1 **TITLE**

2 A multilevel society of herring-eating killer whales indicates adaptation to prey characteristics

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4 Sara B. Tavares[a,*], Filipa I. P. Samarra[a,b], Patrick J.O. Miller[a]

5 [a]Sea Mammal Research Unit, Scottish Oceans Institute, University of St Andrews, St

6 Andrews, Fife KY16 8LB, United Kingdom

7 [b]Marine Research Institute, Skulagata 121, Reykjavik, Iceland

8 [*]Address for reprint requests and correspondence: Sara B. Tavares, Sea Mammal Research

9 Unit, School of Biology, University of St Andrews, Bute Building, St Andrews KY16 9TS,

10 Scotland, United Kingdom. Telephone: +44 01334 463607. E-mail address: sbt3@st-

11 andrews.ac.uk.

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13 **RUNNING TITLE**

14 Multilevel society of herring-feeding killer whales

15

16 **ABSTRACT**

17 Non-social factors can influence animal social structure. In killer whales (*Orcinus orca*), fish-

18 vs. mammal-eating ecological differences are regarded as key ecological drivers of their

19 multilevel society, including group size, but the potential importance of specific target prey

20   remains unclear. Here, we investigate the social structure of herring-eating killer whales in

21   Iceland and compare it to the described social structures of primarily salmon- and seal-eating

22   populations in the Northeast Pacific, which form stable coherent basic units nested within a

23   hierarchical multilevel society. Using 29023 photographs collected over 6 years, we examined

24   the association patterns of 198 individuals combining clustering, social network structure and

25   temporal patterns of association analysis. The Icelandic population had largely weak but non-

26   random associations, which were not completely assorted by known ranging patterns. A

27   fission-fusion dynamic of constant and temporary associations was observed but this was not

28   due to permanent units joining. The population-level society was significantly structured but

29   not in a clear hierarchical tier system. Social clusters were highly diverse in complexity and

30   there were indications of subclusters. There was no indication of dispersal nor strong sex

31   differences in associations. These results indicate that the Icelandic herring-eating killer whale

32   population has a multilevel social structure without clear hierarchical tiers or nested coherent

33   social units, different from other populations of killer whales. We suggest that local ecological

34   context, such as the characteristics of the specific target prey (e.g. predictability, biomass and

35   density) and subsequent foraging strategies may strongly influence killer whale social

36   association patterns.

37   **Key words:** ecological context, hierarchical structure, multilevel societies, social structure,

38   killer whale, orca

INTRODUCTION

The sociality of a group-living species is driven by a trade-off between its specific ecological, evolutionary and social contexts (Krause and Ruxton 2002). Non-social factors, particularly predation risk, finding/catching food, defending resources and resource patchiness, can strongly determine the social structure of simple social systems and provide the context for the development of complex ones (Jarman 1974; Wrangham 1980; Whitehead 2008a). General socioecological frameworks have been developed for various taxa, characterizing how such factors can affect sociality by using broad characteristics of a species/genera, such as occurrence of group foraging, group size or mating system (Emlen and Oring 1977; Wrangham 1980; Gowans et al. 2007). However, with the increase of within-species studies (e.g. Barton et al. 1996, Sinha et al. 2005; Whitehead et al. 2012), it seems clear that it is important to emphasize intraspecific variation which likely reflects variability under different ecological conditions. Investigating different populations of the same species across ecological gradients is therefore valuable to evaluate the influence of ecological drivers.

Multilevel societies are among the social systems found on group-living species and have been described as hierarchical structures of nested social levels (i.e. discrete social stratification of associations among individuals into tiers) with at least one stable core unit (Wittemyer et al. 2005; Grueter, Matsuda, et al. 2012; Grueter, Chapais, et al. 2012). Recently, de Silva and Wittemyer (2012) suggested that multilevel societies should be seen along a continuum of nestedness and that some might present less clearly hierarchically stratified social levels that transition more gradually. Commonly, multilevel societies exhibit fission–fusion dynamics, with frequent association, disassociation, and reassociation of

61 groups of individuals (e.g. Connor et al. 1992). Although multilevel societies have been

62 studied more extensively in terrestrial mammals, particularly in primates (see Grueter,

63 Chapais, et al. 2012), such social systems are also observed in cetaceans and intraspecific

64 variation has been reported (Connor et al. 1998; Whitehead et al. 2012). For example, female

65 sperm whales (*Physeter macrocephalus*) form long-term stable social units which, in the

66 Pacific, temporarily group with other units with which they share part of the acoustic

67 repertoire, but rarely group in the North Atlantic, possibly due to differences in predation risk

68 (Whitehead et al. 2012).

69 One well-described tiered multilevel society among cetaceans is that of the 'resident' fish-

70 eating killer whale (*Orcinus orca*) population in the Northeast Pacific, hereafter termed

71 residents. The basic unit of this society is the matriline, consisting of an oldest surviving

72 female and her philopatric descendants, remaining associated with their mother for life (Bigg

73 et al. 1990; Baird and Whitehead 2000; Barrett-Lennard 2000). Within matrilineal units,

74 individuals associate strongly and at very similar levels, while matrilineal units can frequently

75 interact (Bigg et al. 1990; Baird and Whitehead 2000; Ford et al. 2000). Matrilines that share

76 at least part of their acoustic repertoire, probably due to common maternal ancestry, form the

77 next social level, the clan (Ford 1991). Different clans have no calls in common, and

78 matrilines from the same or different clans frequently travel together (Ford 1991). The next

79 and broadest social level (just under population) is the community, consisting of matrilines

80 that share a common area and associate periodically but not with those of another community

81 (Bigg et al. 1990). This multilevel society is based on distinct fission-fusion patterns of whole

82 coherent family-based units, where stable matrilineal units collectively associate more

83 frequently with other close kin units. The 'sub-pod' and 'pod' were traditionally considered

84 intermediate social levels between the matriline and the clan, consisting of matrilines with

85 recent maternal ancestry that often (> 95% and 50% of the time, respectively) travelled

86 together (Bigg et al. 1990; Ford 1991). However, recent studies have shown fluctuations in

87 the reoccurrence of associations between matrilines (Ford and Ellis 2002; Parsons et al. 2009),

88 as well as changes in the pods originally described (Ford et al. 2000), leading to suggestions

89 that the term 'pod' should only be used to designate aggregations of killer whales or as a

90 synonym for matriline (Ford and Ellis 2002).

91 Intraspecific variation in sociality among killer whales is believed to relate to prey-type.

92 Northeast Pacific resident killer whales mainly prey on salmon, especially Chinook

93 (*Oncorhynchus tshawytscha*) while mammal-eating killer whales (also referred to as

94 'transients' or Bigg's killer whales) feed on marine mammals, especially harbour seals (*Phoca*

95 *vitulina*; Ford et al. 1998). Although sympatric, these two populations comprise two specialist

96 ecotypes that are socially and reproductively segregated (Bigg 1982; Barrett-Lennard 2000).

97 Both ecotypes exhibit coherent and stable matrilineal social units based on long-term kinship

98 associations but there are important distinctions between their social strategies. The resident

99 population forms larger matrilineal units than the mammal-eating population and while the

100 resident population is philopatric, there is some level of adult dispersal in the mammal-eating

101 population (Bigg et al. 1990; Baird and Whitehead 2000). For example, males may disperse to

102 briefly associate with other matrilines or live alone, randomly associating with other adult

103 males. Moreover, some females may disperse from the matriline and stay socially mobile,

104 associating strongly for short periods with different groups (Baird and Dill 1996; Baird and

105 Whitehead 2000). This variation is considered to be due to the different foraging strategies of

106 the populations. Hunting marine mammal prey in large groups incurs greater costs by

107 increasing the probability of detection by the prey. Furthermore, the optimal energetic intake

108 for mammal-eating killer whales (preying upon medium-sized seals) declines for groups

109 larger than 3 individuals (Baird and Dill 1996). In contrast, resident killer whales spread out

110 and coordinate to locate salmon (Ford et al. 2000), potentially benefiting from larger group

111 sizes. With little or no predation risk, populations of this species apparently refine their social

112 systems primarily in relation to foraging efficiency, particularly availability of resources and

113 competition for those resources.

114 In the North Atlantic, the only published study addressing sociality found greater similarities

115 between the Scottish mammal-eating population and Northeast Pacific mammal-eating

116 population relative to residents, despite greater phylogenetic distance, suggesting that ecology

117 drives sociality more than phylogenetic inertia does (Beck et al. 2012). The study included a

118 limited dataset from Icelandic herring-eating killer whales and their social structure was not

119 explored in detail. However, the study's hierarchical display of associations suggested that

120 social tiers were not clearly defined in this population and that associations at a variety of

121 strengths existed. These features were not further addressed, nevertheless the study concluded

122 that the Icelandic fish-eating population is probably more similar to the Northeast Pacific

123 resident population than to mammal-eating populations.

124 Icelandic killer whales are believed to mainly prey upon Atlantic herring (*Clupea harengus*)

125 and follow the Icelandic summer-spawning (ISS) herring stock during its yearly migration

126 (Sigurjónsson et al. 1988) between overwintering, feeding and spawning grounds (Óskarsson

127   et al. 2009). Unlike the salmon prey of resident killer whales, herring form large and dense

128   schools as an antipredator strategy (Nøttestad and Axelsen 1999) and killer whales feeding on

129   herring schools use a coordinated group feeding strategy, encircling their prey to herd and

130   capture it (Similä and Ugarte 1993). Feeding aggregations of killer whales are very common

131   in Iceland, making it difficult to discern isolated groups and confusing the determination of

132   associations in the field (Sigurjónsson et al. 1988; Beck et al. 2012). In addition, herring can

133   undergo large variations in abundance and migration routes (Jakobsson and Stefánsson 1999;

134   Óskarsson et al. 2009) making it a changeable food resource. In fact, recent research suggests

135   not all individuals specialize on ISS herring and follow it year-round. Other killer whales

136   observed only in one season or seasonally moving between Iceland and Scotland exhibited

137   wider trophic niche width, suggesting diversity in foraging strategies (Samarra and Foote

138   2015; Samarra et al., in press; FIP Samarra et al. in prep).

139   In this study we investigate the social structure of herring-eating killer whales in Iceland,

140   based upon patterns of association between photo-identified individuals in spawning and

141   overwintering grounds. We relate our results to the described societies of killer whales in the

142   Northeast Pacific. Specifically, we investigate: 1) the degree and diversity of associations

143   between pairs of individuals; 2) whether social structural units of individuals exist and are

144   hierarchically nested in the social structure; 3) how associations persist or change over time in

145   the population and depending on age-sex class and; 4) whether variations in movement and

146   feeding strategy within the Iceland killer whale population influence sociality by promoting

147   social segregation. Given the differences in historical availability, migration patterns, and

148   anti-predator strategies of herring, salmon and seals, we hypothesize that broad ecology (fish-

149   vs. mammal-eating) alone cannot explain sociality and that local ecological conditions, such

150   as characteristics of prey schools and associated foraging strategy of the population, might

151   also strongly shape the social structure of killer whales.

152

153   **METHODS**

154   **Data collection**

155   Photographs of killer whales were collected in July 2008-2010 and 2013-2015 in

156   Vestmannaeyjar (South Iceland), a spawning ground of ISS herring, and in February-March

157   2013-2014 and mid-February to mid-March 2015 in Grundarfjörður and Kolgrafafjörður

158   (West Iceland), two fjords that were part of the ISS herring overwintering grounds. During

159   daylight hours, when killer whales were encountered, groups were approached and

160   photographs of all individuals surfacing together were taken using a variety of digital single-

161   lens reflex cameras with telephoto lenses. On several occasions, more than one

162   photographer/camera was used. Sampling effort varied across years and seasons, due to

163   weather conditions, research effort priorities, and the number of research vessels used (Table

164   1). In the winters of 2014-2015 a whale-watching platform was also used. Due to the inherent

165   difficulty in approaching and photographing all individuals from whale watching platforms,

166   only encounters when coverage of the groups present was considered complete (i.e. all

167   individuals in the group were identified) were included in the analysis.

168

169   **Photo-identification**

170 Killer whales were individually identified based on the size and shape of the dorsal fin,

171 patterns of the saddle patch and natural markings, such as nicks and scars, using left-side

172 pictures (Bigg 1982). For young animals without distinct natural markings, the eyepatch was

173 also used for identification across seasons/years. The quality of photographs was judged based

174 upon focus, contrast, angle and overall quality assessment (adapted from Friday et al. 2000).

175 Only high and medium quality photographs were used. To avoid false positives, matches were

176 confirmed if 3 distinct features of the individual were unambiguously identified.

177 To differentiate sex and stage of maturity four different categories were used: (1) Adult males

178 – adults that have reached sexual maturity and present distinguishable taller dorsal fin; (2)

179 Adult females – mature size individuals, with relatively smaller dorsal fin, seen during the

180 study period either consistently with a calf in echelon position, or without developing dorsal

181 fin for at least 3 years, or that were matched to a preliminary catalogue from the Marine

182 Research Institute including photos taken between 1981 and 2007, without developing dorsal

183 fin; (3) Juveniles – identifiable individuals > 1 year old that have not reached mature size

184 (both sexes); (4) Other – whales of apparently larger size than juveniles but for which sex and

185 stage of maturity were impossible to determine.

186 Individuals that were only sighted in the summers of 2008-2010 were excluded from the

187 analysis to reduce bias resulting from including individuals that may have died during the first

188 years of the study and reduce the possibility of incomplete group coverage data from

189 fieldwork where photographic data collection was opportunistic. This procedure excluded 25

190 individuals from the study.

191

Association criterion

Due to the common observations of aggregations of individuals in Iceland (Sigurjónsson et al. 1988; Beck et al. 2012), spatiotemporally isolated groups in the field are unclear and it is difficult to rigorously define a group. Despite this, the way in which animals are photographed is related to their inherent social structure, as animals that prefer to associate will undoubtedly be photographed together or in close proximity more often (Bigg et al. 1990). Using the capture time recorded in each photograph's metadata, we can discriminate animals surfacing together in close proximity, since they are photographed within a very short time frame. Individuals were considered associated for the day (sampling period) if photographed by the same camera/photographer within 20 seconds. This value was quantitatively derived by maximum likelihood estimation of photographic bouts (Langton et al. 1995; Luque and Guinet 2007; see Supplementary Material S1). The association criterion matches our field observations that groupings of adjacent associated animals tended to surface (and be available for photographing) close in time to each other and within 20 seconds, whereas non-contiguous animals were generally only available for photographing after a longer time had passed. Shorter and longer temporal association criteria (5 seconds and 1 hour, respectively) were used to test the robustness of the observed association patterns to the temporal criterion used (Supplementary Material S2). These analyses suggested that the association criterion value used in the study is likely meaningful to describe the animals' social structure and appropriate to capture important associates without overloading the analysis with random associations.

Analysis of associations

214

215 Only individuals seen on at least 5 different days were included in the analysis of

216 associations. This value is recommended by Whitehead (2008) as a minimum cut-off and it is

217 a more conservative restriction than several other studies (e.g. minimum cut-off of 4

218 sightings: Ottensmeyer and Whitehead 2003; Tosh et al. 2008; Beck et al. 2012; Esteban et al.

219 2016). We explored the consistency of the results under more restrictive thresholds (≥ 10 days

220 and ≥ 20 days; see Supplementary Material S3). Due to similarity in the obtained results and

221 the fact that restricting the criterion for inclusion to a minimum of 5 sampling periods

222 significantly increased the number of individuals included in the analysis, this was considered

223 an appropriate threshold to describe the population dynamics of this social system.

224 All analyses described below were conducted using SOCPROG 2.6 (Whitehead 2009) in

225 MatLab 8.5 (MathWorks, Natick, MA, U.S.A.), except where noted. To quantify associations

226 between pairs of individuals we calculated the half-weight index (HWI), which estimates the

227 proportion of time individuals spend together: $HWI = 2AB/(A + B)$, where AB is the number

228 of times individuals A and B were identified associating with each other, and A and B are the

229 total number of times each individual was identified (Cairns and Schwager 1987; Whitehead

230 2008a). This symmetric association index was chosen since it minimizes sampling bias when

231 some individuals present were missed. This index was calculated per season (summer and

232 winter) and overall.

233 We used a permutation test, permuting the associations within samples (days), to test whether

234 associations in the population were different from random, with the null hypothesis that

235 between sampling periods there are no preferred/avoided associations (Bejder et al. 1998;

236 Whitehead 2008a). This test reveals whether or not an observed social structure is only due to

237 properties of the dataset used (e.g. the size of aggregations of individuals and the number of

238 encounters or sampling periods) when the associations are not different from random. The

239 association matrix was permuted 10000 times, when the P value stabilized, with 1000 trials

240 (inversion of part of the matrix of associations) per permutation. The random data obtained by

241 this process were also used in the temporal analysis of associations.

242 To measure how diverse the associations were, we calculated the social differentiation (S) of

243 the population. Social differentiation is the estimated coefficient of variation of association

244 indices of the population. If S is close to 0, the associations are very homogenous, and if $S >$

245 1.0 the relationships are very diverse across dyads of animals (Whitehead 2008a; Whitehead

246 2009). The social differentiation was calculated using the likelihood method described by

247 Whitehead (2008b), with non-parametric bootstrap for calculating its standard error (SE) and

248 sampling periods chosen randomly for each of 1000 bootstrap samples.

249

250 **Hierarchical stratification**

251 Hierarchical clustering analysis using a dendogram display (tree diagram where individuals

252 are represented by nodes and the branching pattern represents the degree of associations) have

253 been used to visualize and interpret the social structure of killer whale populations (e.g. Bigg

254 et al. 1990; Baird and Whitehead 2000; Beck et al. 2012). This agglomerative technique

255 imposes a model where the social structure of the population is hierarchically structured: basic

256 social units (permanent or semipermanent social entities at high association values) are nested

257 within larger social units (permanent or semipermanent social entities –'tiers' (Wittemyer et

258 al. 2005) - at low association values) in a stratified fashion (Whitehead 2008a; Whitehead

259 2009).

260 To investigate whether or not the Icelandic population exhibits clear hierarchical stratification

261 we combined the quantification of the distribution of HWI along with a hierarchical display of

262 associations and a visual exploration of the stratification of the population. We displayed

263 associations as a dendogram, using the average-linkage clustering method. To identify the

264 association index at which significant divisions within the population occurred we used

265 modularity, defined by Newman (2004), controlling for differences in gregariousness

266 ('Modularity-G'; Lusseau 2007; Whitehead 2008a). To identify the degree of possible

267 stratification among individuals we explored the fragmentation of the population's social

268 network across lower values of HWI. We displayed the associations between individuals as a

269 social network, where nodes represent individuals and edges (links) between nodes represent

270 an existing association. Then, we sequentially removed edges in the population with

271 increasing HWI values to visualize the fragmentation of the network at each level, and

272 removed isolated (unconnected) nodes from the display for clarity. This was performed in R

273 3.2.3 (R Core Team 2015) using the package igraph (Csardi and Nepusz 2006).

274

275 **Non-hierarchical structure and movement pattern assortative mixing**

276 We used Newman's (2006) eigenvector-based clustering method to detect social clusters

277 within the population. This clustering technique sequentially divides the population into

278   successive clusters and does not assume a hierarchical association between individuals.

279   Maximum modularity (Q) values higher than 0.3 describe a good division of the population

280   into clusters (Newman 2004). We described the composition, mean and maximum HWI,

281   movement pattern of adults and social differentiation (with and without juveniles) of each

282   cluster obtained by the division. The Pearson correlation test, calculated in MatLab 8.5

283   (MathWorks, Natick, MA, U.S.A.), was used to test for correlation between social

284   differentiation and cluster size, with and without juveniles. Associations for each cluster were

285   displayed as sociograms (circular network diagrams), created in in R 3.2.3 (R Core Team

286   2015) using the package igraph (Csardi and Nepusz 2006). To study the possible substructure

287   within clusters we applied Newman's (2006) eigenvector-based clustering method to each

288   cluster individually.

289   We investigated whether the different movement pattern of individuals determined

290   association patterns by examining the assortative mixing in the population, i.e. the tendency

291   for individuals with the same movement pattern to preferentially associate, using Newman's

292   (2002) assortativity coefficient (r). Three different broad movement patterns were considered

293   based on individual sighting history (as in FIP Samarra et al. in prep): (1) only identified in

294   the winter season, (2) only identified in the summer season, (3) identified on both winter and

295   summer seasons. This coefficient ranges from zero to one and high values of r indicate higher

296   assortativity of the population, i.e. individuals associate only with others of the same 'type'.

297   The assortativity coefficient was calculated in R 3.2.3 (R Core Team 2015) using the package

298   assortnet (Farine 2014), for the whole population with and without juveniles, to account for

299 the possibility of juveniles only being identified later in the study period. The SE was

300 calculated using the jackknife method described by Newman (2003).

301

302 **Temporal patterns of associations**

303 To investigate how associations changed over time we calculated the standardized lagged

304 association rate (SLAR). All individuals, regardless of sighting frequency, were used in this

305 analysis to avoid positive bias (Whitehead 2008a). The SLAR is the estimate of the

306 probability that if two individuals are associated after a specified lag, the second individual is

307 a randomly chosen associate of the first (Whitehead 1995; Whitehead 2008a). Standard errors

308 were calculated using a temporal jackknife procedure with 15 day periods of data being

309 omitted in turn (Whitehead 1995; Whitehead 2007). To categorize how the relationships

310 between individuals changed over time, four different theoretical exponential models were

311 fitted (by maximum likelihood and binomial loss) to the full data set. The models are based in

312 the presence/absence of constant and temporary associations (Whitehead 2008a). The model

313 that best fitted the data is indicated by the lowest quasilikelihood Akaike information criterion

314 (QAIC, Whitehead 2007). The difference between the QAIC of the best model and other

315 models (ΔQAIC) indicates the degree of support for the less favored models: differences 0-2

316 indicating substantial support, 4-7 indicating less support and > 10 indicating essentially no

317 support for the alternative models (Burnham and Anderson 2002). Starting values of the

318 parameters for all models were obtained from the estimated parameters of the best-fitted

319 model in a preliminary fitting (with initial values of all parameters set to 0.5). The jackknife

320 method gives standard errors for the parameters of the model and for measures of social

321 structure estimated from them: typical group size (as in Jarman (1974), number of associated

322 individuals in groups, including the individual itself) and typical unit size (number of

323 individuals in permanent units), considering the case where permanent units temporarily

324 group (Whitehead 2008a).

325

Sex differences in association patterns

327 Differences in patterns of association by sex were investigated as in Baird and Whitehead

328 (2000). The mean and maximum HWI within and between sexes were calculated for adults of

329 known sex (Females and Males) seen on 5 or more days. The mean HWI between A-B is an

330 estimate of the probability of a random individual of category A associating with any

331 individual of category B at any sampling period, so it is insensitive to different numbers of

332 individuals in different categories (Baird and Whitehead 2000). The maximum HWI of A-B is

333 the average maximum of association indices between each individual from category A and

334 any individual from category B. We tested the null hypothesis that associations between and

335 within sexes are similar using a Mantel test where associations between categories were

336 permuted 5000 times (Schnell et al. 1985). Variation in temporal patterns of associations were

337 analyzed using the SLAR for associations between all adults of known sex (Females and

338 Males) to avoid positive bias of the SLAR.

339

Adult female-specific analysis

341 Mixing within aggregations of resident killer whales have been noted to differ between males

342 and females: adult males can temporarily travel away from their matrilines, possibly for

343 mating purposes (Bigg et al. 1990; Barrett-Lennard 2000), but adult females generally stay in

344 their matrilineal units, which are spatially dispersed, particularly during foraging (Ford 1989).

345 We therefore separately examined the associations only between the most frequently

346 encountered adult females in the study, as they may show higher levels of association within

347 groups and a more clearly defined tier structure than observed in the overall population. This

348 analysis was performed using 2 restricted datasets: 1) adult females encountered on more than

349 10 days and at least in 3 different years; 2) adult females encountered on at least 20 days and

350 at least in 3 different years. Permutation tests and dendograms were performed as described

351 above, for both datasets. Associations between females were displayed in a sociogram created

352 in R 3.2.3 (R Core Team 2015) using the package igraph (Csardi and Nepusz 2006).

353

RESULTS

355 314 individuals (88 adult males, 94 adult females, 59 juveniles and 73 others) were identified

356 in a total of 29023 photographs taken on 110 different days. The mean ± standard deviation

357 (SD) number of individuals identified per day was 25.1 ± 20.6 individuals (range = 1-121

358 total identifications per day).

359

Analysis of associations

361   198 individuals (56 adult males, 69 adult females, 41 juveniles and 32 others) were identified

362   on at least 5 days (mean of 12.6 ± 7.1 days, range of 5-38 days) and used in the analysis of

363   associations. 51 were only sighted in the winter season (including 8 juveniles), 32 only in the

364   summer season (including 11 juveniles), and 115 on both seasons (including 22 juveniles).

365   Most individuals were seen in several years (mean $\pm$ SD of 3 ± 1.5 years, range of 1-6

366   different years).

367   The mean HWI of the population was low (mean $\pm$ SD = 0.02 ± 0.01, non-zero HWI mean $\pm$

368   SD = 0.18 ± 0.19). Regardless of the season, the distribution of non-zero HWI values

369   observed showed a high proportion of low level associations and relatively fewer strong ties

370   at high HWI values (Figure 1). More than half of the pairs of associations were lower than 0.1

371   (51.4%, 1161 dyads). Only 9.9% (224 dyads) of the associations had HWI ≥ 0.5 (individuals

372   associated more than half of the time). This was the value used by Baird and Whitehead

373   (2000) to define matrilines in the Pacific mammal-eating population and by Bigg et al. (1990)

374   to define pods of matrilines that frequently associated. Only 0.9% of the associations (21

375   dyads) were higher than 0.8, the value used by Beck et al. (2012) to define primary social

376   tiers, equivalent to matrilines.

377   The SD and coefficient of variation (CV) of association indices were significantly higher in

378   the real dataset than in the permuted data (real SD = 0.09, random SD = 0.05, P=0.0001; real

379   CV = 4.12; random CV = 2.59; P = 0.0001). Hence, we could reject the null hypothesis that

380   individuals associated randomly. The social differentiation of the population was close to 1 (S

381   $\pm$ SE = 0.98 ± 0.03), revealing a highly diverse range of associations within the population.

382

Hierarchical stratification

384   Applying the hierarchical dendogram display (cophe

385   netic correlation coefficient [CCC] > 0.8; Figure 2), social clusters diverged at an extremely

386   low association index value (HWI of 0.02, maximum modularity of 0.68). The knot diagram

387   presented an apparent constant rate of cumulative bifurcations, which only slightly increased

388   at very low association indices. This pattern was still visible using a very restrictive

389   association criterion (Figure S3 in Supplementary Material S2). The network of associations

390   was more interconnected at low HWI thresholds (Figure 3). However, without a larger

391   number of strong bonds the network started to fragment very quickly when links were

392   sequentially removed at low HWI thresholds. The network contained few stronger ties, as is

393   visible when HWI = 0.5, with very small sets differentiated and individuals detached from the

394   network. Associations in the Icelandic killer whale population did not appear to be clearly

395   stratified into hierarchical tiers. Considering the wide range of association levels present, this

396   does not mean that individuals only associate with a small set of companions.

397

Examination of structure and movement pattern assortative mixing

399   Using Newman's (2006) clustering technique, the population could be significantly divided in

400   18 distinct clusters (Table 2; $Q = 0.66$). The social clusters obtained in the analysis were of

401   mixed sex-age classes. The cluster sizes varied between 3 and 33 individuals, with a mean $\pm$

402   SD of 11 ± 7.8 individuals per cluster. As expected, mean HWI within clusters was higher

403 than between clusters (within clusters mean HWI ± SD = 0.27 ± 0.17 and maximum HWI ±

404 SD = 0.65 ± 0.17; between clusters mean HWI ± SD = 0.01 ± 0.01 and maximum HWI ± SD

405 = 0.01 ± 0.06). The assortativity coefficient of the network indicated some level of separation

406 of associations according to movement pattern (including juveniles r ± SE = 0.44 ± 0.01; not

407 including juveniles r ± SE = 0.49 ± 0.01) but much lower than would be expected if

408 individuals favored associations with others of equal movement pattern and/or avoided

409 associations with individuals with a different movement pattern. In fact, not all clusters were

410 discriminated by movement pattern: 5 clusters were composed of a mix of individuals sighted

411 in both seasons and individuals sighted in a single season.

412 Clusters were highly variable in their complexity (Table 2). There was a wide range of values

413 of social differentiation by cluster (with juveniles mean ± SE = 0.52 ± 0.1, min-max: 0-1.15;

414 without juveniles mean ± SE = 0.49 ± 0.1, min-max: 0-1.17). The Pearson's correlation test

415 showed that social differentiation was significantly correlated with unit size (with juveniles r

416 = 0.68, P = 0.002; without juveniles r = 0.62, P = 0.006). Within larger clusters not all

417 associations were strong (representing high social preference) or weak, and members

418 associated at many different degrees. In general, only a few individuals within each cluster

419 maintained strong associations (> 0.5 or 0.8) with other members and only 5 clusters had a

420 mean HWI > 0.5. From the measures of social structure, inspection of photographs and direct

421 observations we concluded that we were not able to identify all companions of the members

422 of cluster F. This cluster was most likely incomplete and therefore was not included in further

423 descriptions.

424 Our analysis distinguished three types of social clusters in the population: stable (C, G, K, N,

425 O and P; Figure 4), intermediate complexity (D, H, M, Q and R; Figure 5) and complex (A, B,

426 E, I, J and L; Figure 6) clusters. Stable clusters had high mean HWI values, very low social

427 differentiation and members with equal movement pattern. Only in cluster G two juveniles

428 were subclustered with a very low modularity value, likely because they were born during the

429 study period and only identified later in the study. Therefore, these clusters had no apparent

430 substructuring and associations between members were generally more homogeneous but not

431 equal.

432 Intermediate complexity clusters had intermediate values of mean HWI and social

433 differentiation, showing potential but unclear subclustering (Q values generally < 0.3), since

434 individuals across potential subclusters also associated very frequently. In general, cluster

435 members had equal movement patterns, except for one cluster.

436 Complex clusters had very high values of social differentiation and very low mean HWI, but

437 high maximum HWI. In general, cluster members had different movement patterns, except for

438 two clusters. Complex clusters showed potential substructuring, although this was not clear

439 for all clusters (Q values of about 0.3 for cluster B and J). Associations between members of

440 complex clusters were diverse and only some members maintained strong associations, with

441 most associations being lower and at varying levels.

442

443 **Temporal patterns of associations**

444   The standardized lagged association rate SLAR ($g'(\tau)$) remained higher than would be

445   expected from random associations over the investigated time periods (τ; Figure 7), indicating

446   that non-random associations persisted over time.

447   The two more complex models presented a reasonable fit to the data (see Supplementary

448   Material S4). The model SLAR3, labelled as 'constant companions plus casual acquaintances'

449   in Whitehead (2008a), had the lowest QAIC value, fitting the data best. Adding a second level

450   of dissociation (SLAR4), gave a similar curve and a very small difference of QAIC to SLAR3

451   indicating some support for this model. However, contrary to SLAR3, there was no

452   convergence and stable fit of SLAR4 when varying the parameters start values, which raised

453   doubt on the suitability of this model for the data. For this reason the simpler model SLAR3,

454   which has lowest QAIC and consistent parameters, was chosen to describe the temporal

455   patterning of associations. This model indicated that the population was driven by a

456   combination of longer-term relationships that last for many years, and temporary associations:

457    $g'(t) = 0.06 + 0.02e^{-0.0486t}$. Temporary associations decayed exponentially, with the model

458   suggesting important dissociations over scales of about 21 days (0.0486/days, SE = 0.09). The

459   proportion of long-term associations was 77%, with only 23% of temporary relationships.

460   This model's fit estimated a typical group size of 14.8 individuals (SE = 2.5) and a typical

461   unit size of 11.7 individuals (SE = 3.4).

462

463   **Sex differences in association patterns**

22

464 125 adults of known sex seen on 5 or more days were used in this analysis. Association levels

465 within and between adult sex classes were similar, with low mean association indices and

466 high maximum association indices (Table 3). The Mantel test did not reveal clear significant

467 differences in association between, relative to within adult sex classes (permutation test, P =

468 0.05). If the analysis was restricted to 75 adults of know sex seen on more than 10 days there

469 was no significant difference in association (permutation test, P = 0.13). The temporal

470 analysis suggests that Female-Male, Male-Male and Female-Female associations were

471 somewhat stable across time and remained higher than random (Figure 8). For all types of

472 associations, the SLAR was higher than the SLAR between all individuals (higher probability

473 of association). In general, all SLAR were relatively stable over time and no sex difference

474 was noticeable.

475

476 **Adult female-specific analysis**

477 32 adult females were sighted on more than 10 days over at least 3 years and only 12 of those

478 were sighted on at least 20 days over at least 3 different years (Table 4). On both restriction

479 conditions, associations were non-random (32 females: real SD = 0.11, random SD = 0.08, P

480 = 0.0001 and real CV = 2.33, random CV = 1.72, P = 0.0001; 12 females: real SD = 0.17,

481 random SD = 0.14, P = 0.0001 and real CV = 1.51, random CV = 1.31, P < 0.0001). The

482 classical hierarchical clustering technique displayed dendograms with a varying level of

483 associations between females, with significant clusters discriminated at low HWI values (see

484 Table 4 and Supplementary Material S5). Although the cluster discrimination occurs at a

485 higher HWI value for the set of females with the more restrictive observational threshold, it is

486 still a low value and mostly weak associations are present within the discriminated clusters.

487 The sociogram showed that, regardless the observational threshold, associations between

488 females are mainly weak even between most females from the same cluster (Figure 9). Also,

489 there are several weak associations between females from many different clusters.

490

DISCUSSION

492 Our results showed that associations within the Icelandic population of herring-eating killer

493 whales were non-random but the number of strong associations was small. Although the

494 dendogram display of associations presented a high cophenetic correlation coefficient, social

495 clusters were differentiated at extremely low levels of association. With this technique,

496 individuals were clustered together also by least preferred associations, i.e. weaker

497 associations at very low HWI values, since not all individuals associated strongly within

498 social units.

499 In a hierarchically structured society, transitions between structural tiers are clear because

500 individuals within a social cluster (nested in a tier) associate more strongly than individuals

501 within clusters at the level above. Societies without hierarchical nesting can still display a

502 dendogram with a cophenetic correlation coefficient > 0.8, indicating an acceptable match to

503 the matrix of association indices (Bridge 1993), while being an inappropriate way of

504 realistically displaying associations (Whitehead 2008a; Whitehead 2009). When individuals

505 associate weakly overall the degree of potential hierarchical stratification is limited since an

506 individual cannot represent its social unit because associations within a social unit are not

507 equally strong. Our study showed this to be the case in this population. Thus, a non-stratified

508 way of studying the society was considered more appropriate than techniques that assume a

509 hierarchically-organized social structure.

510 The population could be significantly divided into social clusters, which were highly diverse

511 in complexity (even when using a more restrictive observation threshold; Supplementary

512 Material S3 – Figure S10). A small portion of the clusters presented more coherent

513 associations between members, which might represent cohesive basic structures. The majority

514 of the clusters presented diverse association strengths and potential further subclustering. In

515 some social clusters, many individuals did not strongly associate with all other members. This

516 population presented both constant and temporary associations, not completely assorted by

517 movement pattern and with no clear differences between sexes. Together these results suggest

518 that the Icelandic herring-eating killer whale population has a multilevel society with no clear

519 nested hierarchical structure of coherent social units, different from other populations of killer

520 whales studied to date.

521 The evidence for non-random associations indicates that our results were not merely a

522 consequence of the quality or constraints of the dataset. It is possible that some of the HWI

523 values were negatively biased due to incomplete photographic coverage of

524 groupings/aggregations (Ottensmeyer and Whitehead 2003). However, this type of bias would

525 only increase the probability of not rejecting the null hypothesis of associations being random.

526 The analysis using the most encountered adult females aimed at reducing the potential

527 influence of recording sporadic associations, due to the observation that adult female resident

528 killer whales have lower levels of mixing with other groups than other age-sex classes. Thus,

529   a matrilineal structure may have been more clearly detectable among adult females than in the

530   overall population. However, our population-level results were instead strongly supported by

531   the adult female-specific analysis, with adult females also presenting an unclear hierarchical

532   structure but a complex sociality with rare strong associations and many weak associations

533   between females from the same cluster, and several associations between females from

534   different clusters. There are indications that the weakness of associations is due to a high

535   variability across years (associations on one year might not occur in a different year) but the

536   small yearly number of sightings limits our ability to reach a definitive conclusion on the

537   stability of associations and yearly preferences between these individuals.

538

539   **A complex multilevel society**

540   In the Icelandic herring-eating killer whale population individuals clearly associated at

541   different levels, in some cases forming subcluster units. This society appears to tend towards

542   an incompletely nested multilevel society (as in Figure 6 in de Silva and Wittemyer 2012).

543   The levels of social stratification are not hierarchically distinct because transitions between

544   levels are gradual and may vary among individuals or sets of individuals, i.e. not all

545   individuals associate at similarly higher levels within social units and at distinctly lower levels

546   between social units. The variability in cluster complexity indicates diverse association

547   patterns among individuals and suggests different association strategies within the population.

548   Killer whale movement patterns did not assort their associations. In fact, individuals from

549   different subclusters and clusters with markedly different movement patterns were commonly

550 seen in tight groupings within less than one body length, a measure commonly used in other

551 killer whale social structure studies to define a group (e.g. Ivkovich et al. 2010, Esteban et al.

552 2016; Figure 10). Furthermore, complex cluster A (Figure 6) was formed by 3 highly

553 distinctive subclusters: subcluster A1, composed of individuals seen in Iceland year-round

554 following the movements of the ISS herring stock; subcluster A2 composed of individuals

555 that are only seen in Iceland in the winter; subcluster A3, composed of 5 individuals matched

556 to the Scottish population (only 2 Others and 1 Juvenile from this cluster were not matched)

557 and sighted in Scotland in the summer (Samarra and Foote 2015). Combining social structure

558 analysis with genetics could help to clarify the underlying aspects of social contact reported

559 here between whales with different movement patterns and potentially different feeding

560 ecologies in Iceland. It is worth noting that the individuals matched to the Scottish population

561 were not always sighted together in Scotland (Samarra and Foote 2015) nor in Iceland. It is

562 possible that individuals were missed in Scotland due to the opportunistic nature of data

563 collection. However, in our study we could confirm that these individuals were not always

564 associating at close proximity.

565 The Icelandic multilevel society seems to be driven by a mix of both constant and temporary

566 associations of mean duration of about 21 days. This temporal pattern of fission-fusion

567 dynamics can occur in several types of social systems: 1) one in which constant permanent

568 social units temporarily associate; 2) one in which individuals temporarily maintain casual but

569 preferred associations and; 3) one in which permanent units exist but some individuals are

570 'floaters' who move between units (Whitehead 2008a). When full units of individuals

571 collectively join, the typical group size should be twice the typical unit size, as in Pacific

572   sperm whales representing 2 temporal stable units joining (Whitehead et al. 1991) or larger, as

573   in Nova Scotia long-finned pilot whales where a group is comprised of several units

574   (Ottensmeyer and Whitehead 2003). Our study suggests that the temporal pattern did not

575   result from permanent social units temporarily associating since the estimated typical group

576   size was less than double of the typical unit size. Also, there was no indication of 'floaters'

577   moving between units and no evidence of adult dispersal in the Icelandic population. Instead,

578   temporary associations are probably formed between preferred but casual associates or

579   potentially by small sets of associates who temporarily associate with full permanent units, as

580   small sets of associated 'floaters'. Cluster members with weaker ties might represent these

581   casual but preferred temporary associates. It is unknown if this behavioral flexibility is only

582   maintained when killer whales aggregate in herring grounds or if it is seasonally shaped, so

583   further studies will be necessary to understand this type of affiliation.

584

585   **How can local ecological context shape killer whale social structure?**

586   Methodological differences among studies (e.g. disparity in sampling procedures, definition

587   of association, association index used) prevent a quantitative comparison of social structure

588   between the Icelandic and other killer whale populations. Nevertheless, overall social

589   structure comparisons can still be made. If sociality was determined by fish- vs. mammal-

590   eating ecological differences alone (Beck et al. 2012), we would expect that the Icelandic

591   population would have a similar social structure to fish-eating resident killer whales. Indeed,

592   mammal-eating killer whales show dispersal of either sex from maternal groups and relatively

593   rare and unstable associations between adult males (Baird and Whitehead 2000) which we did

594   not observe in our study and is also not present in residents (Bigg et al. 1990). These specific

595   characteristics of the mammal-eating population are linked to optimal foraging group size

596   adjustment when feeding on seals (Baird and Dill 1996). However, the clear stable matrilineal

597   units (cohesive long-term groups) with members associating strongly and permanently (Bigg

598   et al. 1990; Baird and Whitehead 2000) common to both mammal-eating and residents, was

599   not found in the Icelandic herring-eating population.

600   Coherent basic social units have been described for other killer whale populations regardless

601   of targeted prey (in Alaska: Matkin et al. 1999; Marion Island: Tosh et al. 2008; Northwest

602   Pacific: Ivkovich et al. 2010; and Gibraltar: Esteban et al. 2016) and it has been considered a

603   firm characteristic of the species despite ecological differences. In the Icelandic herring-eating

604   population the possible existence of matrilineal units is not clear, but cannot be rejected. For

605   example, the potential subclustering of cluster D (Figure 5) is matched to direct observations

606   of constant close proximity associates, which could be more similar to basic matrilineal units.

607   Yet, these subclusters were still strongly associated and were seen frequently switching

608   preference for close companions across days and years, as well as with individuals from other

609   clusters. Therefore, if matrilineal units are present in this population it is possible that these

610   are not entirely comparable to the ones present in other killer whale societies. An increase in

611   the timespan of association data and genetic analysis, relating kinship and gene flow with the

612   underlying patterns of associations, will be crucial to inform on the presence and

613   characteristics of family bond-units in this population.

614   Further differences from the resident killer whale society were the lack of clear social tiers

615   and hierarchical nesting in the Icelandic herring-eating society, which included fission-fusion

616   dynamics at an individual (or sets of a few individuals) rather than at a group level (periodic

617   merging of permanent social units). A parallel variation in multilevel structuring has been

618   quantified in elephant societies (de Silva and Wittemyer 2012). African elephants (*Loxodonta*

619   *africana*) maintain a clear multitiered society of coherent basic units that associate

620   hierarchically. In contrast, Asian elephants (*Elephas maximus*) have a complex multilevel

621   society without hierarchical structuring and nested units. Asian elephants do not maintain

622   clear core groups and associations can be either ephemeral or long-term. de Silva and

623   Wittemyer (2012) could not determine whether these differences were due to phylogenetic or

624   ecological factors, but there were significant environmental differences between the two

625   societies, such as differences in primary productivity and predation pressure.

626   Our study points to a different view of killer whale social structure, with a more dynamic and

627   fluid sociality than generally inferred from broad ecology. As argued by Beck et al. (2012),

628   ecology probably influences killer whale sociality rather than simply phylogenetic separation

629   of populations. However, considering only fish- vs. mammal-eating strategies as the

630   ecological condition influencing sociality ignores important particularities of local ecological

631   context. Herring-eating killer whales in Iceland target a prey with particular characteristics

632   different from salmon and seals, such as antipredator behaviors, unpredictability and patchy

633   distribution of high biomass. This shapes the feeding behavior of the population and probably

634   its social structure.

635   Herring is a schooling fish with a diverse repertoire of antipredator maneuvers (Nøttestad and

636   Axelsen 1999). Feeding upon this prey requires a highly coordinated group feeding technique

637   to herd and catch herring (Similä and Ugarte 1993), unlike feeding techniques described for

638   other fish-eating killer whale populations. To efficiently hunt larger concentrations or school

639   sizes using a coordinated foraging technique, killer whales might benefit from larger group

640   sizes to encircle the herring school (Vabø and Nøttestad 1997; Nøttestad et al. 2002). Active

641   adjustment of killer whale numbers hunting herring schools has been observed in Norway

642   (Nøttestad et al. 2002): on 4 observations of feeding groups (range of 22-46 individuals, mean

643      $\pm$ SD = 33.5 $\pm$ 10.6 individuals), the 2 largest groups (38 and 46 individuals in total) occurred

644   when the herring layer was larger (depth range of 150/160 meters to 350 meters) and were

645   composed by different smaller groups of killer whales that gathered before starting to herd

646   herring, arriving from different directions. In these conditions, it might be important to

647   maintain a fission-fusion society where associations are flexible and individuals can actively

648   adjust to these constantly changing requirements.

649   Herring can also undergo substantial changes in density and spatial distribution, particularly

650   in overwintering grounds (Óskarsson et al. 2009). The unpredictability of the prey may

651   additionally promote the maintenance of a more fluid and flexible sociality. A socioecological

652   model proposed for dolphins suggests that when resources are unpredictable, dolphins will

653   present wide range movements, reduced competition by cooperative foraging and larger

654   groups to more effectively find and exploit large prey schools (Gowans et al. 2007). Dusky

655   dolphins (*Lagenorhynchus obscurus*) in Argentina feed on schooling fish and present similar

656   basic herding techniques to herring-eating killer whales (Würsig and Würsig 1980). Their

657   target prey is also unpredictably distributed. The population presents a strong fission-fusion

658   society with constantly fluctuating subgroup memberships (although some associations might

659   be constant) that split for feeding and social purposes (Würsig and Würsig 1980; Würsig and

660   Bastida 1986). This social structure is very different from dusky dolphins of New Zealand

661   (Markowitz 2004), whose target preys are more predictable.

662   Finally, feeding aggregations in Iceland are very common during summer and winter, in

663   grounds where herring are temporarily highly concentrated. The patchiness of a resource will

664   influence whether animals do aggregate and, although these aggregations for feeding are not

665   social structures (spatiotemporal clusters of individuals forced by non-social factors) they

666   might act as catalysts for sociality (Whitehead 2008a). Recurring aggregations due to prey

667   behavior may offer a special local ecological context for the establishment of associations,

668   creating opportunities for social interactions with other individuals and somehow shaping the

669   social structure of this population. The dynamic nature of the society described here may have

670   been uncovered because our data collection took place mostly during periods when large

671   aggregations of whales can occur, due to this particular ecological context. Future work

672   focusing on social associations of herring-eating killer whales during periods when herring

673   are more dispersed may reveal stronger social bonds, and clear long-term stable matrilineal

674   groups, if group sizes are substantially lower than observed during the herring spawning and

675   overwintering periods.

676   Other ecological differences such as habitat characteristics or historical capture might have

677   also shaped the social structure of this population but we lack sufficient information to

678   determine their influence at present. Furthermore, the Icelandic population is comprised of

679   individuals with different seasonal movement patterns that associate at least seasonally. This

680   alone can influence the social structure of the population, since different movement patterns

681   within the same population suggest exposure to different environmental conditions. This

682 might also lead to variation in social factors within the population, e.g. mating competition or

683 avoidance, which can influence the structuring of basic and high-order groups in mammals

684 (Silk 2007). More information on the genetic relatedness of whales with different movement

685 patterns is needed to understand how it may affect the resulting society.

686 We have shown that the Icelandic herring-eating killer whale population has a complex

687 multilevel social structure with no clear hierarchical nesting and no strong social segregation

688 by movement pattern. This social system appears to be different from other populations of

689 killer whales worldwide, but continued photo-identification data will be crucial to investigate

690 these questions over longer time scales and under different seasonal, spatial and prey

691 behavioral contexts. The differences observed suggest that fish vs. marine mammal prey-type

692 alone does not define killer whale social structure and local ecological context, such as prey

693 characteristics and foraging strategy, are probably strong drivers of sociality. The factors

694 constraining hierarchical stratification of societies are little understood and to our knowledge

695 are not addressed in socioecological frameworks (e.g. Emlen and Oring 1977; Wrangham

696 1980; Gowans et al. 2007). Comparative studies of populations targeting similar prey will be

697 extremely important to quantitatively assess the degree of variation in multilevel social

698 structuring with local ecological context.

699

700 **Funding**

719

720   Data accessibility statement

721   Analyses reported in this article can be reproduced using the data provided by Tavares et al.

722   (2016).

723

724 **REFERENCES**

725 Baird RW, Dill LM. 1996. Ecological and social determinants of group size in transient killer

726 whales. Behav. Ecol. 7:408–416.

727 Baird RW, Whitehead H. 2000. Social organization of mammal-eating killer whales: group

728 stability and dispersal patterns. Can. J. Zool. 78:2096–2105.

729 Barrett-Lennard LG. 2000. Population structure and mating patterns of killer whales (*Orcinus*

730 *orca*) as revealed by DNA analysis [PhD thesis]. University of British Columbia.

731 Barton RA, Byrne RW, Whiten A. 1996. Ecology, feeding competition and social structure in

732 baboons. Behav. Ecol. Sociobiol. 38:321–329.

733 Beck S, Kuningas S, Esteban R, Foote AD. 2012. The influence of ecology on sociality in the

734 killer whale (*Orcinus orca*). Behav. Ecol. 23:246–253.

735 Bejder L, Fletcher D, Bräger S. 1998. A method for testing association patterns of social

736 animals. Anim. Behav. 56:719–725.

737 Bigg MA. 1982. An assessment of killer whale (*Orcinus orca*) stocks off Vancouver Island,

738 British Columbia. Rep. Int. Whal. Comm. 32:655–666.

739 Bigg MA, Olesiuk P, Ellis GM, Ford JKB, Balcomb KC. 1990. Social organization and

740 genealogy of resident killer whales (*Orcinus orca*) in the coastal waters of British Columbia

741 and Washington State. Reports Int. Whal. Commision Spec. Issue 12:383–405.

742 Bridge PD. 1993. Classification. In: Fry JC, editor. Biological data analysis. Oxford, UK:

743 Oxford University Press. p. 219–242.

744   Burnham KP, Anderson DR. 2002. Model selection and multimodel inference: a practical

745   information-theoretic approach. New York, USA: Springe-Verlag.

746   Cairns SJ, Schwager SJ. 1987. A comparison of association indices. Anim. Behav. 35:1454–

747   1469.

748   Connor RC, Mann J, Tyack PL, Whitehead H. 1998. Social evolution in toothed whales.

749   Trends Ecol. Evol. 13:228–232.

750   Connor RC, Smolker RA, Richards AF. 1992. Two levels of alliance formation among male

751   bottlenose dolphins (*Tursiops sp.*). Proc. Natl. Acad. Sci. 89:987–990.

752   Csardi G, Nepusz T. 2006. The igraph software package for complex network research.

753   InterJournal, Complex Syst. 1695:1–9.

754   Emlen ST, Oring LW. 1977. Ecology, sexual selection, and the evolution of mating systems.

755   Science. 197:215–223.

756   Esteban R, Verborgh P, Gauffier P, Giménez J, Foote AD, de Stephanis R. 2016. Maternal

757   kinship and fisheries interaction influence killer whale social structure. Behav. Ecol.

758   Sociobiol.:111–122.

759   Farine DR. 2014. Measuring phenotypic assortment in animal social networks: weighted

760   associations are more robust than binary edges. Anim. Behav. 89:141–153.

761   Ford JKB. 1989. Acoustic behaviour of resident killer whales (*Orcinus orca*) off Vancouver

762   Island, British Columbia. Can. J. Zool. 67:727–745.

763   Ford JKB. 1991. Vocal traditions among resident killer whales (*Orcinus orca*) in coastal

764   waters of British Columbia. Can. J. Zool. 69:1454–1483.

765   Ford JKB, Ellis GM, Balcomb KC. 2000. Killer whales: the natural history and genealogy of

766   Orcinus orca in British Columbia and Washington. Vancouver, Canada: UBC Press.

767   Ford JKB, Ellis GM, Barrett-Lennard LG, Morton AB, Palm RS, Balcomb KC. 1998. Dietary

768   specialization in two sympatric populations of killer whales (*Orcinus orca*) in coastal British

769   Columbia and adjacent waters. Can. J. Zool. 76:1456–1471.

770   Friday N, Smith TD, Stevick PT, Allen J. 2000. Measurement of photographic quality and

771   individual distinctiveness for the photographic identification of humpback whales, *Megaptera*

772   *novaeangliae*. Mar. Mammal Sci. 16:355–374.

773   Fruchterman TMJ, Reingold EM. 1991. Graph drawing by force-directed placement. Softw.

774   Pract. Exp. 21:1129–1164.

775   Gowans S, Würsig B, Karczmarski L. 2007. The social structure and strategies of delphinids:

776   predictions based on an ecological framework. Adv. Mar. Biol. 53:195–294.

777   Grueter CC, Chapais B, Zinner D. 2012. Evolution of multilevel social systems in nonhuman

778   primates and humans. Int. J. Primatol. 33:1002–1037.

779   Grueter CC, Matsuda I, Zhang P, Zinner D. 2012. Multilevel societies in primates and other

780   mammals: introduction to the special issue. Int. J. Primatol. 33:993–1001.

781   Ivkovich TV, Filatova OA, Burdin AM, Sato H, Hoyt E. 2010. The social organization of

782   resident-type killer whales (*Orcinus orca*) in Avacha Gulf, Northwest Pacific, as revealed

783   through association patterns and acoustic similarity. Mamm. Biol. Zeitschrift fur Saugetierkd.

784   75:198–210.

785   Jarman PJ. 1974. The social organisation of antelope in relation to their ecology. Behaviour

786   48:215–267.

787   Krause J, Ruxton GD. 2002. Living in Groups. New York, USA: Oxford University Press.

788   Langton SD, Collett D, Sibly RM. 1995. Splitting behaviour into bouts; a maximum

789   likelihood approach. Behaviour 132:781–799.

790   Luque SP, Guinet C. 2007. A maximum likelihood approach for identifying dive bouts

791   improves accuracy, precision and objectivity. Behaviour 144:1315–1332.

792   Lusseau D. 2007. Why are male social relationships complex in the Doubtful Sound

793   bottlenose dolphin population? PLoS One 2:e348.

794   Markowitz TM. 2004. Social organization of the New Zealand dusky dolphin. Texas A&M

795   University.

796   Matkin CO, Ellis GM, Olesiuk P, Saulitis EL. 1999. Association patterns and inferred

797   genealogies of resident killer whales, *Orcinus orca*, in Prince William Sound, Alaska. Fish.

798   Bull. 97:900–919.

799   Newman MEJ. 2002. Assortative mixing in networks. Phys. Rev. Lett. 89:208701.

800   Newman MEJ. 2003. Mixing patterns in networks. Phys. Rev. E 67:026126.

801   Newman MEJ. 2004. Analysis of weighted networks. Phys. Rev. E 70:056131.

802   Newman MEJ. 2006. Modularity and community structure in networks. Proc. Natl. Acad. Sci.

803　U. S. A. 103:8577–8582.

804　Nøttestad L, Axelsen BE. 1999. Herring schooling manoeuvres in response to killer whale

805　attacks. Can. J. Zool. 77:1540–1546.

806　Nøttestad L, Fernö A, Axelsen BE. 2002. Digging in the deep: killer whales' advanced

807　hunting tactic. Polar Biol. 25:939–941.

808　Óskarsson GJ, Gudmundsdottir A, Sigurdsson T. 2009. Variation in spatial distribution and

809　migration of Icelandic summer-spawning herring. ICES J. Mar. Sci. J. du Cons. 66:1762–

810　1767.

811　Ottensmeyer CA, Whitehead H. 2003. Behavioural evidence for social units in long-finned

812　pilot whales. Can. J. Zool. 1338:1327–1338.

813　R Core Team. 2015. R: A language and environment for statistical computing.

814　Samarra FIP, Foote AD. 2015. Seasonal movements of killer whales between Iceland and

815　Scotland. Aquat. Biol. 24:75–79.

816　Samarra FIP, Vighi M, Aguilar A and Víkingsson GA. In press. Intra-population variation in

817　isotopic niche in herring-eating killer whales. Mar. Ecol. Prog. Ser.

818　Schnell GD, Watt DJ, Douglas ME. 1985. Statistical comparison of proximity matrices:

819　applications in animal behaviour. Anim. Behav. 33:239–253.

820　Sigurjónsson J, Lyrholm T, Leatherwood S, Jónsson E, Víkingsson GA. 1988.

821　Photoidentification of killer whales off Iceland 1981 through 1986. Rit Fiskid. 11:99–114.

822　Silk JB. 2007. The adaptive value of sociality in mammalian groups. Philos. Trans. R. Soc.

823   London B Biol. Sci. 362:539–559.

824   de Silva S, Wittemyer G. 2012. A comparison of social organization in Asian elephants and

825   African savannah elephants. Int. J. Primatol. 33:1125–1141.

826   Similä T, Ugarte F. 1993. Surface and underwater observations of cooperatively feeding killer

827   whales in northern Norway. Can. J. Zool. 71:1494–1499.

828   Sinha A, Mukhopadhyay K, Datta-Roy A, Ram S. 2005. Ecology proposes, behaviour

829   disposes: Ecological variability in social organization and male behavioural strategies among

830   wild bonnet macaques. Curr. Sci. 89:1166–1179.

831   Tavares SB, Samarra FIP, Miller PJO. 2016. Data from: A multilevel society of herring-eating

832   killer whales indicates adaptation to prey characteristics. Behavioral Ecology.

833   http://dx.doi.org/10.5061/dryad.j619s.

834   Tosh CA, De Bruyn PJN, Bester MN. 2008. Preliminary analysis of the social structure of

835   killer whales, *Orcinus orca*, at subantarctic Marion Island. Mar. Mammal Sci. 24:929–940.

836   Vabø R, Nøttestad L. 1997. An individual based model of fish school reactions: predicting

837   antipredator behaviour as observed in nature. Fish. Oceanogr. 6:155–171.

838   Whitehead H. 1995. Investigating structure and temporal scale in social organizations using

839   identified individuals. Behav. Ecol. 6:199–208.

840   Whitehead H. 2007. Selection of models of lagged identification rates and lagged association

841   rates using AIC and QAIC. Commun. Stat. - Simul. Comput. 36:1233–1246.

842   Whitehead H. 2008a. Analyzing animal societies: quantitative methods for vertebrate social

843   analysis. Chicago, USA: University Of Chicago Press.

844   Whitehead H. 2008b. Precision and power in the analysis of social structure using

845   associations. Anim. Behav. 75:1093–1099.

846   Whitehead H. 2009. SOCPROG programs: analysing animal social structures. Behav. Ecol.

847   Sociobiol. 63:765–778.

848   Whitehead H, Antunes R, Gero S, Wong SNP, Engelhaupt D, Rendell L. 2012. Multilevel

849   societies of female sperm whales (*Physeter macrocephalus*) in the Atlantic and Pacific: why

850   are they so different? Int. J. Primatol. 33:1142–1164.

851   Whitehead H, Waters S, Lyrholm T. 1991. Social organization of female sperm whales and

852   their offspring: constant companions and casual acquaintances. Behav. Ecol. Sociobiol.

853   29:385–389.

854   Wittemyer G, Douglas-Hamilton I, Getz WM. 2005. The socioecology of elephants: analysis

855   of the processes creating multitiered social structures. Anim. Behav. 69:1357–1371.

856   Wrangham RW. 1980. An ecological model of female-bonded primate groups. Behaviour

857   75:262–300.

858   Würsig B, Bastida R. 1986. Long-range movement and individual associations of two dusky

859   dolphins (*Lagenorhynchus obscurus*) off Argentina. J. Mammal. 67:773–774.

860   Würsig B, Würsig M. 1980. Behavior and ecology of the dusky dolphin, *Lagenorhynchus*

861   *obscurus*, in the South Atlantic. Fish. Bull 77:871–890.

FIGURE LEGENDS

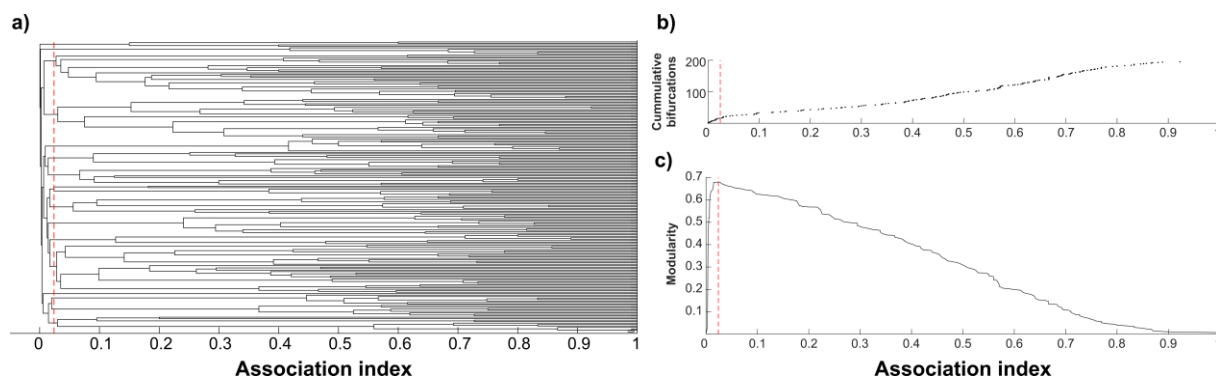863

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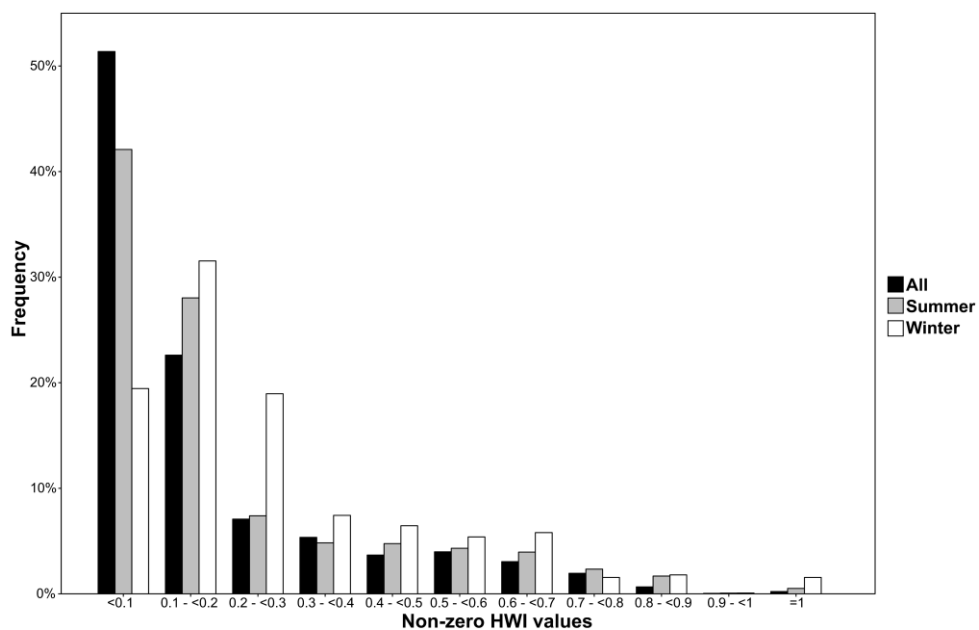
Figure 1. Distribution of non-zero half-weight index (HWI) values in the population using the

full dataset and by season.

867

868

Figure 2. Average-linkage cluster analysis. (a) Dendogram of 198 individuals encountered on

at least 5 days (cophenetic correlation coefficient [CCC] = 0.94). (b) Knot diagram of

871   cumulative number of bifurcations across HWI levels. (c) A maximum modularity-G, within

872   hierarchical clustering, of 0.68 suggests a division into distinct clusters at an HWI of 0.02

873   (dashed line).

874

0.0 (n=198)   0.1 (n=198)   0.2 (n=192)

0.3 (n=191)   0.4 (n=178)   0.5 (n=160)
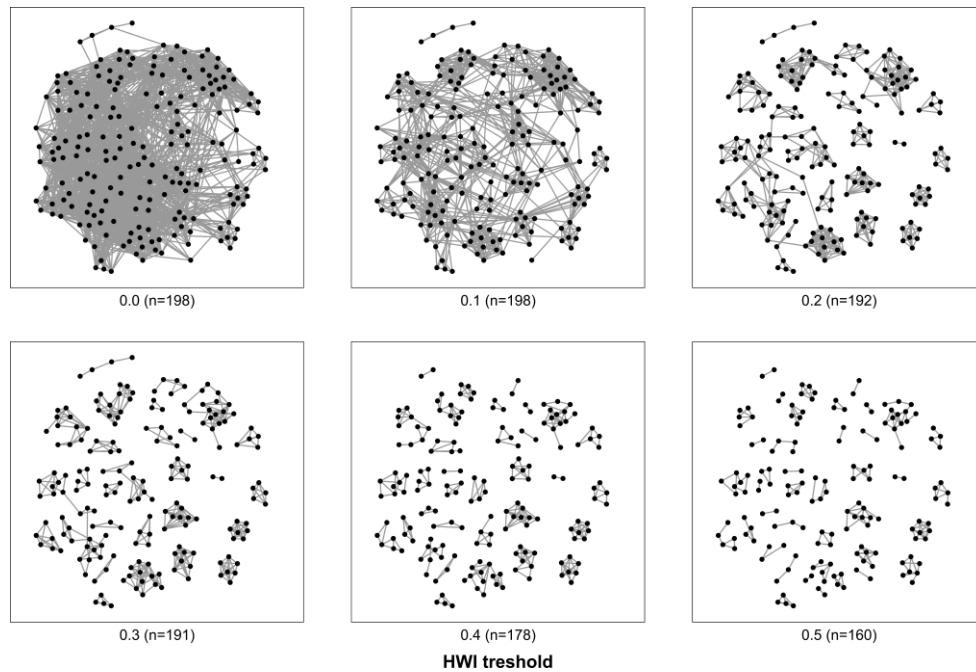
HWI treshold

876   Figure 3. Network fragmentation with increasing HWI threshold. Isolated individuals are

877   removed from the network (n indicates the number of individuals present). Note that at

878   HWI > 0.1 the network starts fragmenting quickly and more individuals become isolated from

879   the network. Plotted using Fruchterman-Reingold force-directed layout (Fruchterman and
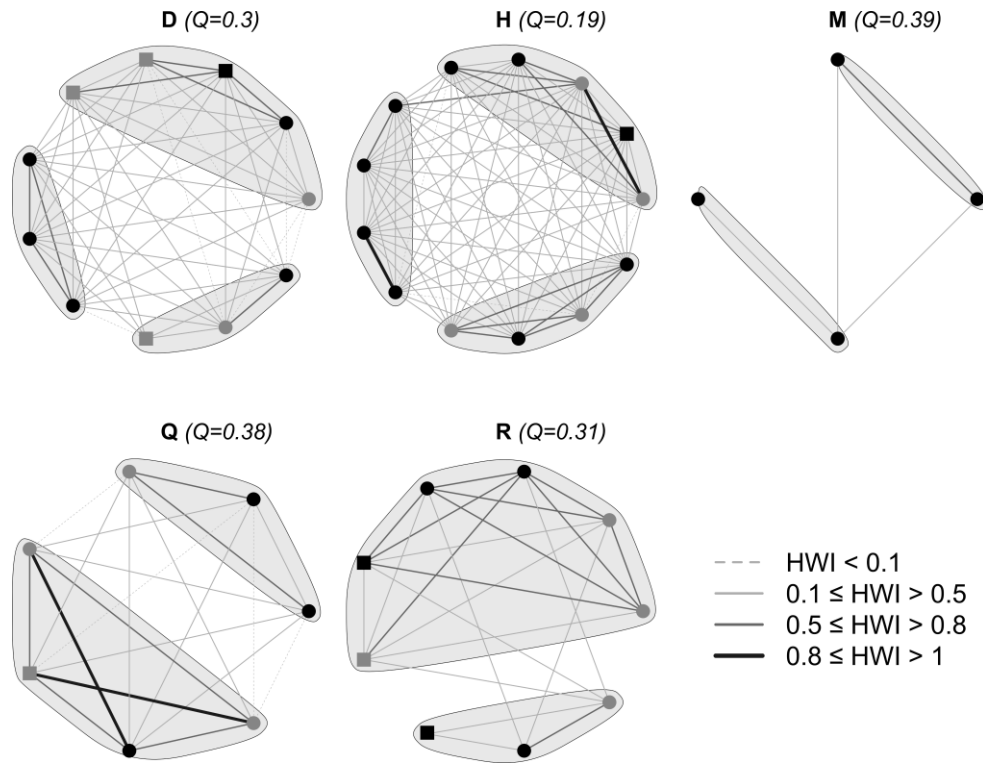
880   Reingold 1991).

881
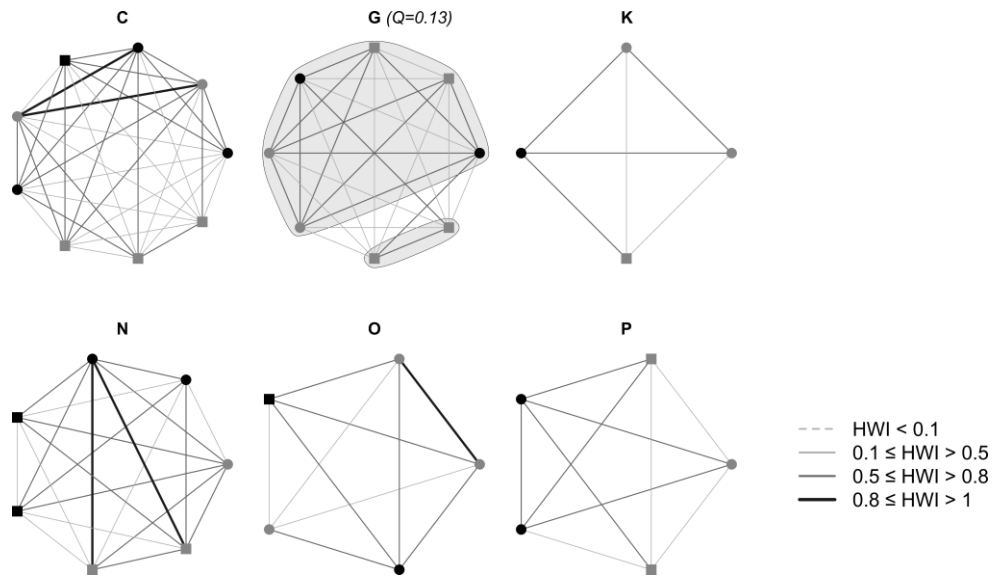
882

883 Figure 4. Sociogram of stable clusters. The thickness of the edges is related to the HWI value

884 of association. Nodes represent individuals and are shaped/colored based on age-sex class

885 (black circle: Female; grey circle: Male; black square: Other; grey square: Juvenile). There

886 was no apparent subcluster division. Two juveniles were subclustered in cluster G but with a

887 very low modularity value (Q), likely because the juveniles were only identified on the later

888 years of the study, contrary to other members.

889

Figure 5. Sociogram of intermediate complexity clusters. The thickness of the edges is related to the HWI value of association. Nodes represent individuals and are shaped/coloured based on age-sex class (black circle: Female; grey circle: Male; black square: Other; grey square: Juvenile). Q indicates the modularity of potential subcluster division.
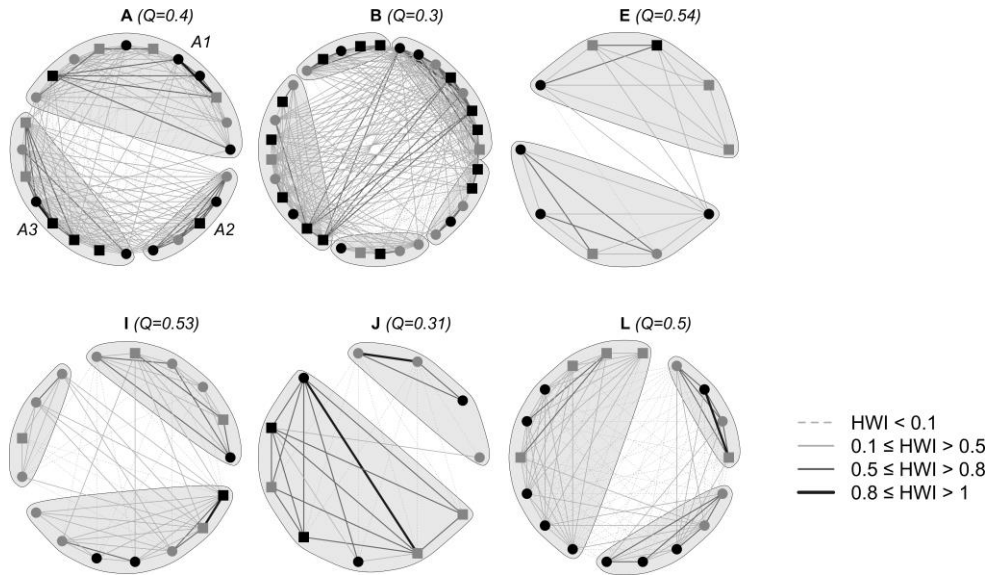
896

897 Figure 6. Sociogram of complex clusters. The thickness of the edges is related to the HWI

898 value of association. Nodes represent individuals and are shaped/colored based on age-sex

899 class (black circle: Female; grey circle: Male; black square: Other; grey square: Juvenile). Q

900 indicates the modularity of potential subcluster division. A1, A2 and A3 indicate the 3

901 subclusters of Cluster A.

902
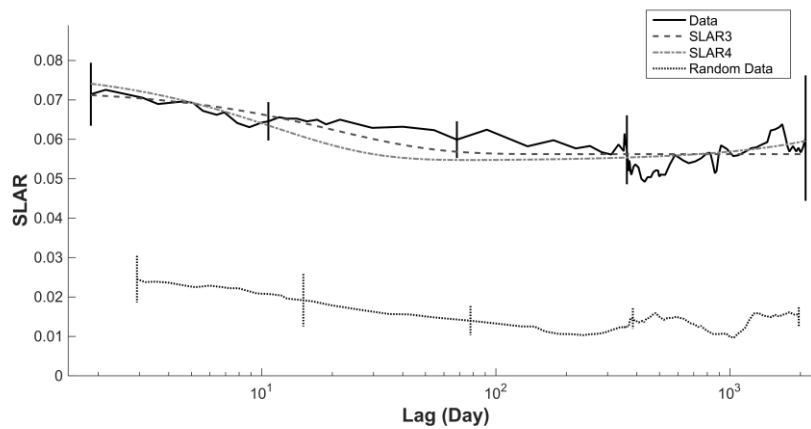
903

904 Figure 7. Standardized random and lagged association rates (SLAR, curve smoothed with

905 30000 moving average). Vertical bars represent temporal jackknife standard errors. The two

906   models of the exponential family with the lowest QAIC values, SLAR3 and SLAR4, are

907   shown (see Supplementary Material S4 for formulas and QAIC values).

908
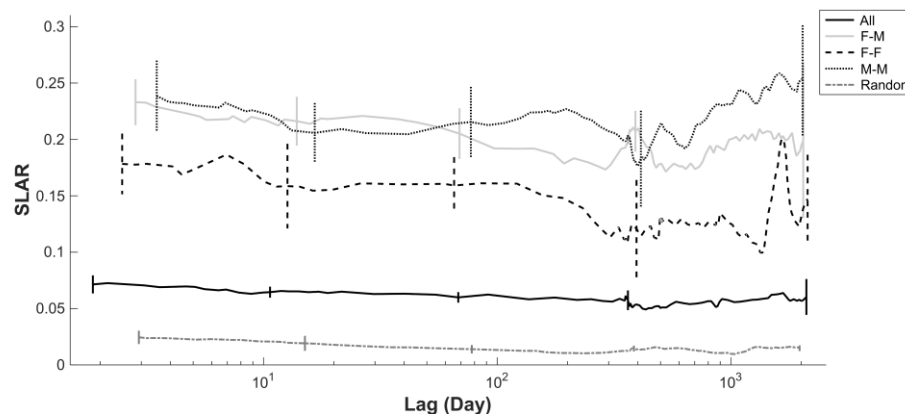
909

910   Figure 8. Standardized lagged association rates (SLAR) for different associations between

911   adults. A different moving average was chosen accordingly to smooth lines. Jackknife

912   grouping factor of 15, shown as vertical bars. SLAR between Females and Males (F-M) and

913   between Males and Males (M-M) are high and relatively stable. Although lower, SLAR

914   between Females and Females (F-F) are also high and much higher than the SLAR between

915   all individuals (All) or if individuals had a random chance of associating (Random).

916
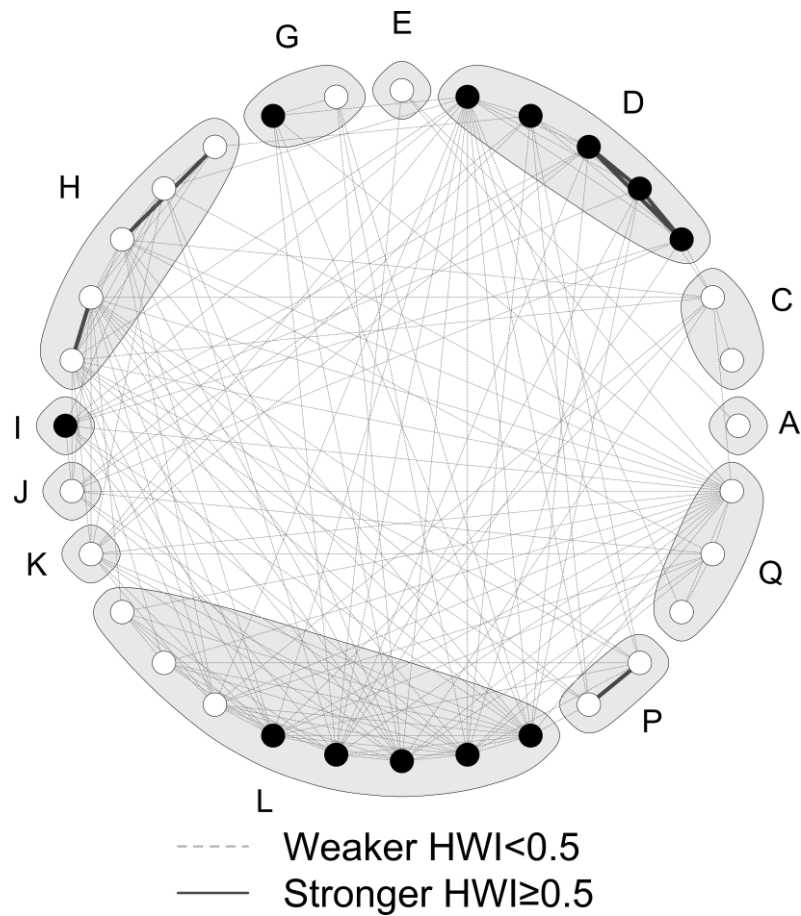
Figure 9. Sociograms of associations for the 32 most frequently encountered adult females (on more than 10 days over at least 3 years) from 12 different clusters. Nodes represent each female and are colored black if the individual was also seen on at least 20 days over at least 3 different years. Members of the same cluster were included within the same grey shading. Note the lack of strong associations and that there are many weak associations between females from different clusters. This is observed regardless of the minimum number of sightings, with predominantly weak associations across black nodes.
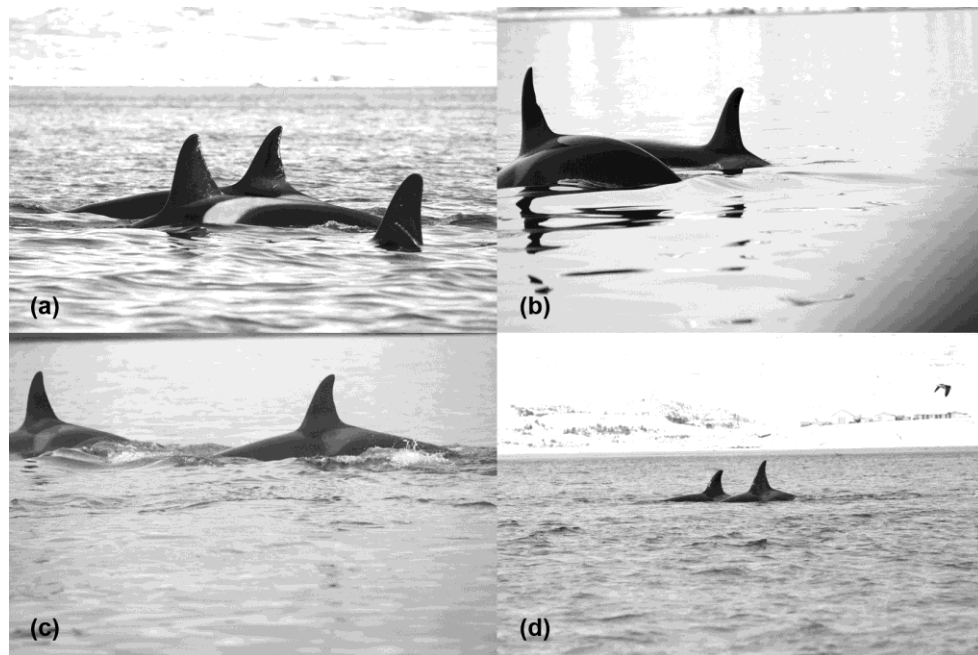
Figure 10. Examples of close associations between individuals from different subclusters and clusters: (a) IF-4 (Female, subcluster A3, Scotland ID 21) in close association with IS121 (Other, subcluster A1); (b) 997 (Female, subcluster A3, Scotland ID 19) in close association with IS041 (Female, cluster L); (c) IS172 (Other, subcluster A3) associating with IS049 (Female, cluster D); (d) IS229 (Other, subcluster A3) associating with IS030 (Female, cluster D).

933 **TABLES**

934 Table 1

935 Summary of the photo-identification sampling effort included in this study.

Year	Season	Sampling periods used (days)		Start-end of sampling periods	Number of	
		Research vessels	WW platform		Photographs	Identified individuals
2008	Summer	6	-	8th – 20th July	382	29
2009	Summer	16	-	7th – 29th July	2552	65
2010	Summer	6	-	4th – 10th July	748	70
2013	Winter	23	-	10th February – 24th March	5649	211
	Summer	4	-	17th – 29th July	1980	51
2014	Winter	19	1	13th February – 31st March	5510	115
	Summer	15	-	6th – 27th July	5265	149
2015	Winter	-	1	1st March	118	3
	Summer	19	-	7th – 29th July	6819	131

936 Days of sampling are discriminated by type of platform: research vessels and whale-watching (WW) boat.

937   Table 2

938   Summary of different clusters identified using Newman's (2006) clustering technique.

Cluster	n	Movement pattern[1]	Days	Identifications[2]	Mean HWI (SD)	Max HWI (SD)	S (SE)	S (SE) excluding juveniles
A	24 (5)	WB	34	2279	0.178 (0.04)	0.67 (0.15)	0.88 (0.1)	0.85 (0.1)
B	33 (3)	W	31	4112	0.12 (0.06)	0.62 (0.15)	1.01 (0.04)	1.01 (0.04)
C	9 (3)	B	15	798	0.54 (0.09)	0.73 (0.11)	0.08 (0.12)	0.05 (0.13)
D	11 (3)	B	60	3883	0.27 (0.06)	0.65 (0.13)	0.66 (0.06)	0.57 (0.08)
E	10 (4)	WB	24	549	0.2 (0.04)	0.55 (0.14)	0.96 (0.05)	0.86 (0.08)
F	3	B	10	91	0.12 (0.05)	0.18 (0)	0 (-)[3]	-
G	8 (4)	B	27	1918	0.49 (0.07)	0.67 (0.08)	0.17 (0.11)	0 (0.07)
H	13	B	31	1817	0.34 (0.04)	0.74 (0.07)	0.36 (0.12)	-
I	17 (4)	SB	65	2754	0.13 (0.05)	0.56 (0.19)	1.15 (0.03)	1.17 (0.04)
J	11 (3)	SB	33	1344	0.31 (0.16)	0.81 (0.25)	0.95 (0.06)	1.08 (0.05)
K	4 (1)	S	19	675	0.6 (0.08)	0.69 (0.08)	0 (0.11)	0 (0.03)
L	18 (5)	B	54	2825	0.16 (0.02)	0.59 (0.15)	1 (0.06)	0.91 (0.1)
M	4	B	8	142	0.27 (0.09)	0.5 (0.12)	0.47 (0.32)	-
N	7 (2)	SB	9	464	0.54 (0.08)	0.73 (0.1)	0 (0.19)	0 (0.12)
O	5	B	8	456	0.6 (0.1)	0.74 (0.12)	0 (0.2)	-
P	5 (2)	B	22	680	0.53 (0.09)	0.68 (0.11)	0.17 (0.09)	0 (0.09)
Q	7 (1)	B	31	1137	0.37 (0.1)	0.75 (0.13)	0.67 (0.14)	0.68 (0.14)
R	9 (1)	B	18	511	0.28 (0.13)	0.64 (0.18)	0.79 (0.09)	0.86 (0.09)

939   n, number of members with number of juveniles in brackets; HWI, half-weight index of association; SD, standard deviation;

940   S, social differentiation; SE, standard error.

941   [1] Movement pattern of non-juvenile members: W – only seen in the winter, S – only seen in the summer, B – seen in both

942   seasons, WB – seen only in the winter or in both seasons, SB – seen only in the summer or in both seasons.

943   [2] Total number of photographic record of identified individuals of each cluster.

944   [3] There was insufficient association data to calculate SE of S for Cluster F.

945   Table 3

946   Distribution of HWI for adult individuals seen at least 5 times, between and within sex

947   classes.

Adult sex classes	Mean HWI (SD)	Max HWI (SD)
Females-All	0.02 (0.01)	0.59 (0.18)
Males-All	0.02 (0.01)	0.62 (0.21)
Females-Females	0.02 (0.01)	0.44 (0.21)
Females-Males	0.02 (0.01)	0.48 (0.24)
Males-Females	0.02 (0.01)	0.56 (0.23)
Males-Males	0.02 (0.01)	0.48 (0.26)
Within classes	0.02 (0.01)	0.46 (0.24)
Between classes	0.02 (0.01)	0.52 (0.23)
All-All	0.02 (0.01)	0.6 (0.19)

948   HWI, half-weight index of association; SD, standard deviation.

949 Table 4

950 Summary of the results of the adult female-specific analysis under two different observational

951 thresholds.

Observational threshold	> 10 days, ≥ 3 years	≥ 20 days, ≥ 3 years
n	32	12
Mean ± SD sightings	19.1 ± 6.6 days (range of 11-34 days) over 4.6 ± 1 years (range of 3-6 years)	26.3 ± 4.5 days (range of 20-34 days) over 5.3 ± 0.5 years (from 5-6 years)
Non-random associations?	Yes	Yes
Dendogram	Figure S10 - Supplementary Material S5	Figure S11 - Supplementary Material S5
Divergence of clusters at HWI	0.04	0.21
Modularity	0.48	0.39

952 n, number of adult females in the analysis; HWI, half-weight index of association; SD, standard deviation.