

1 Dolphin social phenotypes vary in response to food availability but not
2 climate

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13 Abstract

14 Social behaviours can allow individuals to flexibly respond to environmental change, potentially
15 buffering adverse effects. However, individuals may respond differently to the same environmental
16 stimulus, complicating predictions for population-level response to environmental change. Here we
17 show that bottlenose dolphins (*Tursiops truncatus*) alter their social behaviour at yearly and monthly
18 scales in response to a proxy for food availability (salmon abundance) but do not respond to
19 variation in a proxy for climate (the North Atlantic Oscillation index). There was also individual
20 variation in plasticity for gregariousness and connectedness to distant parts of the social network,
21 although these traits showed limited repeatability. In contrast, individuals showed consistent
22 differences in clustering with their immediate social environment at the yearly scale but no
23 individual variation in plasticity for this trait at either time scale. These results indicate that social
24 behaviour in free-ranging cetaceans can be highly resource dependent with individuals increasing
25 their connectedness over short timescales but possibly reducing their wider range of connection at
26 longer timescales. Some social traits showed more individual variation in plasticity or mean
27 behaviour than others, highlighting how predictions for the responses of populations to
28 environmental variation must consider the type of individual variation present in the population.

29

30 **Keywords:** dolphin, environmental change, individual variation, plasticity, social network, *Tursiops*

31 Introduction

32 Animals engage in social interactions with conspecifics which are fundamental for determining
33 health, access to resources, and reproductive success [1]. Consequently, social interactions have a
34 strong influence on ecological processes such as population dynamics and evolutionary processes
35 such as the response to selection [2–4]. To maintain the best fit with their environment, animals may
36 adjust their social behaviour as conditions change [5], for instance being more gregarious when
37 resources are plentiful but less tolerant of conspecifics when resources are scarce [6]. Animals may
38 also change their behaviour through development and during senescence [7], and may non-
39 adaptively adjust their behaviour due to direct effects of the environment and other limitations [8].
40 Such plasticity is a hallmark of behavioural traits and gives behaviour an important role in how
41 animals interact with their environment.

42 When trying to understand how animals may respond plastically to changing environments, most
43 examine responses at the population level [e.g., 9], presuming that any individual variation in
44 response is absent or simply aggregates to give the population-level response. However, individuals
45 may show variation in plasticity, and so each will respond differently to change [10,11, sometimes
46 referred to as 'I x E' i.e., individual by environment interactions,12,13]. For example, European field
47 crickets (*Gryllus campestris*) become bolder and more active as they age, but individuals vary in the
48 extent of this, with some not increasing or even decreasing [14]. The degree of plasticity animals
49 show can be correlated with their mean behaviour (an “intercept-slope correlation”) which
50 determines how the magnitude of among-individual differences varies across environments and
51 indicates the extent to which plasticity is a separate trait in its own right [11,15]. Individuality in
52 plasticity can influence biological processes such as population growth and adaptive change at a
53 range of scales [16, see: 17 and accompanying papers], giving fundamentally different results to
54 when population-level only effects are assumed [15,18]. For example, Seebacher and Little
55 demonstrated that mosquitofish (*Gambusia holbrooki*) differ in how their performance changes with
56 temperature, resulting in a switching of the rank of swimming speed of individuals between cool and

57 warm temperatures. This changed which individuals might be predated, with a lower fraction of the
58 population reaching the critical speed to avoid predation in cool temperatures [19]. Therefore,
59 variation in plasticity will alter both the strength of selection and which genotypes produce
60 phenotypes that are selected for, altering evolution trajectories. Additionally, the extent of among-
61 individual variation in plasticity gives an upper-limit to the heritability of plasticity, which indicates
62 how rapidly plasticity itself can evolve [20–22]. Understanding how plasticity as a trait in its own
63 right can evolve is key for understanding how animals will adapt to more variable climates [22,23].

64 Marine mammals are a key group to study individual variation in response to environmental change.
65 They are typically long-lived, increasing the relative importance of plasticity versus adaptive
66 evolution for coping with contemporary environmental change [24]. They are also exposed to a wide
67 range of changing conditions during their lifetimes including climate, food availability, and pollution,
68 and their populations are often of conservation concern. All of these factors increase the need for us
69 to understand how they respond to changes in their environment [25–32].

70 Here, we studied a population of bottlenose dolphins (*Tursiops truncatus*) in the North Sea for over
71 30 years, regularly recording their social associations. Previous work in this study population has
72 demonstrated that critical group sizes increase in years of higher salmon abundance [33], and we
73 extend this by examining multiple facets of individual-level social behaviour at both the monthly and
74 yearly temporal scales. We achieved this by using social network analysis to quantify three different
75 dimensions of individual social behaviour: an individual's gregariousness (strength), how tightly its
76 immediate social group interact together (clustering coefficient), and how well connected an
77 individual is to the entire population (closeness; each described in more detail below). We then used
78 random regression models to quantify individual social phenotypes and determine how these social
79 phenotypes depend on yearly and monthly variation in available proxies for climate (at a broad
80 scale) and food availability (at a local scale). Our analyses also indicated whether bottlenose dolphins

81 show individual changes in response to the environment, or if population-level change was more
82 prominent.

83 Specifically, we were interested in how social behaviour depends on current environmental
84 conditions. Social behaviours are often highly dependent on both resource availability and spatial
85 distribution [6] and current climatic conditions can impose energetic constraints on individuals
86 [34,35] and impact their ability to move around their environment [36]. Bottlenose dolphin group
87 sizes off the north west coast of Spain showed a nonlinear relationship with the North Atlantic
88 Oscillation (NAO) index [37], while abundances of Indo-Pacific bottlenose dolphins (*T. aduncus*) are
89 impacted by a combination of the El Nino Southern Oscillation and season [38]. In our study system,
90 previous work indicated that the NAO index at a two-year lag was associated with dolphin critical
91 group size, but this appears to be entirely mediated through food availability [33], something we are
92 testing for directly. As such, we did not consider lagged effects here. We summarised climate
93 through the NAO index (see Methods), where positive values in this region indicate warmer and
94 wetter periods which would make rougher sea conditions, potentially resulting in the dolphins
95 travelling shorter distances. We therefore expect higher NAO values to lead to higher clustering
96 coefficients and lower closeness, but not to affect strength, at monthly and yearly scales. We
97 summarised resource availability through salmon abundances (see Methods). We expect that higher
98 salmon abundances allow dolphins to form larger groups (as found previously) and travel shorter
99 distances to find sufficient food, leading to higher strengths, higher clustering coefficients, and lower
100 closeness at both temporal scales.

101

102 [Material and methods](#)

103 Study site & group data collection

104 This study used data from a bottlenose dolphin population on the east coast of Scotland (Fig. 1). The
105 population of over 200 individuals [39] has been studied intensively as part of a long-term individual

106 based study [40–42]. We use data from boat-based photo-identification surveys carried out annually
107 between 1990 and 2021 which regularly recorded dolphin groups within the Moray Firth Special
108 Area of Conservation (SAC; 92/43/EEC), a core part of the population’s range which over 50% of the
109 population use each year (40). All surveys were made from small (5-6m) boats with outboard
110 engines, carefully and slowly manoeuvring the boat around each group to obtain high quality images
111 of the left and right side of as many dorsal fins as possible. Surveys initially followed a fixed survey
112 route until 2001 when, as a result of changing dolphin distribution within the SAC, flexible survey
113 routes were introduced to maximise sightings probability [more details in: ,43]. Data were available
114 from a total of 690 surveys (between 9 and 35 surveys each year; average of 22) with the majority
115 carried out between May to September.

116 During surveys, when we located a bottlenose dolphin group (one or more individuals in close
117 proximity within 100m, hereafter an “encounter”) we collected photo-identification data following a
118 standardised protocol [43]. We identified individuals from high-quality photographs based on unique
119 markings matched against a photo catalogue of previously identified individuals from the area
120 [40,41,44]. On average in a group 84% are successfully photographed, a rate of identification well
121 above the level at which social network metrics in incomplete networks are reliable [45]. All
122 individual identifications from photographs were confirmed by at least two experienced researchers.
123 For individuals first sighted as calves we could determine their year of birth and so their age [46], but
124 for individuals first sighted as juveniles or adults their exact age is unknown. Sex was determined
125 using genital photographs or if an adult was seen in repeat associations with a known calf [46].

126

127 Social network construction

128 Individuals sighted during the same encounter were assumed to be in the same group and therefore
129 associating [known as the ‘Gambit of the Group’ 47]. Aggregating many of these records of groups
130 allows one to infer which individuals are frequently associated and which individuals infrequently or

131 never associate. We removed observations of individuals younger than three years old (n = 2668
132 observations of 242 individuals), as these individuals are not likely to be independent of the mother
133 and so their social associations most likely represent her preferences. We then converted the
134 records of encounters into group by individual matrices (indicating which individuals were seen
135 together in each encounter) and then into weighted, undirected social networks using the R package
136 *asnipe* [48]. Edge weights were set as the simple ratio index, where the number of times two
137 individuals are seen together is divided by the total number of times they are seen, both together
138 and apart [49]. This measure ranges from 0 (individuals never seen together) to 1 (individuals always
139 seen together). We did this separately for each year, creating yearly social networks to assess how
140 social phenotypes vary at this temporal scale in response to environmental conditions. To assess
141 how social phenotypes vary at the monthly scale in response to environmental conditions we then
142 reconstructed social networks per month and removed any months with fewer than 10 encounters
143 [excluding 110 out of 215 months; as networks constructed using fewer than 10 observations can be
144 biased; ,50]. Histograms of the frequency of the number of encounters per year and per month are
145 shown in Fig. S1.

146 For each individual present in the network, for each year and again for each month we calculated
147 three network metrics. First was “strength”, the sum of all an individual’s associations, which as our
148 associations are based on observations of co-occurrence in groups is analogous to typical size of
149 groups an individual is in. Second was “weighted clustering coefficient”, the rate at which an
150 individual associates with other individuals who also associate with each other. This metric
151 represents how tightly individuals interact in their immediate social environment (possibly
152 analogous to “alliances” between three or more individuals, see also: [51,52]), at the expense of
153 interacting with a wider range of individuals. Finally, we quantified “closeness”, the inverse of the
154 mean of the path lengths between that individual and each other individual in the network,
155 corrected for network size to allow comparisons among networks which vary in the number of
156 individuals. Closeness represents the dolphin’s connectedness to the wider population, and would

157 be high if an individual linked two communities or moved between different areas each containing
158 more sedentary individuals.

159 We removed an individual's scores for a given year if they had fewer than five observations in that
160 year (removing 811 observations and leaving 874), as the social network position of those individuals
161 would be highly uncertain. They would however still contribute to the social environments and
162 therefore social network measures of individuals in that year who had five or more observations. We
163 repeated this at the month level, removing individuals' monthly scores when they had fewer than
164 five observations that month (removing 3423 observations and leaving 320). Histograms of the
165 frequency of the number of encounters per individual per year and per month are shown in Fig. S2.
166 The social network measures were not strongly correlated; Pearson correlations between
167 individuals' strength and clustering coefficient were 0.141 (yearly) and 0.346 (monthly), for strength
168 and closeness they were -0.004 (yearly) and -0.245 (monthly), and for clustering coefficient and
169 closeness they were 0.129 (yearly) and 0.170 (monthly).

170

171 Environmental data

172 We used the NAO index in the same time period the grouping observations were made as a measure
173 of climate. We used monthly and yearly measures of the NAO index between 1990 and 2021
174 downloaded from <https://www.cpc.ncep.noaa.gov/products/precip/CWlink/pna/nao.shtml> (Fig. S3).
175 This index indicates the atmospheric pressure difference between the low pressure zone over
176 Iceland and the high pressure zone over the Azores [53,54]. This index has frequently been linked to
177 the ecology of animal populations [55,56], for example influencing the foraging behaviour of Cory's
178 shearwaters [*Calonectris borealis*; ,57]. Climatic effects on cetaceans are typically thought to occur
179 via changes in prey species [31,58]; for instance Lusseau *et al.* found the NAO at a two-year lag
180 influenced critical group size in our study population through the lagged variable's effect on food

181 availability [33]. However, it is also possible that cetaceans respond directly to climate, sometimes at
182 even faster rates than their prey species [37,38,59].

183 For our index of food availability we followed Lusseau *et al.* [33], using data on monthly catches by
184 fishing rods (as opposed to nets) from the wild of both one season and multiple season adult Atlantic
185 salmon (*Salmo salar*) from the Alness, Beaully, Canon, Ness, and Nairn rivers. These feed into the sea
186 where observations of dolphin groups take place and hence are expected to be a good proxy for
187 salmon availability in that area. Further, catches on rods are positively correlated among rivers and
188 among months and with automatic counter data, indicating they are a good proxy for actual
189 abundance [60,61]. Atlantic salmon are an important food source for this dolphin population [62,63],
190 with dolphins forming larger groups when salmon are more abundant [33]. We downloaded monthly
191 data from [https://marine.gov.scot/data/marine-scotland-salmon-and-sea-trout-catches-salmon-](https://marine.gov.scot/data/marine-scotland-salmon-and-sea-trout-catches-salmon-district-shinyapp)
192 [district-shinyapp](https://marine.gov.scot/data/marine-scotland-salmon-and-sea-trout-catches-salmon-district-shinyapp) (using “rod data” and summing retained and released fish for both MSW and 1SW)
193 and summed monthly catches within a calendar year for yearly measures of fish abundance (Fig. S4).

194

195 Data analysis

196 All analyses were performed in R [ver 4.3.1; ,64] using linear mixed-effect models in *glmmTMB* [65].
197 Using regression-based models as opposed to randomisation-based tests has been recommended
198 for analysing questions about node-level social network traits as it improves the ability to make
199 inference while accounting equally well as node permutations for common types of data non-
200 independence [66]. We fitted 12 models, with all combinations across the three social traits, the two
201 environmental variables, and the yearly and monthly timescales. Clustering coefficient cannot be
202 calculated when an individual only associates with one other individual, and so the datasets for
203 these models were slightly smaller than the dataset for strength and closeness (see below). We
204 included individuals with unknown birth and death dates to maximise our sample size, and so
205 neither age nor lifespan could be included as predictor variables. In all models we included the fixed

206 effect of sex [as males and females can differ in social behaviour; ,67,68; ranging behaviour, and
207 survival; ,69], and either the NAO index or the count of caught salmon for that month or year. We
208 did not include both the NAO index and salmon abundance in the same model as we encountered
209 estimation problems with two random slopes. Including sex meant we excluded individuals of
210 unknown sex (140 observations of 66 individuals for the yearly networks, 30 observations of 21
211 individuals for the monthly networks), but the interactions between individuals of known and
212 unknown sex were still used to build the networks and so associations with individuals of unknown
213 sex still influenced the social network traits of males and females. We mean centred and scaled to
214 unit variance the environmental variable [70], and included the interaction between it and sex, to
215 see if male and female social behaviour responded differently to environmental variation. Random
216 effects were the random intercept for individual ID, the random slope of individual ID with the
217 environmental variable fitted as a fixed effect in the model (again mean centred and with a standard
218 deviation of 1), and the correlation between these two terms. We also included a temporal
219 autocorrelation term ($ar1$) among years to account for unmodelled environmental variation that
220 changes slowly across years, which could influence social behaviour to make adjacent years more
221 similar than non-adjacent years. Similarly, in the models for monthly variation we included a random
222 effect of month alongside the yearly temporal autocorrelation term. We used a Gaussian error
223 structure for all models. For strength and closeness, we used log link functions as the distributions
224 were right skewed. For clustering coefficient, which is bounded between 0 and 1, we used a logit link
225 function, which is preferable to an arcsine transformation when handling response variables
226 bounded in this way [71]. We used the default optimising algorithm for all models except for both
227 the yearly models for clustering coefficient and closeness, the model for strength in response to
228 monthly variation in the NAO index, and the models for clustering coefficient and closeness in
229 response to monthly variation in salmon abundance, where we used the “BFGS” optimiser, as
230 otherwise the models did not converge [65].

231 We report the coefficients and standard errors for each fixed effect, along with p-values, to give an
232 idea of the magnitude and uncertainty of each effect. We used the p-values from the Anova function
233 of the *car* package [72], using a Chi-squared test with type III sum of squares. We describe these p-
234 values in terms of “clarity” rather than “significance”; see Dushoff *et al.* [73] for a discussion on this.
235 To test whether individuals clearly differed in their response to the environmental variable, we first
236 tested whether there was a correlation between an individual’s plasticity and its mean behaviour by
237 re-fitting each model (12 in total) with the correlation between random intercepts and slopes
238 suppressed to zero and conducted a likelihood ratio test between the full model and this reduced
239 model with a single degree of freedom. If there was a clear difference between the models, we
240 concluded that the correlation between intercepts and slopes was non-zero. If there was no clear
241 difference between the models, we then tested the importance of the random slopes by comparing
242 the model with an intercept-slope correlation of zero to a model without the random slopes (but still
243 with the random intercepts) using a likelihood ratio test with a mix of zero and one degree of
244 freedom [as is appropriate for testing the clarity of single variance components, 74]. If there was a
245 clear difference between the models, we concluded that individuals differ in their response to the
246 environmental variable. When there is variation in plasticity, the magnitude of among-individual
247 differences varies across environments. We therefore calculated the marginal repeatability for each
248 trait following Schielzeth and Nakagawa [75]. We did this for all trait-environmental variable-time
249 scale combinations (12 in total), even when there was no evidence for random slopes, to aid
250 comparison among traits. Data and R code are available online [76].

251

252 Results

253

254 Change with environmental variables at a yearly scale

255 For the analysis of how dolphin social phenotypes change at the yearly scale in response to
256 environmental variables, our dataset included 129 unique individuals. For strength and closeness
257 there were 874 measures, and for clustering coefficient there were 873 measures. All traits had a
258 mean of 6.78 (sd = 5.39) measures per individual.

259 Dolphins' strength and clustering coefficient were not affected by the NAO index (Fig. 2a and b) or
260 salmon abundance (Fig. 2d and e) in both sexes, and the sexes did not differ in mean strength or
261 clustering coefficient (Table 1, full model results in Tables S1-4, Supplementary Materials). For both
262 strength and clustering coefficient with the NAO index there were no intercept-slope correlations
263 and the random slopes were not statistically clear (Table 2). Individuals did differ in how their
264 strengths changed with salmon abundance, with a clear negative intercept-slope correlation (Table
265 2). There was no intercept-slope correlation and no random slopes for the change of clustering
266 coefficient with salmon abundance (Table 2). The marginal repeatabilities for strength were low:
267 0.017 in the NAO index model and 0.018 in the salmon abundance model, suggesting the trait has
268 limited repeatability. The marginal repeatabilities for clustering coefficient were higher: 0.172 and
269 0.178 for the NAO index and salmon abundance models respectively.

270 Closeness did not vary with NAO index in either sex (Fig. 2c), but it did decrease with increasing
271 salmon numbers in both sexes (Fig. 2f ; Table 1; full results in Supplementary Material Tables S5 &
272 S6). Dolphins showed a negative mean-plasticity relationship for the NAO index, with individuals
273 with lower than average mean closeness increasing their closeness with increasing NAO indices and
274 individuals with higher than average closeness decreasing their closeness. This also indicates there
275 was individual variation in plasticity (Table 2). In contrast, there was a positive intercept-slope
276 correlation for closeness in response to salmon abundance (Table 2), indicating that individuals with
277 lower means also decreased the most. The marginal repeatabilities were low for closeness: 0.003 in
278 the NAO index model and 0.002 in the salmon abundance model.

279 For all social traits there was substantial among-year variation and social traits in consecutive years
280 were positively correlated (year to year correlations: strength; $r_{NAO} = 0.452$, $r_{Salmon} = 0.566$; clustering
281 coefficient; $r_{NAO} = 0.590$, $r_{Salmon} = 0.657$; and closeness; $r_{NAO} = 0.283$, $r_{Salmon} = 0.472$), showing that, as
282 expected, adjacent years were more similar than non-adjacent years.

283 In summary, dolphins had lower closeness scores in years of high salmon abundance, but there were
284 no trait-environment associations at the yearly scale for the other two social traits or for the effect
285 of NAO. For closeness, individuals showed variation in plasticity that was related to their mean
286 behaviour for both NAO and salmon abundance, but for clustering coefficient individuals showed no
287 variation in individual plasticity. Individual dolphins showed variation in their plasticity of strength in
288 response to salmon abundance only, with a great spread of values at high than low values. Clustering
289 coefficient showed consistent differences between individuals across environments, but strength
290 and closeness did not.

291

292 Change with environmental variables at a monthly scale

293 We analysed how dolphin social phenotypes change in response to environmental variables at the
294 monthly scale with a dataset of 88 unique individuals and 320 measures for all traits. Traits had a
295 mean of 3.64 measures (sd = 2.64) each.

296 Strength increased with monthly salmon abundance for both sexes (Fig. 3d, Table 1), and there was
297 individual variation in plasticity and a negative intercept-slope correlation, with individuals with
298 lower means increasing more than those with higher means (Table 2). However, strength did not
299 respond to the monthly NAO index (Fig. 3a) and there was no individual variation in plasticity due to
300 the NAO (Table 1, full model results in Tables S7-12 in the supplementary materials). As for the
301 yearly models, the marginal repeatability of strength was low (0.003 in the NAO index model, 0.007
302 in the salmon abundance model).

303 Clustering coefficient showed no clear relationships with either the monthly NAO index (Fig. 3b), or
304 the monthly salmon abundance (Fig. 3e and Table 1), and the sexes did not differ in their mean
305 clustering coefficient or how it varied. Individuals showed no mean-plasticity relationship and no
306 individual variation in response to either variable (Table 2, note that the model for clustering
307 coefficient and monthly salmon would not converge with random intercepts and slopes but no
308 correlation between them, so we compared the full model with the model without random slopes
309 using two degrees of freedom). Clustering coefficient was slightly repeatable, with marginal
310 repeatabilities of 0.038 and 0.020 in the NAO index and salmon abundance models respectively.

311 Both sexes increased their closeness with higher monthly salmon abundance (Fig. 3f), but individuals
312 did not vary in how their closeness changed in response to salmon abundance (Table 2). There was
313 no response to the NAO index (Fig. 3c and Table 1), with no mean-plasticity relationship. However,
314 individuals did vary around the population-level stability in their responses to the NAO index (Table
315 2). There was limited repeatability of closeness at the monthly scale, with a marginal repeatability of
316 0.063 in the NAO index model and 0.033 in the salmon abundance model.

317 There was among-month and among-year variation, but in the monthly models social traits in
318 consecutive years were either negatively or not correlated (year to year correlations: strength: $r_{\text{NAO}} =$
319 -0.016 , $r_{\text{Salmon}} = 0.024$; clustering coefficient: $r_{\text{NAO}} = -0.307$, $r_{\text{Salmon}} = -0.399$; closeness: $r_{\text{NAO}} = -0.144$,
320 $r_{\text{Salmon}} = -0.139$).

321 In summary, months with higher salmon numbers led to higher strength and higher closeness.
322 Meanwhile, the NAO index did not clearly affect any network trait. Individuals differed in how their
323 strength changed in response to salmon abundance, and they also showed variation in responses of
324 closeness to the NAO index, but they did not differ in how their clustering coefficient changed for
325 either variable. Clustering coefficient and closeness were slightly repeatable across environments
326 but strength was not.

327

328 Discussion

329

330 We explored whether bottlenose dolphin social behaviour responded to environmental variation.
331 Social behaviour responded to variation in food availability, with a measure of connectedness to the
332 wider network (closeness) decreasing at higher salmon abundances at a yearly scale, and both
333 overall gregariousness (strength) and closeness increasing at higher salmon abundances at a
334 monthly scale. Clustering of the local social environment, clustering coefficient, also showed an
335 increase with monthly salmon abundance but this trend was statistically unclear. In contrast, social
336 behaviours showed no population-level responses to climatic change at either scale. In addition, we
337 found that individuals showed consistent differences in mean clustering coefficient, especially at the
338 yearly scale, but not in individual plasticities, while strength and closeness showed some variation in
339 individual plasticity but limited consistent differences in mean behaviour. This plasticity was often,
340 but not always, negatively associated with mean behaviour, causing among individual differences to
341 typically be greater for low values of salmon abundance and the NAO index.

342 Months of higher salmon abundance led to increase in all three social behaviours, although this was
343 not statistically clear for clustering coefficient (see Fig. 4 for a comparison of networks between
344 months with low vs. high salmon abundance). This indicates that dolphins were increasing all kinds
345 of social associations in response to increased immediate food availability. Similar results have been
346 found in spotted hyenas (*Crocuta crocuta*) where seasons with high prey availability have denser
347 social networks [77], and in Grant's gazelles (*Nanger granti*), where increased rainfall (and so food
348 availability) led to higher closeness scores [78]. It is presumed that an increase in social interactions
349 at higher food availability is facilitated by a reduction in the intensity of resource competition
350 [reviewed in: ,6,see also: ,79]. Therefore, in our study system higher rates of social interaction may
351 be beneficial for non-foraging reasons, such as mating. Both mating and calving seasons
352 approximately align with the months of highest salmon abundance in the summer (Fig. S4),

353 supporting this suggestion. Additionally, dolphins could move into areas where food availability is
354 especially high [42,80], causing more individuals to be seen together and therefore inferred social
355 networks to be denser, even if actual rates of social interaction are not changing, or only changing as
356 a byproduct. Finally, it is possible that months with fewer salmon also differ in an unidentified
357 variable which causes dolphins to group less. However, it is unlikely that this unidentified factor is
358 predation threat that changes month to month, as predators are absent in this area [81]. Therefore,
359 a change in social behaviour and/or movement related to the seasonal availability of salmon,
360 perhaps influenced by reproductive behaviour, seems the most likely.

361 Interestingly, the change in closeness at the yearly scale was in opposite direction to that at the
362 monthly scale, showing a decrease with increased salmon abundance, as well as being a
363 considerably stronger effect (standardised effect size of -0.258 compared to 0.087). A decrease in
364 yearly closeness suggests dolphins are more poorly connected to distant parts of the network when
365 salmon are more abundant. This decrease might be indicative of a reduced need to travel long
366 distances to find food, generating a network with a smaller diameter and so lower individual
367 closeness [see also 82 who demonstrated that more patchy food availability increases network
368 connectedness]. This effect might not be apparent at the monthly scale as the increase in strength in
369 months of high salmon abundance could also lead to higher closeness scores. Whether this is the
370 case or not, the fact that changes in different timescales can be in opposite directions is intriguing
371 and should be kept in mind when attempting to generalise results from one timescale to another.

372 Despite the changes in response to salmon abundance, we did not see any responses to climatic
373 variation (the NAO index) on a yearly or monthly scale. The NAO index varied considerably at both
374 scales, ranging from -1.15 to 1.08 at the yearly scale and -3.18 to 2.12 at the monthly scale (Fig. S3),
375 hence a lack of necessary variability seems unlikely. Lusseau *et al.* [33] also observed no variation in
376 group size in our study population in response to contemporary variation in the NAO index (they did
377 see an effect at a two-year lag, likely mediated by food availability). The robustness or inflexibility of

378 social behaviour in response to variation in climatic conditions might indicate that the variation in
379 the NAO index is inconsequential and so they have no need to respond to it. Additionally or
380 alternatively, dolphins may change other phenotypes, such as foraging behaviour or metabolism, to
381 cope with this stressor [31], leaving social behaviour unchanged. Finally, local conditions might be
382 more relevant to dolphin behaviour, as opposed to the regional conditions summarised by the NAO
383 index. For example, movements of bottlenose dolphins depend on tidal currents and fronts [83], and
384 changes to these might be important for their social behaviour.

385 Alongside the plasticity at the population level in strength and closeness, these traits also showed
386 individual variation in plasticity (although strength only showed this for salmon abundance, and
387 closeness only at the yearly level). Therefore, even if the population as a whole showed no overall
388 change for some trait-environmental variable combinations, some individuals might still show an
389 increase in their overall gregariousness and/or connectedness to wider parts of the network, while
390 others a decrease. Variation in individual plasticity leads to environment-dependent repeatability
391 (and possibly heritability), can dampen population responses to environmental variability, and
392 enhance population persistence [18]. For example, due to the negative intercept-slope correlation,
393 individual strength shows the most among-individual variation at low salmon abundances (the
394 approximate marginal repeatability of strength at the monthly scale two standard deviations below
395 the mean salmon abundance was 0.124, compared to 0.02 at the mean). If strength is linked to
396 foraging strategy, for instance if individuals with more social connections have access to more
397 information about prey availability [82], a wider range of social phenotypes could increase the
398 possibility that at least some individuals are successful despite low food availability. Determining the
399 genetic basis and importance of early life conditions for the development of these different
400 responses [12] and how this variation impacts population dynamics [84] is key. Models projecting
401 how these traits in dolphin populations will change in the future should account for both among-
402 individual variation in mean behaviour and in behavioural plasticity. Additionally, Kebke *et al.* [31]
403 suggest that cetacean ranging and foraging behaviour may well be under selection for increased

404 plasticity as environments change, and so estimating selection on both means and plasticities of
405 behaviours is a logical and important next step.

406 In contrast, clustering coefficient showed no individual variation in plasticity at any timescale-
407 environmental variable combination. Clustering coefficient at the yearly scale was the only trait with
408 more than slight repeatability, indicating some individual consistency [see also 85 who found
409 consistency over lifetime in the social behaviours of Indo-Pacific bottlenose dolphins, *T. aduncus*].

410 Therefore, plasticity might be more limited with individuals keeping the same pattern of local
411 connections across environmental conditions. As clustering coefficient depends on the frequency of
412 connections among triads, an individual's trait value cannot change without impacting the trait value
413 of others. This interdependence may then constrain the degree of plasticity possible at the individual
414 level. There is no evidence for male alliances in this population [86], and so determining what these
415 clusters of individuals represent and why they might be so stable would be useful.

416 In conclusion, we found that, at the population level, individual dolphin social behaviour is more
417 responsive to variation in food availability than climatic variation, with this being particularly
418 apparent at the monthly scale. We observed that individuals increased overall gregariousness and
419 connectedness to wider parts of the network in months of higher salmon abundance. In contrast,
420 dolphins decreased their connectedness to wider parts of the network in years of high salmon
421 availability. Traits that tended to show higher repeatability tended to show limited individual
422 variation in plasticity, although there was considerable variation in this trend. As such, whether
423 individual heterogeneity in both mean and plasticity in behaviour needs to be accounted for when
424 predicting species responses to environmental change might have to be considered on a case-by-
425 case basis, and individual plasticities as well as means may be targets of selection and hence
426 evolvable.

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438 Tables

439

440 **Table 1.** Main effects (“M”) and interactions with sex (“I”, also shaded in grey) for the two
 441 environmental variables effects on the three social network traits, at each of the monthly and yearly
 442 scales. Effects clearly different from zero ($p < 0.05$) are highlighted in bold, while effects with p
 443 values between 0.07 and 0.05 are shown in italics.

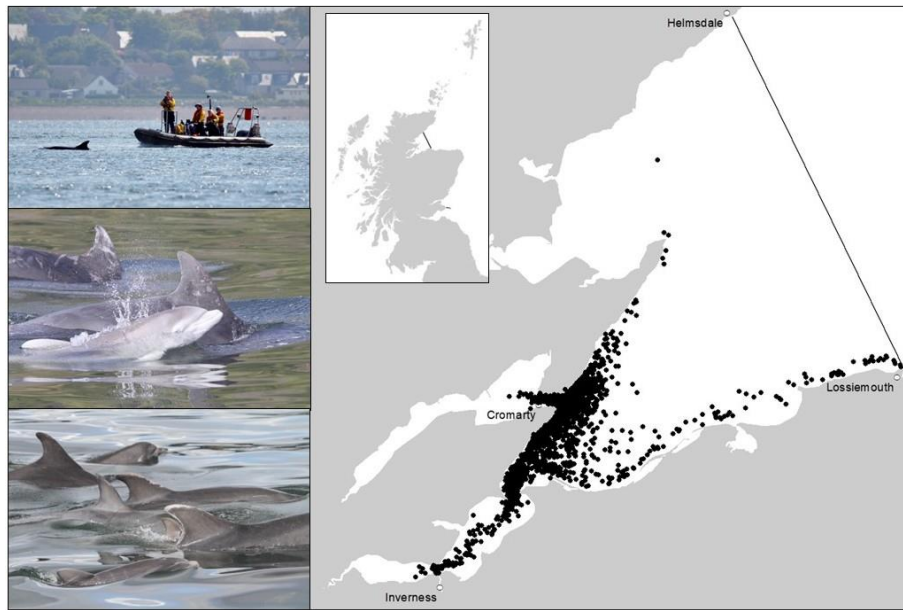
			Strength	Clustering coefficient	Closeness
NAO index	Yearly	M	$\beta = -0.035 \pm 0.066, \chi^2 = 0.280, p = 0.597$	$\beta = -0.102 \pm 0.081, \chi^2 = 1.595, p = 0.207$	$\beta = -0.115 \pm 0.102, \chi^2 = 1.275, p = 0.259$
		I	$\beta = -0.002 \pm 0.021, \chi^2 = 0.005, p = 0.942$	$\beta = 0.031 \pm 0.035, \chi^2 = 0.793, p = 0.373$	$\beta = 0.006 \pm 0.008, \chi^2 = 0.458, p = 0.499$
	Monthly	M	$\beta = 0.053 \pm 0.034, \chi^2 = 2.437, p = 0.119$	$\beta = -0.102 \pm 0.056, \chi^2 = 3.304, p = 0.069$	$\beta = 0.023 \pm 0.033, \chi^2 = 0.464, p = 0.496$
		I	$\beta = 0.039 \pm 0.037, \chi^2 = 1.105, p = 0.293$	$\beta = 0.057 \pm 0.069, \chi^2 = 0.678, p = 0.410$	$\beta = 0.031 \pm 0.037, \chi^2 = 0.713, p = 0.398$
Salmon	Yearly	M	$\beta = 0.108 \pm 0.069, \chi^2 = 2.422, p = 0.120$	$\beta = -0.027 \pm 0.091, \chi^2 = 1.595, p = 0.207$	$\beta = -0.258 \pm 0.094, \chi^2 = 7.489, p = 0.006$
		I	$\beta = -0.009 \pm 0.026, \chi^2 = 0.126, p = 0.723$	$\beta = -0.070 \pm 0.038, \chi^2 = 0.794, p = 0.373$	$\beta = -0.002 \pm 0.008, \chi^2 = 0.091, p = 0.763$
	Monthly	M	$\beta = 0.137 \pm 0.038, \chi^2 = 12.755, p < 0.001$	<i>$\beta = 0.116 \pm 0.062, \chi^2 = 3.569, p = 0.059$</i>	$\beta = 0.087 \pm 0.040, \chi^2 = 4.714, p = 0.030$
		I	$\beta = -0.011 \pm 0.045, \chi^2 = 0.065, p = 0.799$	$\beta = -0.105 \pm 0.074, \chi^2 = 2.011, p = 0.156$	$\beta = 0.009 \pm 0.030, \chi^2 = 0.081, p = 0.777$

444

445

446 **Table 2.** Intercept slope correlations (“ISC”) and their statistical tests, and whether random slopes
 447 (“RS”) were present or absent and their statistical tests (likelihood ratio tests in all cases, an asterix is
 448 given for the test of the random slopes if it was not performed as the intercept-slope correlation was
 449 first found to be clear). Clear positive correlations are noted in bold text and highlighted with blue
 450 fill, and clear negative correlations with bold text and orange fill, while clear random slopes are
 451 highlighted in bold text and the same colour as the associated correlation.

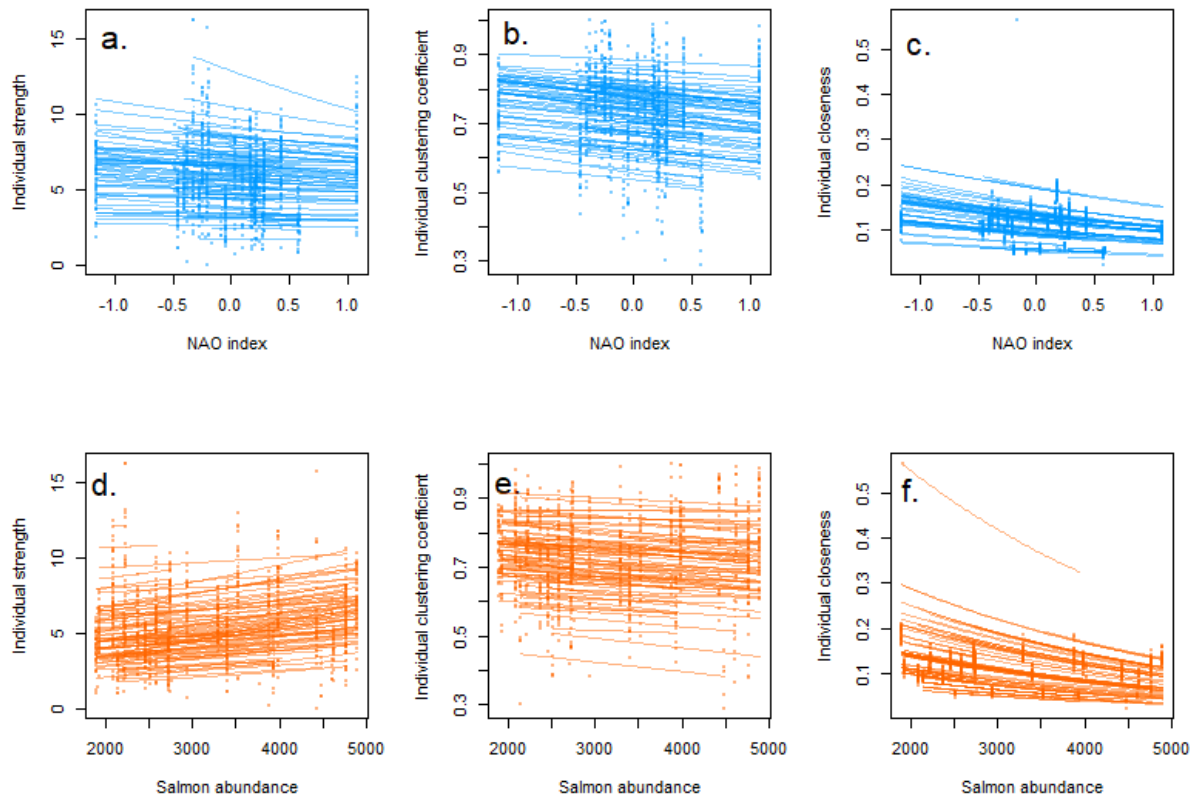
			Strength	Clustering coefficient	Closeness
NAO index	Yearly	ISC	-0.377 ($\chi_1^2 = 1597, p = 0.206$)	0.996 ($\chi_1^2 = 1.274, p = 0.259$)	-0.957 ($\chi_1^2 = 5.269, p = 0.022$)
		RS	Absent ($\chi_{0,1}^2 = 1.688, p = 0.097$)	Absent ($\chi_{0,1}^2 = 0.023, p = 0.500$)	Present *
	Monthly	ISC	-0.976 ($\chi_1^2 = 0.868, p = 0.352$)	0.075 ($\chi_1^2 = 0.000, p = 0.985$)	-0.486 ($\chi_1^2 = 0.447, p = 0.504$)
		RS	Absent ($\chi_{0,1}^2 = 0.001, p = 0.486$)	Absent ($\chi_{0,1}^2 = 0.030, p = 0.431$)	Present ($\chi_{0,1}^2 = 3.448, p = 0.032$)
Salmon	Yearly	ISC	-0.603 ($\chi_1^2 = 7.195, p = 0.007$)	0.998 ($\chi_1^2 = 2.660, p = 0.103$)	0.982 ($\chi_1^2 = 3.967, p = 0.046$)
		RS	Present *	Absent ($\chi_{0,1}^2 = 0.000, p = 0.500$)	Present *
	Monthly	ISC	-0.769 ($\chi_1^2 = 6.191, p = 0.013$)	-0.967 (NA, model did not converge)	-0.999 ($\chi_1^2 = 2.005, p = 0.157$)
		RS	Present *	Absent ($\chi_2^2 = 0.035, p = 0.983$)	Absent ($\chi_{0,1}^2 = 0.000, p = 0.500$)



453

454 **Figure 1.** Images depicting a photo-identification survey (top left), a newborn calf with mother
455 (middle left), unique markings used to identify individuals (bottom left), and location of encounters
456 with bottlenose dolphins within the Moray Firth Special Area of Conservation from 1990 to 2021
457 (right).

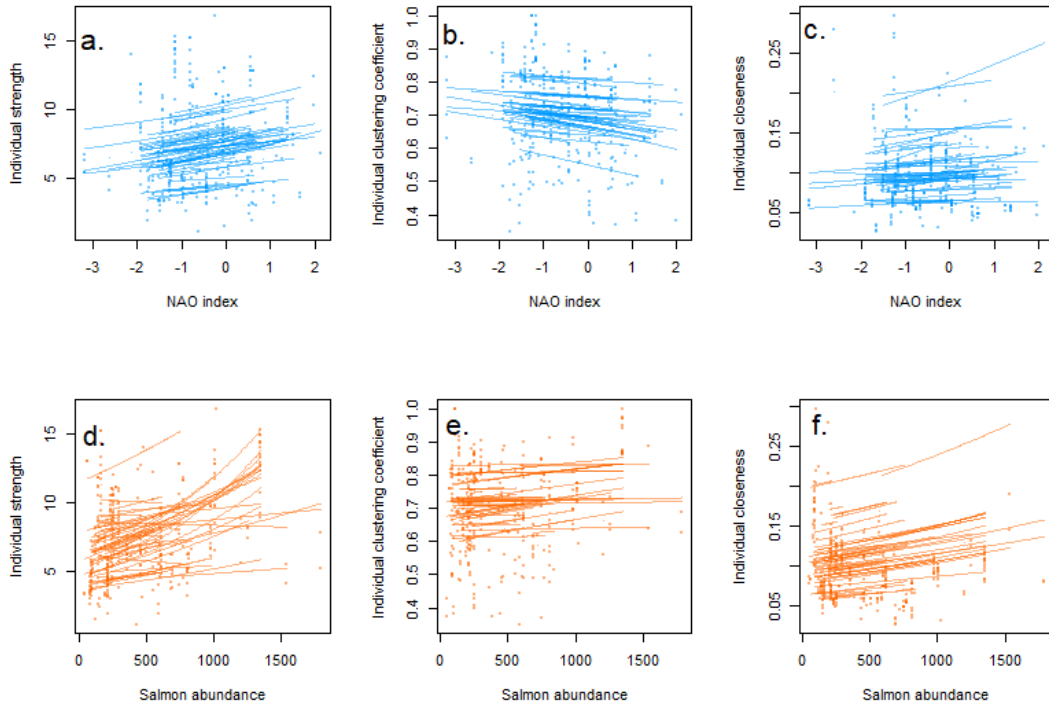
458



459

460 **Figure 2.** Plots of each of the three social network traits and yearly variation in the North Atlantic
 461 Oscillation (NAO) index (a. strength, b. clustering coefficient, c. closeness) and salmon abundances
 462 (d. strength, e. clustering coefficient, f. closeness). For each individual dolphin we have predicted its
 463 network trait on the observed scale based on the model results, using the “predict” function in R
 464 with the individual’s sex, the range of NAO values or salmon counts that individual was exposed to,
 465 and picking a random year that individual experienced.

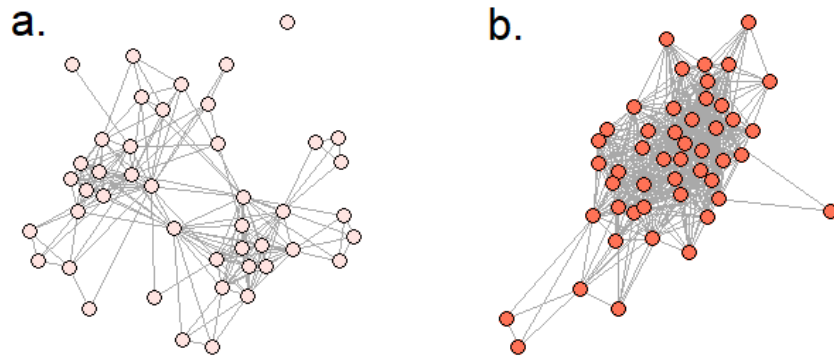
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467

468 **Figure 3.** Plots of each of the three social network traits and monthly variation in the North Atlantic
 469 Oscillation (NAO) index (a. strength, b. clustering coefficient, c. closeness) and salmon abundances
 470 (d. strength, e. clustering coefficient, f. closeness). For each individual dolphin we have predicted its
 471 network trait on the observed scale based on the model results, using the “predict” function in R
 472 with the individual’s sex, the range of NAO values or salmon counts that individual was exposed to,
 473 picking a random year that individual experienced, and the month to June (an arbitrary choice that
 474 was approximately in the middle of the calendar year).

475



476

477 **Figure 4.** Plots of dolphin social networks in a month of low salmon abundance (May 1990) and a
 478 month of high salmon abundance (August 2007). Circles are individual dolphins and grey lines
 479 indicate associations i.e., those seen in the same group at least once in that month.

480

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