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1 **Geographic variation in the time-frequency characteristics of high-**  
2 **frequency whistles produced by killer whales (*Orcinus orca*)**

3

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16

17 **Abstract**

18 Investigating intra-specific variation in acoustic signals can indicate the extent of  
19 isolation and divergence between populations and adaptations to local  
20 environments. Here we analyze the variation in killer whale high-frequency (>17  
21 kHz) whistles recorded off Norway, Iceland, and the North Pacific. We used a  
22 combination of methods including multivariate comparisons of spectral and  
23 temporal parameters and categorization of contours to types. Our results show that  
24 spectral and temporal characteristics of high-frequency whistles recorded in the  
25 North Pacific show significant differences from whistles recorded in the Northeast  
26 Atlantic, being generally stereotyped, lower in frequency, and slightly longer in  
27 duration. Most high-frequency whistles from the North Pacific were downsweeps,  
28 while this was one of the least common types recorded in the Northeast Atlantic.  
29 The repertoire of whistles recorded in Norway was similar to Iceland, but whistles  
30 produced in Norway had significantly lower maximum frequency and frequency  
31 range. Most methods were able to discriminate between whistles of the North  
32 Pacific and the Northeast Atlantic, but were unable to consistently distinguish  
33 whistles from Iceland and Norway. This suggests that macro- and  
34 microgeographic differences in high-frequency whistles of killer whales may  
35 reflect historical geographic isolation between ocean basins and more recent  
36 divergence between adjacent populations.

37

38 **Keywords:** ultrasonic whistles, orcas, geographic variation

39

## 40 **Introduction**

41 When describing geographic variation in acoustic signals it is useful to divide  
42 differences into macrogeographic or microgeographic variation, depending on  
43 whether populations being compared are neighboring, making interbreeding and  
44 social interaction a possibility, or geographically separated, and thus socially and  
45 reproductively isolated (Mundinger 1982). Comparative studies of odontocete  
46 whistles have shown more pronounced inter- than intra-specific variation in whistle  
47 spectral parameters, which could arise if intra-specific variability is constrained to  
48 occur within a species-specific framework (Steiner 1981, Ding *et al.* 1995a, Matthews  
49 *et al.* 1999, Rendell *et al.* 1999, Podos *et al.* 2002). Variation in whistle structural  
50 parameters has previously been described for populations of the same dolphin species  
51 both at microgeographic (*e.g.*, Azevedo and Van Sluys 2005, Morisaka *et al.* 2005)  
52 and macrogeographic levels (*e.g.*, Camargo *et al.* 2006, Baron *et al.* 2008). Intra-  
53 specific geographic variations may occur due to genetic divergence, adaptations to  
54 local environments or cultural differences (Janik 2009). A general correlation of  
55 whistle variation with distance has been proposed whereby neighboring populations  
56 appear to have more similar whistle structure than geographically distant populations  
57 (Ding *et al.* 1995b, Azevedo and Van Sluys 2005, Rossi-Santos and Podos 2006,  
58 May-Collado and Wartzok 2008), although this is not always the case (Camargo *et al.*  
59 2006). Within populations, there is often variation in duration and complexity of  
60 signals (*i.e.*, number of inflection points) (Steiner 1981, Azevedo and Van Sluys  
61 2005, Morisaka *et al.* 2005), while the time-frequency contour of whistles often varies  
62 among individuals, providing information on individual identity (*e.g.*, bottlenose  
63 dolphin, *Tursiops truncatus*; Janik *et al.* 2006; common dolphin, *Delphinus delphis*:  
64 Caldwell and Caldwell 1968; Pacific humpback dolphin, *Sousa chinensis*: Van Parijs

65 and Corkeron 2001). Understanding the variation in the acoustic repertoire within and  
66 between different populations may shed light on the evolution, movements, and  
67 cultural traditions of a species.

68       There are known differences in the structure and use of pulsed calls and whistles  
69 between different killer whale populations. In the North Pacific, pods of resident  
70 (fish-eating) killer whales produce unique and stable repertoires of stereotyped pulsed  
71 calls (Ford 1989, 1991). These calls differ between matriline within pods (Ford 1991,  
72 Miller and Bain 2000, Deecke *et al.* 2010), and to a lesser degree between individuals  
73 within the same matriline (Nousek *et al.* 2006). The stability of resident pods may  
74 explain why the variation in pulsed calls primarily encodes group, rather than  
75 individual, identity (Tyack 1986). Killer whale whistles are generally more complex  
76 and longer than other delphinid whistles (Thomsen *et al.* 2001) and some have  
77 stereotyped frequency contours that are often produced in complex sequences (Riesch  
78 *et al.* 2006, 2008). Resident killer whale groups in British Columbia that do not share  
79 pulsed calls share stereotyped whistles, which may provide a community-level means  
80 of recognition, facilitating social interactions (Riesch *et al.* 2006). Transient  
81 (mammal-eating) killer whales in the North Pacific also produce stereotyped whistles  
82 and the repertoire seems to be shared by all members of the population (Riesch and  
83 Deecke 2011). Despite being sympatric with resident killer whales, transients have  
84 distinct, population-specific repertoires of both pulsed calls and whistles (Ford and  
85 Fisher 1982, Riesch and Deecke 2011).

86       In Iceland and Norway, early studies suggested that killer whales also produce  
87 group-specific call repertoires (Moore *et al.* 1988, Strager 1995). A common ecotype,  
88 known as the “herring-eating Scandinavian killer whale” (Simon *et al.* 2007) has been  
89 suggested for killer whales in this region due to close genetic relatedness (Foote *et al.*

90 2009b, Morin *et al.* 2010) and similar acoustic and foraging behavior. Killer whales  
91 are thought to have regularly migrated between these two locations (Jonsgård and  
92 Lyshoel 1970) due to the distribution of their main prey, Atlantic herring *Clupea*  
93 *harengus* (Sigurjónsson *et al.* 1988, Similä *et al.* 1996, Simon *et al.* 2007). The  
94 migration route of the Atlanto-Scandian herring stock spanned from western Norway  
95 to eastern Iceland prior to the stock collapse in the 1960's (Jakobsson and Østvedt  
96 1999). The migration patterns of the Icelandic and Norwegian herring stocks changed  
97 following the collapse and remained closer to each country's coast (Jakobsson and  
98 Stefánsson 1999, Kvamme *et al.* 2003). Photo-identification studies dating to the  
99 1980's show no matches between Iceland and Norway (Sigurjónsson *et al.* 1988,  
100 Foote *et al.* 2009a), suggesting that if killer whales migrated between those two  
101 locations in the past, there is currently little to no interaction between these  
102 populations. Nevertheless, some Icelandic killer whales have been re-identified as far  
103 east as Shetland (Foote *et al.* 2009a), showing that the movements of some  
104 individuals do extend beyond coastal waters. The suggested historic contact of killer  
105 whales between Iceland and Norway may have influenced their acoustic repertoire.  
106 However, comparisons of their pulsed call type repertoire have found apparently little  
107 repertoire sharing between the two locations (Moore *et al.* 1988, Strager 1995,  
108 Stenersen and Similä 2004, Shamir *et al.* 2014). If killer whales in Iceland and  
109 Norway were in contact in the past and their acoustic repertoires were similar, it is  
110 possible that sufficient time has passed for call repertoires to have diverged -  
111 explaining the pattern observed today. We might then expect that other signals  
112 produced by these whales may also show divergence. A divergent call repertoire may  
113 serve as a population-identifier, however, the extent of stereotypy and geographic  
114 variation in other signals is little understood.

115 High-frequency whistles ranging up to 75 kHz were first reported from herring-  
116 eating Northeast Atlantic killer whales (Samarra *et al.* 2010). High-frequency whistles  
117 have since been described from killer whale recordings made in the North Pacific  
118 (referred to as ‘high-frequency modulated signals’ and ‘ultrasonic whistles’; Simonis  
119 *et al.* 2012, Filatova *et al.* 2012) and in the Antarctic (Trickey *et al.* 2014), indicating  
120 that this is a widespread sound type produced by several populations although they do  
121 not appear to be ubiquitous (Samarra *et al.* 2010, Filatova *et al.* 2012). In the North  
122 Pacific, whistles were consistently downsweeps and, in some cases, highly  
123 stereotyped (Simonis *et al.* 2012, Filatova *et al.* 2012). Here, we analyze qualitatively  
124 and quantitatively the variation in time-frequency contours of high-frequency whistles  
125 recorded from herring-eating killer whales in Norway and Iceland, and compare them  
126 to stereotyped high-frequency whistles recorded in the North Pacific. Our objectives  
127 were: 1) to investigate the degree of micro and macro-geographic variation of time-  
128 frequency parameters and; 2) to investigate whether high-frequency whistles  
129 produced by killer whales in Iceland and Norway were also stereotyped and, if so,  
130 evaluate the spatial distribution of different whistle types. This study of geographic  
131 variation is a starting point to considering the potential function(s) of these poorly  
132 understood signals.

133

#### 134 **Methods**

135 In the Northeast Atlantic, acoustic recordings were collected in Tysfjord, Vestfjord  
136 and Ofotfjord (Northern Norway) between 2005 and 2009 and off the Vestmannaeyjar  
137 archipelago and the Reykjanes peninsula in 2004, 2008 and 2009 (Iceland, Fig. 1). In  
138 both locations, recordings were collected during the day and most sounds were  
139 recorded from feeding or socializing whales. No other cetaceans were concurrently

140 sighted. Recording systems used varied with year and location and included towed  
141 and vertical hydrophone arrays, as well as sound recording tags attached to whales  
142 using suction cups (“Dtags”; Johnson and Tyack 2003). All systems sampled at 96 or  
143 192 kHz (Table 1). Further details of all systems used and data collected are given in  
144 Samarra *et al.* (2010). High-frequency whistles analyzed here are the same as those  
145 reported in that study, including whistles with frequency contours at least partially  
146 below 48 kHz (up to 48 kHz whistles) and whistles with frequency contours entirely  
147 above 48 kHz (>48 kHz whistles), when available. Only 2.6% of whistles at least  
148 partially below 48 kHz recorded at 192 kHz sampling rate crossed 48 kHz, i.e. had  
149 minimum frequency below 48 kHz and maximum frequency above 48 kHz. This  
150 suggests that the lower sampling rate of 96 kHz likely resulted in a negligible loss of  
151 whistles with frequency contours at least partially below 48 kHz that could be  
152 sampled. High-frequency whistles were defined as signals with contours entirely  
153 above 17 kHz (Samarra *et al.*, 2010), as this was the maximum frequency previously  
154 reported for killer whale whistles (Thomsen *et al.* 2001).

155 To compare whistles produced in the Northeast Atlantic with those produced by killer  
156 whales in the North Pacific, we analyzed high-frequency whistles described by  
157 Simonis *et al.* (2012). The recordings were collected at sampling rates of 192 or 200  
158 kHz from either a ship-based hydrophone array or a high-frequency acoustic  
159 recording package (HARP) and were scanned for high-frequency whistles through the  
160 use of Long-Term Spectral Averages (LTSAs) (Wiggins and Hildebrand 2007). To  
161 date, recordings from 19.9 cumulative years at 18 different sites across the North  
162 Pacific have been examined by analysts trained to recognize the presence of these  
163 signals (Fig. 1). There have been 19 acoustic encounters of killer whales at 9 different  
164 locations that included HFM signals, of which the temporal and spectral



165 characteristics of a subset from 6 locations are described here. The recording locations  
166 of signals described here include: Aleutian Islands, Washington Coast, Southern  
167 California Bight, Hoke Seamount, Kauai, and Pearl and Hermes Atoll (Table 1, Fig.  
168 1). High-frequency whistles were attributed to killer whales by their clear association  
169 with other sounds known to be produced by killer whales or by visual observations of  
170 killer whales present in the area (Simonis *et al.* 2012). To ensure the data sets from  
171 the two ocean basins were comparable we only used signals detected in the North  
172 Pacific where contours were also entirely above 17 kHz. Table 1 shows the total  
173 number of whistles analyzed from each location. We pooled all data from the North  
174 Pacific for subsequent analyses, as sample sizes were too small to compare each  
175 location separately. Following inspection of recordings using Adobe Audition 2.0©  
176 (Blackmann-Harris window; FFT=2048 and 4096, for 96 kHz and 192 or 200 kHz  
177 sampling rates, respectively; 100% window width) whistle contours were traced from  
178 visual inspection of the spectrogram using a peaks contour extraction algorithm as  
179 developed by Buck and Tyack (1993; Hann window; frequency resolution=46.875  
180 Hz; time resolution=0.667 ms). The following descriptive parameters were measured  
181 from the extracted fundamental frequency contour: start, half-way duration point  
182 (mid) and end frequency, minimum and maximum frequency, frequency range  
183 (maximum-minimum frequency) and duration.

184 All high-frequency whistles were assigned a quality score based on visual  
185 assessment of signal to noise ratio and overlap with other sounds, between 1 (poor,  
186 when the signal was barely detectable in the spectrogram) and 3 (high, when the full  
187 contour was clearly visible). Only clearly visible contours (of quality 3) with  
188 sufficient signal-to-noise ratio to extract the measurements required were extracted in  
189 our data sets from both ocean basins. It is likely that some whistles in our sample

190 were produced by the same group or the same individuals (mean  $\pm$  stdv [min; max] of  
191 number of whistles per recording day:  $22.4 \pm 22$  [1; 95]). Photographs of whales were  
192 opportunistically collected while recordings were made in Iceland and Norway.  
193 Estimates of group size were not consistently collected across recording sessions in  
194 these two locations, but in general varied between 4-15 animals to large aggregations  
195 containing 50-100 individuals. Photo-identification was particularly challenging in  
196 Norway due to low-light conditions in winter and analysis has not been completed. In  
197 Iceland, on average  $17 \pm 14$  [2; 41] individuals were identified per recording session  
198 and for those individuals that were resighted at least once (52 of 86) the number of  
199 resightings was  $4 \pm 2$  [1; 9]. Recordings in the North Pacific were mostly from a  
200 single day in each location, and group sizes were generally not available (Table 1). It  
201 was not possible to identify which individuals produced high-frequency whistles  
202 recorded in this study, however, it is unlikely that the sampling procedure across  
203 different days or across wide geographic areas (such as for the North Pacific data)  
204 biased the repeated sampling of a small number of individuals within each location.

205

#### 206 *Stereotypy of high-frequency whistles*

207 To investigate whether, like pulsed calls, high-frequency whistles fell into stereotyped  
208 categories, the data set was categorized using two different methods: 1) visual  
209 categorization by human observers as commonly used to identify whistle types and; 2)  
210 automated categorization using ARTwarp (Deecke and Janik 2006).

211

#### 212 *1) Categorization by a human observer*

213 We first conducted visual classification by a human observer using the entire sample  
214 of high-frequency whistles to identify differences in the repertoires of different

215 whistle types across locations. Spectrograms of all whistles were generated in  
216 MATLAB (version 7.0.4; spectrogram parameters: FFT=2048 or 4096, for 96 kHz  
217 and 192 or 200 kHz sampling rates, respectively; overlap=87.5%; window  
218 function=Hann). The observer was blind to the origin of high-frequency whistles  
219 being classified. High-frequency whistles seemed to show continuous rather than  
220 discrete variation, and as a result were grouped into broad categories (e.g., Azevedo  
221 and Van Sluys 2005): upsweeps (rise in frequency with no inflection points),  
222 downsweeps (decrease in frequency with no inflection points), ascending-descending  
223 (rise in frequency followed by one inflection point and then a decrease in frequency),  
224 descending-ascending (decrease in frequency followed by one inflection point and  
225 then an increase in frequency), constant (small or no change in frequency and no  
226 inflection point), and other (if a contour did not fit any of the previous categories, Fig.  
227 2).

228

#### 229 *2) Categorization using an automated method*

230 To inspect variation at a finer scale, we conducted an independent automated  
231 categorization in MATLAB (version 7.11). A subset of the extracted fundamental  
232 frequency contours were analyzed by an adaptive resonance theory neural network  
233 that uses dynamic time-warping to calculate contour similarity (ARTwarp; Deecke  
234 and Janik 2006). Computation time constraints meant that it was impossible to input  
235 all extracted contours unless whistles were downsampled, reducing their time  
236 resolution. However, downsampling by a factor of 3 resulted in severe  
237 misclassification of the data (18 out of 19 categories included misclassified whistles)  
238 based upon visual inspection of generated categories. Therefore, the original time

239 resolution was used (0.667 ms), but only a subset of randomly chosen whistle  
240 contours was categorized.

241 ARTwarp compares the similarity between an input contour and a contour that  
242 defines each category (reference contour) to a user-defined similarity value, called the  
243 vigilance parameter, to decide how each input contour should be categorized (Deecke  
244 and Janik 2006). To find the categorization that would explain most variation in high-  
245 frequency whistles with the least number of categories, the vigilance parameter was  
246 set to values between 0% and 100% in 50 logarithmic steps, and the subset of  
247 contours was categorized for each vigilance parameter value. The optimal  
248 categorization should have the highest variance ratio, calculated as the ratio of  
249 average within-category similarity over average between-category similarity as in  
250 Deecke and Janik (2006). This method was adopted because it has successfully  
251 classified the signature whistles of bottlenose dolphins and pulsed calls of killer  
252 whales (Deecke and Janik 2006).

253

#### 254 *Multivariate analysis of variation in time-frequency parameters*

255 We conducted a multivariate discriminant function analysis (DFA) to investigate  
256 differences between whistles from different locations. All frequency and time  
257 parameters were included, except frequency range, as it is already represented by  
258 minimum and maximum frequency. We used location as the grouping variable  
259 ('Iceland', 'Norway' or 'North Pacific') and used a jackknife cross-validation  
260 technique implemented in the `lda` function of package MASS version 7.3-16  
261 (Venables and Ripley 2002) in R 2.11.1 for Mac OS (R Development Core Team  
262 2011). The overall proportion of correct classifications and the proportion of correct  
263 classifications by location were calculated. These were compared to the proportion of

264 by-chance accuracy, calculated as the sum of the squares of all prior probabilities,  
265 assumed to be equal for all locations.

266

## 267 **Results**

268 We measured the parameters of 985 high-frequency whistles ( $n_{\text{Iceland}} = 570$ ;  
269  $n_{\text{Norway}} = 256$ ;  $n_{\text{Pacific}} = 159$ ). One of the whistles in our sample (from Norway) was a  
270 clear outlier, with duration of 4.2 s, much longer than the majority of remaining  
271 whistles and was removed from the analyses. Table 2 presents the descriptive  
272 statistics of all contour parameters measured. Duration and frequency range showed  
273 the highest coefficients of variation across all locations. All other frequency  
274 parameters had much lower coefficients of variation, however variation for Iceland  
275 and Norway was consistently larger than variation in the North Pacific. This could be  
276 due to the smaller sample size of whistles from the Pacific. However, in the North  
277 Atlantic very high-frequency whistles were recorded that likely explain the larger  
278 coefficients of variation observed here. There was a clear gap in the distribution of  
279 frequency parameters between whistles with fundamental contours up to 48 kHz and  
280 whistles with fundamental frequency contours entirely above 48 kHz (Fig. 3).  
281 Whistles with contours entirely above 48 kHz were recorded in a small number of  
282 encounters ( $n_{\text{Iceland}} = 4$ ;  $n_{\text{Norway}} = 2$ ). They appeared as clear outliers in the  
283 distributions and were thus removed from the comparisons of parameter distributions  
284 (Fig. 3).

285 There was considerable overlap between the distributions of some of the contour  
286 parameters from Iceland and Norway (Fig. 3). To compare these parameters across  
287 locations, we employed a Mann-Whitney U test, due to the non-normality of most  
288 distributions (Shapiro-Wilk normality tests:  $P < 0.0001$ , except for frequency range in

289 the North Pacific with  $p=0.09$ ). We used Bonferroni correction to adjust the  
290 significance level to account for multiple comparisons ( $0.05/21=0.002$ ). Despite the  
291 apparent overlap, comparisons between the parameter distributions from Iceland and  
292 Norway revealed significant differences in end frequency (Mann-Whitney U test:  
293  $W=74148$ ;  $P=0.0004$ ), frequency range (Mann-Whitney U test:  $W=81867$ ;  $P<0.0001$ )  
294 and maximum frequency (Mann-Whitney U test:  $W=74203$ ;  $P=0.0003$ ). End  
295 frequency and maximum frequency were significantly correlated within the two  
296 locations (Pearson correlation; Iceland: end vs. maximum frequency:  $r=0.96$ ,  
297  $P<0.001$ ; Norway: end vs. maximum frequency:  $r=0.98$ ,  $P<0.001$ ), which likely  
298 reflects a whistle upsweep shape. Whistles recorded in the North Pacific tended to  
299 have lower start, mid, end, minimum, and maximum frequencies, a slightly longer  
300 duration and a greater frequency range. The start frequency was not significantly  
301 different between Iceland and the Pacific (Mann-Whitney U test:  $W=49578$ ;  
302  $P=0.008$ ), while all other parameters were ( $P$ -values $<0.0001$ ). All parameters were  
303 also significantly different between the North Pacific and Norway, with the exception  
304 of duration (Mann-Whitney U test:  $W=16777$ ;  $P=0.11$ ).

305

### 306 *Categorization by a human observer*

307 The visual classification of whistles showed that in Iceland the majority of  
308 whistles were upsweeps, followed by descending-ascending whistle types, while in  
309 Norway, upsweeps and descending-ascending whistles were equally common (Table  
310 3). Overall, the different whistle types recorded from Norway and Iceland largely  
311 resembled each other in spectral and temporal characteristics (Fig. 2), in agreement  
312 with the similarities suggested by the overlapping parameter distributions. In contrast,  
313 whistles from the North Pacific were all downsweeps, with only one whistle being

314 classified as ‘Other’. These clear differences in repertoire correspond to the  
315 differences in extracted frequency parameters (above). Nevertheless, the simple  
316 structure of downsweeps recorded in the North Pacific was similar to that of the few  
317 downsweeps recorded in the Northeast Atlantic (Fig. 2).

318

319 *Categorization using an automated method*

320 An assessment of the geographic variation of whistles was also completed using  
321 50 randomly chosen whistles from each location. The results of the ARTwarp  
322 categorization showed that an increase in the vigilance parameter resulted in an  
323 increase in the number of categories generated. The chosen categorization divided the  
324 150 high-frequency whistles into 27 categories, containing between 1 and 18 contours  
325 (mean  $\pm$  standard deviation of contours in each category:  $6 \pm 4.6$ ). This categorization  
326 corresponded to the local maximum in variance ratio achieved when the vigilance  
327 parameter was 95.6%. All but five categories included more than one whistle. Of the  
328 five categories containing only one whistle one category contained one whistle from  
329 the Pacific, two categories contained single whistles from Norway, and two categories  
330 contained single whistles from Iceland. Of the 22 categories with more than one  
331 whistle, five included only high-frequency whistles from the Pacific. The remaining  
332 high-frequency whistles from the Pacific were grouped into three more categories that  
333 also included whistles from Norway: two categories containing only two whistles  
334 (one from the Pacific and one from Norway) and; one category including 17 whistles  
335 from the Pacific and one whistle from Norway. All remaining categories included  
336 whistles from both Norway and Iceland.

337

338 *Multivariate analysis of variation in time-frequency parameters*

339       The multivariate DFA showed high macrogeographic variation between the  
340 Northeast Atlantic and North Pacific groups, with the first discriminant function  
341 accounting for 98.9% of between group variability. The loadings of the first  
342 discriminant function revealed that duration, maximum frequency, and end frequency  
343 were the main discriminating predictors (Loadings: duration = -2.81; maximum  
344 frequency = 0.33; end frequency = -0.46). The cross-validated classification showed  
345 an overall correct classification of 62.4% of whistles to the correct location, compared  
346 to a by-chance proportion of 33.3%, calculated as the sum of the squares of all prior  
347 probabilities. Correct classification scores per location revealed that the North Pacific  
348 was the location with the highest score (95.0%), with only 8 of its 159 whistles  
349 misclassified as being from Norway. Lower correct classification scores (63.9% and  
350 52.4%) were achieved for whistles from Norway and Iceland, respectively. Most  
351 misclassifications for Norway (77 of 84) were assigned to Iceland and conversely,  
352 most misclassifications for Iceland (254 of 261) were assigned to Norway. The  
353 remaining 7 misclassifications from each location were assigned to the North Pacific.  
354 Figure 4 shows the first two discriminant functions and illustrates how the first  
355 discriminant function achieved the most discrimination between locations, with  
356 whistles from the North Pacific being clearly different from those recorded in the  
357 Northeast Atlantic, while whistles from Norway and Iceland overlapped to a much  
358 greater extent. However, at high values of the second discriminant function there was  
359 little overlap between Iceland and Norway (Fig. 4). Inspection of these whistles  
360 revealed that these have high frequency range and possibly are driving observed  
361 statistically significant differences in this parameter between locations.



362 To investigate whether discrimination between Iceland and Norway was more  
363 apparent within whistle types, discriminant function analyses were carried out for the  
364 two most common whistle types (upsweeps and descending-ascending) at these  
365 locations. Descending-ascending whistles were correctly classified at rates of 60%  
366 and 66.7% for Iceland and Norway, respectively. Overall correct classification was of  
367 62.7%, compared to a by-chance proportion of 50%, suggesting a slight improvement  
368 in classification when using this whistle type, but still considerable similarity between  
369 locations. The overlap in the distribution of the discriminant scores resulting from the  
370 first discriminant function is presented in Figure 5, illustrating how the discrimination  
371 between these two locations was poor. Correct classification of upsweeps was 58.7%  
372 and 58.5% for Iceland and Norway, respectively. For upsweeps, overall correct  
373 classification was 58.6%, compared to a by-chance proportion of 50%, which also  
374 suggests an overlap in the discriminant scores within this type (Fig. 5).

375

## 376 **Discussion**

377 We found clear macrogeographic variation between high-frequency whistles  
378 recorded in the North Pacific and the Northeast Atlantic, while within the Northeast  
379 Atlantic only subtle microgeographic variation was observed. In all locations whistles  
380 could be manually classified into broad stereotyped categories, but the diversity of  
381 whistle types identified varied between ocean basins. While the majority of whistles  
382 recorded in the North Pacific consisted of only one whistle type, the Northeast  
383 Atlantic repertoires included more types and the repertoires were similar between  
384 locations. In all locations the within-location variation in most frequency parameters  
385 was small in comparison to variation in frequency range and duration. It is possible  
386 that some degree of this variation is due to varied signal-to-noise ratio conditions

387 under which recordings were collected. Nevertheless, in other delphinids intra-  
388 specific variation in frequency parameters was generally low, while variation in  
389 whistle duration tended to be comparatively higher (*e.g.*, Ding *et al.* 1995*b*, Morisaka  
390 *et al.* 2005). It is possible that frequency parameters are constrained by morphology,  
391 while the variability of whistle duration may be related to social and non-social  
392 behavior or environmental factors, or random individual variation (*e.g.*, May-Collado  
393 and Wartzok 2008).

394

#### 395 *Macrogeographic variation in high-frequency whistles*

396 Within the North Pacific, acoustic encounters of killer whales were not common at  
397 any of the recording sites, and high-frequency whistles were infrequently observed.  
398 There was broad similarity in the recorded whistles despite the considerable  
399 geographic range covered by the recordings. The consistency in whistle type  
400 (downsweeps) and similarities in frequency characteristics to those reported by  
401 Filatova *et al.* (2012) suggests that within the Pacific Ocean there may be little  
402 variability in high-frequency whistles. However, not all populations appear to produce  
403 these signals; both Northeast Pacific resident and transient killer whales apparently do  
404 not produce high-frequency whistles (Samarra *et al.* 2010, Filatova *et al.* 2012) but  
405 the ecotypes of those whales that do produce them in the North Pacific remain largely  
406 unknown, with the exception of North Pacific offshores (Simonis *et al.* 2012, Filatova  
407 *et al.* 2012). While Pacific offshore, resident and Northeast Atlantic killer whales are  
408 all closely related genetically (Morin *et al.* 2010), it is curious that Pacific resident  
409 killer whales have not been recorded using the signals shared by their nearest  
410 relatives. In contrast to the apparent similarity within the Pacific Ocean, there were  
411 clear differences between whistles recorded in the Pacific and Atlantic Ocean basins.

412 Whistles recorded in the North Pacific had consistently lower frequency  
413 parameters, while frequency range was significantly higher in the North Pacific than  
414 in either of the Northeast Atlantic populations. Differences in duration were less  
415 pronounced and significant differences were only detected in comparison to Iceland.  
416 The discriminant function analysis was able to correctly classify the vast majority of  
417 whistles from the North Pacific, assigning duration and maximum and end frequency  
418 as main discriminating predictors. Whistle types identified were also considerably  
419 different between ocean basins; while downsweeps were the most common whistle  
420 type in the North Pacific, this whistle type was uncommon in the Northeast Atlantic.  
421 The automated categorization also grouped most whistles from the Pacific into  
422 distinct categories. This divergence in whistle types will likely influence some of the  
423 observed differences in frequency parameters particularly the start, mid and end  
424 frequency but does not explain differences in minimum and maximum frequencies,  
425 which should not be affected by whistle shape. Thus, we believe that the observed  
426 differences in frequency parameters between ocean basins are not exclusively due to  
427 differences in whistle type usage but reflect a real divergence in the whistle frequency  
428 produced.

429 Divergence in frequency at macrogeographic scales could reflect divergence in  
430 geographically isolated populations that could originate from a wide range of genetic  
431 and social mechanisms. Indeed genetic data suggests considerable variation between  
432 populations in the Atlantic and the Pacific in comparison to variation between Iceland  
433 and Norway (Morin *et al.* 2010, Foote *et al.*, 2011). Differences in the acoustic  
434 environment, such as background noise or transmission properties (*e.g.*, Morisaka *et*  
435 *al.* 2005, May-Collado and Wartzok 2008), have also been proposed as factors  
436 explaining variations in signal frequency characteristics between populations. In both

437 ocean basins recordings were collected over wide geographic areas, and we therefore  
438 cannot identify large and consistent habitat differences that could clearly explain the  
439 patterns of variation observed in this study. Body size, however, is known to vary  
440 between the two ocean basins; killer whales in the Northeast Atlantic in general have  
441 smaller body sizes than killer whales in the Northeast Pacific (Christensen 1984,  
442 Stenersen and Similä 2006), but Northeast Pacific offshores have smaller body size  
443 than resident and transient killer whales (Ford *et al.* 2000, Dahlheim *et al.* 2008).  
444 Nevertheless, we cannot exclude the possibility that divergence in frequency  
445 characteristics between these ocean basins may be related to morphological  
446 constraints. The reasons behind the consistent production of downsweeps in the North  
447 Pacific in contrast to the more variable repertoires recorded in the Northeast Atlantic  
448 are unknown. Although intriguing, to fully understand the reasons behind variations  
449 in frequency and usage of whistle types across ocean basins more effort is required to  
450 record killer whales with adequate sampling rates in other locations. This will reveal  
451 the extent of the consistent downsweep repertoire across the North Pacific or the  
452 existence of variable repertoires in other ocean basins as well as how frequency  
453 characteristics may vary in other habitats.

454

#### 455 *Microgeographic variation in high-frequency whistles*

456 Within the Northeast Atlantic, we found similarities in the repertoire and  
457 characteristics of high-frequency whistles produced by killer whales in Norway and  
458 Iceland. None of the quantitative methods employed was able to distinguish between  
459 whistles from Iceland and Norway as clearly as between whistles from Northeast  
460 Atlantic and North Pacific, suggesting different levels of divergence between  
461 locations. Despite the apparent overlap in parameter distributions in the Northeast

462 Atlantic, whistles from Norway showed significantly lower end frequency, maximum  
463 frequency and frequency range when compared to Iceland. The discriminant function  
464 analysis showed some degree of correct classifications, although many whistles from  
465 both locations were misclassified, while the automated categorization included  
466 whistles from both locations in most of the categories generated. Although the overall  
467 repertoire was similar between the two locations, there were some differences in the  
468 usage of whistle types. Upsweeps were the most common whistle type in Iceland,  
469 while in Norway both upsweeps and descending-ascending whistles were equally  
470 common. Even when trying to discriminate between locations within whistles of the  
471 same type, discriminant function analyses still misclassified a large proportion of  
472 whistles, suggesting similarity between whistles produced. The similarity in both  
473 time-frequency parameters and overall repertoire of high-frequency whistles between  
474 Norway and Iceland is in striking contrast to the divergence in pulsed call repertoires  
475 (Moore *et al.* 1988, Strager 1995, Stenersen and Similä 2004, Shamir *et al.* 2014). At  
476 present we have little evidence of contextual production of high-frequency whistles to  
477 help us identify their function. Nevertheless, this divergence between pulsed calls and  
478 high-frequency whistles possibly reflects different functions of these different signal  
479 types.

480 Microgeographic variation in acoustic signals may be shaped by genealogy, the  
481 timing of separation, ranging behavior of individuals, or cultural divergence in the  
482 case of learned acoustic signals (*e.g.*, Ding *et al.* 1995b, Azevedo and Van Sluys  
483 2005, Papale *et al.* 2013). For killer whales in Norway and Iceland evidence for (a  
484 recent) common ancestor comes from historic ranging patterns of prey, genetics  
485 (Jonsgård and Lyshoel 1970, Foote *et al.* 2009a), and high-frequency whistle  
486 repertoires, while the unique pulsed call repertoires of each region may reflect more

487 recent divergence (Moore *et al.* 1988, Strager 1995, Stenersen and Similä 2004,  
488 Shamir *et al.* 2014). A small number of high-frequency whistles have also been  
489 recorded from killer whales in Shetland (Samarra *et al.* 2010), an archipelago situated  
490 between Iceland and Norway where some Icelandic killer whales are known to travel  
491 (Foote *et al.* 2009a). Further recordings from this location and others should provide  
492 an interesting comparison to evaluate the degree of divergence between adjacent  
493 populations. Although the function(s) of these high-frequency whistles remain  
494 unclear, the signals analyzed in this study offer a window to understanding how  
495 acoustic behavior may relate to ancestry and dispersal patterns of killer whale  
496 populations on multiple scales.

497

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522

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691 **Table 1.** Specifications of recordings containing high-frequency whistles analyzed in this study (further details are given in Samarra *et al.* 2010  
 692 and Simonis *et al.* 2012).

Ocean basin	Location	Recording days	Recording time (h)	Sampling rate (kHz)	Recording method	Whistles analyzed
Northeast Atlantic	Iceland	19	64	96 and 192	Vertical hydrophone array	570
					Towed hydrophone array Dtag	
	Norway	18	104	96 and 192	Towed hydrophone array Dtag	257
North Pacific	Aleutian islands	2	3.1	200	HARP (depth 783 m)	44
	Hoke Seamount	1	0.6	200	HARP (depth 770 m)	22
	Kauai	1	0.6	200	HARP (depth 706 m)	36
	Pearl and Hermes Atoll	1	0.6	200	HARP (depth 753 m)	10
	Southern California	1	1.9	200	HARP (depth 1295 m)	22

---

Bight						
Southern California	1	0.5	200	Ship-based hydrophone	11	
Bight				array		
Washington Coast	1	0.7	192	Ship-based hydrophone	14	
				array		

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695 **Table 2.** Descriptive statistics of high-frequency whistles analyzed in this study.  
 696 Sample sizes for each location are included in brackets. For each parameter, values  
 697 given are mean  $\pm$  standard deviation [minimum – maximum], with coefficient of  
 698 variation (calculated as the ratio of the standard deviation to the mean) given as a  
 699 percentage within brackets. All frequency parameters are presented in kHz and  
 700 duration is presented in milliseconds (ms).

Location	Iceland ( <i>n</i> =570)	Norway ( <i>n</i> =256)	North Pacific ( <i>n</i> = 159)
Start frequency	32.6 $\pm$ 9.1 (27.9%) [16.9 – 71.2]	34.7 $\pm$ 11.0 (31.7%) [18.3 – 71.0]	29.6 $\pm$ 5.1 (17.2%) [19.3 – 44.0]
End frequency	38.2 $\pm$ 8.7 (22.8%) [19.4 – 74.7]	37.4 $\pm$ 9.0 (24.1%) [21.5 – 68.3]	20.8 $\pm$ 3.2 (15.4%) [17.1 – 33.4]
Mid frequency	33.8 $\pm$ 8.6 (25.4%) [17.6 – 68.8]	34.6 $\pm$ 9.6 (27.7%) [19.0 - 64.3]	25.3 $\pm$ 4.3 (16.9%) [18.4 – 39.4]
Minimum frequency	31.7 $\pm$ 8.6 (27.1%) [16.9 - 68.3]	33.0 $\pm$ 9.2 (27.9%) [18.1 – 64.3]	20.8 $\pm$ 3.2 (15.3%) [17.1 – 33.4]
Maximum frequency	38.4 $\pm$ 8.7 (22.7%) [19.4 – 74.7]	38.4 $\pm$ 10.2 (26.6%) [22.3 – 71.0]	29.7 $\pm$ 5.1 (17.1%) [19.3 – 44.0]
Frequency range	6.8 $\pm$ 3.7 (54.4%)	5.4 $\pm$ 2.9 (53.7%)	8.9 $\pm$ 3.8 (42.6%)

	[0.7 – 21.2]	[1.0 – 19.9]	[1.6 – 20.2]
Duration	138.1 ± 135.9	143.6 ± 143.1	142.6 ± 74.2
	(98.4%)	(99.7%)	(52.1%)
	[6 - 814]	[10 - 1300]	[37.8 – 371.2]

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703 **Table 3.** Proportion of high-frequency whistle types produced in different locations.

704 Desc-Asc stands for descending-ascending and Asc-Desc stands for ascending-

705 descending whistles.

Whistle categories							
Location	Upsweep	Downsweep	Desc-Asc	Asc-Desc	Constant	Other	Total
Iceland	68.4%	1.4%	28.6%	0%	0.2%	1.4%	570
Norway	41.2%	9.3%	42.8%	0.8%	0%	5.8%	257
North Pacific	0%	99.4%	0%	0%	0%	0.6%	159
Total	50.3%	19.3%	27.7%	0.2%	0.1%	2.4%	986

706

707

708 **Figure captions**

709 **Figure 1.** Map illustrating the approximate locations (stars) where recordings  
710 containing high-frequency whistles were collected in: top) the Northeast Atlantic and;  
711 bottom) the North Pacific. SCB stands for Southern California Bight. Locations where  
712 recordings were conducted but no high-frequency whistles were detected are also  
713 shown (circles).

714

715 **Figure 2.** Spectrograms showing examples of different high-frequency whistle types  
716 from Iceland, Norway and the North Pacific. If a specific whistle type was only  
717 produced in one location only one example was shown. Note the different y-axis  
718 scaling for the Constant whistle type.

719

720 **Figure 3.** Distribution of all frequency parameters extracted from whistle contours.  
721 Horizontal lines represent medians, boxes represent inter-quartiles, and whiskers  
722 represent values within 1.5 times the inter-quartile range from the boxes. Outliers are  
723 plotted as single points. Frequency range is plotted separately due to its different y-  
724 axis scale, as is duration.

725

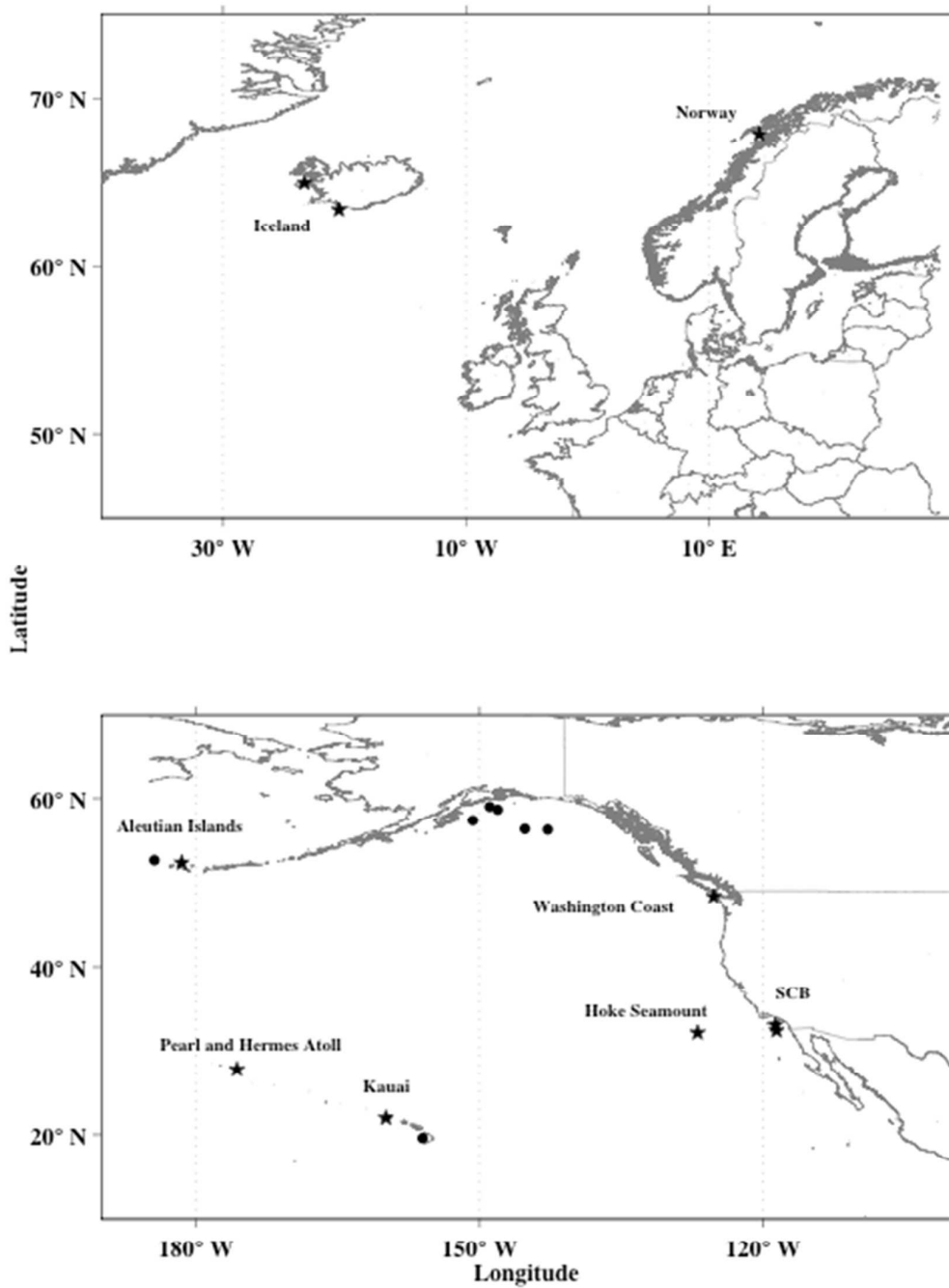
726 **Figure 4.** Plot of the first two discriminant functions for the comparison between  
727 whistles recorded in Iceland (I), Norway (N) and the North Pacific (P). Colors follow  
728 the same legend as in Figure 2. Note the overlap between whistles from Norway (N)  
729 and Iceland (I) in contrast to discrimination between whistles from the NE Atlantic  
730 and whistles from the Pacific (P).

731

732 **Figure 5.** Boxplots illustrating the distribution of discriminant scores (DF1) for  
733 descending-ascending whistles (Desc-Asc) for the two groups (Iceland and Norway)  
734 and discriminant scores for upsweep whistles for the two groups. Colors follow the  
735 same legend as in Figure 2.  
736

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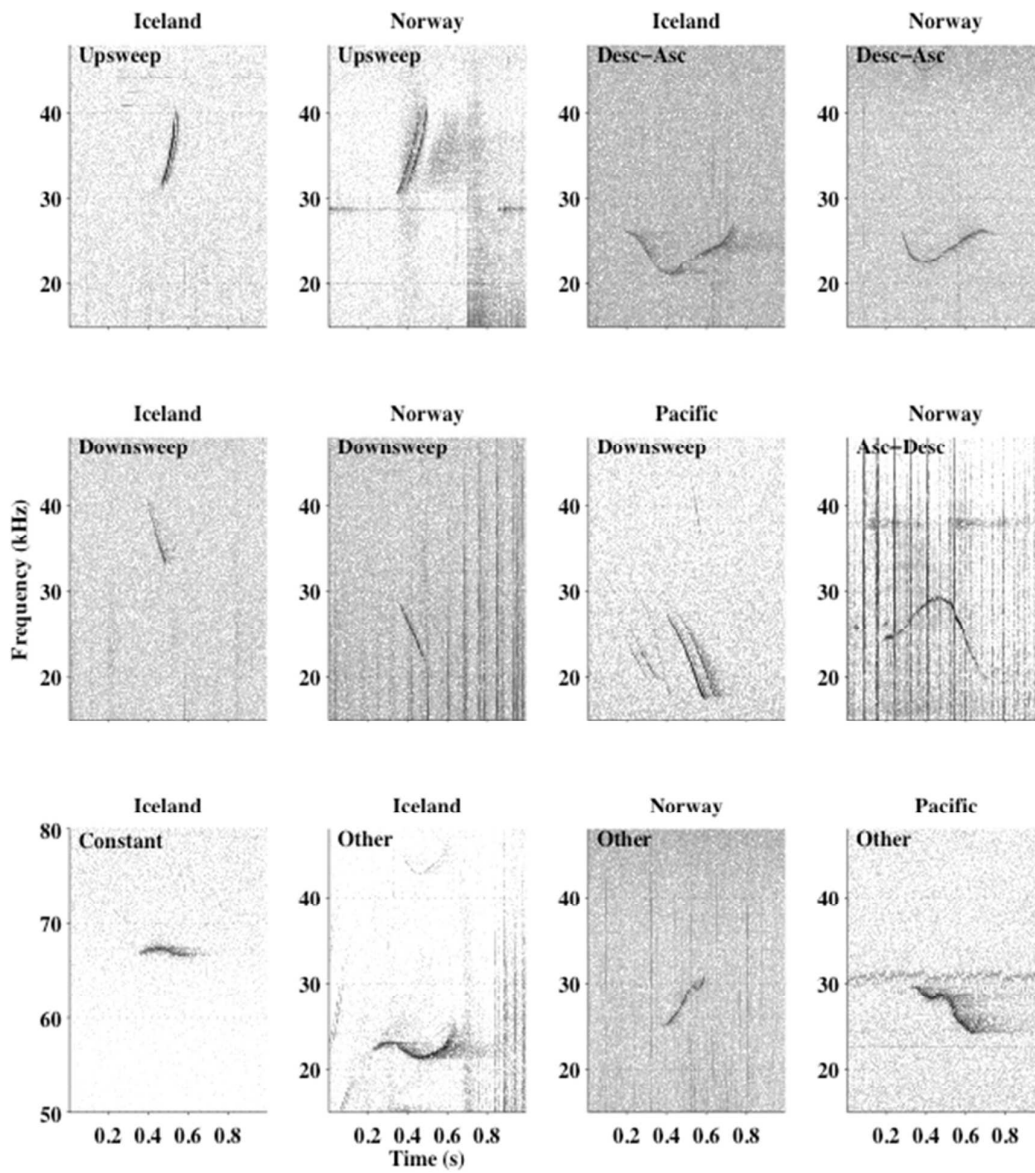
737 **Figure 1**



738

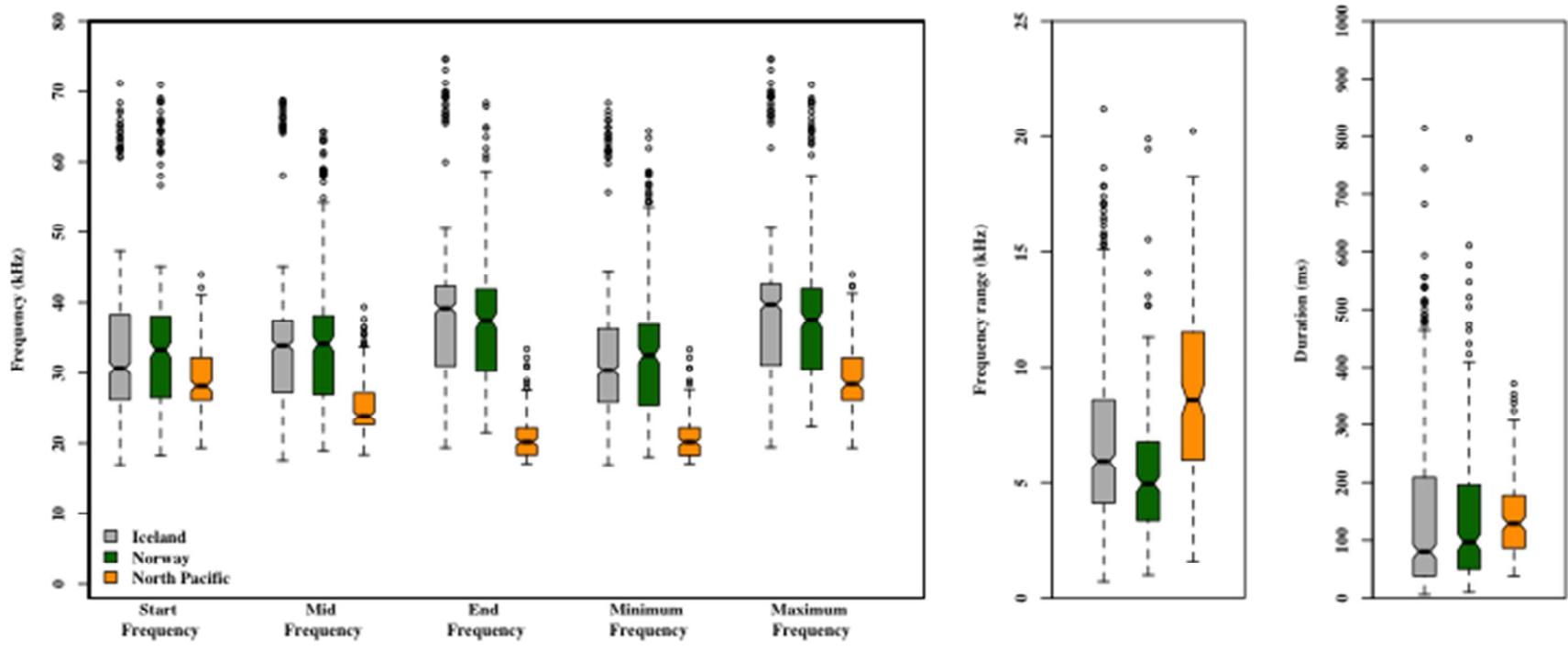
739

740 **Figure 2**



741

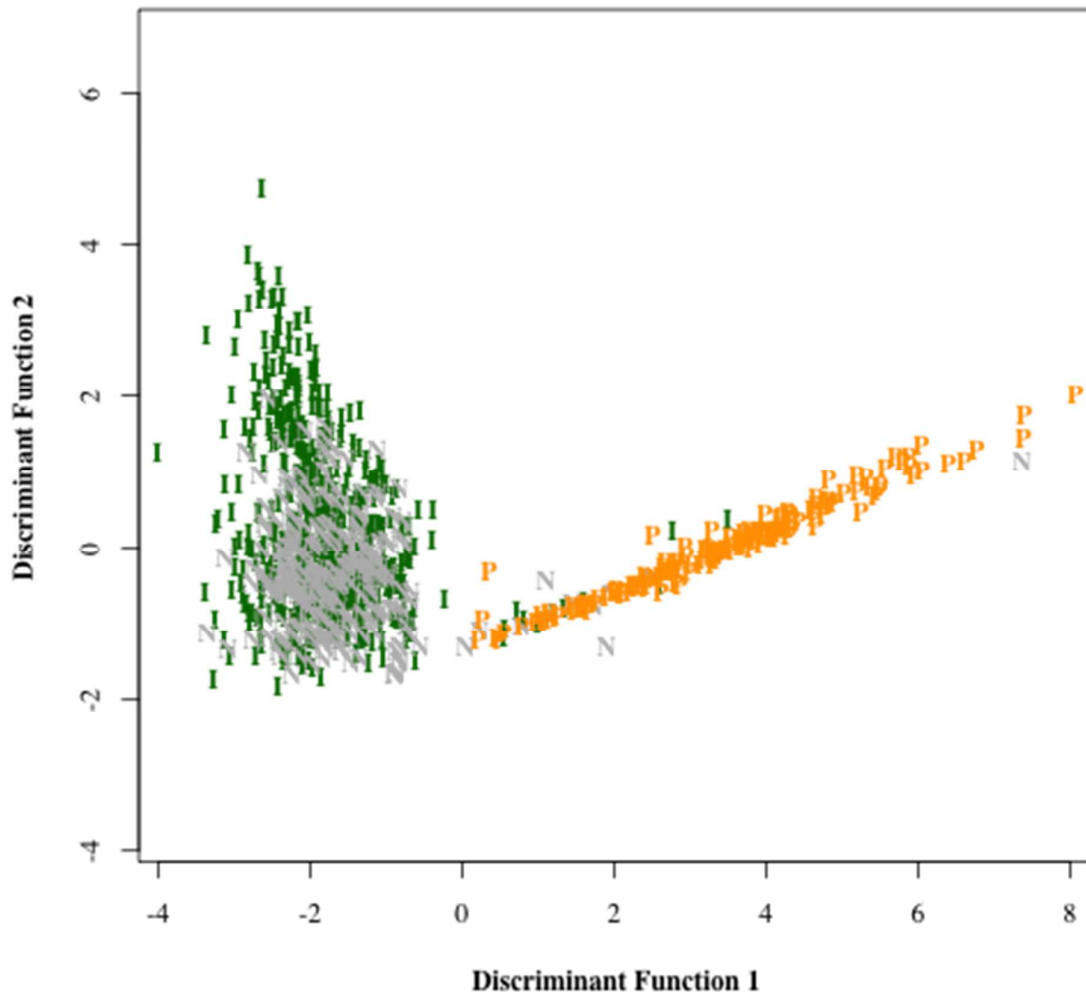
742 Figure 3



743

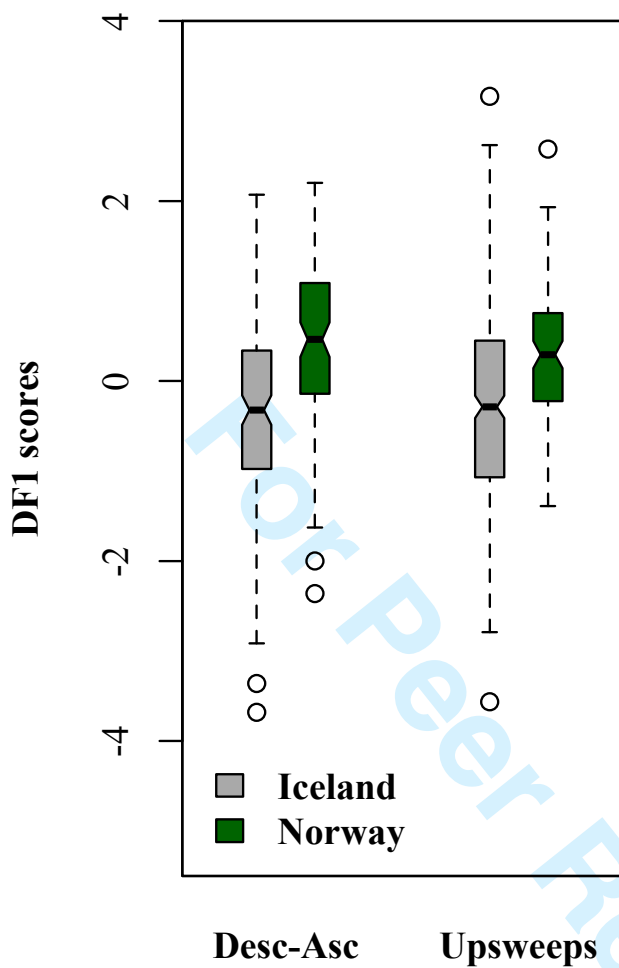


744 **Figure 4**



745

746 **Figure 5**



747