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 to variation in proxies of food availability and climate, against a background of population-level stability. Individual dolphins did not consistently respond to yearly variation in environmental factors. However, at the monthly scale individuals became better connected to their local social environment in months of high salmon abundance, but their overall gregariousness and connectedness to the wider network did not change. This stability in social network position suggests there are important drivers maintaining a consistent structure. These results indicate that forecasting population responses to environmental change should account for among-individual variation in 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 (Snyder-Mackler *et al.* 2020). Consequently, social interactions have a strong influence on ecological processes such as population dynamics and evolutionary processes such as the response to selection (Moore *et al.* 1997; Wolf *et al.* 1999; McGlothlin *et al.* 2010). To maintain the best fit with their environment, animals may adjust their social behaviour as conditions change (Komdeur & Ma 2021), for instance being more gregarious when resources are plentiful but less tolerant of conspecifics when resources are scarce (Fisher *et al.* 2021). Animals may also change their behaviour through development and during senescence (White *et al.* 2012). 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., Abrahms *et al.* 2022), implying that all individuals respond similarly. However, individuals typically show variation in plasticity, and so each will respond differently to change (Nussey *et al.* 2007; Dingemanse *et al.* 2010, sometimes referred to as "I x E" i.e., individual by environment interactions; Stamps 2016; Stamps & Biro 2016). 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 (Fisher *et al.* 2015). This individuality can influence biological processes such as population growth and adaptive change at a range of scales (Vindenes & Langangen 2015; see: Hamel *et al.* 2018 and accompanying papers), giving fundamentally different results to when population-level only effects are assumed (Brommer 2013b; Dingemanse & Wolf 2013). 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 (Nussey *et al.* 2005; Chevin 2013; Araya-Ajoy & Dingemanse 2017). Understanding how plasticity as a trait in its own right can evolve is key in understanding how animals will adapt to more variable climates (Nussey *et al.* 2005; Brommer 2013a).

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 (Hoffmann & Sgrò 2011). 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 (Simmonds & Isaac 2007; Tyack 2008; MacLeod 2009; Evans & Bjørge 2013; Avila *et al.* 2018; van Weelden *et al.* 2021; Kebke *et al.* 2022).

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 (Arso Civil *et al.* 2021) has been studied intensively as part of a long term individual based study (Wilson *et al.* 1999; Cheney *et al.* 2013; Arso Civil *et al.* 2019b). 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) (Cheney *et al.* 2014). 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 (Cheney *et al.* 2014). Additional data were also available from Whale and Dolphin Conservation land based photo-identification surveys (Cheney *et al.* 2013). 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.

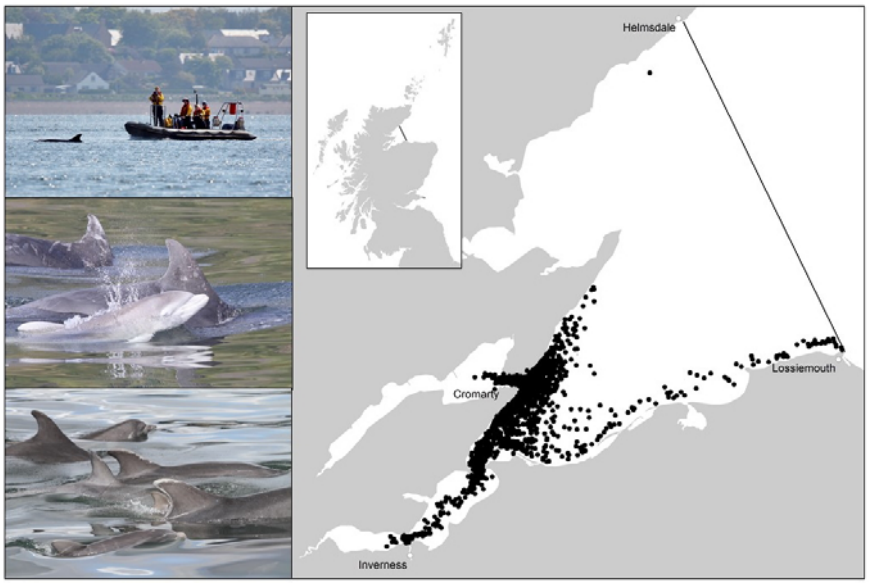


Figure 1. Images depicting a photo-identification survey (top let), a newborn calf with mother (middle left), unique markings used to identify individuals (bottom left). and location of encounters with bottlenose dolphins within the Moray Firth Special Area of Conservation from May to September 1990 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 (Cheney *et al.* 2014). We identified individuals from high-quality photographs based on unique markings matched against a photo catalogue of

96 previously identified individuals from the area (Würsig & Jefferson 1990; Wilson *et al.* 1999; Cheney
97 *et al.* 2013). On average, in a group 84% are successfully photographed, and all individual
98 identifications are confirmed by at least two experienced researchers. For individuals first sighted as
99 calves we could determine their year of birth and so their age (Cheney *et al.* 2022), but for
100 individuals first sighted as juveniles or adults their exact age is unknown. Sex was determined using
101 genital photographs or if an adult was seen in repeat associations with a known calf (Cheney *et al.*
102 2022).

103

104 ## Social network construction

105 Individuals sighted during the same encounter were assumed to be in the same group and therefore
106 associating (known as the "Gambit of the Group"; Whitehead & Dufault 1999). Aggregating many of
107 these records of groups allows one to infer which individuals are frequently associated and which
108 individuals infrequently or never associate. We removed observations of individuals younger than
109 three years old (n = 2634 observations of 233 individuals), as these individuals are not likely to be
110 independent of the mother and so their social associations most likely represent her preferences.
111 We then converted the records of encounters into group by individual matrices (indicating which
112 individuals were seen together in each encounter) and then into weighted, undirected social
113 networks using the R package *asnipe* (Farine 2013). Edge weights were set as the simple ratio index,
114 where the number of times two individuals are seen together is divided by the total number of times
115 they are seen, both together and apart (Cairns & Schwager 1987). This measure ranges from 0
116 (individuals never seen together) to 1 (individuals always seen together). We did this separately for
117 each year, creating a social network per year to assess how social phenotypes vary at the yearly
118 scale in response to environmental conditions. To assess how social phenotypes vary at the monthly
119 scale in response to environmental conditions we then reconstructed social networks per month and
120 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.* (2004), 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 (Hurrell 1995; Stenseth *et al.* 2003). This index has frequently been linked to the ecology of animal populations (Gordo *et al.* 2011; Wan *et al.* 2022), for example influencing the foraging behaviour of Cory's shearwaters (Calonectris borealis; Pereira *et al.* 2020). While climatic effects on cetaceans are typically thought to occur via changes in prey species (Víkingsson *et al.* 2015; Kebke *et al.* 2022), a phenomenon also observed in our study population (Lusseau *et al.* 2004), it is also possible that cetaceans respond directly to climate, sometimes at even faster rates than their prey species (Sprogis *et al.* 2018; Thorne & Nye 2021; Methion *et al.* 2022).

For our index of food availability we again followed Lusseau *et al.* (2004), 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 (Youngson *et al.* 2002; Thorley *et al.* 2005). Atlantic salmon are an important food source for this dolphin population (Janik 2000; Santos *et al.* 2001), with dolphins forming larger groups when salmon are more abundant (which is correlated with the two-year lagged winter NAO index; Lusseau *et al.* 2004). 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; R Development Core Team & Team 2016) using linear mixed effect models in *glmmTMB* (Brooks *et al.* 2017). Using regression-based models as opposed to randomisation-based tests has been recommended for analysing questions about node-level social network traits as it improves the ability to make inference while accounting as well as node permutations for common types of data non-independence (Hart *et al.* 2021). We fitted 12 models, with all combinations across the three social traits, the two environmental variables, and the yearly and monthly timescales. Clustering coefficient cannot be calculated when an individual only associates with one other individual, and closeness cannot be calculated for individuals without any connections, and so the datasets for these models were slightly smaller than the dataset for strength (see below). We included individuals with unknown birth and death dates to maximise our sample size, and so neither age nor lifespan could be included as predictor variables. In all models we included the fixed effect of sex (as males and females can differ in social behaviour; Shane *et al.* 1986; Mann *et al.* 2012; ranging behaviour, and survival; Arso Civil *et al.* 2019a), and either the NAO index or the count of caught salmon for that month or year. We did not include both the NAO index and salmon abundance in the same model as we encountered estimation problems with two random slopes. Including sex meant we excluded individuals of unknown sex (258 observations of 103 individuals for the yearly networks, 281 observations of 91 individuals for the monthly networks), but the interactions between individuals of known and unknown sex were still used to build the networks and so associations with individuals of unknown sex still influenced the social network traits of males and females. We mean centred and scaled to unit variance the environmental variable (Schielzeth 2010), and included the interaction between it and sex, to see if male and female social behaviour responded differently to environmental variation. Random effects were the random intercept for individual ID, the random slope of individual ID with the environmental variable fitted as a fixed effect in the model (again mean centred and with a standard deviation of 1), and the correlation between these two terms. We also included a temporal

autocorrelation term (ar1) among years to account for variation among years and that adjacent years may be more similar than non-adjacent years. Similarly, in the models for monthly variation we included a random effect of month. We used a Gaussian error structure for all models. For strength and closeness, we used log 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 (Warton & Hui 2011). 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 (Brooks *et al.* 2017).

We used the p-values from the Anova function of the *car* package (Fox & Weisberg 2019), 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. (2019) for a discussion on this. To test whether including random slopes improved our models, and so whether individuals clearly differed in their response to the environmental variable, for each model (12 in total) we re-fitted it without the random slope (and the covariance between random intercepts and slopes) and conducted a likelihood ratio test between the two models. If random slopes did not improve the model we concluded the intercept-slope correlation was zero.

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. 3a and b) 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). In addition, the random slopes were not statistically clear, suggesting that individual dolphins did not differ in their (lack of) response to the NAO index. A lack of variation in individual slopes leads us to assume that the intercept slope correlations for the NAO index were not different from zero (Table 2), indicating an individual's mean behaviour is not related to how it responds to the NAO index. But individuals did differ in their responses to salmon abundance, with a negative intercept slope correlation for strength (individuals with lower mean strength increased their strength at higher values of the NAO index) and a positive one for clustering coefficient (individuals with lower mean clustering coefficient decreased it with increasing NAOI index; Table 2).

Similarly, closeness did not vary with NAO index (Fig. 2c) or salmon numbers (Fig. 3c) 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 did not differ in their response to the NAO index, but they did show different responses to salmon abundance (Table 2). Like strength, individuals with lower mean closeness increased their closeness more with increasing salmon abundance, and there was no relationship between an individual's mean closeness and its response to the NAO index model (Table 2).

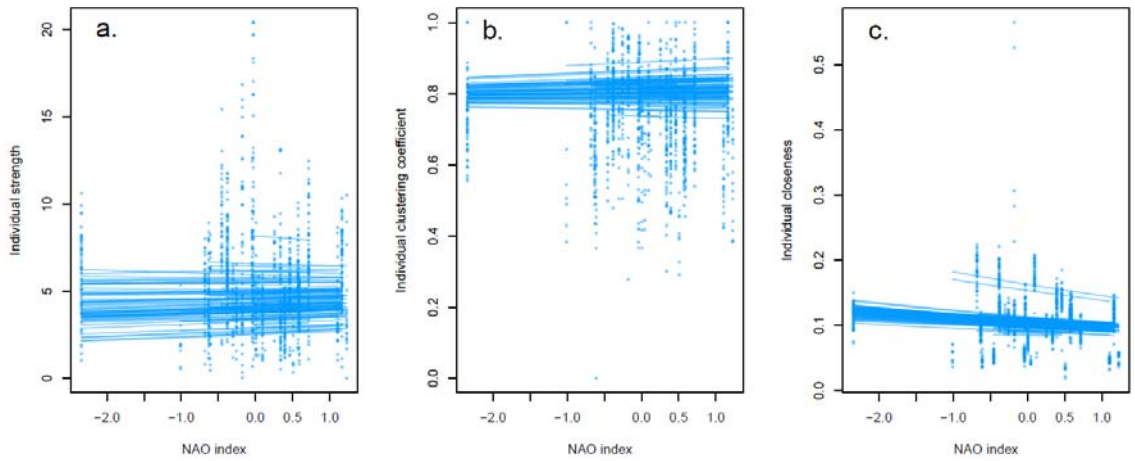


Figure 2. Plots of each of the three social network traits and yearly variation in the North Atlantic Oscillation (NAO) index (a. strength, b. clustering coefficient, c. closeness). For each individual dolphin we have predicted its network trait based on the model results, using the "predict" function in R with the individual's sex, the range of NAO values that individual was exposed to, and setting the year to 2005.

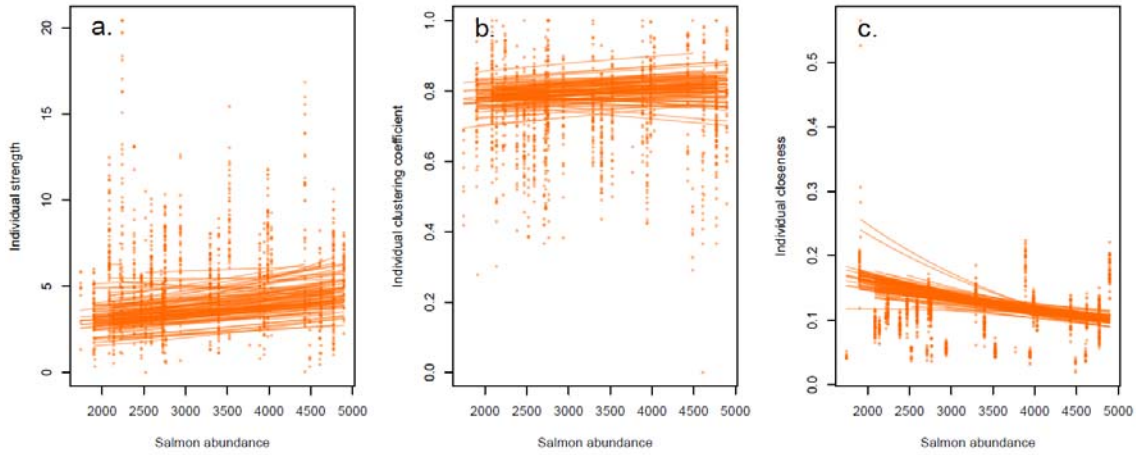


Figure 3. Plots of each of the three social network traits and yearly variation in salmon abundance (a. strength, b. clustering coefficient, c. closeness). For each individual dolphin we have predicted its

network trait based on the model results, using the "predict" function in R with the individual's sex, the range of salmon counts that individual was exposed to, and setting the year to 2005.

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

Table 1. Main effects (prefixed with "M:") and interactions with sex (prefixed with "I:" and shaded in grey) for the two environmental variables effects on the three social network traits, at each of the monthly and yearly scales. Effects clearly different from zero ($p < 0.05$) are highlighted in bold, while effects with p values between 0.1 and 0.05 are highlight in italics.

For all social traits there was substantial among-year variation and consecutive years were positively correlated (year to year correlations: strength; $r_{NAO} = 0.314$, $r_{Salmon} = 0.429$; clustering coefficient; $r_{NAO} = 0.559$, $r_{Salmon} = 0.560$; and closeness; $r_{NAO} = 0.455$, $r_{Salmon} = 0.543$), showing that, as expected, adjacent years were more similar than non-adjacent years.

In summary, there were no trait-environment association at the yearly scale. However, individuals always differed in their response to salmon abundance but never in their (lack of) response to the NAO index.

		Strength	Clustering coefficient	Closeness
NAO index	Yearly	- (χ^2 = 1.5345, df = 2, p = 0.464)	- (χ^2 = 0.896, df = 2, p = 0.639)	- (χ^2 = 1.490, df = 2, p = 0.475)
	Monthly	-0.963 (χ^2 = 6.904, df = 2, p = 0.032)	- (χ^2 = 1.632, df = 2, p = 0.442)	-0.792 (χ^2 = 49.643, df = 2, p < 0.001)
Salmon	Yearly	-0.321 (χ^2 = 18.927, df = 2, p < 0.001)	0.268 (χ^2 = 8.568, df = 2, p = 0.014)	-0.510 (χ^2 = 71.013, df = 2, p < 0.001)
	Monthly	-0.299 (χ^2 = 31.096, df = 2, p < 0.001)	- (χ^2 = 1.946, df = 2, p = 0.378)	-0.350 (χ^2 = 194.29, df = 2, p < 0.001)

Table 2. Intercept slope correlations and statistical tests of clarity of random slopes. Positive correlations in blue, negative in red, those where slopes were not clearly different from zero and so intercept slope correlation assumed to be not different from zero are indicated with a dash and not coloured in.

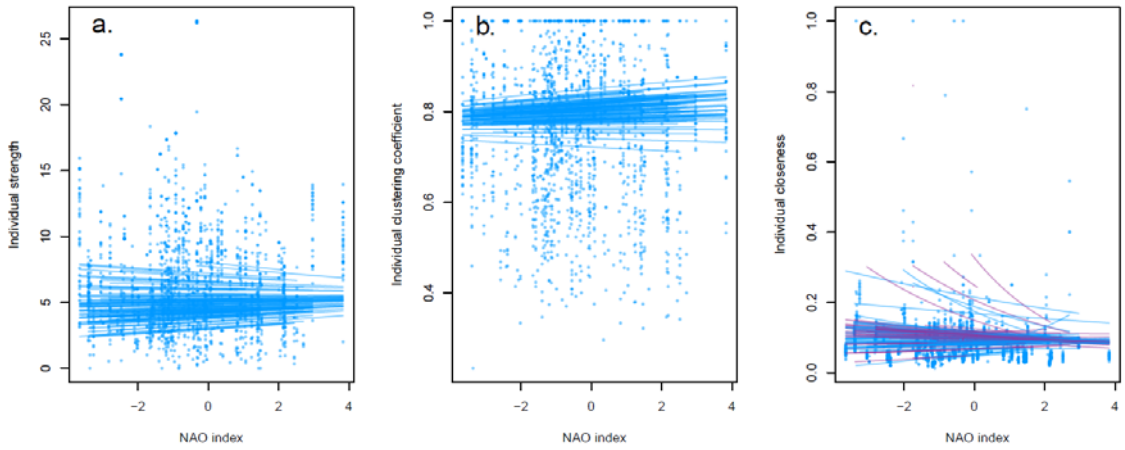
Change with environmental variables at a monthly scale

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

Strength was not affected by the monthly NOA index (Fig. 4a) or monthly salmon abundance (Fig. 5a) 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, with individuals with high values decreasing their strength with higher values of the environmental factor and individuals with low values increasing their strength (Table 2).

Months of higher salmon abundance led to higher clustering coefficients in both sexes (Figs. 5b & 6 and Table 1). Clustering coefficient did not however vary in response to monthly NOA index in either

289 sex (Fig. 4b and Table 1). The sexes did not differ in their mean clustering coefficient. Individuals did
290 not vary in their response to salmon abundance, or in their lack of response to the NAO index, and
291 so in both cases the intercept-slope correlation is not different from zero (Table 2).



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293 **Figure 4**. Plots of each of the three social network traits and monthly variation in the North Atlantic
294 Oscillation (NAO) index (a. strength, b. clustering coefficient, c. closeness). In c., males are shown in
295 purple, females in blue, to visualise the possible difference between the sexes (see Results). For each
296 individual dolphin we have predicted its network trait based on the model results, using the
297 "predict" function in R with the individual's sex, the range of NAO values that individual was exposed
298 to, setting the year to 2005, and the month to June.

299

300 Females had a lower average closeness than males, although this effect was only clear in the model
301 for the NAO index (Table S11). Further, the sexes may have differed in their response to the NAO
302 index; while males showed a marginally unclear decrease with higher NAO index, females may have
303 shown no change or even a slight increase (Fig. 4c and Table 1). Closeness did not respond to
304 monthly salmon numbers in either sex (Fig. 5c and Table 1). Individuals differed in their responses to
305 the NAO index and to salmon abundance (Table 2), with individuals with high values decreasing their
306 closeness with higher values of the environmental factor and individuals with low values increasing
307 their closeness.

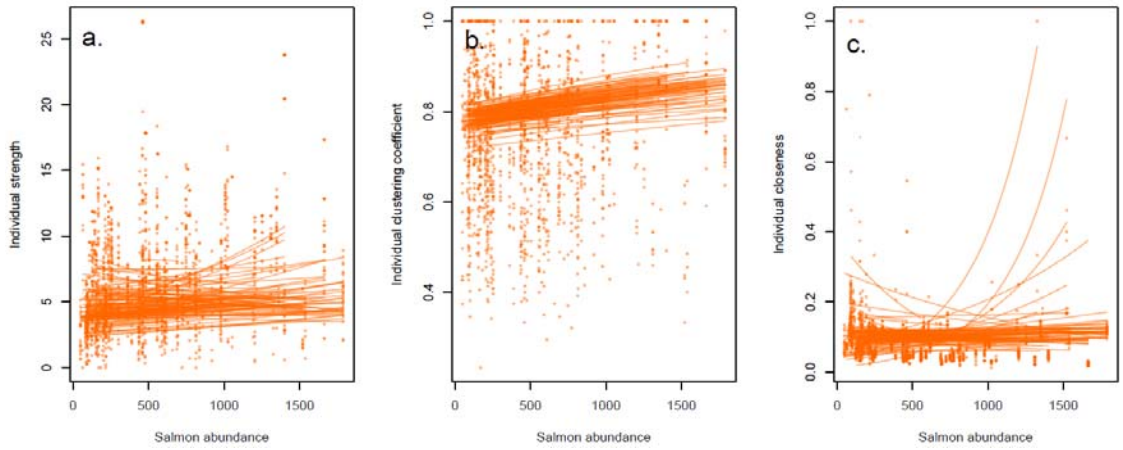

Figure 5. Plots of each of the three social network traits and monthly variation in salmon abundance (a. strength, b. clustering coefficient, c. closeness). For each individual dolphin we have predicted its network trait based on the model results, using the "predict" function in R with the individual's sex, the range of salmon counts that individual was exposed to, setting the year to 2005, and the month to June.

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.

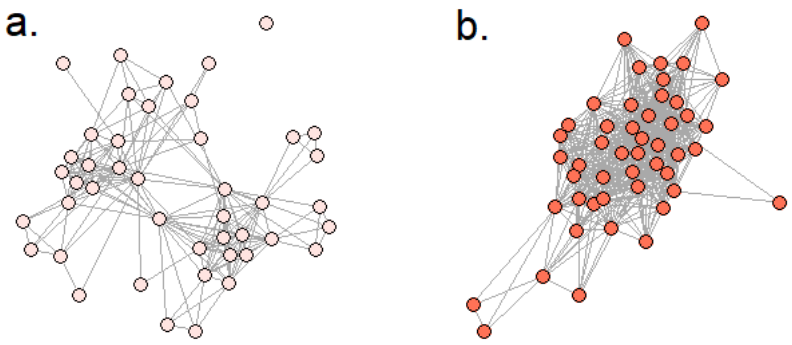

Figure 6. Plots of dolphin social networks in a month of low salmon abundance (May 1990) and a month of high salmon abundance (August 2007). Circles are individual dolphins and grey lines indicate associations i.e., those seen in the same group at least once.

Discussion

We explored whether bottlenose dolphin social behaviour responded to environmental variation. Typically, social behaviour was stable, with 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, alongside differences in mean behaviour, 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. Otherwise, the stability

345 of social behaviour implies that maintaining a consistent social structure is important (see also Evans
346 *et al.* 2021 who found consistency over lifetime in the social behaviours of Indo-Pacific bottlenose
347 dolphins, T. aduncus), and so testing the importance of social network stability on fitness in dolphins
348 is key.

349 Despite the population-level stability, in most cases individual dolphins differed in how their social
350 behaviour changed in response to environmental variation (i.e., they showed among-individual
351 variation in plasticity). Therefore, while the population as a whole showed no overall change, some
352 individuals would show an increase in the social behaviour, while others a decrease. Variation in
353 individual plasticity leads to environment-dependent repeatability (and possibly heritability), can
354 dampen population responses to environmental variability, and enhance population persistence
355 (Dingemanse & Wolf 2013). For example, due to the negative intercept-slope correlation, individual
356 strength shows the most among-individual variation at low monthly salmon abundances. This wider
357 range of social phenotypes could increase the possibility that at least some individuals are successful
358 despite low food availability. Determining the genetic basis and importance of early life conditions
359 for the development of these different responses (Stamps 2016) and how this variation impacts
360 population dynamics (Vindenes *et al.* 2008) is key. Models projecting how dolphin populations will
361 change in the future should account for both among-individual variation in mean behaviour and in
362 behavioural plasticity.

363 In general, the lack of plasticity in social network traits suggests dolphin social behaviour will show
364 limited changes at the population level if salmon abundances or climate change over time (based on
365 similar changes to environmental variables studied here). Populations of animals with relatively long
366 generation times are more reliant on phenotypic plasticity than adaptive evolution to track rapid
367 environmental change (Hoffmann & Sgrò 2011). Therefore, if dolphins do not change plastically
368 there is limited scope for evolution to compensate to enhance phenotype-environment fit. If social

369 behaviours are important for coping with detrimental environments, this could potentially be
370 problematic, leading to reduced reproduction and possibly population decline.

371 The one exception to stability was that individual clustering coefficient increased in months with
372 higher salmon abundance (see Fig. 6 for a comparison of months with low vs. high salmon
373 abundance). This indicates that dolphins were "closing triads" and interacting more often with those
374 who they shared a mutual third association. The increase in clustering coefficient occurred without a
375 change in strength or closeness, suggesting a nuanced change in behaviour. Interestingly, individuals
376 did not show variability in this increase, suggesting it is important or unavoidable for all. Similar
377 results have been found in spotted hyenas (*Crocuta crocuta*) where seasons with high prey
378 availability have denser social networks (Holekamp *et al.* 2012). However, other systems have found
379 lower food availability leads to decreased sociability (Randall *et al.* 2005; Williams *et al.* 2017), and it
380 is presumed this response reduces the intensity of resource competition (Lin *et al.* 2019; reviewed
381 in: Fisher *et al.* 2021). Therefore, higher clustering may be beneficial for non-foraging reasons, such
382 as mating. Both mating and calving seasons approximately align with the months of highest salmon
383 abundance in the summer (Fig. S4), supporting this suggestion. Dolphins could also reduce travel
384 distances when food availability is high (Shane *et al.* 1986), leading to them stay in the same place
385 and so interact more with a tight circle of others; increasing their clustering coefficient.
386 Alternatively, it is possible that months with fewer salmon also differ in an unidentified variable
387 which causes dolphins to cluster less. However, it is unlikely that this unidentified factor is predation
388 threat that changes month to month, as predators are absent in this area (Cheney *et al.* 2019).
389 Therefore, a change in social behaviour and/or movement related to the seasonal availability of
390 salmon, perhaps influenced by reproductive behaviour, seems the most likely.

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

394 varied by more than 2.8 times between years (Fig. S4), hence a lack of relevant variability seems
395 unlikely. Lusseau *et al*. (2004) observed larger groups in years of higher salmon abundance, but this
396 was over fewer years and was not an individual-level analysis. The robustness or inflexibility of social
397 behaviour in response to year-to-year variation in climatic conditions and food availability might
398 indicate that the yearly environmental variation is inconsequential and so they have no need to
399 respond to it. However, it seems unlikely that variation in food availability of 2.8 times does not
400 matter to this population, as their distribution in space reflects foraging opportunities (Hastie *et al.*
401 2004). Alternatively, dolphins may change other phenotypes, such as foraging behaviour or
402 metabolism, to cope with these stressors (Kebke *et al.* 2022), leaving social behaviour unchanged.
403 For example, salmon are not this dolphin population's only prey (Santos *et al.* 2001), and so they
404 may switch to other prey if salmon are scarce, obviating the need to modify their social networks.

405 We estimated correlations between an individual's mean behaviour (its intercept) and its plasticity in
406 behaviour (its slope). For strength and closeness, intercept-slope correlations were negative if they
407 were different from zero. Therefore, individuals typically converged to similar behaviour at higher
408 NAO index values and salmon abundances. Negative intercept-slope correlations can constrain
409 evolution if higher mean values *and* higher plasticities are favoured, as selection is favouring a
410 combination of phenotypes that is rare (Dingemanse & Wolf 2013). In contrast, intercept-slope
411 correlations for clustering coefficient were either zero or, in the case of the response to salmon
412 abundance at the yearly scale, positive. The positive correlation shows behaviours diverging among
413 individuals at higher yearly salmon abundances. Additionally, while a positive intercept slope
414 correlation means that selection on either intercept or slope causes the other to increase too, no
415 correlation means intercepts and slopes can be independent targets of selection. Kebke *et al*. (2022)
416 suggest that cetacean ranging and foraging behaviour may well be under selection for increased
417 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. 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 will be made publicly available upon acceptance.

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