# Dolphin social phenotypes typically show individual variation in response to environmental change alongside population-level stability

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## Abstract

Social behaviours can allow individuals to flexibly respond to environmental change, potentially buffering adverse effects. However, individuals may respond differently to the same environmental stimulus, complicating our ability to predict population-level response to environmental change. Here we show that bottlenose dolphins (*Tursiops truncatus*) show a high degree of individual variability in responses of social network traits to variation in proxies of food availability (salmon abundance) and climate (the North Atlantic Oscillation index), against a background of population-level stability. Individual dolphins did not reliably respond to yearly variation in environmental factors and showed limited consistency in their overall gregariousness or connectedness to distant parts of the network. However, individuals showed consistent differences in mean connectedness to their immediate social environment and at the monthly scale these connections became denser in months of high salmon abundance. Negative relationships between mean behaviour and plasticity in behaviour suggest greater levels of variation during times of low North Atlantic Oscillation index or salmon abundance. These results indicate that forecasting population responses to environmental change should account for among-individual variation in both mean and plasticity of social behaviour.

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

## Introduction

Animals engage in social interactions with conspecifics which are fundamental for determining health, access to resources, and reproductive success (1). Consequently, social interactions have a strong influence on ecological processes such as population dynamics and evolutionary processes such as the response to selection (2–4). To maintain the best fit with their environment, animals may adjust their social behaviour as conditions change (5), for instance being more gregarious when resources are plentiful but less tolerant of conspecifics when resources are scarce (6). Animals may also change their behaviour through development and during senescence (7). Such plasticity is a hallmark of behavioural traits and gives behaviour an important role in how animals interact with their environment.

When trying to understand how animals may respond through plasticity to changing environments, most examine responses at the population level (e.g., 8), implying that all individuals respond similarly. However, individuals typically show variation in plasticity, and so each will respond differently to change (9,10, sometimes referred to as 'I x E' i.e., individual by environment interactions,11,12). For example, European field crickets (*Gryllus campestris*) become bolder and more active as they age, but individuals vary in the extent of this, with some not increasing or even decreasing (13). The degree of plasticity animals show can be correlated with their mean behaviour (an "intercept-slope correlation") which determines how the magnitude of among-individual differences varies across environments and indicates the extent to which plasticity is a separate trait in its own right (10,14). Individuality in plasticity can influence biological processes such as population growth and adaptive change at a range of scales (15,see: 16 and accompanying papers), giving fundamentally different results to when population-level only effects are assumed (14,17).

Additionally, the extent of among-individual variation in plasticity gives an upper-limit to the heritability of plasticity, which indicates how rapidly plasticity itself can evolve (18–20). Understanding how plasticity as a trait in its own right can evolve is key in understanding how animals will adapt to more variable climates (20,21).

Marine mammals are a key group to study individual variation in response to environmental change. They are typically long-lived, increasing the relative importance of plasticity versus adaptive evolution for coping with contemporary environmental change (22). They are also exposed to a wide range of changing conditions including climate, food availability, and pollution, and their populations are often of conservation concern. All of these factors increase the need for us to understand how they respond to changes in their environment (23–30).

Here, we studied a population of bottlenose dolphins (*Tursiops truncatus*) in the North Sea for 30 years, and regularly recorded their social associations. We use social network analysis to quantify three different dimensions of individual social behaviour: an individual's gregariousness (strength), how tightly its immediate social group interact together (clustering coefficient), and how well connected an individual is to the entire population (closeness). We then used random regression models to quantify individual social phenotypes and determine how these social phenotypes depend on yearly and monthly variation in available proxies for climate and food availability. These models also indicated whether bottlenose dolphins show individual changes in response to the environment, or if population-level change was more prominent.

## Material and methods

### Study site & group data collection

This study used data from a bottlenose dolphin population on the east coast of Scotland (Fig. 1). The population of over 200 individuals (31) has been studied intensively as part of a long term individual

based study (32–34). We use data from boat-based photo-identification surveys carried out annually between 1990 and 2020 which regularly recorded dolphin groups within the Moray Firth Special Area of Conservation (SAC) (92/43/EEC) (35). The SAC is a core part of the population's range with over 50% of the population using this area each year, with regular annual summer survey effort aimed at maximising sighting probability, and consistent and adaptive protocols (35). Additional data were also available from Whale and Dolphin Conservation land based photo-identification surveys (33). Data were available from a total of 913 surveys (between 10 and 90 surveys each year; average of 30) with the majority carried out between May to September.

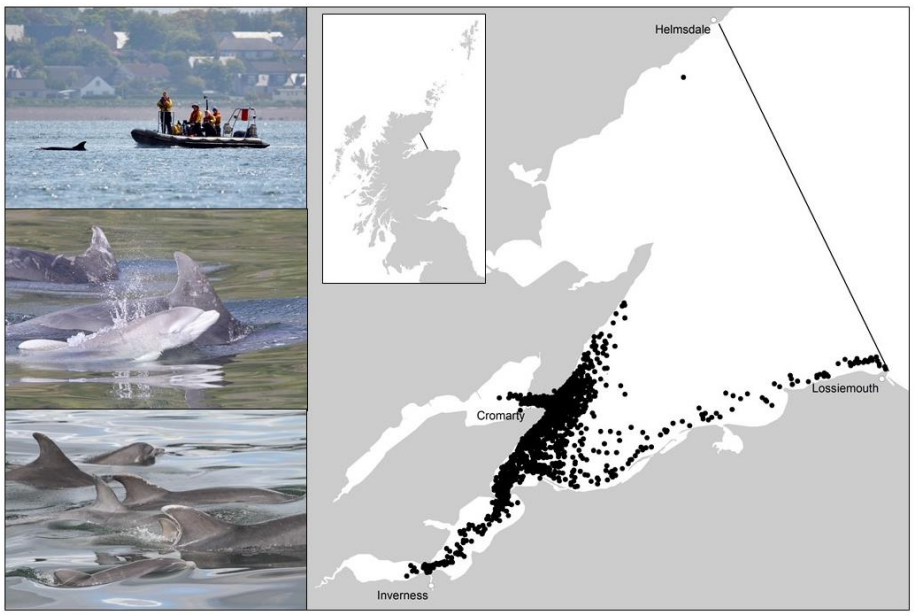



**Figure 1**. Images depicting a photo-identification survey (top let), a newborn calf with mother (middle left), unique markings used to identify individuals (bottom left). and location of encounters with bottlenose dolphins within the Moray Firth Special Area of Conservation from May to September 1990 to 2020 (right).

During surveys, when we located a bottlenose dolphin group (one or more individuals in close proximity and engaging in similar behaviours such as travelling and foraging) we collected photo-identification data following a standardised protocol (35). We identified individuals from high-quality

photographs based on unique markings matched against a photo catalogue of previously identified individuals from the area (32,33,36). On average, in a group 84% are successfully photographed, a rate of identification well above the level at which social network metrics in incomplete networks are reliable (37). All individual identifications from photographs are confirmed by at least two experienced researchers. For individuals first sighted as calves we could determine their year of birth and so their age (38), but for individuals first sighted as juveniles or adults their exact age is unknown. Sex was determined using genital photographs or if an adult was seen in repeat associations with a known calf (38).

### Social network construction

Individuals sighted during the same encounter were assumed to be in the same group and therefore associating (known as the 'Gambit of the Group'; ,39). Aggregating many of these records of groups allows one to infer which individuals are frequently associated and which individuals infrequently or never associate. We removed observations of individuals younger than three years old (n = 2634 observations of 233 individuals), as these individuals are not likely to be independent of the mother and so their social associations most likely represent her preferences. We then converted the records of encounters into group by individual matrices (indicating which individuals were seen together in each encounter) and then into weighted, undirected social networks using the R package *asnipe* (40). Edge weights were set as the simple ratio index, where the number of times two individuals are seen together is divided by the total number of times they are seen, both together and apart (41). This measure ranges from 0 (individuals never seen together) to 1 (individuals always seen together). We did this separately for each year, creating a social network per year to assess how social phenotypes vary at the yearly scale in response to environmental conditions. To assess how social phenotypes vary at the monthly scale in response to environmental conditions we then reconstructed social networks per month and removed any months with fewer than 10 encounters

(excluding 98 out of 217 months; as networks constructed using fewer than 10 observations can be biased; Franks *et al.* 2010). Histograms of the frequency of the number of encounters per year and per month are shown in Fig. S1.

For each individual present in the network for each year, we calculated the following: strength (the sum of all an individual's associations, representing its gregariousness), weighted clustering coefficient (the rate at which an individual associates with other individuals who also associate with each other, representing how tightly individuals in its immediate social environment interact), and closeness (the mean of the path lengths between that individual and each other individual in the network, corrected for network size to allow comparisons among networks which vary in the number of individuals, representing its connectedness to the wider population). We removed an individual's scores for a given year if they had fewer than three observations in that year (removing 498 and leaving 1133), as the social network position of those individuals would be highly uncertain. They would however still contribute to the social environments and therefore social network measures of individuals in that year who had three or more observations. We repeated this at the month level, again removing individuals' monthly scores when they had fewer than three observations that month (removing 2215 and leaving 1704). Histograms of the frequency of the number of encounters per individual per year and per month are shown in Fig. S2. We also removed instances where an individual's closeness was over 1, which occurs when an individual is only connected to a single other (n = 2 in the yearly networks, n = 18 in the monthly networks). The social network measures were not well correlated; Pearson correlations between individuals' strength and clustering coefficient were 0.136 (yearly) and 0.101 (monthly), for strength and closeness they were -0.042 (yearly) and -0.314 (monthly), and for clustering coefficient and closeness they were 0.157 (yearly) and 0.032 (monthly).

## Environmental data

Following Lusseau *et al*. (43), we used the North Atlantic Oscillation (NAO) index as a measure of climate. We used monthly and yearly measures of the NAO index between 1990 and 2020 downloaded from https://www.cpc.ncep.noaa.gov/products/precip/CWlink/pna/nao.shtml (Fig. S3). This index indicates the atmospheric pressure difference between the low pressure zone over Iceland and the high pressure zone over the Azores (44,45). This index has frequently been linked to the ecology of animal populations (46,47), for example influencing the foraging behaviour of Cory's shearwaters (Calonectris borealis; ,48). While climatic effects on cetaceans are typically thought to occur via changes in prey species (29,49), a phenomenon also observed in our study population (43), it is also possible that cetaceans respond directly to climate, sometimes at even faster rates than their prey species (50–52).

For our index of food availability we again followed Lusseau *et al*. (43), using data on monthly catches by fishing rods (as opposed to nets) from the wild of both one season and multiple season adult Atlantic salmon (*Salmo salar*) from the Alness, Beauly, Canon, Ness, and Nairn rivers. These feed into the sea where observations take place and hence are expected to be a good proxy for salmon availability in that area. Further, catches on rods are positively correlated among rivers and among months and with automatic counter data, indicating they are a good proxy for actual abundance (53,54). Atlantic salmon are an important food source for this dolphin population (55,56), with dolphins forming larger groups when salmon are more abundant (which is correlated with the two-year lagged winter NAO index; ,43). We downloaded monthly data from https://scotland.shinyapps.io/sg-salmon-sea-trout-catch/ (summing retained and released fish) and summed monthly catches within a calendar year for yearly measures of fish abundance (Fig. S4).

## Data analysis

All analyses were performed in R (ver 4.1.0; ,57) using linear mixed effect models in *glmmTMB* (58). Using regression-based models as opposed to randomisation-based tests has been recommended

169 for analysing questions about node-level social network traits as it improves the ability to make
170 inference while accounting as well as node permutations for common types of data non-
171 independence (59). We fitted 12 models, with all combinations across the three social traits, the two
172 environmental variables, and the yearly and monthly timescales. Clustering coefficient cannot be
173 calculated when an individual only associates with one other individual, and closeness cannot be
174 calculated for individuals without any connections, and so the datasets for these models were
175 slightly smaller than the dataset for strength (see below). We included individuals with unknown
176 birth and death dates to maximise our sample size, and so neither age nor lifespan could be included
177 as predictor variables. In all models we included the fixed effect of sex (as males and females can
178 differ in social behaviour; ,60,61; ranging behaviour, and survival; ,62), and either the NAO index or
179 the count of caught salmon for that month or year. We did not include both the NAO index and
180 salmon abundance in the same model as we encountered estimation problems with two random
181 slopes. Including sex meant we excluded individuals of unknown sex (258 observations of 103
182 individuals for the yearly networks, 281 observations of 91 individuals for the monthly networks),
183 but the interactions between individuals of known and unknown sex were still used to build the
184 networks and so associations with individuals of unknown sex still influenced the social network
185 traits of males and females. We mean centred and scaled to unit variance the environmental
186 variable (63), and included the interaction between it and sex, to see if male and female social
187 behaviour responded differently to environmental variation. Random effects were the random
188 intercept for individual ID, the random slope of individual ID with the environmental variable fitted
189 as a fixed effect in the model (again mean centred and with a standard deviation of 1), and the
190 correlation between these two terms. We also included a temporal autocorrelation term (ar1)
191 among years to account for variation among years and that adjacent years may be more similar than
192 non-adjacent years. Similarly, in the models for monthly variation we included a random effect of
193 month. We used a Gaussian error structure for all models. For strength and closeness, we used log
194 link functions as the distributions were right skewed, adding 0.001 to all strength measures before

transformation to allow us to include zero values (although zeroes were rare; n = 1 for the yearly analysis and n = 6 for the monthly analysis). For clustering coefficient, which is bounded between 0 and 1, we used a logit link function, which is preferable to an arcsine transformation when handling response variables bounded in this way (64). We used the default optimising algorithm for all models except the model for strength in response to monthly variation in salmon abundance, and the models for clustering coefficient in response to monthly variation in both NAO index and salmon abundance, where we used the "BFGS" optimiser, as otherwise the model did not converge (58).

We report the coefficients and standard errors for each fixed effect, along with p-values, to give an idea of the magnitude and uncertainty of each effect. We used the p-values from the Anova function of the *car* package (65), using a Chi-squared test with type III sum of squares. We describe these p-values in terms of "clarity" rather than "significance", see Dushoff et al. (66) for a discussion on this. To test whether individuals clearly differed in their response to the environmental variable, we first tested whether there was a correlation between an individual's plasticity and its mean behaviour by re-fitting each model (12 in total) with the correlation between random intercepts and slopes supressed to zero and conducted a likelihood ratio test between the full model and this reduced model with a single degree of freedom. If there was no clear difference between the models, we then tested the importance of the random slopes by comparing the model with an intercept-slope correlation of zero to a model without the random slopes (but still with the random intercepts) using a likelihood ratio test with a mix of zero and one degrees of freedom (as is appropriate for testing the clarity of single variance components, 67). When there is variation in plasticity, the magnitude of among-individual differences varies across environments. We therefore calculate the marginal repeatability for each trait following Schielzeth and Nakagawa (68). We did this for all trait-environmental variable-time scale combinations (12 in total), even when there was no evidence for random slopes, to aid comparison among traits.

## Results

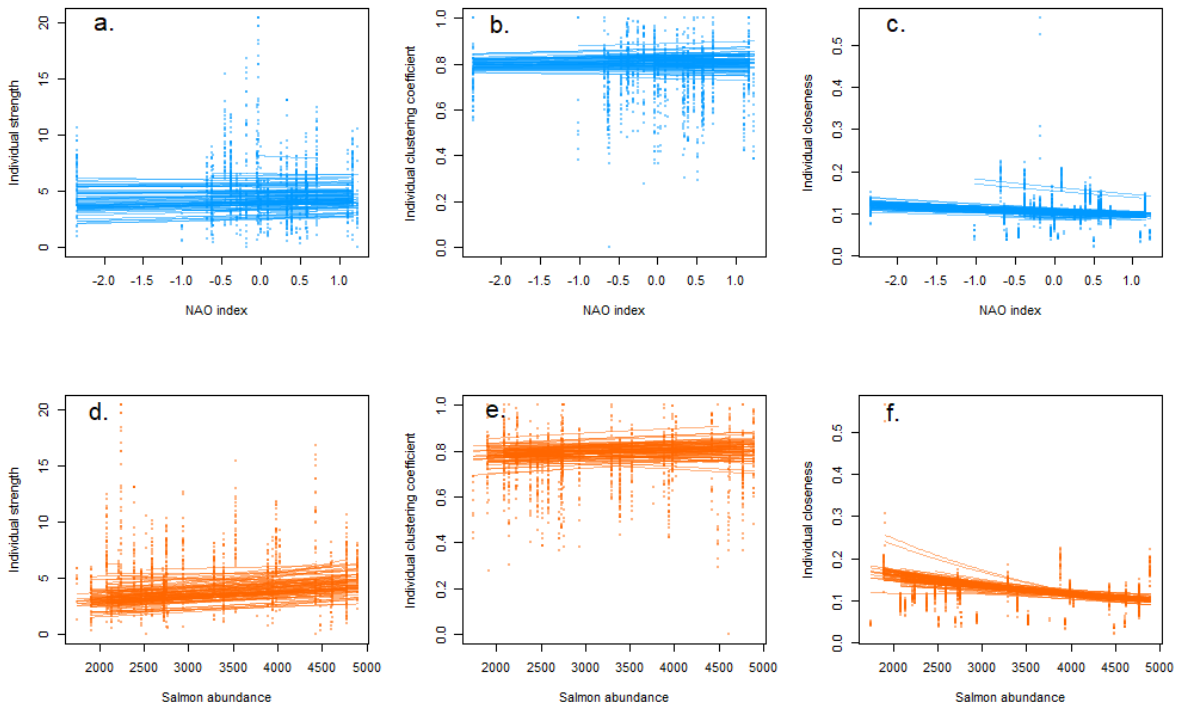
### Change with environmental variables at a yearly scale

For the analysis of how dolphin social phenotypes change at the yearly scale in response to environmental variables, our dataset included 155 unique individuals. For strength there were 1133 measures, for clustering coefficient there were 1129 and for closeness there were 1132. Traits had a mean of 7.31 (sd = 5.99), 7.28 (sd = 5.92), and 7.30 (sd = 5.99) measures per individual for strength, clustering coefficient and closeness respectively

Dolphins' strength and clustering coefficient were not affected by the NAO index (Fig. 2a and b) or salmon abundance (Fig. 2d and e) in both sexes, and the sexes did not differ in mean strength or clustering coefficient (Table 1, full model results in Tables S1-6, supplementary materials). There were no intercept-slope correlations, and the random slopes were not statistically clear, suggesting that individual dolphins did not differ in their (lack of) response to the NAO index (Table 2). However, individuals did differ in their responses to salmon abundance, with clear random slopes for both strength and clustering coefficient. For both traits the intercept-slope correlation was not clearly different from zero, although it was negative and close to clarity for strength (suggesting individuals with lower mean strength increased their strength at higher values of the NAO index; Table 2). The marginal repeatabilities for strength were low: 0.017 in the NAO index model and 0.019 in the salmon abundance model, suggesting the trait has limited repeatability. The marginal repeatabilities for clustering coefficient were higher: 0.173 and 0.204 for the NAO index and salmon abundance models respectively.

Similarly, closeness did not vary with NAO index (Fig. 2c) or salmon numbers (Fig. 2f) in either sex (Table 1). Although females may have had higher mean closeness than males, the effect was not statistically clear (Supplementary Material Tables S5 & S6). Again, individuals' mean behaviour and plasticities in response to the NAO were not related, and dolphins did not show differences in their

245 plasticities (Table 2). However, dolphins did show a mean-plasticity relationship for salmon
246 abundance, with individuals with lower mean closeness increasing their closeness more with
247 increasing salmon abundance. This also indicates there was individual variation in plasticity (Table 2).
248 The marginal repeatabilities were low for closeness: 0.030 in the NAO index model and 0.023 in the
249 salmon abundance model.

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251 **Figure 2.** Plots of each of the three social network traits and yearly variation in the North Atlantic
252 Oscillation (NAO) index (a. strength, b. clustering coefficient, c. closeness) and salmon abundances
253 (d. strength, e. clustering coefficient, f. closeness). For each individual dolphin we have predicted its
254 network trait on the observed scale based on the model results, using the "predict" function in R
255 with the individual's sex, the range of NAO values or salmon counts that individual was exposed to,
256 and setting the year to 2005.

257

258 For all social traits there was substantial among-year variation and consecutive years were positively
259 correlated (year to year correlations: strength; $r_{NAO}$ = 0.314, $r_{Salmon}$ = 0.429; clustering coefficient; $r_{NAO}$

260 = 0.559, $r_{Salmon}$ = 0.560; and closeness; $r_{NAO}$ =0.455, $r_{Salmon}$ = 0.543), showing that, as expected,

261 adjacent years were more similar than non-adjacent years.

262 In summary, there were no trait-environment association at the yearly scale. However, individuals

263 always differed in their response to salmon abundance but never in their (lack of) response to the

264 NAO index. Clustering coefficient showed some repeatability across environments, but strength and

265 closeness did not.

266

267 **Table 1**. Main effects ("M") and interactions with sex ("I", also shaded in grey) for the two

268 environmental variables effects on the three social network traits, at each of the monthly and yearly

269 scales. Effects clearly different from zero ($p < 0.05$) are highlighted in bold, while

270 effects with p values between 0.1 and 0.05 are highlight in italics.

| | | | Strength | Clustering coefficient | Closeness |
|---|---|---|---|---|---|
| NAO index | Yearly | M | β = 0.013 ± 0.075, $\chi^2$ = 0.032, p = 0.858 | β = 0.012 ± 0.086, $\chi^2$ = 0.019, p = 0.891 | β = -0.053 ± 0.093, $\chi^2$ = 0.324, p = 0.569 |
| | | I | β = 0.009 ± 0.023, $\chi^2$ = 0.163, p = 0.687 | β = 0.005 ± 0.034, $\chi^2$ = 0.019, p = 0.889 | β = -0.011 ± 0.013, $\chi^2$ = 0.733, p = 0.392 |
| | Monthly | M | β = 0.029 ± 0.021, $\chi^2$ = 1.902, p = 0.168 | β = 0.038 ± 0.038, $\chi^2$ = 0.968, p = 0.325 | *β = -0.077 ± 0.044, $\chi^2$ = 3.004, p = 0.083* |
| | | I | β = -0.002 ± 0.024, $\chi^2$ = 0.009, p = 0.924 | β = 0.009 ± 0.042, $\chi^2$ = 0.045, p = 0.832 | *β = 0.103 ± 0.053, $\chi^2$ = 3.724, p = 0.054* |
| Salmon | Yearly | M | β = 0.123 ± 0.077, $\chi^2$ = 2.523, p = 0.112 | β = 0.040 ± 0.088, $\chi^2$ = 0.019, p = 0.891 | β = -0.142 ± 0.088, $\chi^2$ = 2.609, p = 0.106 |
| | | I | β = -0.009 ± 0.031, $\chi^2$ = 0.091, p = 0.762 | β = 0.012 ± 0.043, $\chi^2$ = 0.019, p = 0.890 | β = -0.011 ± 0.013, $\chi^2$ = 0.733, p = 0.392 |
| | Monthly | M | β = 0.015 ± 0.034, $\chi^2$ = 0.199, p = 0.655 | **β = 0.170 ± 0.051, $\chi^2$ = 11.290, p = 0.001** | β = 0.019 ± 0.064, $\chi^2$ = 0.086, p = 0.769 |
| | | I | β = 0.050 ± 0.035, $\chi^2$ = 2.131, p = 0.144 | β = -0.060 ± 0.049, $\chi^2$ = 1.495, p = 0.221 | β = 0.006 ± 0.069, $\chi^2$ = 0.006, p = 0.936 |

271

272 ## Change with environmental variables at a monthly scale

273 We analysed how dolphin social phenotypes change in response to environmental variables at the

274 monthly scale with a dataset of 151 unique individuals for strength and closeness and 149 for

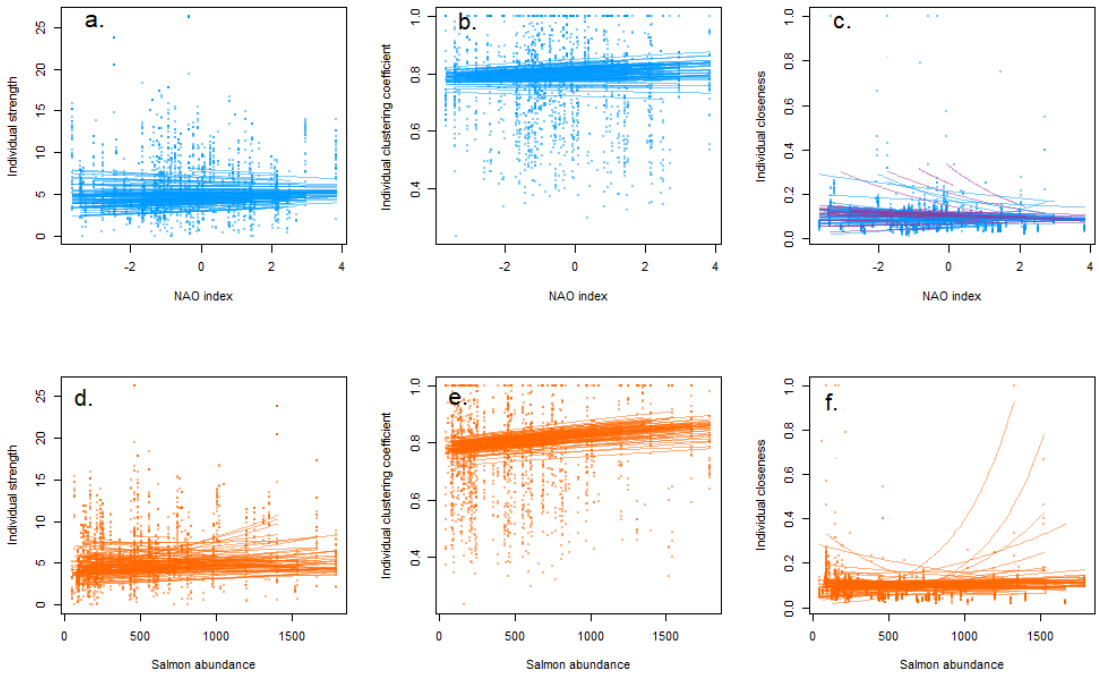
clustering coefficient. For strength there were 1704 measures, for clustering coefficient 1688, and for closeness 1696. Traits had a mean of 11.3, 11.3, and 11.2 measures per individual for strength, clustering coefficient, and closeness respectively (sd = 10.7 for all).

**Table 2**. Intercept slope correlations ("ISC") and their statistical tests, and whether random slopes ("RS") were present or absent and their statistical tests (likelihood ratio tests in all cases, an asterix is given for the test of the random slopes if it was not performed as the intercept-slope correlation was first found to be clear). Clear positive correlations are noted in bold text and highlighted with blue fill, and clear negative correlations with bold text and orange fill, with the two intercept-slope correlations with p values between 0.1 and 0.05 indicted in italics.

| | | | Strength | Clustering coefficient | Closeness |
|---|---|---|---|---|---|
| NAO index | Yearly | ISC | -0.539 ($\chi_1^2$ = 1.299, p = 0.254) | -0.999 ($\chi_1^2$ = 0.896, p = 0.344) | -0.784 ($\chi_1^2$ = 1.477, p = 0.224) |
| | | RS | Absent ($\chi_{0,1}^2$ = 0.236, p = 0.314) | Absent ($\chi_{0,1}^2$ = 0.000, p = 0.500) | Absent ($\chi_{0,1}^2$ = 0.013, p = 0.455) |
| | Monthly | ISC | **-0.963 ($\chi_1^2$ = 6.864, p = 0.009)** | 0.975 ($\chi_1^2$ = 1.660, p = 0.198) | **-0.792 ($\chi_1^2$ = 22.911, p < 0.001)** |
| | | RS | **Present** * | Absent ($\chi_{0,1}^2$ = -0.027, p = 0.500) | **Present** * |
| Salmon | Yearly | ISC | *-0.321 ($\chi_1^2$ = 3.002, p = 0.083)* | 0.268 ($\chi_1^2$ = 1.182, p = 0.277) | **-0.510 ($\chi_1^2$ = 9.389, p = 0.002)** |
| | | RS | **Present ($\chi_{0,1}^2$ = 15.925, p < 0.001)** | **Present ($\chi_{0,1}^2$ = 7.385, p = 0.003)** | **Present** * |
| | Monthly | ISC | *-0.299 ($\chi_1^2$ = 2.838, p = 0.092)* | 0.994 ($\chi_1^2$ = 1.946, p = 0.163) | **-0.350 ($\chi_1^2$ = 5.891, p = 0.015)** |
| | | RS | **Present ($\chi_{0,1}^2$ = 28.258, p < 0.001)** | Absent ($\chi_{0,1}^2$ = 0.000, p = 0.500) | **Present** * |

Strength was not affected by the monthly NOA index (Fig. 3a) or monthly salmon abundance (Fig. 3d) in either sex and the sexes did not differ in their mean strength (Table 1, full model results in Tables S7-12 in the supplementary materials). Individuals differed in their responses to the monthly NAO index and salmon abundances (Table 2). For the NAO index, individuals with high values decreased their strength as the NAO index increased while individuals with low values increased their strength (Table 2). There was no clear intercept-slope correlation for salmon abundance although it was also negative. As for the yearly models, the marginal repeatability of strength was low (0.007 in the NAO index model, 0.009 in the salmon abundance model).

293 Months of higher salmon abundance led to higher clustering coefficients in both sexes (Figs. 3e and
294 4 and Table 1). Clustering coefficient did not however vary in response to monthly NOA index in
295 either sex (Fig. 3b and Table 1). The sexes did not differ in their mean clustering coefficient.
296 Individuals showed no mean-plasticity relationship and did not vary in their responses to salmon
297 abundance, or in their lack of response to the NAO index (Table 2). Clustering coefficient was
298 moderately repeatable, with marginal repeatabilities of 0.337 and 0.284 in the NAO index and
299 salmon abundance models respectively.




300

301 **Figure 3**. Plots of each of the three social network traits and monthly variation in the North Atlantic
302 Oscillation (NAO) index (a. strength, b. clustering coefficient, c. closeness) and salmon abundances
303 (d. strength, e. clustering coefficient, f. closeness). In c., males are shown in purple, females in blue,
304 to visualise the possible difference between the sexes (see Results). For each individual dolphin we
305 have predicted its network trait on the observed scale based on the model results, using the
306 "predict" function in R with the individual's sex, the range of NAO values or salmon counts that
307 individual was exposed to, setting the year to 2005, and the month to June.

Females had a lower average closeness than males, although this effect was only clear in the model for the NAO index (Table S11). Further, the sexes may have differed in their response to the NAO index; while males showed a marginally unclear decrease with higher NAO index, females may have shown no change or even a slight increase (Fig. 3c and Table 1). Closeness did not respond to monthly salmon numbers in either sex (Fig. 3f and Table 1). Individuals differed in their responses to the NAO index and to salmon abundance (Table 2), with individuals with high values decreasing their closeness with higher values of the environmental factor and individuals with low values increasing their closeness. Unlike for the yearly scale there was some repeatability of closeness at the monthly scale, with a marginal repeatability of 0.216 in the NAO index model and 0.168 in the salmon abundance model.

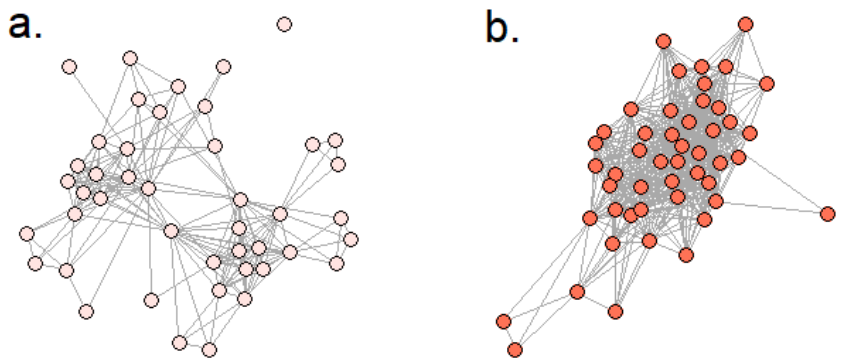



**Figure 4**. Plots of dolphin social networks in a month of low salmon abundance (May 1990) and a month of high salmon abundance (August 2007). Circles are individual dolphins and grey lines indicate associations i.e., those seen in the same group at least once in that month.

There was among-month and among-year variation, and consecutive years were always positive correlated (year to year correlations: strength: $r_{NAO}$ = 0.553, $r_{Salmon}$ = 0.529; clustering coefficient: $r_{NAO}$ = 0.228, $r_{Salmon}$ =0.074; closeness: $r_{NAO}$ = 0.467, $r_{Salmon}$ = 0.475).

In summary, months with higher salmon numbers led to higher clustering coefficient in both sexes but did not impact strength or closeness. Meanwhile, months with a higher NAO index were

associated with a higher closeness in females and a lower closeness in males, although both these effects were not clearly different from zero. The NAO index did not affect strength or clustering coefficient. Individuals differed in how their strength and closeness changed in response to both the NAO index and salmon abundance, but they did not differ in how their clustering coefficient changed for either variable. Clustering coefficient was somewhat repeatable across environments, closeness marginally so, and strength not at all.

## Discussion

We explored whether bottlenose dolphin social behaviour responded to environmental variation. Typically, social behaviour showed no variation at the yearly scale in response to the NAO index or salmon abundance. Similarly, two social behaviours showed no variation to environmental change at the monthly scale, although, how tightly individuals in the immediate social environment interacted (clustering coefficient) did increase in response to increases in monthly salmon abundance. We also showed that individuals differed in their behavioural responses to changes in salmon abundance at both yearly and monthly scales, and to the NAO index at the monthly scale, indicating variation in plasticity. This plasticity was often, but not always, negatively associated with mean behaviour, causing among individual differences to typically be greater for low values of salmon abundance and the NAO index. Interestingly, when males and females increased their clustering coefficient in response to higher monthly salmon abundances, there was limited among-individual variation in this change. This conformity of response perhaps suggests a particularly important or unavoidable change. Among-individual variation in mean behaviour was limited for strength at both timescales and for closeness at the yearly timescale, marginal for closeness at the monthly scale and clustering coefficient at the yearly scale, and most apparent for clustering coefficient at the monthly scale (see also 69 who found consistency over lifetime in the social behaviours of Indo-Pacific bottlenose

353 dolphins, T. aduncus). Social traits differed therefore in either showing limited population-level
354 plasticity and little repeatability, but some variation in individual slopes (strength and closeness),
355 and some population-level plasticity and repeatability, and less variation among individual slopes
356 (clustering coefficient).

357 Despite the population-level stability in strength and closeness, in most cases individual dolphins
358 differed in how their social behaviour changed in response to environmental variation (i.e., they
359 showed among-individual variation in plasticity). Therefore, while the population as a whole showed
360 no overall change, some individuals would show an increase in their overall gregariousness and/or
361 connectedness to wider parts of the network, while others a decrease. Variation in individual
362 plasticity leads to environment-dependent repeatability (and possibly heritability), can dampen
363 population responses to environmental variability, and enhance population persistence (17). For
364 example, due to the negative intercept-slope correlation, individual closeness shows the most
365 among-individual variation at low monthly salmon abundances (the approximate marginal
366 repeatability two standard deviations below the mean salmon abundance was 0.54, compared to
367 0.07 at the mean). This wider range of social phenotypes could increase the possibility that at least
368 some individuals are successful despite low food availability. Determining the genetic basis and
369 importance of early life conditions for the development of these different responses (11) and how
370 this variation impacts population dynamics (70) is key. Models projecting how dolphin populations
371 will change in the future should account for both among-individual variation in mean behaviour and
372 in behavioural plasticity.

373 In general, the lack of plasticity in social network traits suggests dolphin social behaviour will show
374 limited changes at the population level if salmon abundances or climate change over time (based on
375 similar changes to environmental variables studied here). Populations of animals with relatively long
376 generation times are more reliant on phenotypic plasticity than adaptive evolution to track rapid
377 environmental change (22). Therefore, if dolphins do not change plastically there is limited scope for

evolution to compensate to enhance phenotype-environment fit. If social behaviours are important for coping with detrimental environments, this could potentially be problematic, leading to reduced reproduction and possibly population decline.

The one exception to stability was that individual clustering coefficient increased in months with higher salmon abundance (see Fig. 4 for a comparison of months with low vs. high salmon abundance). This indicates that dolphins were “closing triads” and interacting more often with those who they shared a mutual third association. The increase in clustering coefficient occurred without a change in strength or closeness, suggesting a nuanced change in behaviour. Interestingly, individuals did not show variability in this increase, suggesting it is important or unavoidable for all. Similar results have been found in spotted hyenas (*Crocuta crocuta*) where seasons with high prey availability have denser social networks (71). However, other systems have found lower food availability leads to decreased sociability (72,73), and it is presumed this response reduces the intensity of resource competition (reviewed in: ,6,see also: ,74). Therefore, higher clustering may be beneficial for non-foraging reasons, such as mating. Both mating and calving seasons approximately align with the months of highest salmon abundance in the summer (Fig. S4), supporting this suggestion. Dolphins could also reduce travel distances when food availability is high (60), leading to them stay in the same place and so interact more with a tight circle of others; increasing their clustering coefficient. Alternatively, it is possible that months with fewer salmon also differ in an unidentified variable which causes dolphins to cluster less. However, it is unlikely that this unidentified factor is predation threat that changes month to month, as predators are absent in this area (75). Therefore, a change in social behaviour and/or movement related to the seasonal availability of salmon, perhaps influenced by reproductive behaviour, seems the most likely.

Notwithstanding the response of dolphins to changes in environmental factors on a monthly scale, we did not see any responses to environmental variation on a yearly scale. Both factors varied considerably year-to-year; the NAO index ranged from -2.35 to 1.23 (Fig. S3) and salmon abundance

varied by more than 2.8 times between years (Fig. S4), hence a lack of relevant variability seems unlikely. Lusseau *et al*. (43) observed larger groups in years of higher salmon abundance, but this was over fewer years and was not an individual-level analysis. The robustness or inflexibility of social behaviour in response to year-to-year variation in climatic conditions and food availability might indicate that the yearly environmental variation is inconsequential and so they have no need to respond to it. However, it seems unlikely that variation in food availability of 2.8 times does not matter to this population, as their distribution in space reflects foraging opportunities (76). Alternatively, dolphins may change other phenotypes, such as foraging behaviour or metabolism, to cope with these stressors (29), leaving social behaviour unchanged. For example, salmon are not this dolphin population's only prey (56), and so they may switch to other prey if salmon are scarce, obviating the need to modify their social networks.

We estimated correlations between an individual's mean behaviour (its intercept) and its plasticity in behaviour (its slope). For strength and closeness, intercept-slope correlations were negative if they were different from zero. Therefore, individuals typically converged to similar behaviour at higher NAO index values and salmon abundances (among-individual differences in mean behaviours were also low for these traits). Negative intercept-slope correlations can constrain evolution if higher mean values *and* higher plasticities are favoured, as selection is favouring a combination of phenotypes that is rare (17). In contrast, intercept-slope correlations for clustering coefficient were either zero or, in the case of the response to salmon abundance at the yearly scale, positive. The positive correlation shows behaviours diverging among individuals at higher yearly salmon abundances. Additionally, while a positive intercept slope correlation means that selection on either intercept or slope causes the other to increase too, no correlation means intercepts and slopes can be independent targets of selection. Kebke *et al*. (29) suggest that cetacean ranging and foraging behaviour may well be under selection for increased plasticity as environments change, and so testing this directly is a logical and important next step.

In conclusion, we found that at the population-level dolphin social behaviour is relatively stable across years despite year-to-year variation in environmental conditions. At the monthly scale, we observed all individuals increased clustering of local social associations due to higher salmon abundance. However, at both monthly and yearly scales there was lots of variability at the individual level in responses to environmental factors, and variation among both traits and timescales in how repeatable traits were. As such, individual heterogeneity in both mean and plasticity in behaviour both should be more widely accounted for when predicting species responses to environmental change, and individual plasticities as well as means may be targets of selection and hence evolvable.

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## Statement of authorship

DF conceived the idea for the manuscript, BC provided data, DF ran analyses with guidance from BC, DF wrote first draft of the manuscript and both authors contributed to revisions.

## Data accessibility statement

Data and R code used for the analysis are available to reviewers and will be made publicly available upon acceptance.

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