

Individual foraging variation drives social organization in bottlenose dolphins

Séverine Methion^{1,2}, Bruno Díaz López¹

1. Bottlenose Dolphin Research Institute (BDRI), Avenida Beiramar 192, 36980 O Grove, Pontevedra, Spain

2. Université Bordeaux, UMR CNRS 5805 EPOC, Allée Geoffroy St Hilaire, 33615 Pessac Cedex, France

Address correspondence to S. Methion. E-mail: severine@thebdri.com

ABSTRACT

Identifying foraging variation within a population and assessing its relationship with social structure is essential to increase knowledge about the evolution of social systems. Here, we investigated individual foraging variation in bottlenose dolphins and its potential influence on their social organization. We used generalized affiliation indices and applied social network analysis to data collected over 4 consecutive years of research in a coastal area subject to significant use and pressure by humans. Our findings revealed variation in foraging behavior among individual bottlenose dolphins, which in turn shapes their social organization. Our results indicated that individuals that frequently foraged within human-altered areas (i.e., shellfish farms) exhibited weaker Strength, Reach, and Affinity compared to others. These bottlenose dolphins profit from a reliable and easily located food source which may increase their energy intake and inter-individual competition. In contrast, individuals that foraged less frequently within the shellfish farms occupied a central position within the network and exhibited strong associations. These individuals may benefit from increased cooperation and reduced intragroup competition, thus increasing learning and information-sharing, as they may face a patchy and irregular distribution of prey. We also demonstrated that bottlenose dolphins preferred to affiliate with other individuals with similar foraging strategies (i.e., homophily), which could promote, through time, a segregation of the population into behaviorally distinct groups. These findings provide valuable insight into the evolution of bottlenose dolphin social systems and their response to human-induced changes in the marine environment.

Key words: aquaculture, association patterns, bottlenose dolphins, foraging behavior, generalized affiliation indices, social network.

INTRODUCTION

Animals commonly form groups to reduce predation risk, increase mating opportunity and access to resources (Alexander 1974). Yet, grouping is also associated with costs, such as intraspecific competition for food (Clark and Mangel 1986; Krause and Ruxton 2002). Societies with flexible grouping patterns limit the effect of within-group competition through group splits during periods of low resource availability and enhance cooperative effects through group cohesion when the ecological costs of aggregating are low (Chapman 1990; van Schaik 1999). Several group-living mammal species exhibit such fission-fusion dynamics (e.g., chimpanzee, *Pan troglodytes*: Lehmann and Boesch 2004; African elephant, *Loxodonta africana*: Fishlock and Lee 2013; giraffe, *Giraffa Camelopardalis*: Muller et al. 2018; zebra, *Equus spp.*: Sundaresan et al. 2007; bottlenose dolphin, *Tursiops spp.*: Connor et al. 2000; Bechstein's bat, *Myotis bechsteinii*: Kerth et al. 2011).

To balance the effect of competition for resources, individuals within a population can also differ substantially in resource use (Svånback and Bolnick 2006). Foraging variation may arise from differences in sex, age, or morphology (Gustafsson 1988). Alternatively, foraging variation may arise from individual specialization, with individuals differing in prey preferences, habitat use, or foraging behavior (Bolnick et al. 2002; Robertson et al. 2014), independently of environmental or phenotypic variation (Estes et al. 2003). Individual foraging variation has been documented in several mammals with dynamic grouping patterns including macaques, *Macaca fascicularis* (Maria and Van Schaik 1986), African elephants (Woolley et al. 2009), and bottlenose dolphins (Sargeant et al. 2007; Díaz López 2012) and has important ecological implications. Previous studies reported that individual foraging variation can alter the structure of animal societies (Chilvers and Corkeron 2001; Díaz López and Shirai 2008; Ansmann et al. 2012), which in turn may influence population fitness (Formica et al. 2012), reproductive success (Cameron et al. 2009), genetic structure (Altmann et al. 1996), and transmission of learned behavior (Whitehead 2010) and pathogens (Keeling and Eames 2005). Given such broad implications, identifying foraging variation within a population and

assessing its relationship with population social structure is essential to increase knowledge about the evolution of social systems (Cantor and Farine 2018).

Social network analyses have been increasingly used to accurately describe animal societies (Farine and Whitehead 2015). A common challenge when analyzing social network, is distinguishing true affiliations from other structural variables (e.g., sex; gregariousness: Godde et al. 2013; sample size: Farine and Strandburg-Peshkin 2015) that may influence the association patterns among individuals (Whitehead and James 2015). The incorporation of structural variables into social network analysis is important for revealing true association patterns, and a growing number of studies on animal societies take these into account (e.g., Muller et al. 2018; Diaz-Aguirre et al. 2019; Hunt et al. 2019; Machado et al. 2019). Generalized affiliation indices, which have been recently developed, enable control of structural variables in social network analyses (Whitehead and James 2015), therefore providing an encouraging approach for understanding complex animal societies.

Exhibiting social systems characterized by fission-fusion dynamics, bottlenose dolphins provide a useful framework for analyzing variation in social relationships within a population. In various locations around the world, bottlenose dolphins associate in temporary groups of variable size and composition yet also show long term association among individuals within these fluid groups (Connor et al. 2000). Multiple variables may play a role in shaping bottlenose dolphin societies including predation risk (Heithaus and Dill 2002), mating opportunity (Möller et al. 2001), access to resources (Gowans et al. 2007), human activities (Díaz López and Shirai 2008), sex (Diaz-Aguirre et al. 2018), and kinship (Wisniewski et al. 2010).

Bottlenose dolphins display numerous foraging techniques that vary substantially among and within populations (e.g., mud plume feeding: Lewis and Schroeder 2003; fish herding: Gazda et al. 2005; benthic feeding: Rossbach and Herzing 1997; sponge feeding: Sargeant et al. 2007). In some areas, bottlenose dolphins have adapted their foraging techniques to maximize their

energy intakes, capitalizing on anthropogenic activities such as fisheries (e.g., trawler fisheries: Corkeron et al. 1990; Bearzi et al. 2009; gillnet fisheries: Read et al. 2003; Díaz López 2006) and aquaculture (e.g., finfish aquaculture: Díaz López, 2009; shellfish aquaculture: Methion and Díaz López 2019a). Such interactions influence bottlenose dolphin social structure: in Australia, bottlenose dolphins feeding in association with trawlers were part of a different social community than the ones not using this feeding technique (Chilvers and Corkeron 2001); in Brazil, bottlenose dolphins cooperating with beach-casting fishermen were socially segregated from non-cooperative dolphins (Daura-Jorge et al. 2012); and in Italy, the level of association between individuals was significantly lower for bottlenose dolphins engaged in opportunistic feeding activities in finfish farm areas than during not-opportunistic feeding activities (Díaz López and Shirai 2008; Díaz López 2019).

Along the northwestern coast of Spain (Galicia), shellfish aquaculture leads to a variation in resource distribution and abundance. Shellfish are grown on floating rafts with a concentration of ropes in the same area, submerged in the water, increasing the abundance of fish species within shellfish farm areas relative to adjacent areas (Chesney and Iglesias 1979), thus providing high prey density for common bottlenose dolphins (*Tursiops truncatus*) (Díaz López and Methion 2017). When foraging in shellfish farms, bottlenose dolphins swim around the floating rafts to herd school of fish, rush toward the ropes, and feed (Methion and Díaz López 2019a). Although bottlenose dolphin habitat-use and foraging behavior have previously been associated with shellfish aquaculture areas, potential variation in the frequency with which individuals use shellfish farms as foraging grounds and its influence on social interactions have never been studied.

In light of the above considerations, we used behavioral and photo-identification data to investigate individual foraging variation in bottlenose dolphins and its potential influence on their social organization (affiliation indices and network metrics). First, we evaluated whether individual bottlenose dolphins varied in the frequency with which they use human-altered areas (i.e., shellfish farms) as foraging grounds.

Second, we evaluated whether this variation was linked to individual associations and social structure characteristics using generalized affiliation indices (Whitehead and James 2015) and social network analysis (Lusseau et al. 2003; Whitehead 2008). Given the findings of previous research (Díaz López and Methion 2017; Methion and Díaz López 2019a), we expected that the concentration of food resources associated with shellfish aquaculture would induce individual foraging variation, with some individuals foraging more frequently within shellfish farms than others. Subsequently, we expected that this foraging variation would influence bottlenose dolphin social organization, with weaker associations between individuals showing foraging preferences for high food availability areas, where inter-individual competition is higher (Holekamp et al. 2012). Through this framework, we aimed to further our understanding of individual foraging variation driving social organization in bottlenose dolphins.

METHODS

Study area

The present study was conducted in the Ría de Arousa (Galicia, northwest Spain) (Figure 1). Intense upwelling events occur in the area, leading to high biodiversity, productive fisheries, and important aquaculture activities, particularly the production of shellfish (Tenore et al. 1995). Shellfish farming has occurred in Galicia since the late 1940s (Miguez et. 2009) and has developed over the years. Shellfish are grown on ropes suspended from wooden floating rafts which cover approximately 17% of the study area (Figure 1) (Díaz López and Methion 2017). The rafts act as fish aggregation devices, increasing the abundance of fish species within shellfish farm areas compared to adjacent areas (Chesney and Iglesias 1979). Bottlenose dolphins are present year-round in the Ría de Arousa (Díaz López and Methion 2017; Methion and Díaz López 2018) and frequently use the shellfish farm areas as foraging grounds (Methion and Díaz López 2019a).

Data collection

Boat-based surveys were conducted on-board a 12 m research vessel between April 2014 and

November 2017. The study area was monitored during daylight hours when the sea conditions were no greater than 3 on the Douglas sea force scale and visibility was not reduced by rain or fog (Díaz López and Methion 2017). A group of bottlenose dolphin was defined as one or more individuals observed within a 100-m radius, interacting with each other, and engaging in the same behavioral activity (Methion and Díaz López 2019a). All encounters continued until the group composition changed, the group was lost, or until weather conditions became unfavorable. Upon sighting a group of bottlenose dolphins, the date, time, and GPS location were recorded, and group size and composition were estimated. The presence of the group of bottlenose dolphins inside or outside the shellfish farm areas was also recorded. Photographs were taken for photo-identification purposes using digital single lens reflex (DSLR) cameras equipped with a 35- to 300-mm telephoto zoom lens. Attempts were made to photograph both sides of the dorsal fin of every dolphin present in the group, regardless of the degree of marking, age class, or behavior. Bottlenose dolphins were identified based on natural markings on their dorsal fin from high-quality photographs (Würsig and Jefferson 1990). Only individuals with distinctive marks (referred as identified individuals) were included in the analysis to avoid misidentification. Details on the photo-identification procedure can be found in Methion and Díaz López (2018). The predominant behavior of the group was assessed and classified into four categories: foraging, resting, socializing, and travelling (detailed in Methion and Díaz López 2019a). The age of individuals was classified as either dependent calves or adults based on behavioral cues and visual assessment of the size (following Methion and Díaz López 2019a). All males were sexed by the observation of an erection or by the gap (>2.5 cm) between the genital and anal slits, with photographs of the genital area (N = 37). Females were sexed either (i) by the observation of mammary slits and absence of gap between the genital and anal slits, with photographs of the genital area (N = 20), or (ii) by the repeated observation with a new-born swimming in infant position (a minimum of 7 consecutive sampling days, N = 9). Data collection complies with the current laws of Spain, the country in which the study was performed.

Individual foraging variation and spatial distribution

Individual foraging variation was assessed through the difference in use of shellfish farm areas as foraging grounds. To explore the use of shellfish farm areas as foraging grounds by an individual bottlenose dolphin, a “farm foraging rate” was calculated for each individual. The farm foraging rate was defined as the number of times an identified individual was observed foraging in the shellfish farm areas as a proportion of the total number of times the same individual was observed foraging. The farm foraging rate was then used as a continuous measure in further analysis.

Spatial distribution of the sightings for each individual was plotted using a geographical information system (QGIS software, <http://www.qgis.org>). Minimum convex polygon was used to compare space-use between individuals (Burgman and Fox 2003). Space-use overlap between each pair of individuals was determined by using the vector overlay features in QGIS. The central tendency of an individual space-use was represented by the centroid of the minimum convex polygon of all sightings of the individual (Figure 1).

Defining association and estimating affiliation indices

Bottlenose dolphins identified within the same group during a single day were considered associated. To ensure accurate behavioral assessment and individual identification, only groups monitored for at least 15 minutes and where at least 75% of the estimated group size were reliably photographed were included in the analysis. In order to reduce inaccuracies and biases associated with small sample size, analyses were further limited to individual bottlenose dolphins observed (a) foraging more than 6 times (greater than the median number of sightings in which individuals were observed foraging) and (b) in at least 3 calendar years. Dependent calves were not included in the analysis because of their dependent relationship with their mothers (Mann and Smuts 1998).

Social and network analyses were carried out in Socprog 2.8 (Whitehead 2009). Daily sampling periods were used to remove possible demographic effects occurring during the study period (Whitehead 2008). A matrix of association was generated based on the half-weight index (HWI) to reduce biases due to sampling techniques (Cairns and Schwager 1987).

The coefficient of variation of the true association indexes (S) was estimated to measure the social differentiation of the observed HWI using maximum likelihood (Whitehead 2008). Coefficient of variation S values greater than 0.5 indicate well differentiated societies (Whitehead 2008). The correlation between true and estimated association indices (r) was calculated to assess whether the observed association accurately described the social structure (Whitehead 2008). Values of the correlation coefficient, r , close to 1 indicate a good representation of social structure.

The generalized affiliation index (GAI) was used as a measure of strength of the association between dyads (Whitehead and James 2015). The GAI was used to account for the effects of confounding structural factors that might influence the affiliation pattern between individuals (Whitehead and James 2015). The multiple regression quadratic assignment procedure (MRQAP) was used to test the correlation between the association indices (HWI; response variable) and four predictor variables: sex similarity, gregariousness, space-use overlap, and cumulative number of sightings for each pair of individuals. The correlations were calculated for each predictor variable while controlling for the others. GAIs were calculated as the residuals of a generalized linear model, where the dependent variable was the association index (HWI), and the structural factors were the predictor variables (Whitehead and James 2015).

Analysis of affiliation patterns

To assess whether observed associations occurred at random, a Monte Carlo simulation test was conducted, where association matrices were randomly permuted until the P-value stabilized (Bejder et al. 1998; Whitehead 2009). To account for non-independence of group

membership, randomizations permuting associations among groups within each sampling period were carried out (Whitehead 2009). A significantly higher standard deviation (SD) of observed affiliation indices compared to that of randomly permuted data indicated the presence of non-random associations (Whitehead 1999).

To assess whether affiliation patterns (mean and maximum GAI) were related to the farm foraging rate, a non-parametric Spearman's correlation test was performed using the psych package in v. 1.8.1. of the statistics and graphics tool R (R Development Core Team 2011).

Additionally, to test whether individuals preferred to affiliate with other individuals having a similar farm foraging rate, an arbitrary threshold using the mean value was fixed and individuals were pooled in two foraging classes: (i) "Frequent Farmers", individuals with a farm foraging rate equal to or higher than the mean and (ii) "Occasional Farmers", individuals with a farm foraging rate lower than the mean. A two-tailed Mantel test was then run to compare affiliation indices within and between the two foraging classes (Whitehead 2008).

Network metrics and social structure

A social network approach was used to investigate the social association patterns. Social network was modelled as weighted networks based on the association matrices defined by the GAI among individuals. We calculated five egocentric network measures (Whitehead 2008) to investigate differences in centrality of individuals: (i) the Strength, which is a measure of gregariousness and is the sum of the GAI of each individual (Barrat et al. 2004); (ii) the Eigenvector Centrality, which is a measure of an individual's importance in the network and is determined as the distance from other central individuals relative to all others in the network (Newman 2004); (iii) the Reach, which is a measure of indirect connectedness in the network (Whitehead 2008); (iv) the Clustering Coefficient, which describes how well associated an individual associates are (Holme et al. 2007); and (v) the Affinity, which is a measure of how strongly an individual is associated to other individuals with high strength (Barthélemy 2005).

To assess whether network metrics were related to the farm foraging rate, non-parametric spearman's correlation tests were performed.

A social network diagram was drawn using the program Netdraw (Borgatti et al. 2002), with lines (edges) representing GAI between individuals (nodes).

Potential subgrouping within the network was explored using the clustering algorithm and eigenvector-based approach of Newman (2006) to select the community partition that maximizes the modularity coefficient (Q) (implemented in Socprog 2.8; Whitehead 2009). To define the most parsimonious clustering step, the social network is iteratively divided into clusters until a peak in Q is reached (Newman 2006). Q values above 0.3 are generally considered to present a meaningful delineation of the data (Newman 2004).

RESULTS

During the study period, 265 groups of bottlenose dolphins were encountered and 171 individual dolphins were identified. Of the groups containing two or more adult individuals, 84% were mixed-sex. Of the total number of identified individuals, 66 met the restriction criteria including 37 males and 29 females. Total sightings per selected individual ranged from 7 to 82 (mean \pm SE = 32 ± 1.83 , median = 28).

Individual foraging variation and spatial distribution

Individual farm foraging rate varied from 0.00 to 0.57 (mean \pm SE = 0.30 ± 0.01 , median = 0.30). Males and females did not show significant differences in farm foraging rate (males: mean \pm SE = 0.32 ± 0.02 , median = 0.30; females: mean \pm SE = 0.28 ± 0.02 , median = 0.30) (Mann-Whitney U test with 10000 permutations, $P > 0.05$).

Association patterns, network metrics, and social structure

The coefficient of variation of the true association indexes indicated a well-differentiated society ($S = 0.81 \pm 0.02$ SE). The correlation between the true association indexes and estimated

association indexes indicated that the association data had good power to detect the true social system within the population ($r = 0.86 \pm 0.02$ SE).

MRQAP tests indicated a significant correlation of associations with sex similarity, gregariousness, space-use overlap, and cumulative number of sightings for each pair of individuals (Table 1) and were, therefore, included in GAI analyses. The SD of the mean of the observed matrix was significantly higher than the one from random data (observed SD = 0.090, random SD = 0.085) (1000 permutations, 1000 trials per permutations, $P < 0.001$).

The mean and maximum GAI were negatively correlated to the farm foraging rate (Spearman's rho, $P < 0.01$) (Figure 2). Likewise, the analysis indicated a negative relationship between the network metrics and the farm foraging rate. Indeed, Strength, Reach, and Affinity were negatively related to the farm foraging rate (Figure 2).

Both the network analysis and the network diagram (Figure 3) indicated the rather peripheral positions of those individuals with higher foraging rates and emphasized the central role of individuals that forage less frequently between mussel rafts.

Modularity analysis identified four social clusters that ranged in size from 12 to 23 individuals. However, analysis did not show conclusive partitioning into separated social units as the modularity of this assignment was 0.09 (Newman 2004).

Affiliations were significantly higher within foraging classes than between foraging classes (two-tailed Mantel test with 1000 permutations, $t = 5.4$, matrix correlation = 0.12, $P < 0.01$) (within foraging classes: mean GAI \pm SD = 0.02 ± 0.04 ; between foraging classes: mean GAI \pm SD = 0.00 ± 0.03), indicating that individuals preferentially associate with individuals having a similar farm foraging rate. Thirty-nine dolphins were categorized as Frequent Farmers (including 24 males and 15 females) and 27 dolphins were categorized as Occasional Farmers (including 13 males and 14 females).

DISCUSSION

The current study reveals that behavioral variation among individual bottlenose dolphins shapes their social organization. In particular, bottlenose dolphins that frequently foraged within human-altered areas (i.e., shellfish farms) exhibited weaker associations when compared to others. Furthermore, we demonstrated that bottlenose dolphins preferred to affiliate with other individuals with similar foraging strategies. These findings provide valuable insight into the evolution of bottlenose dolphin social systems and their response to human-induced changes in the marine environment.

Our results indicate that bottlenose dolphins used shellfish farm areas as foraging grounds with varying intensity. Individual variation in foraging behavior has been previously documented in other parts of the world for bottlenose dolphins (e.g., Sardinia, Italy: Díaz López and Shirai 2008; Florida, USA: Nowacek 2002; Torres and Read 2009; Shark Bay, Australia: Mann and Sargeant 2003, Sargeant et al. 2007, Sargeant and Mann 2009; Brazil: Simões-Lopes et al. 1998) as well as other social mammals (e.g., European badger, *Meles meles*: Robertson et al. 2014; mink, *Mustela spp*: Sidorovich et al. 2001; sea otter, *Enhydra lutris*: Estes et al. 2003). Behavioral variation may reduce competition between group members and facilitate a stable society, playing an important role in the evolution of the social system (Barta 2016). In Galicia, competition for food resources may motivate individual bottlenose dolphins to adopt different foraging strategies, and thus induce the observed differences in foraging behavior. The behavioral variation reported in this study, therefore, likely reflects differences in the utilization of distinct foraging strategies rather than differences in spatial distribution and between sexes.

Along the north-west coast of Spain (Galicia), shellfish aquaculture has introduced spatial habitat complexity, leading to a variation in resource distribution and abundance (Chesney and Iglesias 1979) and has fragmented bottlenose dolphin habitat (Díaz López and Methion 2017). Certain individual bottlenose dolphins frequently used the shellfish farm areas as foraging grounds, using specific foraging strategies to catch prey in between the floating

rafts (Methion and Díaz López 2019a). These individuals therefore profit from a reliable and easily located (i.e., lower energetic and time expenditure when foraging) food source, which may increase their energy intake (Díaz López 2012; Methion and Díaz López 2019a). A frequent interaction with shellfish aquaculture may have led some individuals to have an intimate knowledge of the characteristics of these human-altered areas and be able to efficiently obtain the food resources concentrated within these structures.

Social network analyses reveal that the observed variation in foraging behavior among individual bottlenose dolphins was associated with their social organization. Network metrics including Strength, Reach, and Affinity were negatively correlated to the farm foraging rate. Bottlenose dolphins frequently foraging within the shellfish farm areas had a peripheral position within the network and exhibited weaker Strength, Reach, and Affinity compared to individuals with a lower foraging rate. The reliable, easily located, and large food source present within the shellfish farm areas, may have made it less necessary for dolphins to cooperate with a large number of conspecifics. The presence of concentrated food resources within these human-altered areas could increase the level of intraspecific competition between individuals (Díaz López 2019). In contrast, individuals that foraged less frequently within the shellfish farms occupied a central position within the network and had strong associations. These individuals may benefit from increased cooperation and reduced intragroup competition, thus increasing learning and information-sharing, as they may face a patchy and irregular distribution of prey. Cooperative foraging tactics, such as ‘carousel swim’ (i.e., dolphins surrounding wild fish schools, forcing the fish to swim in a concentrated ball), have been described in bottlenose dolphins hunting wild prey (Díaz López 2009). By coordinating their behaviors, individuals that foraged less frequently within the shellfish farms may maximize their foraging efficiency, and presumably their overall fitness. Relationships between association patterns and foraging behavior have been suggested to be a result of individual adaptations to local ecological conditions. In Sardinia Island (Italy), association levels between bottlenose dolphins became

weaker as a consequence of an increase in intragroup competition due to human-induced changes (i.e., fin-fish farming and coastal fisheries) in the marine environment (Díaz López 2019). In Australia, Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) were socially more connected after the reduction of commercial fisheries (Ansmann et al. 2012). In Kenya, associations between spotted hyenas (*Crocuta crocuta*) were weakest when competition for resources was most intense (Holekamp et al. 2012).

Our findings indicate that bottlenose dolphins preferred to affiliate with other individuals that foraged within shellfish farms at similar frequencies. Homophily based on foraging strategies has been previously shown in other bottlenose dolphin populations (e.g., sponge foraging in Australia: Mann et al. 2012; foraging in interaction with fishermen in Brazil: Daura-Jorge et al. 2012; Machado et al. 2019; “Feeding associates” interacting with finfish farm in Italy: Díaz López and Shirai 2008). The observed tendency to associate with similar individuals (i.e., homophily) may influence a range of social processes in this population of bottlenose dolphins, including social segregation (Best et al. 2013), social contagion (i.e., spread of behavior patterns in a group through imitation) (Sah et al. 2018), and the evolution of cooperation (Massen and Koski 2014). As social bonds take investment of time, energy, and trust, maintaining associations with individuals that are more trustworthy is beneficial (Massen and Koski 2014). By associating with individuals of similar foraging preferences, bottlenose dolphins may facilitate the cooperation and the transmission of information (i.e., learning) within foraging groups rather than between foraging groups.

Efficient foraging requires knowledge of prey locations and foraging strategies, which may be learned by interacting with conspecifics (Sargeant et al. 2007; Díaz López 2009; Mann et al. 2012). The higher Strength, Reach (which has been associated with behavioral contagion; Flack et al. 2006), and Affinity observed in individuals foraging less frequently within the shellfish farm areas further suggest that these individuals play an important role in cooperation, communication, and social learning (Wey et al. 2008). Social learning is commonly used among

mammals to acquire information about the environment and is a suggested process behind the development of individual foraging variation (e.g., meerkat, *Suricata suricatta*: Thornton and Malapert 2009; sea otter: Estes et al. 2003; bottlenose dolphin: Daura-Jorge et al. 2012; Mann et al. 2012). Given the observational learning skills of bottlenose dolphins (Kuczaj and Yeater 2006), the foraging strategies for capturing prey may be perpetuated by transmission of information between individuals (Rendell and Whitehead 2001). Learning through observation may help to maintain behavioral strategies by facilitating the transmission of behavior from one bottlenose dolphin to another (Kuczaj and Yeater 2006). In bottlenose dolphins, there is ample opportunity for social learning since mothers care for their offspring for several years (Mann and Smuts 1998), and since they exhibit social systems characterized by fission-fusion dynamics, allowing both vertical and horizontal transmission of behavior. The presence of females which had calves during the study period supports the fact that foraging strategies could be passed down from mother to offspring (vertical transmission). Bottlenose dolphins may also learn these foraging strategies from individuals within a generation (horizontal transmission). The flow of information could, therefore, be increased between individuals exhibiting similar foraging behavior. This learning homophily could promote, through time, a segregation of the population into behaviorally distinct groups (Centola et al. 2007).

Given bottlenose dolphins’ inconspicuous nature and the changing environment they inhabit, there are inherent difficulties in studying their behavior and social organization. Bottlenose dolphin social organization is likely to be driven by multiple factors acting synergistically, including behavior (Díaz López and Shirai 2008), reproductive state (Connor et al. 2000), sex (Mann et al. 2012), kinship (Wiszniewski et al. 2010), age (Gero et al. 2005), and environmental conditions (Díaz López 2019). Our analytical approach, taking into account adult individuals only and the effects of four structural variables (sex, gregariousness, space-use overlap, and cumulative number of sightings for each pair of individuals) when estimating affiliation indices (GAI), provides reliable results when estimating social interactions (Whitehead and James 2015).

Other factors may contribute to social interactions in this bottlenose dolphin population such as kinship (Parsons et al. 2003; Wiszniewski et al. 2010; Carter et al. 2013) and similarity of interaction partners in terms of consistent individual differences in behavior (i.e., “behavioral syndromes” or “personality”). Individual differences in personality have been documented for captive bottlenose dolphins (Highfill and Kuczaj 2007) and may potentially correlate with the observed differences in foraging behavior (i.e. risk-taking behavior). These factors, together with ecological pressures (Yamagiwa 1999; Belton et al. 2018; Díaz López 2019), may play important roles in the development of non-random and long-term associations among individual bottlenose dolphins.

In conclusion, this study highlights the relationship between individual foraging variation in bottlenose dolphin and their social organization. The observed foraging variation may have further implication for bottlenose dolphin ranging behavior (Cantor et al. 2018) and genetics (Estes et al. 2003). From a conservation perspective, individual bottlenose dolphins frequently foraging within human-altered areas (i.e., shellfish farms) may face higher risk of injury or death due to the interaction with human activities (i.e., boat strikes, entanglement, water pollution; Methion and Díaz López 2019a) which could alter the population social dynamics and structure. Further information about the willingness to interact with human activities (i.e., risk-taking behavior) through specific studies on personality will be crucial to further understand the social organization and the emergence of specialized behaviors in wild bottlenose dolphins.

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Figure 1. Map of the study area (Ría de Arousa, northwest Spain) showing the minimum convex polygon centroids for each of the 66 bottlenose dolphins studied. Polygons represent shellfish farm areas.

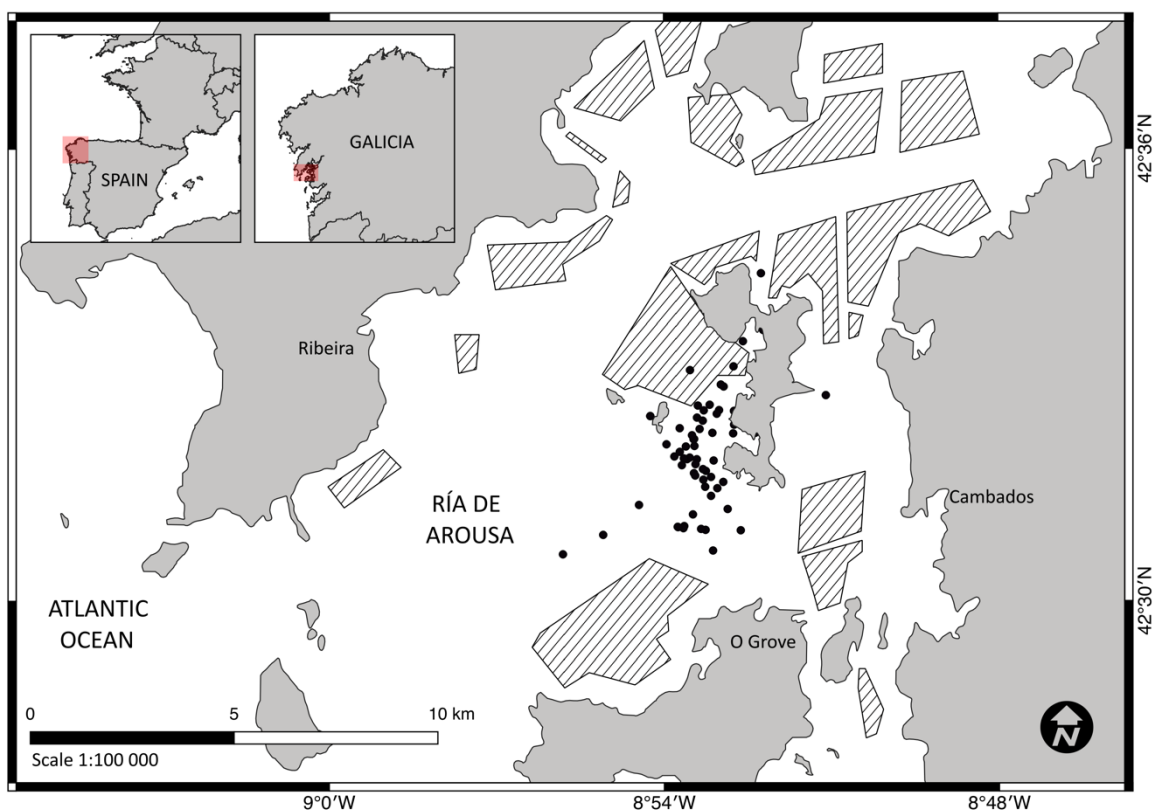


Figure 2. Scatter plot with fitted line and Spearman rho coefficient between farm foraging rate (x-axis) and each affiliation (mean GAI and max GAI) and network metrics (Strength, Eigenvector Centrality, Clustering Coefficient, Reach, and Affinity) (y-axis). Histograms with rug plot are provided for each variable. Significance codes: * = $P < 0.05$, ** = $P < 0.01$; *** = $P < 0.001$.

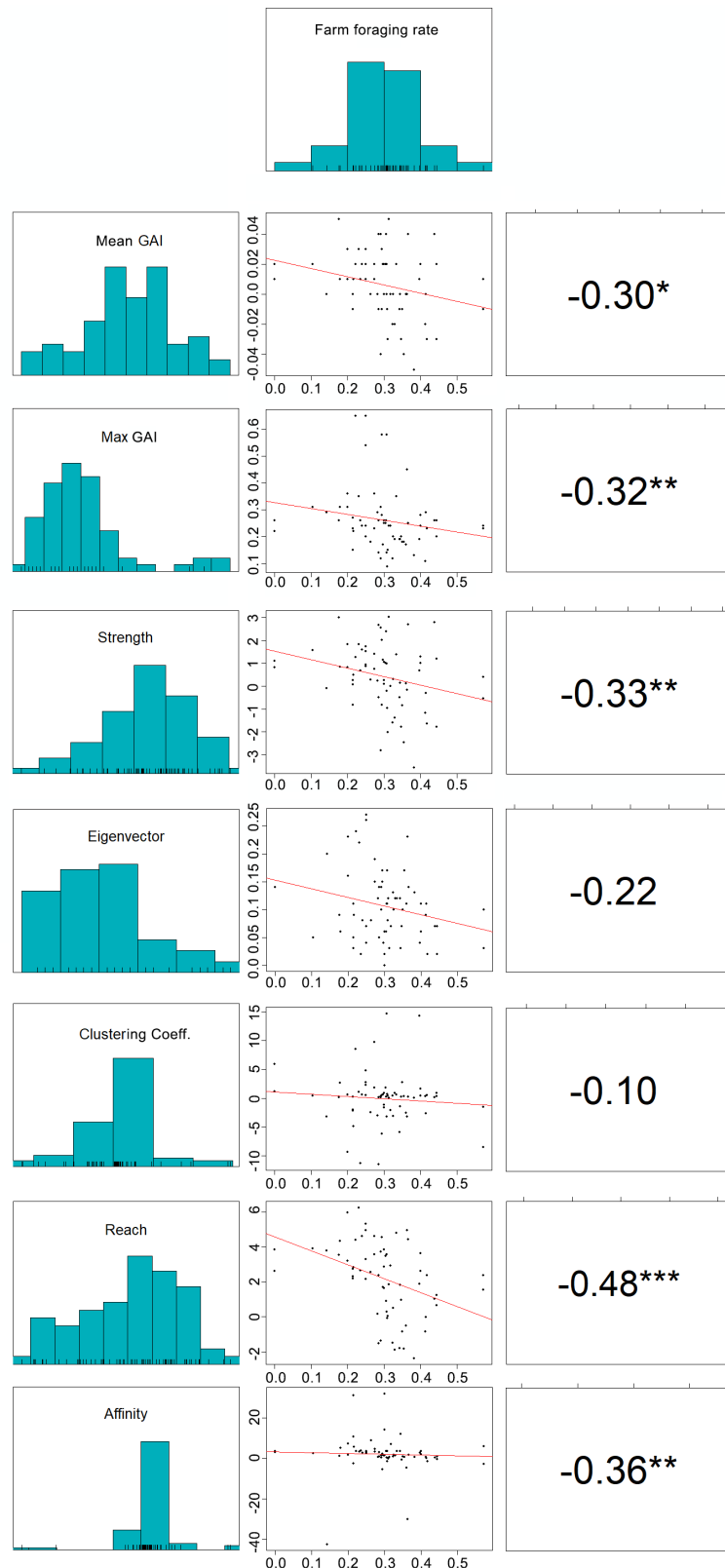


Figure 3. Social network of bottlenose dolphins in the Ría de Arousa (northwest Spain). Each individual is represented by a node. Only edges with GAI greater than 0.02 are displayed. Node sizes represent the farm foraging rate of the individuals, and edge width is proportional to the strength of the affiliations.

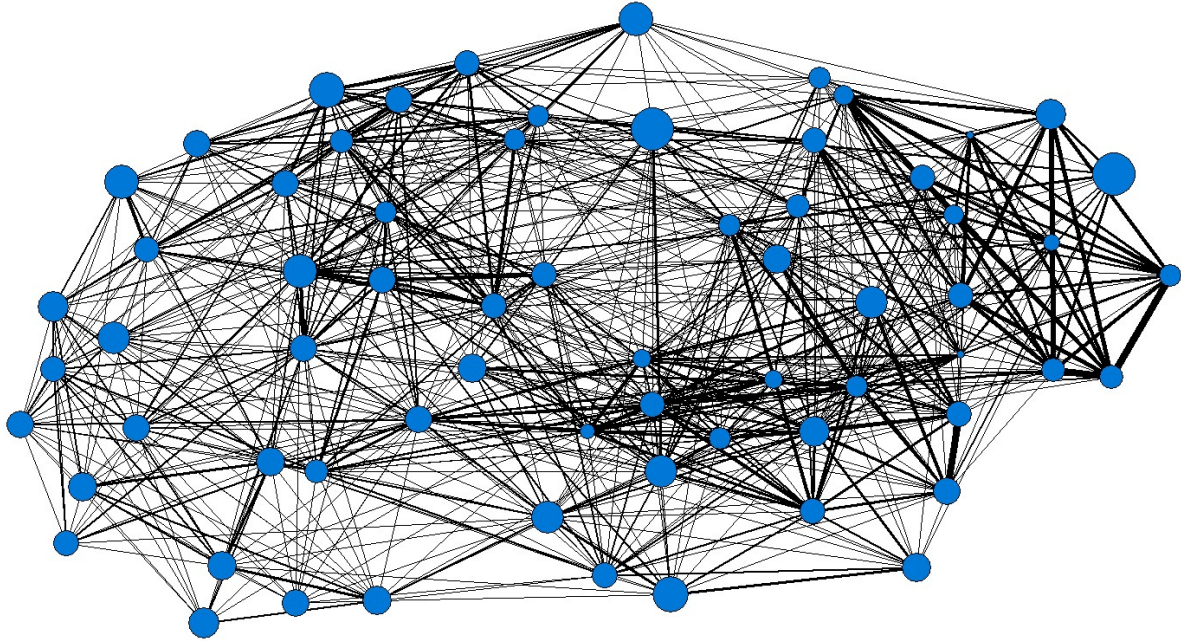


Table 1. Significance of predictor variables on association indices using multiple regression quadratic assignment procedures (N = 66 individuals).

Predictor variable	Partial correlation coefficient	P
Sex similarity	0.1016	< 0.01
Gregariousness	0.3915	< 0.001
Cumulative number of sightings per pair of individuals	0.3293	< 0.001
Space-use overlap	0.3004	< 0.001