1   **Geographic variation in the time-frequency characteristics of high-**

2   **frequency whistles produced by killer whales (*Orcinus orca*)**

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4   Filipa I. P. Samarra [1,2,a], Volker B. Deecke[1,3], Anne E. Simonis[4] and Patrick J. O.

5   Miller[1]

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7   [1] Sea Mammal Research Unit, Scottish Oceans Institute, University of St Andrews, St

8   Andrews, Fife KY16 8LB, UK

9   [2] Current address: Marine Research Institute, Skúlagata 4, 121 Reykjavík, Iceland

10   [3] Current address: Centre for Wildlife Conservation, University of Cumbria, Rydal

11   Road, Ambleside, Cumbria, LA22 9BB. UK

12   [4] Scripps Institution of Oceanography, University of California, San Diego, 9500

13   Gilman Drive, La Jolla, California 92093-0205, USA

14

15   [a] email: filipa@hafro.is

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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.

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

39

Introduction

When describing geographic variation in acoustic signals it is useful to divide

differences into macrogeographic or microgeographic variation, depending on

whether populations being compared are neighboring, making interbreeding and

social interaction a possibility, or geographically separated, and thus socially and

reproductively isolated (Mundinger 1982). Comparative studies of odontocete

whistles have shown more pronounced inter- than intra-specific variation in whistle

spectral parameters, which could arise if intra-specific variability is constrained to

occur within a species-specific framework (Steiner 1981, Ding *et al*. 1995*a*, Matthews

et al. 1999, Rendell *et al*. 1999, Podos *et al*. 2002). Variation in whistle structural

parameters has previously been described for populations of the same dolphin species

both at microgeographic (*e.g*., Azevedo and Van Sluys 2005, Morisaka *et al*. 2005)

and macrogeographic levels (*e.g*., Camargo *et al*. 2006, Baron *et al*. 2008). Intra-

specific geographic variations may occur due to genetic divergence, adaptations to

local environments or cultural differences (Janik 2009). A general correlation of

whistle variation with distance has been proposed whereby neighboring populations

appear to have more similar whistle structure than geographically distant populations

(Ding *et al*. 1995*b*, Azevedo and Van Sluys 2005, Rossi-Santos and Podos 2006,

May-Collado and Wartzok 2008), although this is not always the case (Camargo *et al*.

2006). Within populations, there is often variation in duration and complexity of

signals (*i.e*., number of inflection points) (Steiner 1981, Azevedo and Van Sluys

2005, Morisaka *et al*. 2005), while the time-frequency contour of whistles often varies

among individuals, providing information on individual identity (*e.g*., bottlenose

dolphin, *Tursiops truncatus*; Janik *et al*. 2006; common dolphin, *Delphinus delphis*:

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 matrilines 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.*

4

90   2009*b*, 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.* 2009*a*), 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.* 2009*a*), 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 ± stdv [min; max] of

191　number of whistles per recording day: 22.4 ± 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 ± 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 ± 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 ($n_{Iceland}$ = 570;

269   n_{Norway} = 256; $n_{Pacific}$ = 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 ($n_{Iceland}$ = 4; n_{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 ± standard deviation of contours in each category: 6 ± 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

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*. 1995*b*, 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*. 2009*a*), 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*. 2009*a*). 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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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	257
					Dtag	
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	

693

694

31

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

701

702

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

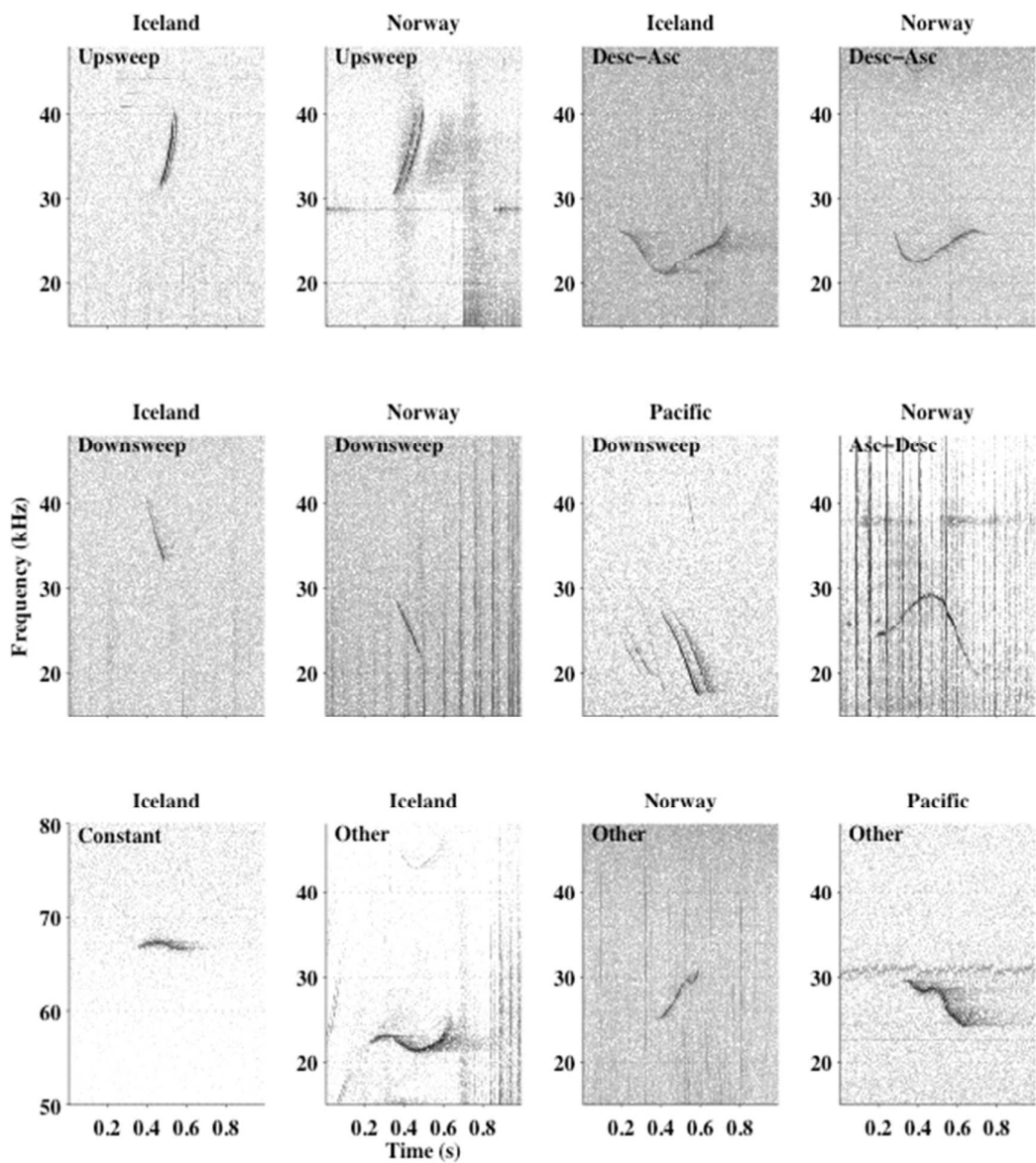735   same legend as in Figure 2.
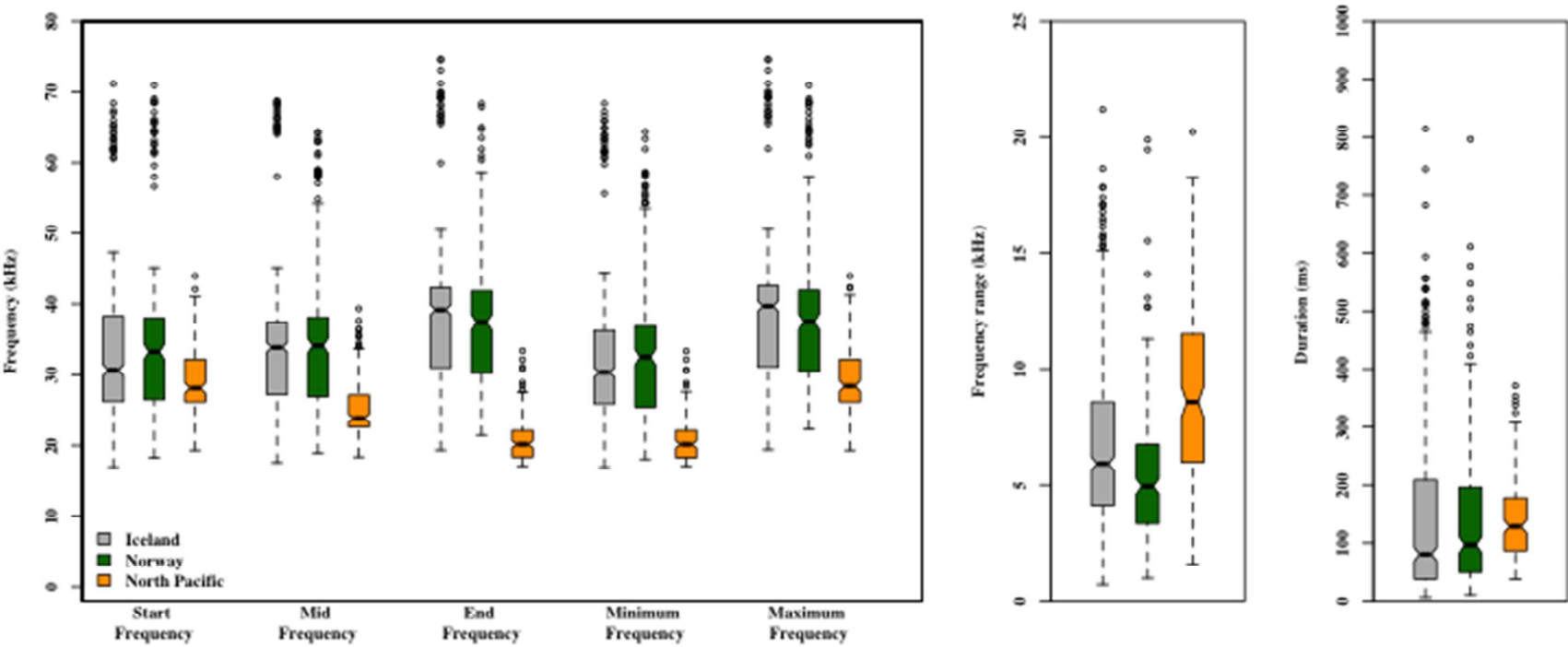
736

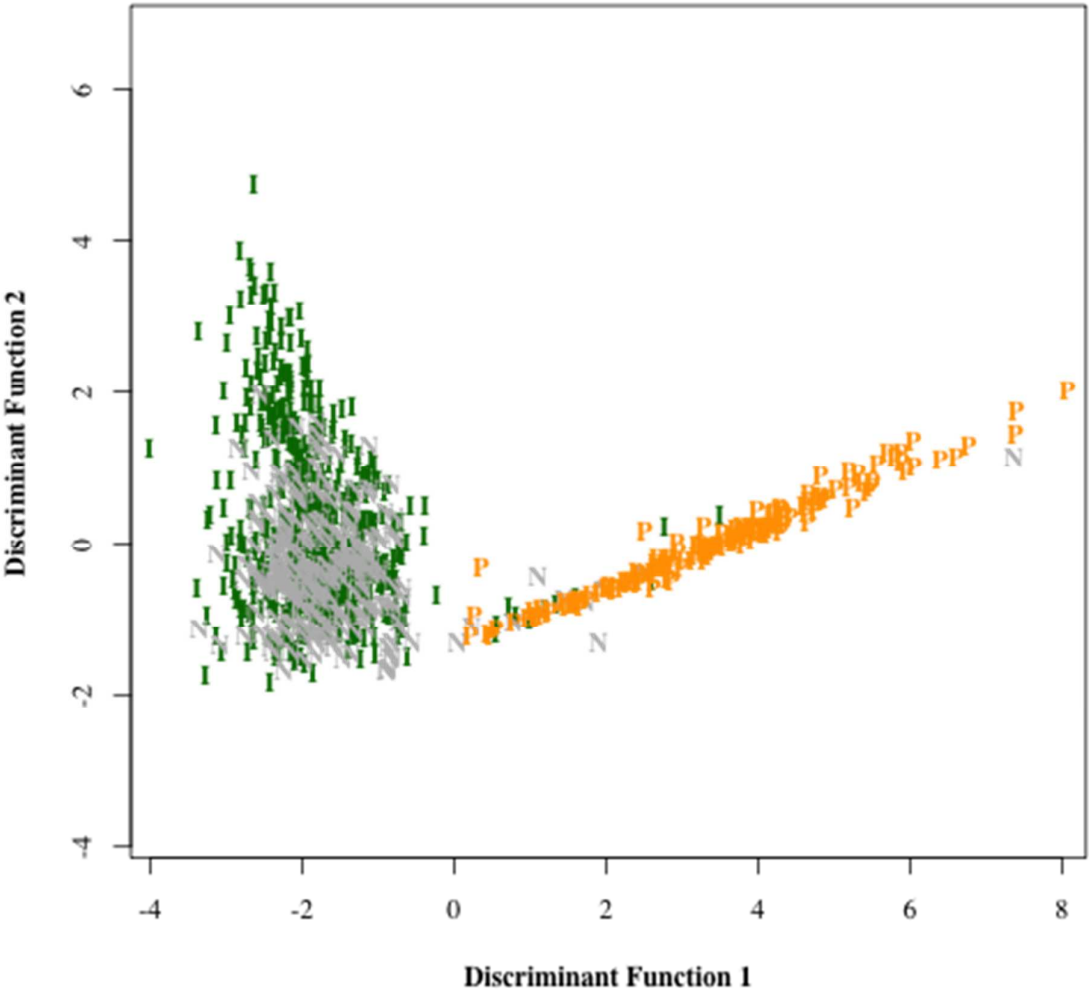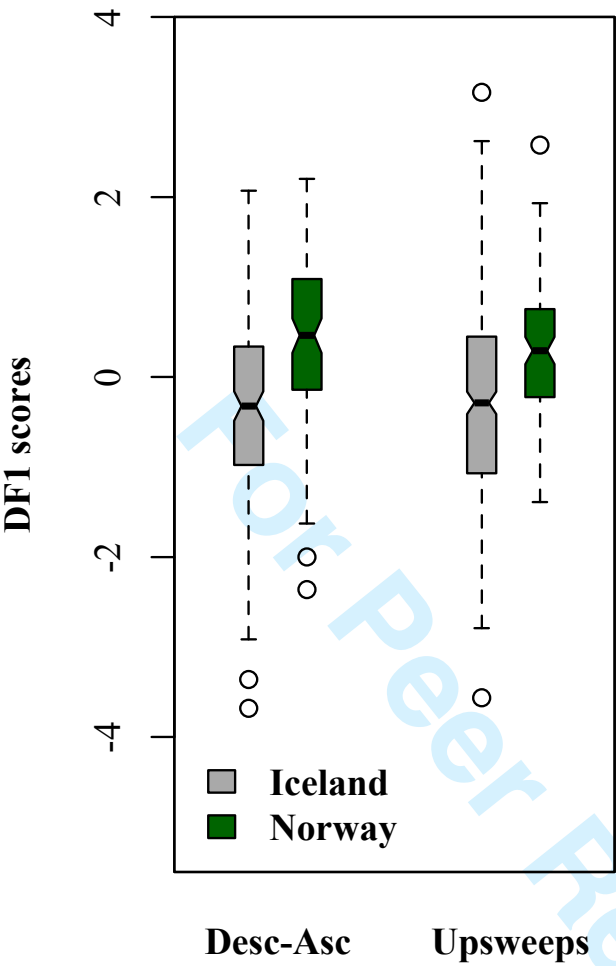737　　**Figure 1**
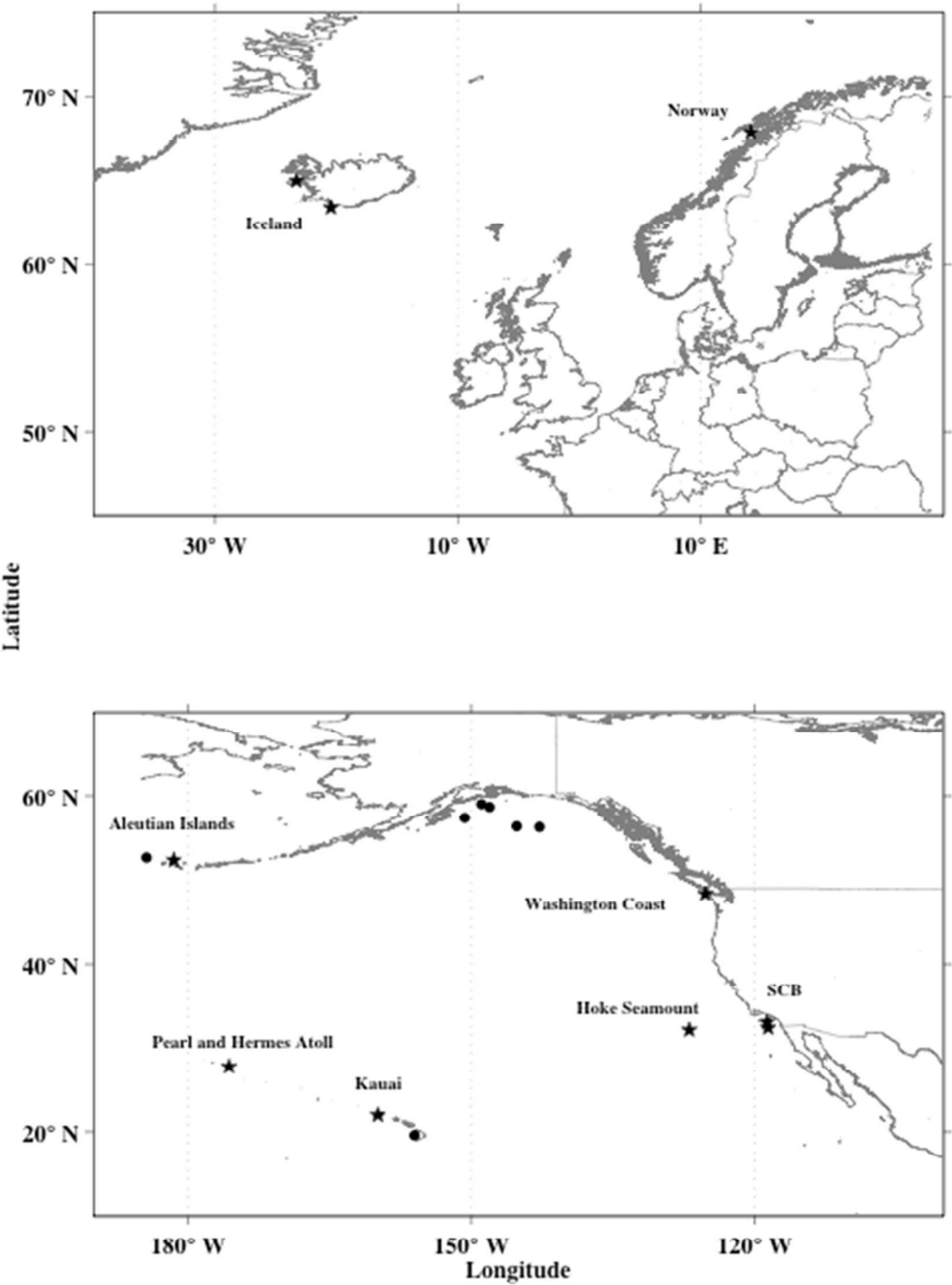
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740 **Figure 2**

741

742 **Figure 3**

743

744   **Figure 4**

745

746   **Figure 5**

747