Intraspecific variation in the cochleae of harbour porpoises (Phocoena phocoena) and its implications for comparative studies across odontocetes

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In morphological traits, variation within species is generally considered to be lower than variation among species, although this assumption is rarely tested. This is particularly important in fields like palaeontology, where it is common to use a single individual as representative of a species due to the rarity of fossils. Here, we investigated intraspecific variation in the cochleae of harbour porpoises (*Phocoena phocoena*). Intraspecific variation of cochlear morphology is well characterised among odontocetes (toothed whales) because of the importance of the structure in echolocation, but generally these studies use only a single cochlea to represent each species. In this study we compare variation within the cochleae of 18 specimens of *P. phocoena* with variations in cochlear morphology across 51 other odontocete species. Using both 3D landmark and linear measurement data, we performed Generalised Procrustes and principal component analyses to quantify shape variation. We then quantified intraspecific variation in our sample of *P. phocoena* by estimating disparity and the coefficient of variation for our 3D and linear data respectively. Finally, to determine whether intraspecific variation may confound the results of studies of interspecific variation, we used multivariate and univariate analyses of variance to test whether variation within the specimens of *P. phocoena* was significantly lower than that across odontocetes. We found low levels of intraspecific variation in the cochleae of *P. phocoena*, and that cochlear shape within *P. phocoena* was significantly less variable than across odontocetes. Although future studies should attempt to use multiple cochleae for every species, our results suggest that using just one cochlea for each species should not strongly influence the conclusions of comparative studies if our results are consistent

across Cetacea.

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2 **implications for comparative studies across odontocetes.**

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26   variation among species, although this assumption is rarely tested. This is particularly important

27   in fields like palaeontology, where it is common to use a single individual as representative of a

28   species due to the rarity of fossils. Here, we investigated intraspecific variation in the cochleae

29   of harbour porpoises (*Phocoena phocoena*). Interspecific variation of cochlear morphology is

30   well characterised among odontocetes (toothed whales) because of the importance of the

31   structure in echolocation, but generally these studies use only a single cochlea to represent

32   each species. In this study we compare variation within the cochleae of 18 specimens of *P.*

33   *phocoena* with variations in cochlear morphology across 51 other odontocete species. Using

34   both 3D landmark and linear measurement data, we performed Generalised Procrustes and

35   principal component analyses to quantify shape variation. We then quantified intraspecific

36   variation in our sample of *P. phocoena* by estimating disparity and the coefficient of variation for

37   our 3D and linear data respectively. Finally, to determine whether intraspecific variation may

38   confound the results of studies of interspecific variation, we used multivariate and univariate

39   analyses of variance to test whether variation within the specimens of *P. phocoena* was

40   significantly lower than that across odontocetes. We found low levels of intraspecific variation in

41   the cochleae of *P. phocoena*, and that cochlear shape within *P. phocoena* was significantly less

42   variable than across odontocetes. Although future studies should attempt to use multiple

43   cochleae for every species, our results suggest that using just one cochlea for each species

44   should not strongly influence the conclusions of comparative studies if our results are consistent

45   across Cetacea.

46

47   **Introduction**

48

49   Intraspecific variation, the diversity of genotypes and phenotypes within a single species, is a

50   key component of adaptation and evolution by natural selection (O'Dell & Rajakaruna, 2011;

51 Des Roches et al., 2018). Intraspecific variation includes variation related to size, allometry, sex,

52 and differences related to environment or genetics. It can influence community structure and

53 ecosystem function as much as interspecific variation (Des Roches et al., 2018). Within species,

54 there can be variation in predator defences, parasite resistance, resource manipulation and

55 many more, all of which can alter the number and strength of interactions, shifting the dynamics

56 of an ecosystem (Bolnick et al., 2011). Intraspecific variation also allows local adaptation and

57 the formation of ecotypes leading to phenotypic or genotypic divergence (Ishikawa, Onoda &

58 Hikosaka, 2007; O'Dell & Rajakaruna, 2011).

59

60 For most morphological traits, it is assumed that degrees of intraspecific variation are generally

61 smaller than those of interspecific variation. Nevertheless, in many studies this assumption is

62 not (or cannot be) tested because of logistical constraints, for example, where using multiple

63 specimens for each species is not feasible due to time or cost restrictions, or because samples

64 are limited. Palaeontological studies, for example, commonly use a single individual as

65 representative of a whole population or species because of the rarity of fossils (Ekdale &

66 Racicot, 2015; Ekdale, 2016; Park et al., 2017a; Gonzales, Malinzak & Kay 2018; Marx et al.,

67 2018; Racicot et al., 2019).

68

69 One field where this assumption has been made is the study of cetacean cochleae. The

70 cochlea, the organ of hearing, is a complex structure with a vital role in species survival (Cantos

71 et al., 2000). Odontocetes (toothed cetaceans) are reliant on their hearing abilities using

72 echolocation for feeding, communicating and navigating their habitat, among other functions

73 (Ketten, 1992a; Ketten, 1992b). Most cross-species studies of cetacean cochlear morphology

74 use only one cochlea for each species (e.g. Luo & Marsh, 1996; Ekdale & Racicot, 2015; Park,

75 Fitzgerald & Evans, 2016; Churchill et al., 2016) due to the rarity of specimens in natural history

76 collections and because µCT scanning them takes time and money. Many studies also focus on

77   using the cochlea to study interspecific variation among mammal groups (Ekdale & Rowe, 2011;

78   Ekdale 2013, Benoit et al., 2015; Billet, Hautier & Lebrun, 2015; Ekdale, 2016; Costeur, et al.,

79   2018; Racicot, et al. 2016; Racicot, Darroch & Kohno, 2018) rather than just within cetaceans.

80   However, increasing numbers of studies are using cochlear morphology (e.g. number of turns,

81   shape of endolymphatic sac) for phylogenetic purposes using geometric morphometrics (e.g.

82   Spoor et al., 2007; Billet, Hautier & Lebrun, 2015; Mennecart & Costeur, 2016; Costeur et al.,

83   2018), which could have implications in comparative studies (Ekdale, 2010; Ekdale, 2015;

84   Thean, Kardjilov & Asher, 2017).

85

86   Here, we tested whether intraspecific variation is a major confounding factor in cross-species

87   analyses by comparing morphological variation among the cochleae of 18 specimens of harbour

88   porpoise (*Phocoena phocoena*) with those across 51 other species of odontocete. Specifically

89   we investigate whether variation within *P. phocoena* cochleae is significantly lower than

90   variation across all odontocete cochleae. Intraspecific variation has not been quantified relative

91   to interspecific variation in odontocete cochleae. Previous studies have either briefly noted

92   clustering of taxa in morphospace, differences between left and right ears (Racicot, Darroch &

93   Kohno, 2018), or only focused on population-level differences within a single species (Schnitzler

94   et al., 2017). Our 18 conspecific specimens represent a large advance in our ability to quantify

95   intraspecific variation in this feature.

96

97   **Material and Methods**

98

99   *DATA COLLECTION*

100   We chose the harbour porpoise (*Phocoena phocoena*) for this study because of the large

101   number of specimens in natural history collections making it possible to obtain a large sample

102   size for the species, something that is not available for most odontocetes. We assumed that

103 results from *P. phocoena* can be generalised across odontocetes, but were unable to test this

104 assumption with the available data.

105

106 *3D shape data*

107 TP collected the majority of the 3D shape data for an earlier paper (Park et al., 2019). 18

108 cochleae of *P. phocoena* were added to this study by MCIM (Table S1). For all cochleae we

109 obtained µCT scans of the periotics - the bone containing the inner ear - of 52 species

110 (comprising 94% of extant genera) of odontocetes by imaging osteological specimens from

111 museum collections. Scan parameters for cochleae of *P. phocoena* are available in Table S2

112 and scan parameters for previously collected data on the other species are available from Park

113 *et al.* (2019). For this study we obtained periotics from 18 specimens of *P. phocoena*. Of these

114 15 are from the left-hand side of the skull, and three from the right-hand side; 17 are from the

115 UK coast, and one is from the USA coast; four are female, five are male, and nine are unsexed

116 (see Table S3). All specimens are adult animals.

117

118 Using these data, we reconstructed 3D models of the inner ears using the segmentation and

119 thresholding editors in Avizo 9.0 (Visualization Sciences Group-a FEI Company, 2016), and

120 then cleaned the resulting 3D models using Geomagic Wrap® (3D Systems, 2017). Next we

121 landmarked the digital models with 40 sliding semilandmark curves comprising a total of 361

122 landmarks (Figure 1), using IDAV Landmark (Wiley, 2005). The position of these curves

123 followed the protocols of Costeur *et al.* (2018), using only the curves from the cochlea because

124 the semi-circular canals are not phylogenetically or ecologically informative in odontocetes

125 (Costeur et al., 2018). Landmarks were placed by a single investigator (TP) to avoid multi-user

126 bias in placement. Finally we exported coordinates from the landmarked models as .pts files

127 from IDAV Landmark (Wiley, 2005).

128

129   *Geometric morphometrics*

130   We performed all geometric morphometric analyses in R version 3.4.3 (R Core Team, 2019),

131   using the R package GEOMORPH (Adams, Collyer & Kaliontzopoulou, 2018). First, we used

132   Generalised Procrustes Analysis (GPA) to remove the effects of position, scale and orientation.

133   The semilandmarks were 'slid' along their tangent vectors between adjacent semilandmarks

134   until their positions minimised the shape difference between specimens (using the Procrustes

135   distance criterion), to reduce the effect of their initially arbitrary placement (Bookstein et al.,

136   1999; Gunz, Mitteroecker & Bookstein 2005; Adams, Rohlf & Slice, 2013). We then performed a

137   principal component analysis (PCA) on the resulting Procrustes coordinates using the

138   'plotTangentSpace' function; and used these principal components (PCs) in further analyses.

139

140   *Linear measurements*

141   One of us (MCIM) took the following measurements of the cochlea (Figure 2) in Avizo 9.2.0

142   using the *Measure* and *Spline Probe* tools and following protocols from Park*,* Fitzgerald &

143   Evans (2016): (1) cochlear height; (2) cochlear width; (3) number of turns of cochlear canal; (4)

144   cochlear volume; (5) cochlear canal length; (6) length of secondary spiral lamina (SSL); (7)

145   basal ratio (cochlear height/cochlear width); (8) axial pitch (cochlear height/number of turns);

146   and (9) percentage of extent of secondary spiral lamina ((secondary spiral lamina

147   length/cochlear canal length)*100). We also measured (10) width of basal turn perpendicular to

148   cochlear width (W2); (11) maximum distance between turns of the cochlea (ITD); and (12) area

149   of fenestra cochlearis (FC) following Churchill *et al.* (2016). Where possible (n = 7) for the

150   specimens of *P. phocoena,* we also collected condylobasal length (skull length in mm) as a

151   proxy for body size as body mass data was not available for all specimens.

152

153   We chose these measurements because they relate to auditory function in cetaceans. Cochlear

154   height (1) and width (2, 10) relate to the auditory abilities of odontocetes (West, 1985; Ketten &

155   Wartzok, 1990). The number of turns of the cochlear canal (3) also relates to auditory abilities

156   and differs among mammal groups (West, 1985; Ketten & Wartzok, 1990; Ekdale & Rowe,

157   2011). Cochlear volume (4) is used as an estimate of size which relates to body mass and

158   length (Racicot et al., 2016). Cochlear canal length (5) correlates with body size in odontocetes

159   and is used as a quantitative measurement for comparison (Ketten, 1992a). Length of

160   secondary spiral lamina (6) was measured to calculate percentage of extent of secondary spiral

161   lamina (9), an indicator of the stiffness of the basilar membrane that is associated with high

162   frequency hearing (Ekdale & Racicot, 2015; Park et al., 2017a). Basal ratio (7) and axial pitch

163   (8) are two quantitative ways to examine cochlear shape and size for comparative studies

164   (Racicot et al., 2016). Both measurements are negatively correlated with frequency of hearing

165   (Ketten & Wartzok, 1990). Taxa that use high frequency hearing also tend to have a larger inter-

166   turn distance (11; Ekdale & Racicot, 2015). The area of the fenestra cochleae (12) tends to be

167   larger in low frequency species, although beaked whales and sperm whales also have large

168   areas.

169

170   We then performed a principal component analysis (PCA) on the scaled and centred linear

171   measurements listed above using the 'prcomp' function in R; and used these principal

172   components (PCs) in further analyses.

173

174   All data used in this study are available on the NHM Data Portal (data.nhm.ac.uk). The 3D

175   shape data for cochleae of *P. phocoena*, linear measurements of all cochleae, and other data

176   used in this paper are deposited in Martins, Park & Cooper (2019). 3D shape data for cochleae

177   of other odontocetes were collected for Park *et al.* (2019) and are deposited in Park *et al.*

178   (2018).

179

180   *ANALYSES*

181

182   All analyses were carried out in R version 3.4.3 (R Core Team, 2019), and reproducible R

183   scripts are available on GitHub (github.com/nhcooper123/intraspecific-porpoise; Cooper,

184   Martins & Park, 2020).

185

186   *Quantifying intraspecific variation in Phocoena phocoena*

187   To quantify intraspecific variation in cochleae of *P. phocoena* we estimated disparity for all

188   principal components of the 3D shape data and linear measurements separately, using the R

189   package dispRity (Guillerme, 2018). We used the sum of variances and median centroid

190   distance metrics as our disparity metrics. For each linear measurement we also calculated the

191   coefficient of variation (CV), i.e. (standard deviation/mean)*100. Generally values of CV below

192   30% represent low levels of variation (Brown, 1998), and previous studies that found low levels

193   of intraspecific variation in cochleae find values of CV below 20% (Ekdale & Rowe, 2011;

194   Mennecart & Costeur, 2016; Racicot, Darroch & Kohno, 2018). We also calculated values of CV

195   for our measurements using data from previous studies of cochleae intraspecific variation in

196   odontocetes so we could compare the values to those of *P. phocoena.* Where these studies

197   contained right and left cochleae from one individual we first took the mean for the individual,

198   then calculated CV across individuals.

199

200   *Comparing intraspecific variation and interspecific variation*

201   Quantifying the amount of intraspecific variation alone does not tell us whether intraspecific

202   variation may confound the results of studies of interspecific variation. To investigate this we

203   tested whether there were significantly higher levels of variation in cochlear shape among *P.*

204   *phocoena* and the other odontocetes than within the specimens of *P. phocoena*. For the 3D

205   shape data, we first conducted a Procrustes MANOVA (multivariate analysis of variance) using

206   the 'proc.lm' function from GEOMORPH using the Procrustes aligned coordinates as the

207   response variable, and the grouping variable (*P. phocoena* vs. other odontocetes) as the

208   explanatory variable. Next we fitted a standard MANOVA using the 'manova' function in R, with

209   the first 26 PC axes scores (comprising 95% of the variance in cochlear shape) as the response

210   variable. To identify which PCs, if any, were most important in driving any differences among

211   the cochleae of *P. phocoena* and other odontocetes we also used analysis of variance (ANOVA)

212   to test each PC separately. To account for multiple testing we Bonferroni corrected our p values.

213   Finally, we repeated the latter two analyses, i.e. MANOVA and ANOVAs, using the first six PC

214   axes (comprising 95% of the variance) extracted from the linear measurements.

215

216   We visualised specimen position in 2D morphospace across combinations of PCs 1, 2, and 3

217   (3D shape data) and PCs 1-4 (linear measurement data) as these PCs were significant in our

218   ANOVAs (see Results). To aid the interpretation of our results we also created morphospace

219   plots of PC1 and PC2 where species were coloured based on taxonomic family and a selection

220   of ecological variables; specifically habitat (riverine = > 50% of time spent in river, nearshore = >

221   50% of time spent in coastal waters, oceanic = > 50% of time spent in pelagic waters), diet

222   (generalist = consumes a wide variety of prey types, fish = > 50% of diet is fish, cephalopods =

223   > 50% of diet is cephalopods), feeding mode (raptorial = prey capture occurs mainly via

224   snapping or ram feeding, suction = prey capture occurs mainly via suction, i.e. obligate suction

225   feeders), and dive type (shallow = maximum estimated dive depth less than 100m; middle depth

226   = maximum estimated dive depth ~500m; deep = maximum estimated dive depth ~ 1000m; very

227   deep = maximum estimated dive depth greater than 1000m) and hearing type (NBHF = known

228   or presumed to use narrow band high-frequency sonar; Type 2 = do not use NBHF). Some taxa

229   fall into several of these categories so we assigned these to composite categories e.g. *Tursiops*

230 is classed as nearshore/oceanic. Details of the categories for each species, and the references

231 these were taken from, are in Tables S4 and S5. We also tested whether these variables were

232 correlated with overall cochlear shape using MANOVAs.

233

234 *Sensitivity analyses*

235 Because we have 18 specimens of *P. phocoena* and only one specimen of each of the other

236 species, cochleae of *P. phocoena* will have a stronger effect on the principal components

237 scores than other cochleae, distorting the morphospace. Ideally we would collate an equal

238 number of cochleae for each species, but these specimens simply do not exist in these numbers

239 for the majority of species. Specimens of *P. phocoena* are the most readily available because

240 they are common and often strand (Coombs et al., 2019). Their skulls are also small enough to

241 store in bulk within natural history collections. To determine whether this distortion problem

242 influenced our conclusions, we sampled two specimens of *P. phocoena* from the 18 and then

243 repeated the GPA, PCA, and MANOVA analyses described above for the 3D shape dataset.

244 We repeated this for every possible combination of two specimens of *P. phocoena*, and then for

245 every combination of three specimens and so on until reaching every combination of 17

246 specimens.

247

248 To determine whether our results apply only to broad-scale taxonomic comparisons, i.e.

249 *P. phocoena* vs. other odontocetes, we also repeated our GPA, PCA and MANOVA analyses

250 comparing *P. phocoena* with other species of *Phocoena* only (*P.dioptrica, P.sinus,*

251 *P.spinipinnis*). 3D shape analyses used PC1 - PC14, and linear measurement analyses used

252 PC1 - PC7 as these were the PCs required to account for 95% of the variation in cochlear

253 shape in each case.

254

255 Finally, variation within cochleae of *P. phocoena* may be explained by the differences among

256 the specimens (Table S3) in terms of whether the cochleae came from the left or right side of

257 the animal, their sex, origin or body size. We therefore tested whether variation in cochleae of *P.*

258 *phocoena* was significantly correlated with the side of the head the cochlea came from, or the

259 sex, origin (UK vs. USA) or skull length (as a proxy for body size) of the specimens. We

260 repeated our GPA and PCA analyses for the specimens of *P. phocoena* only, and then used the

261 resulting Procrustes coordinates or PCs as response variables in Procrustes ANOVAs or

262 MANOVAs with either side, sex, origin or log skull length as predictors. 3D shape analyses used

263 PC1 - PC16, and linear measurement analyses used PC1 - PC7 as these were the PCs

264 required to account for 95% of the variation in cochlear shape in each case. For 3D shape

265 analyses where sex or skull length were the predictors we used only PC1 - PC6 (accounting for

266 75% of the variation on cochlear shape) because there were not enough observations to fit

267 MANOVAs for all 16 PCs.

268

269 **Results**

270

271 *3D shape variation*

272 The first 26 principal components (PC) axes comprised 95% of the variance in cochlear shape.

273 PC1 accounted for 34.08% of the cochlear shape variation (Figure 3), and represents cochleae

274 that are positively correlated with having a less oval-shaped and more circular fenestra vestibuli.

275 PC2 accounted for 12.15% of the shape variation and represents cochleae that are negatively

276 correlated with having a radial expansion of the scala tympani (i.e. a tympanal recess, *sensu*

277 Park et al., 2017b; Park, Fitzgerald & Evans, 2017c; Figure 3), and PC3 accounted for 8.956%

278 of the shape variation (Figure 3), and represents cochleae that are positively correlated with

279 having cochlear canals that do not overlap the basal turn.

280

281 *Linear measurements*

282 The first six PC axes comprised 95% of the variance in cochlear linear measurements. PC1

283 accounted for 54.28% of the variation (Figure 4), which is best described by a combination of

284 cochlea width, W2, ITD and cochlea height. PC2 accounted for 18.65% of the variation best

285 described by basal ratio and extent of secondary spiral lamina (Figure 4). PC3 (8.579% of the

286 variation) and PC4 (6.355% of the variation) are best described by secondary spiral lamina

287 extent and number of turns respectively (Figure 4).

288

289 *Quantifying intraspecific variation in Phocoena phocoena*

290 The disparity of *P. phocoena* in the 3D shape data (sum of variances = 0.014, median centroid

291 distance = 0.100) is lower than in the linear measurement data (sum of variances = 1.487,

292 median centroid distance = 1.091), although the morphospace occupied is larger compared with

293 other odontocetes in the 3D shape data (Figures 3 and 4). Values of CV vary across the linear

294 measurements (Table 1) but all are below 30% and only area of fenestra cochlearis (FC)

295 exceeds 20%. This reflects low levels of intraspecific variation in cochleae of *P. phocoena*.

296 Values of CV for all measurements except cochlear volume, axial pitch and ITD are higher than

297 those found in previous studies (Table 1; Table S6).

298

299 *Comparing intraspecific variation and interspecific variation*

300 There was significantly more variation among odontocete species than within the specimens of

301 *P. phocoena* (Table 2; Figures 3 and 4) when the entire shape of the cochlea was considered,

302 whether we used Procrustes coordinates or PCs from the 3D shape data or linear

303 measurements.

304

305 When we investigated individual PC axes (Table S7), for the 3D shape data we found that only

306 PC1 and PC3 of the 26 PCs significantly differed between *P. phocoena* and other odontocetes,

307 and for linear measurements only PC1, PC2 and PC4 (only PC1 and PC2 are significant after

308 Bonferroni correction) showed significant differences among the two groups.

309

310 Figures S1 and S2 show how species are spread across PC1/PC2 morphospace according to

311 taxonomic family, habitat, diet, feeding mode, dive type and hearing type. All of these variables

312 except feeding mode were also significantly correlated with cochlear shape (Table S8).

313

314 *Sensitivity analyses*

315 In our sensitivity analyses, MANOVAs for 3D shape data remained significant provided at least

316 four specimens of *P. phocoena* were included in the analyses (Figures S3 and S4).

317

318 When the specimens of *P. phocoena* were compared to other *Phocoena* species only, there

319 was still significantly less variation within the specimens of *P. phocoena* using Procrustes

320 coordinates from the 3D shape data (but not for PCs) and linear measurements (Table S9).

321

322 Variation in cochleae of *P. phocoena* was not significantly correlated with the side of the head

323 the cochlea came from, the sex, or skull length of the specimens for either 3D shape data or

324 linear measurements (Table S10). Origin (UK vs. USA) was not significantly correlated with

325 variation in cochleae of *P. phocoena* for the linear measurements, but was significantly

326 correlated with variation in the 3D shape data (p = 0.038; after Bonferroni correction p = 0.152).

327 This is driven by the large negative value of PC1 for the USA specimen. To ensure this did not

328 influence our intraspecific variation results (see above) we repeated our 3D shape analyses

329 (including the GPA and PCA steps) removing this specimen (NHMUK_1873.6.3.45). The results

330 are qualitatively identical to those including the USA specimen (Table S11).

331

332   **Discussion**

333

334   In this study, we tested whether intraspecific variation is a major confounding factor in cross-

335   species analyses by comparing variation within the cochleae of the harbour porpoise (*Phocoena*

336   *phocoena*) with those across a broad sample of other odontocete species. Levels of

337   intraspecific variation in cochleae of *P. phocoena* were lower than the levels of variation seen

338   across other odontocetes. *P. phocoena* showed higher values of coefficient of variation (CV)

339   overall (ranging from 3.394 - 26.80%; Table 1) compared to other odontocetes (ranging from 0 -

340   23.33%; Table S6), however, for most cochlear measurements the values of CV were similar.

341   The greatest difference in values of CV was for the fenestra cochlearis, which may be artificially

342   variable due to a lack of standardised protocol for measuring it (Racicot et al., 2016; Churchill et

343   al., 2016). Intraspecific variation in *P. phocoena* might be expected to be higher than in other

344   odontocetes because of their large geographic range which stretches across almost all shallow

345   cool temperate to subpolar waters of the northern hemisphere, within which they encounter

346   many different kinds of habitats (Jefferson, 2014). This suggests that *P. phocoena* should

347   generally have a higher level of intraspecific variation compared to other odontocetes with more

348   limited geographic ranges and habitats. We cannot test this here, due to the paucity of studies

349   containing more than one specimen for each species, but future research should compare the

350   values of CV found for *P. phocoena* here with those of another similarly widespread species, for

351   example *Tursiops truncatus* (common bottlenose dolphin) or *Delphinus delphis* (short-beaked

352   common dolphin).

353

354   Although there was significantly more variation among odontocete species than among the

355   specimens of *P. phocoena*, for at least some principal components, specimens from other

356   species overlapped with *P. phocoena.* Cochlear morphology was also related to habitat, diet,

357   mode of echolocation, and dive type (Table S8), suggesting that species identity alone is not

358   enough to explain variation across all principal components. In addition, not all of the specimens

359   of *P. phocoena* cluster together tightly (Figure 3). This could reflect differences in cochlear

360   morphology among populations (although this does not appear to be the case for these data as

361   only one specimen is from the USA and the rest are from the UK), or variability within the

362   species. Cochleae also exhibit convergent evolution (Park et al., 2019), so individuals or

363   species that live in similar acoustic environments (regions where variables such as water

364   temperature, pressure, and salinity result in sound travelling through the water at similar

365   velocities) as *P. phocoena* may have similar cochleae. The relatively low levels of intraspecific

366   variation found in *P. phocoena* adds further support for the acoustic environment being a

367   constraint on cochlear morphology. This is additionally demonstrated in the morphospace plot of

368   PC1 and PC2 (Figure 3), the area occupied by *P. phocoena* is shared with taxa such as *P.*

369   *sinus* (vaquita)*, Cephalorhynchus commersonii* (Commerson's dolphin), and *Inia geoffrensis*

370   (Amazon river dolphin), all of which also live in shallow waters. However, other taxa that spend

371   more time in deeper waters, for example *Pseudorca crassidens* (false killer whale) and *Tursiops*

372   *truncatus*, also occupy this region of morphospace, indicating that additional factors are also in

373   play, although they may also frequent shallower waters or have coastal ecotypes (Jefferson,

374   Webber & Pitman, 2015). Previous studies have also suggested that constraints on cochlear

375   morphology are strong, due to several factors including frequency propagation (Manoussaki et

376   al., 2008), spatial constraints (Pietsch et al., 2017), and its vital importance for survival in

377   odontocetes (Ketten,1992a). As such the capacity for elaboration or innovation in cochlear

378   shape may be limited, which could force all odontocete cochleae to fall within the same limited

379   morphospace. Other sources of error, such as mislabelling of specimens in collections or errors

380   in µCT scanning or landmarking, are unlikely due to the care taken during these stages, and

381   assistance from expert curators in museum collections.

382

383 Although, as described above, the specimens of *P. phocoena* did not cluster together closely in

384 our PC plots, we note that PC plots only show two dimensions of the data, not all of the 26 PC

385 axes that comprised 95% of the variance in cochlear shape. Our MANOVA results, however,

386 showed that there was significantly more variation in cochlear shape among odontocete species

387 than within *P. phocoena* specimens. This highlights that clustering (or not) in several PC axes,

388 does not necessarily equate to clustering across the entire morphospace, although limitations in

389 how we visualise more than three dimensions mean that PC plots are still valuable visualisation

390 tools. In addition, although PCAs on different datasets are not directly comparable, shape

391 variation in the cochleae of odontocetes appears to be spread across a much higher number of

392 PCs than that seen in most studies involving skulls (e.g. Cardini & Polly, 2013; McCurry et al.,

393 2017; Page & Cooper 2017; Randau, Sanfelice & Goswami, 2019).

394

395 **Conclusion**

396

397 The 18 specimens of *P. phocoena* used in this study represent the highest number of records

398 for one species used in intraspecific studies of cochlear morphology (the next highest is 12

399 individual sperm whales; Schnitzler et al., 2017) in cetaceans. Overall, our results show that

400 intraspecific variation of cochlea shape in *P. phocoena* is lower than interspecific variation of

401 cochlea shape across odontocetes. Assuming that interspecific variation of *P. phocoena* is

402 representative of patterns across odontocetes, this suggests we can still be reasonably

403 confident in our conclusions when using n = 1 for comparative studies of cochlea morphology,

404 as done in most previous studies (Ekdale & Racicot, 2015; Ekdale, 2016; Park, Fitzgerald &

405 Evans, 2016; Park et al., 2017a; Park et al., 2017b). It is possible that *P. phocoena* is not

406 representative of patterns across odontocetes. If *P. phocoena* is less variable than other

407 odontocetes this would reduce our confidence that using just one specimen for comparative

408 studies is sufficient. However, as discussed above, we believe this is unlikely because *P.*

409   *phocoena* has a broad geographic range, and shows variability in habitat use and trophic

410   ecology across that range (Bjørge 2003; Jefferson 2014). As such we speculate that *P.*

411   *phocoena* is instead likely to be more variable than most species making our conclusions more

412   conservative. Ideally, future studies should use multiple cochleae for each species, but where

413   this is impossible due to the rarity of specimens, or expense of specimen loans and/or μCT

414   scanning, this should not influence the conclusions of comparative studies, assuming results

415   from *P.phocoena* can be generalised across odontocetes.

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628 **Acknowledgements**

629 We thank: Oliver Lambert (IRNSB), Gabriel Aguirre Fernandez (UZH), Brett Clark and Vincent

630 Fernandez (NHM), Alistair Evans (MU) and Loïc Costeur (UB) for scanning several of the

631 specimens in this study; Richard Sabin and Roberto Portela Miguez (NHM), Erich Fitzgerald

632 and Karen Roberts (NMV), Neil Duncan and Eileen Westwig (AMNH) for access to specimens.

633

634

635 **Data and code availability**

636 All data are available on the NHM Data Portal (data.nhm.ac.uk). 3D data for cochleae of *P.*

637 *phocoena*, linear measurements of all cochleae, and other data used in this paper are in

638 Martins, Park & Cooper (2019; doi.org/10.5519/0091362). 3D data for cochleae of the other

639 odontocete species are available from Park *et al.* (2018; doi.org/10.5519/0082968).

640 Reproducible R scripts are available on GitHub (github.com/nhcooper123/intraspecific-porpoise;

641 Cooper, Martins & Park, 2020).

[i]Table 1: Coefficients of variation (CV) of 12 linear measurements for 18 Phocoena phocoena specimens, along with the mean CV of these measurements from previous odontocete studies (see Table S3 for raw data), the number of studies featuring each measur

SSL = length of secondary spiral lamina; W2 = Width of basal turn perpendicular to cochlear width; ITD = Inter-turn distance, maximum distance between turns; FC = area of fenestra cochlearis (FC). No previous studies measured intraspecific variation in SSL or extent of SSL.

1   *Table 1: Coefficients of variation (CV) of 12 linear measurements for 18 Phocoena*

2   *phocoena specimens, along with the mean CV of these measurements from previous*

3   *odontocete studies (see Table S3 for raw data), the number of studies featuring each*

4   *measurement (N), and the maximum number of individuals in each of these previous*

5   *studies. SSL = length of secondary spiral lamina; W2 = Width of basal turn*

6   *perpendicular to cochlear width; ITD = Inter-turn distance, maximum distance between*

7   *turns; FC = area of fenestra cochlearis (FC). No previous studies measured intraspecific*

8   *variation in SSL or extent of SSL.*

	This study	Previous studies		
measurement	**CV (%)**	**Mean CV (%)**	**N**	**maximum number of individuals**
cochlea height	7.783	6.793	8	12
cochlea width	4.842	3.364	4	12
number of turns of the cochlear canal	3.394	2.478	7	5
cochlear volume	8.015	10.23	1	2
cochlear canal length	6.189	3.401	4	12
SSL	6.619	-	-	-
basal ratio	8.846	0.000	1	2
axial pitch	8.688	8.736	5	4

extent of SSL	3.089	-	-	-
W2	7.612	2.544	2	5
ITD	11.93	12.622	2	5
FC	**26.80**	9.838	2	5

Table 2. Results of Procrustes MANOVA and standard MANOVA analyses using either Procrustes aligned coordinates [i]or principal components (PCs) accounting for 95% of the variance as the response variable, and whether a specimen was Phocoena phocoena

3D shape data analyses used PCs 1 to 26; linear measurements analyses used PCs 1 to 6.

1   *Table 2. Results of Procrustes MANOVA and standard MANOVA analyses using either*

2   *Procrustes aligned coordinates or principal components (PCs) accounting for 95% of*

3   *the variance as the response variable, and whether a specimen was Phocoena*

4   *phocoena or another odontocete species as the explanatory variable. 3D shape data*

5   *analyses used PCs 1 to 26; linear measurements analyses used PCs 1 to 6.*

3D shape data				
test	**df**	**F/approx F**	**Pillai**	**p**
Procrustes ANOVA	1,67	6.005	NA	0.001
MANOVA	1,67	8.623	0.842	< 0.001
Linear measurements				
MANOVA	1,67	9.090	0.468	< 0.001

Figure 1

Endocast of NHMUK_SW1934.31 in anterior, lateral, dorsal and ventral views showing semi-landmark curves.

A-anterior view, B-lateral view, C-dorsal view, D-ventral view. Dotted lines show the semi-landmark curves.

Secondary Spiral Lamina

Primary bony Lamina

Anterior View

A

Fenestra Vestibuli

Fenestra Cochlearis

Lateral View

B

Posterior Semi-Circular Canal

Lateral Semi-Circular Canal

Anterior Semi-Circular Canal

Dorsal View

C

Cochlear Canal

Vestibular Curve

Ventral View

D
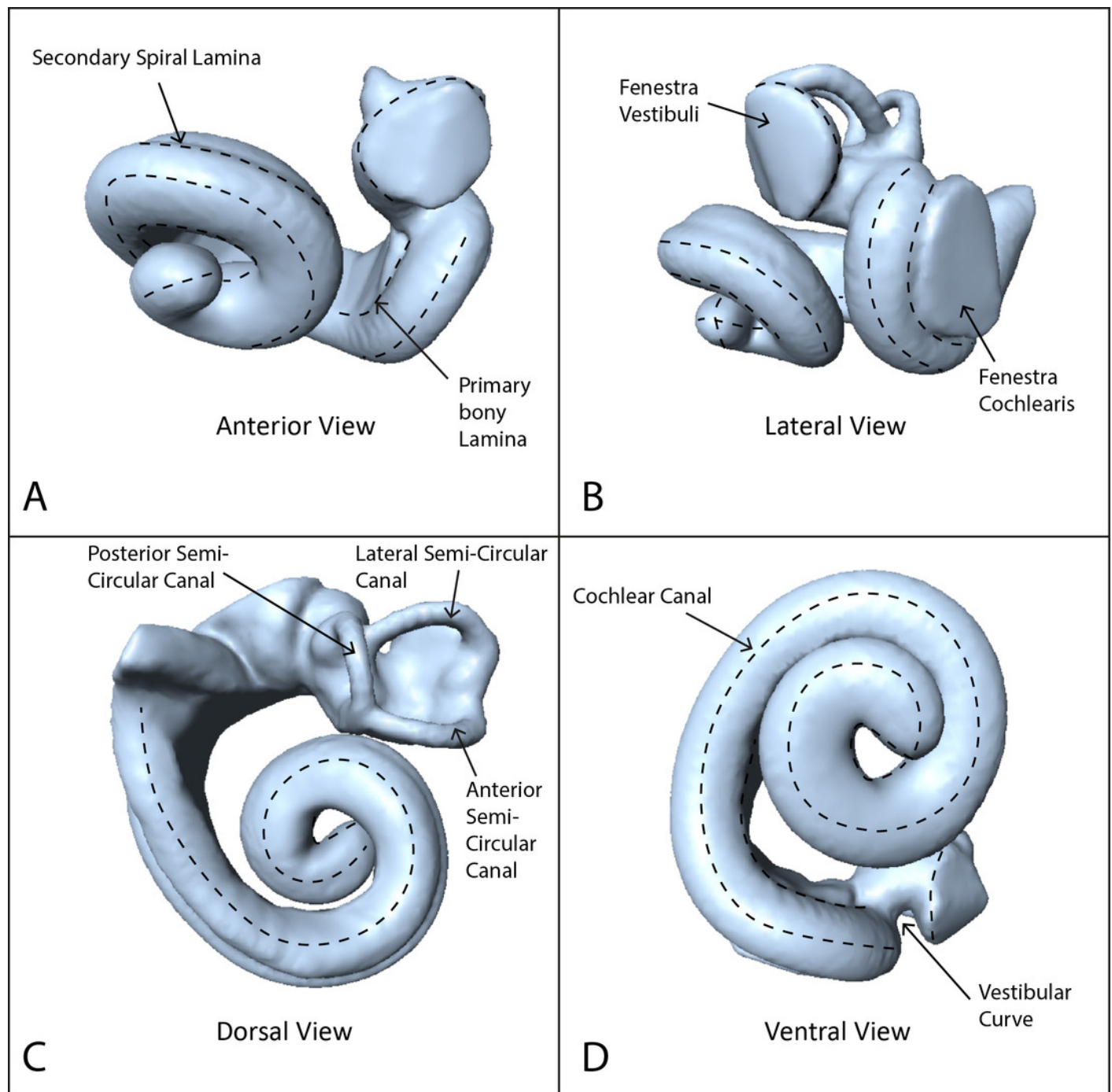
Figure 2

Line drawing of Phocoena phocoena (NHMUK_SW1934.31) cochlea in vestibular and posterior view, illustrating key measurements.

A-vestibular view, B-posterior view
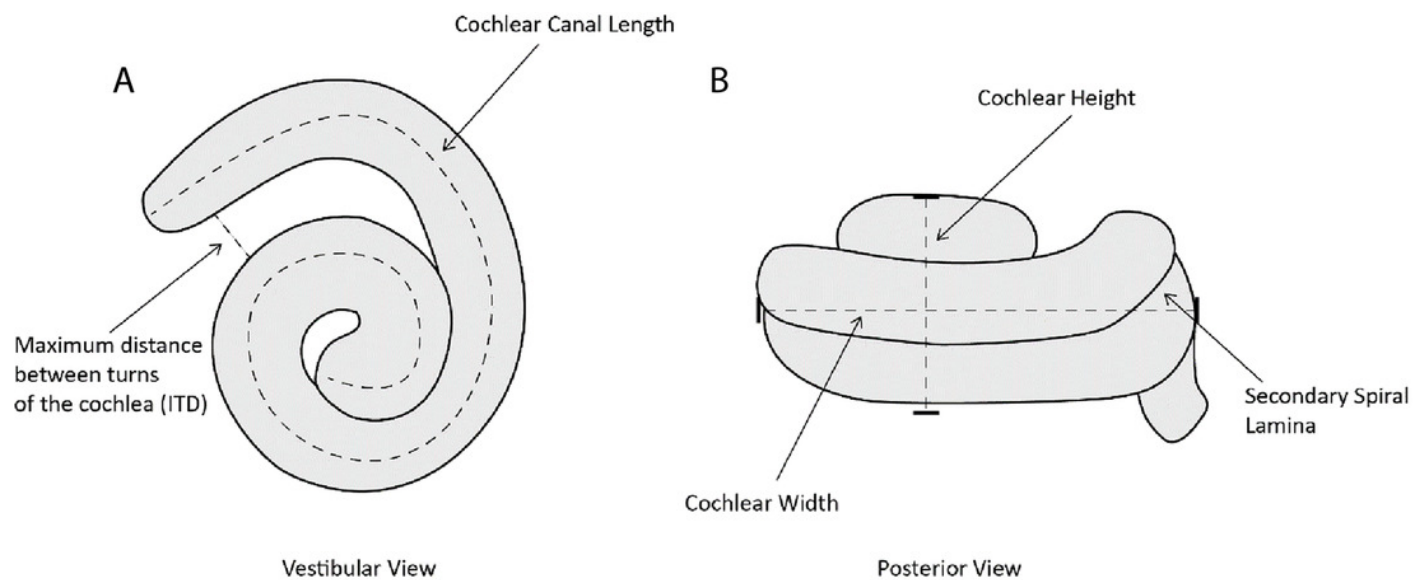
Figure 3

Principal components (PC) plots for 3D cochlea shape data for PCs 1-3.

Purple points and convex hulls are Phocoena phocoena specimens; green points are all other odontocete species. Numbers in brackets show the percentage variance explained for each PC.
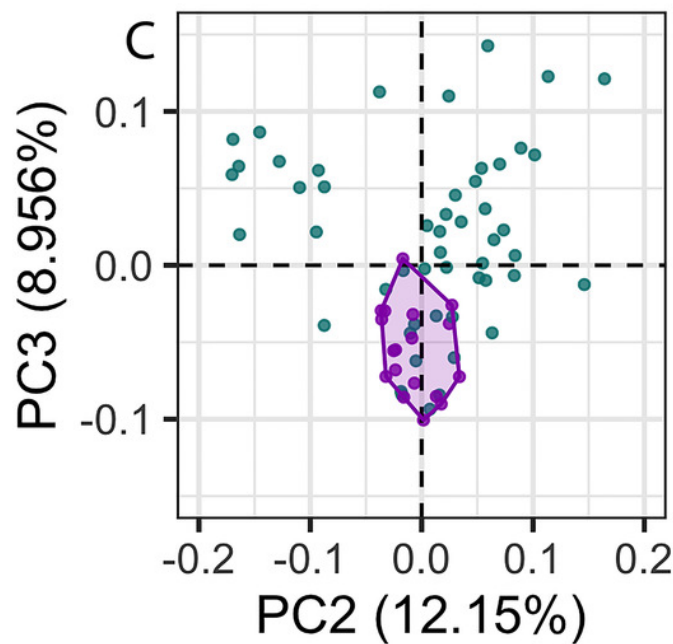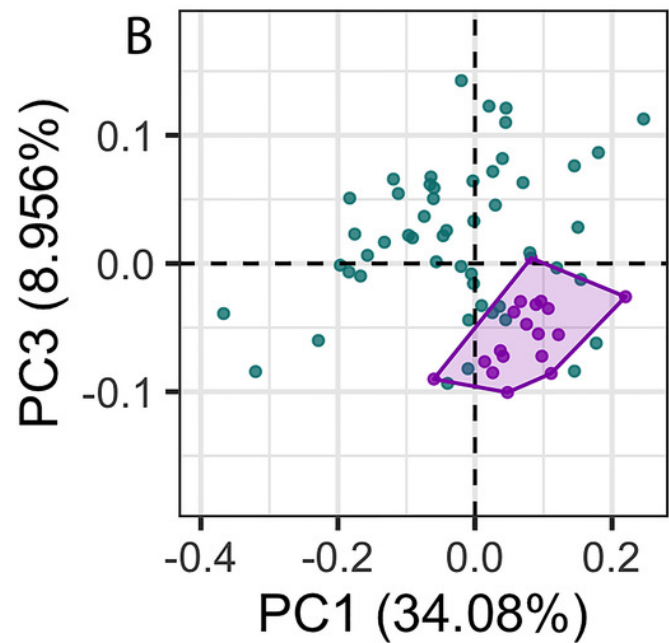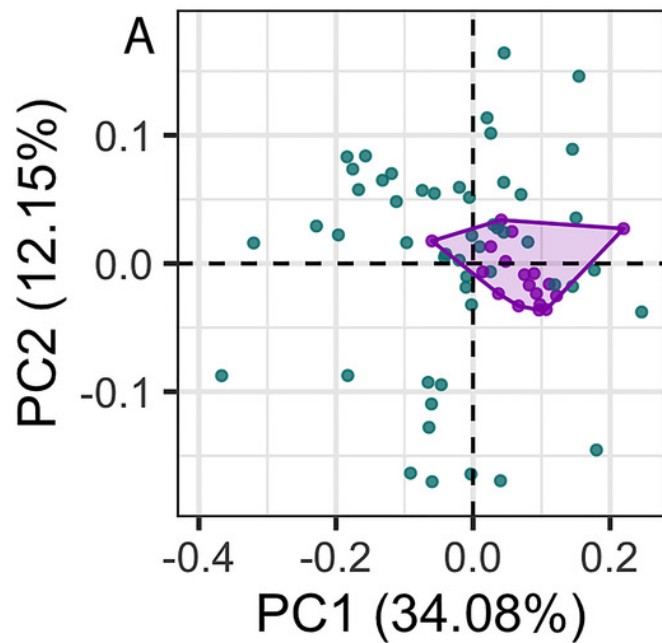
Figure 4

Cochleae of taxa near the extremes of the morphospace shown in figure 3 (not to scale)

A: Mesoplodon mirus (PC1 max); B: Globicephala melas (PC1 min); C: Sousa teuszii ; D: Tasmacetus shepherdi.

A

*Mesoplodon
mirus*

B

*Globicephala
melas*

C

*Sousa
teuszii*

D

*Tasmacetus
shepherdi*