Risso's dolphin: Corkeron  
239 and Van Parijs, 2001; common dolphin: Moore and Ridgway, 1995; short-finned pilot whale:  
240 Sayigh et al., 2013; long-finned pilot whale: Nemiroff and Whitehead, 2009; false killer  
241 whale: Murray et al., 1998; beluga whale: Belikov and Bel'kovich, 2006; Garland et al.,  
242 2015), but the structure of these sounds varies across species. An upper component is  
243 typically a high-frequency tonal sound ('whistle') in all species, but most dolphins (bottlenose  
244 dolphin, common dolphin, Risso's dolphin) and beluga whales typically produce burst-pulse  
245 sounds or click trains as a lower component, and only killer whales, false killer whales and  
246 both species of pilot whales have been reported to regularly produce calls as a lower  
247 component of two-voiced sounds.

248 Research on sound production in odontocetes has been so far mostly focused on bottlenose  
249 dolphins that typically produce click trains (echolocation clicks and burst pulse sounds) and  
250 high-frequency whistles, but rarely emit "calls" – the sound category intermediate between  
251 click trains and whistles (Murray et al., 1998). Even in the study of sound production where a  
252 false killer whale *Pseudorca crassidens* was involved (Madsen et al., 2013), the authors  
253 referred to the tonal vocalizations as "whistles" and did not provide any sonograms that could  
254 clarify the structure of these sounds. In many cases, the terminology used to classify sounds  
255 into categories is still poorly linked to sound production mechanisms, often due to a lack of  
256 knowledge on the mechanisms involved in producing different types of sound. In the future,  
257 advances in the understanding of delphinid sound production would benefit from  
258 collaboration between morphologists and bioacousticians familiar with vocal repertoires.

259 The frequency of the lower component of two-voiced call segments had narrower range than  
260 single-voiced calls and call segments in all populations: single-voiced calls had lower

261 minimum and higher maximum frequency values. The higher maximum frequency values are  
262 easy to explain: we did not make a distinction between upper and lower components in single-  
263 voiced calls and call segments, so some single-voiced calls and call parts are homologous to  
264 the lower component while others are homologous to the upper component of two-voiced  
265 calls. This distinction is important to consider in future studies of killer whale acoustic  
266 behavior, because "upper" and "lower" single-voiced calls can potentially have different  
267 communicative functions.

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

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

284 Dolphin sounds are produced by two pairs of phonic lips (Cranford et al., 2011; Madsen et al.,  
285 2013). Two-voiced calls most likely arise from both pairs of phonic lips oscillating

286 simultaneously with different frequencies, one pair producing the upper and another – the  
287 lower component. In this case, the lack of the upper component in calls below 300 Hz can  
288 indicate that both pairs of phonic lips are involved in their production (i.e., technically the  
289 low-frequency sounds are two-voiced, but both pairs of lips oscillate with low frequency).

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

300 Terrestrial mammals can produce biphonic calls without specific anatomical adaptations of  
301 the sound-producing structures (Frey et al., 2016). Humans produce sounds with two  
302 independent, but similar frequencies by asynchronous vibration of the left and right vocal  
303 folds (Tigges et al., 1997). Other proposed sources of biphonation in terrestrial mammals  
304 include air vortices at the narrowings of the vocal tract (Solomon et al., 1995) and source-  
305 filter interaction when the vocal folds start oscillating at one of the resonance frequencies of  
306 the vocal tract (Titze et al., 2008; Volodin et al., 2013). Both of these mechanisms are  
307 however unlikely to occur in cetaceans because these mechanisms relate on air resonances  
308 depending on the air volume in the vocal tract. This would lead to the shift in the fundamental  
309 frequency when the whales dive and air cavities contract under pressure. However, both lower  
310 and upper components of stereotyped two-voiced calls in killer whales are produced with

311 stable fundamental frequencies (Ford, 1991; Yurk et al., 2002; Miller et al., 2007). Miller et  
312 al. (2007) demonstrated the differences in the relative intensity of harmonics between male  
313 and female killer whales, suggesting that air volume in odontocete's nasal sacs can act as a  
314 filter similarly to the vocal tract in terrestrial mammals.

315 If a sound source besides right and left pairs of phonic lips exists, three-voiced sounds are  
316 theoretically possible. Such sounds have not been reported in killer whales, but Sayigh et al.  
317 (2013) provides a sonogram (Fig. 2C and Fig. 5 in Sayigh et al., 2013) of a call of short-  
318 finned pilot whale *Globicephala macrorhynchus* that apparently contains three independently  
319 modulated components: an upsweep upper component, a downsweep lower component and a  
320 low-frequency buzz or squeak. The upper component has clear heterodynes, indicating that  
321 the upper and lower components are produced by coupled sources, most likely phonic lips,  
322 but the source for the overlapping low-frequency buzz is unknown. Future studies are  
323 required to understand the sound production of two-voiced (and possibly three-voiced) calls  
324 in killer and pilot whales using similar experimental approaches as used in bottlenose  
325 dolphins.

326 We found that constraints were especially pronounced in two-voiced calls. Single-voiced calls  
327 ranged further down than the lower component of two-voiced calls. Upper component ranged  
328 higher than single-voiced calls; however, in this study we have not considered so-called  
329 'whistles' that can occur at much higher frequencies (Samarra et al., 2010; Filatova et al.,  
330 2012b; Simonis et al., 2012). Whistles were not a part of this study because we included only  
331 stereotyped calls that allow consistent sampling, while whistles are typically not stereotyped  
332 (Ford, 1991). Stereotyped whistles were reported in killer whales, but they were less common  
333 than calls and not specific to a particular pod or clan (Riesch et al., 2006). This suggests that  
334 they have other communicative function than stereotyped calls, probably due to the  
335 differences in their propagation range (Thomsen et al., 2002; Miller, 2006).

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

#### 340 **B. Implications for cultural evolution**

341 Calls with either lower or upper component frequencies that go far beyond the assumed  
342 boundary of 4 kHz were rare in general and completely absent in some populations. Calls  
343 with the frequencies of the lower component above 4 kHz were found only in the Alaskan and  
344 Icelandic populations. Of note, Alaskan AKS18 call has sidebands (Fig. 3) in some (but not  
345 all) samples, suggesting that the real fundamental frequency can be lower, and the energy is  
346 shifted to the upper harmonic due to filtering. The lower limit of the upper component is not  
347 as strict, but only in transient populations the 5% quantile of the upper component goes below  
348 4 kHz, confirming that transients generally have lower call frequencies than residents and  
349 North Atlantic killer whales (Filatova et al., 2015a). Besides, the lower component in two-  
350 voiced calls rarely goes below 300 Hz, though killer whales often produce such low-  
351 frequency sounds separately as single-voiced calls.

352 If some socially learned sounds are easier to produce than others, the morphology of the  
353 phonic lips plays a role in the formation of a cultural attractor. The idea of cultural attraction  
354 (Sperber, 1996) is based on two contradicting observations: a) social learning is generally not  
355 a copying process and typically results in modifications of the transmitted information or  
356 behavior; but b) cultural information/behavior is often relatively stable within whole  
357 populations and across generations. Cultural attractors are abstract 'centers of gravity' in the  
358 space of possibilities, which exist because some factors affect the probability that individual  
359 memes will depart from their models in one direction rather than in another. In killer whales,  
360 it appears that such 'centers of gravity' occur at frequencies around 1 kHz for the lower

361 component and around 5-10 kHz for the upper component of two-voiced calls. This would  
362 define the most probable direction of call change, causing multiple convergences in different  
363 populations.

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

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

379 This phenomenon is especially important to understand while interpreting the similarities in  
380 calls of captive-born killer whales. For example, Kremers et al. (2012) found some vague  
381 similarities of calls of captive-born killer whales of Icelandic maternal origin with calls of  
382 Canadian Northern and Southern residents (even though none of them was related to Northern  
383 residents, and only two of the four whales had Southern resident grandfathers). Kremers et al.  
384 (2012) explain this finding by multiple chain learning events among captive individuals,  
385 ignoring the arguably more plausible explanation of random call convergence.



386 Sounds of killer whales and other cetaceans are usually referred to as culturally transmitted, as  
387 opposed to genetically inherited sounds of most other mammals. However, Laland and Janik  
388 (2006) emphasize that it is counterproductive to interpret behavior as being either genetic or  
389 cultural, because every learned behavior has some genetic basis. This basis can include the  
390 tendency to learn specific behaviors as well as physical ability to perform them. Our work  
391 illustrates the genetically inherited constraints of socially learned killer whale sounds that  
392 shall be considered in the further studies of their cultural evolution.

393

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#### 405 **References**

406 Alvarez, Y., Juste, J., Tabares, E., Garrido-Pertierra, A., Ibáñez, C., and Bautista, J.M. (1999).  
407 "Molecular phylogeny and morphological homoplasy in fruitbats," *Mol. Biol. Evol.* 16, 1061-  
408 1067.

409 Bowles, A. E., Young, W. G., and Asper, E. D. (1988). "Ontogeny of stereotyped calling of a  
410 killer whale calf, *Orcinus orca*, during her first year," *Rit Fiskideildar* 11, 251–275.

411 Belikov, R. A., and Bel'kovich, V. M. (2006). "High-pitched tonal signals of beluga whales  
412 (*Delphinapterus leucas*) in a summer assemblage off Solovetskii Island in the White Sea,"  
413 *Acoustical Physics* 52(2), 125-131.

414 Bickford, A. (2006). "Articulatory Phonetics: Tools For Analyzing The World's Languages,"  
415 (4th ed.). Summer Institute of Linguistics.

416 Brown, J. C. (2008). "Mathematics of pulsed vocalizations with application to killer whale  
417 biphonation," *J. Acoust. Soc. Am.* 123(5), 2875-2883.

418 Corkeron, P. J., and Van Parijs, S. M. (2001). "Vocalizations of eastern Australian Risso's  
419 dolphins, *Grampus griseus*," *Can. J. Zool.* 79(1), 160-164.

420 Crance, J. L., Bowles, A. E., and Garver, A. (2014). "Evidence for vocal learning in juvenile  
421 male killer whales, *Orcinus orca*, from an adventitious cross-socializing experiment," *J.*  
422 *Exper. Biol.* 217(8), 1229-1237.

423 Cranford, T. W., Amundin, M., and Norris, K. S. (1996). "Functional morphology and  
424 homology in the odontocete nasal complex: implications for sound generation," *J. Morphol.*  
425 228(3), 223-285.

426 Cranford, T. W., and Amundin, M. (2003). "Biosonar pulse production in odontocetes: the  
427 state of our knowledge," *Echolocation in bats and dolphins*, 27-35.

428 Cranford, T. W., Elsberry, W. R., Van Bonn, W. G., Jeffress, J. A., Chaplin, M. S.,  
429 Blackwood, D. J., ... & Ridgway, S. H. (2011). "Observation and analysis of sonar signal  
430 generation in the bottlenose dolphin (*Tursiops truncatus*): evidence for two sonar sources," *J.*  
431 *Exper. Mar. Biol. Ecol.* 407(1), 81-96.

432 Deecke, V. B., Ford, J. K. B., and Spong, P. (2000). "Dialect change in resident killer whales:  
433 implications for vocal learning and cultural transmission," *Anim. Behav.* 60, 629-638.

434 Deecke, V. B., Barrett-Lennard, L. G., Spong, P., and Ford, J. K. B. (2010). The structure of  
435 stereotyped calls reflects kinship and social affiliation in resident killer whales (*Orcinus*  
436 *orca*). *Naturwissenschaften* 97, 513-518.

437 Delsuc, F., Brinkmann, H., Philippe, H., (2005). "Phylogenomics and the reconstruction of the  
438 tree of life," *Nat. Rev. Genet.* 6, 361–375.

439 Duc, A. V. (2011). "A comparison of the discrete call repertoires of Northeast Atlantic killer  
440 whales (*Orcinus orca*)," Master of Science dissertation, Uppsala University.

441 Filatova, O. A., Burdin, A. M., Hoyt, E., and Sato, H. (2004). "A catalogue of discrete calls of  
442 resident killer whales (*Orcinus orca*) from the Avacha Gulf of Kamchatka Peninsula,"  
443 *Zoologicheskii Journal* 83,1169-1180 (in Russian).

444 Filatova, O. A., Deecke, V. B., Ford, J. K. B., Matkin, C. O., Barrett-Lennard, L. G., Guzeev,  
445 M. A., Burdin, A. M., and Hoyt, E. (2012a). "Call diversity in the North Pacific killer whale  
446 populations: implications for dialect evolution and population history," *Anim. Behav.* 83,  
447 595-603.

448 Filatova, O. A., Ford, J. K., Matkin, C. O., Barrett-Lennard, L. G., Burdin, A. M., and Hoyt,  
449 E. (2012b). "Ultrasonic whistles of killer whales (*Orcinus orca*) recorded in the North  
450 Pacific," (L). *J. Acoust. Soc. Am.* 132(6), 3618-3621. Filatova, O. A., Burdin A. M., and  
451 Hoyt, E. (2013). "Is killer whale dialect evolution random?" *Behav. Proc.* 99, 34-41.

452 Filatova, O. A., Miller, P. J., Yurk, H., Samarra, F. I., Hoyt, E., Ford, J. K., ... & Barrett-  
453 Lennard, L. G. (2015a). "Killer whale call frequency is similar across the oceans, but varies  
454 across sympatric ecotypes," *J. Acoust. Soc. Am.* 138(1), 251-257.

455 Filatova, O. A., Samarra, F. I., Deecke, V. B., Ford, J. K., Miller, P. J., & Yurk, H. (2015b).  
456 "Cultural evolution of killer whale calls: background, mechanisms and consequences,"  
457 Behaviour 152(15), 2001-2038.

458 Foote, A. D., Griffin, R. M., Howitt, D., Larsson, L., Miller, P. J., and Hoelzel, A. R. (2006).  
459 "Killer whales are capable of vocal learning," Biol. Let. 2(4), 509-512.

460 Foote, A. D., Osborne, R. W., Hoelzel, A. R. (2008). "Temporal and contextual patterns of  
461 killer whale (*Orcinus orca*) call type production," Ethol. 114, 599-606.

462 Ford, J. K. B. (1987). "A catalogue of underwater calls produced by killer whales (*Orcinus*  
463 *orca*) in British Columbia," Canadian Data Report of Fisheries and Aquatic Sciences, 633 pp.

464 Ford, J. K. B. (1989). "Acoustic behaviour of resident killer whales (*Orcinus orca*) off  
465 Vancouver Island, British Columbia," Can. J. Zool. 67, 727-745.

466 Ford, J. K. B. (1991). "Vocal traditions among resident killer whales (*Orcinus orca*) in coastal  
467 waters of British Columbia," Can. J. Zool. 69, 1454-1483.

468 Frey, R., Volodin, I. A., Fritsch, G., and Volodina, E. V. (2016). "Potential sources of high  
469 frequency and biphonic vocalization in the dhole (*Cuon alpinus*)," PloS one, 11(1), e0146330,  
470 1-26.

471 Garland, E. C., Castellote, M., and Berchok, C. L. (2015). "Beluga whale (*Delphinapterus*  
472 *leucas*) vocalizations and call classification from the eastern Beaufort Sea population," The J.  
473 Acoust. Soc. Am. 137(6), 3054-3067.

474 Gedamke, J., Costa, D. P., and Dustan, A. (2001). "Localization and visual verification of a  
475 complex minke whale vocalization," J. Acoust. Soc. Am. 109, 3038-3047.

476 Janik, V. M., and Sayigh, L. S. (2013). "Communication in bottlenose dolphins: 50 years of  
477 signature whistle research," J. Comp. Physiol. A, 199(6), 479-489.

478 Johnson, M. P., and Tyack, P. L. (2003). "A digital acoustic recording tag for measuring the  
479 response of wild marine mammals to sound," IEEE J. Oceanic Eng. 28, 3e12.

480 Kremers, D., Lemasson, A., Almunia, J., and Wanker, R. (2012). "Vocal sharing and  
481 individual acoustic distinctiveness within a group of captive orcas (*Orcinus orca*)," J.  
482 Compar. Psychol. 126(4), 433.

483 Labov W. (2011). "Principles of linguistic change, cognitive and cultural factors (Vol. 3),"  
484 John Wiley and Sons.

485 Laland, K. N., and Janik, V. M. (2006). "The animal cultures debate," Trends Ecol. Evol.  
486 21(10), 542-547.

487 Lilly, J. C., and Miller, A. M. (1961). "Vocal exchanges between dolphins ," Science,  
488 134(3493), 1873-1876.

489 Madsen, P. T., Jensen, F. H., Carder, D., and Ridgway, S. (2012). "Dolphin whistles: a  
490 functional misnomer revealed by heliox breathing," Biol. Lett. 8(2), 211-213.

491 Madsen, P. T., Lammers, M., Wisniewska, D., and Beedholm, K. (2013). "Nasal sound  
492 production in echolocating delphinids (*Tursiops truncatus* and *Pseudorca crassidens*) is  
493 dynamic, but unilateral: clicking on the right side and whistling on the left side," J. Exper.  
494 Biol. 216(21), 4091-4102.

495 Miller, P. J. (2006). "Diversity in sound pressure levels and estimated active space of resident  
496 killer whale vocalizations," J. Comp. Physiol. A 192(5), 449-459.

497 Miller, P. J., Samarra, F. I., and Perthuisson, A. D. (2007). "Caller sex and orientation  
498 influence spectral characteristics of "two-voice" stereotyped calls produced by free-ranging  
499 killer whales," J. Acoust. Soc. Am. 121(6), 3932-3937.

500 Moore, S. E., and Ridgway, S. H. (1995). "Whistles produced by common dolphins from the  
501 Southern California Bight," *Aquat. Mamm.* 21(1), 55-63.

502 Moran, S., McCloy, D. and Wright, R. (eds.). (2014). "PHOIBLE Online," Leipzig: Max  
503 Planck Institute for Evolutionary Anthropology. (available online at <http://phoible.org>)

504 Mueller, R.L., Macey, J.R., Jaekel, M., Wake, D.B., Boore, J.L., (2004). "Morphological  
505 homoplasy, life history evolution, and historical biogeography of plethodontid salamanders  
506 inferred from complete mitochondrial genomes," *PNAS* 101, 13820-13825.

507 Murray, S. O., Mercado, E., and Roitblat, H. L. (1998). "Characterizing the graded structure  
508 of false killer whale (*Pseudorca crassidens*) vocalizations," *J. Acoust. Soc. Am.* 104(3), 1679-  
509 1688.

510 Nemiroff, L., and Whitehead, H. (2009). "Structural characteristics of pulsed calls of long-  
511 finned pilot whales *Globicephala melas*," *Bioacoustics*, 19(1-2), 67-92.

512 Norris, K. S. (1968). "The evolution of acoustic mechanisms in odontocete cetaceans,"  
513 *Evolution and Environment*, 297-324.

514 Papale, E., Buffa, G., Filiciotto, F., Maccarrone, V., Mazzola, S., Ceraulo, M., ... and  
515 Buscaino, G. (2015). "Biphonic calls as signature whistles in a free-ranging bottlenose  
516 dolphin," *Bioacoustics*, 24(3), 223-231.

517 R Core Team (2014). "R: A language and environment for statistical computing," R  
518 Foundation for Statistical Computing, Vienna, Austria. URL <http://www.R-project.org/>.

519 Riesch, R., Ford, J. K., and Thomsen, F. (2006). "Stability and group specificity of  
520 stereotyped whistles in resident killer whales, *Orcinus orca*, off British Columbia," *Anim.*  
521 *Behav.* 71(1), 79-91.

522 Samarra, F. I., Deecke, V. B., Vinding, K., Rasmussen, M. H., Swift, R. J., and Miller, P. J.  
523 (2010). "Killer whales (*Orcinus orca*) produce ultrasonic whistles," J. Acoust. Soc. Am.  
524 128(5), EL205-EL210.

525 Saulitis, E. L., Matkin, C. O., & Fay, F. H. (2005). "Vocal repertoire and acoustic behavior of  
526 the isolated AT1 killer whale subpopulation in southern Alaska," Can. J. Zool. 83(8), 1015-  
527 1029.

528 Sayigh, L., Quick, N., Hastie, G., and Tyack, P. (2013). "Repeated call types in short-finned  
529 pilot whales, *Globicephala macrorhynchus*," Mar. Mam. Sci. 29(2), 312-324.

530 Shamir, L., Yerby, C., Simpson, R., von Benda-Beckmann, A. M., Tyack, P., Samarra, F.,  
531 Miller, P. J. O., and Wallin, J. (2014). "Classification of large acoustic datasets using machine  
532 learning and crowdsourcing: Application to whale calls," J. Acoust. Soc. Am. 135(2), 953-962.

533 Shapiro, A. D. (2008). "Orchestration: the movement and vocal behavior of free-ranging  
534 Norwegian killer whales (*Orcinus orca*)," Doctoral dissertation, Massachusetts Institute of  
535 Technology and Woods Hole Oceanographic Institution.

536 Shapiro, A. D., Tyack, P. L., and Seneff, S. (2011). "Comparing call-based versus subunit-  
537 based methods for categorizing Norwegian killer whale, *Orcinus orca*, vocalizations," Anim.  
538 Behav. 81, 377-386.

539 Simonis, A. E., Baumann-Pickering, S., Oleson, E., Melcón, M. L., Gassmann, M., Wiggins,  
540 S. M., and Hildebrand, J. A. (2012). "High-frequency modulated signals of killer whales  
541 (*Orcinus orca*) in the North Pacific," J. Acoust. Soc. Am. 131(4), EL295-EL301.

542 Solomon, N.P., Luschei, E., and Kang, L. (1995). "Fundamental frequency and tracheal  
543 pressure during three types of vocalizations elicited from anaesthetized dogs," J. Voice. 9,  
544 403-412.

545 Sperber, D. 1996. "Explaining Culture: a Naturalistic Approach," Oxford: Blackwell.

546 Strager, H. (1995). "Pod-specific call repertoires and compound calls of killer whales, *Orcinus*  
547 *orca* Linnaeus, 1758, in the waters of northern Norway," *Can. J. Zool.* 73, 1037-1047.

548 Taylor, A. M., and Reby, D. (2010). "The contribution of source-filter theory to mammal  
549 vocal communication research," *J. Zool.* 280(3), 221-236.

550 Tervo, O. M., Christoffersen, M. F., Parks, S. E., Kristensen, R. M., and Madsen, P. T.  
551 (2011). "Evidence for simultaneous sound production in the bowhead whale (*Balaena*  
552 *mysticetus*)," *J. Acoust. Soc. Am.* 130(4), 2257-2262.

553 Thomsen, F., Franck, D. and Ford, J. K. B. (2002). "On the communicative significance of  
554 whistles in wild killer whales (*Orcinus orca*)," *Naturwissenschaften* 89, 404-407.

555 Tigges, M., Mergell, P., Herzel, H., Wittenberg, T., and Eysholdt, U. (1997). "Observation  
556 and modelling of glottal biphonation," *Acta Acustica united with Acustica* 83, 707-714.

557 Titze, I.R., Riede, T., and Popollo, P. (2008). "Nonlinear source-filter coupling in phonation:  
558 Vocal exercises," *J. Acoust. Soc. Am.* 123, 1902-1915.

559 Tyack, P. L., and Sayigh, L. S. (1997). "Vocal learning in cetaceans. Social influences on  
560 vocal development," Cambridge University Press.

561 Tyson, R. B., Nowacek, D. P., and Miller, P. J. (2007). "Nonlinear phenomena in the  
562 vocalizations of North Atlantic right whales (*Eubalaena glacialis*) and killer whales (*Orcinus*  
563 *orca*)," *J. Acoust. Soc. Am.* 122(3), 1365-1373.

564 Volodin, I.A., Volodina, E.V., Frey, R., Carranza, J., and Torres-Porras, J. (2013).  
565 "Spectrographic analysis points to source-filter coupling in rutting roars of Iberian red deer,"  
566 *Acta Ethol.* 16, 57-63.



567 Wieland, M., Jones, A., and Renn, S. C. (2010). "Changing durations of southern resident  
568 killer whale (*Orcinus orca*) discrete calls between two periods spanning 28 years," Mar.  
569 Mam. Sci. 26,195-201.

570 Wilden, I., Herzel, H., Peters, G., and Tembrock, G. (1998). "Subharmonics, biphonation, and  
571 deterministic chaos in mammal vocalization," Bioacoustics 9(3), 171-196.

572 Yurk, H., Barrett-Lennard, L. G., Ford, J. K. B., and Matkin, C. O. (2002). "Cultural  
573 transmission within maternal lineages: vocal clans in resident killer whales in southern  
574 Alaska," Anim. Behav. 63, 1103-1119.

575

576 Table 1. 5% and 95% quantiles of frequency values (in kHz) of single-voiced and both  
 577 components 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
Northern residents	0.05	4.63	0.54	2.17	5.12	10.66
Southern residents	0.04	4.80	0.36	2.02	4.51	8.12
West Coast transients	0.23	2.99	0.20	0.90	3.32	6.71
Eastern Aleutian transients	0.25	4.73	0.40	1.49	3.28	5.42
Iceland	0.25	4.33	0.66	2.14	5.01	10.47
Norway	0.27	7.52	0.32	2.50	5.21	11.28

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579

580 **Figure captions**

581 Fig. 1. (color online) The start and the end of the lower-frequency component (LFC) and  
582 upper-frequency component (UFC) in two-voiced call do not match, so that only the middle  
583 segment of the call is two-voiced, while the beginning and the end of the call are single-  
584 voiced. Heterodyne frequencies arise from the interaction of LFC and UFC; the lower  
585 heterodyne in each point is equal to  $LFC-UFC$ , and the higher heterodyne is equal to  
586  $LFC+UFC$ .

587 Fig. 2. (color online) Scatterplot with marginal histograms showing the distribution of  
588 frequency points of the lower and upper components in two-voiced calls from all populations:  
589 KR – Kamchatkan residents, AR – Alaskan residents, NR – Northern residents, SR –  
590 Southern residents, WT – West Coast transients, AT – Eastern Aleutian transients, Ice –  
591 Iceland, NrW – Norway.

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

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

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

601 Fig. 6. Examples of convergence of call structure in different populations.

602

