

RESEARCH ARTICLE

Complex Social Structure of an Endangered Population of Bottlenose Dolphins (*Tursiops truncatus*) in the Aeolian Archipelago (Italy)

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Abstract

We investigated social structure and association patterns for a small population of Mediterranean bottlenose dolphins, *Tursiops truncatus*, inhabiting the Aeolian Archipelago (southern Italy). Specifically we evaluate the role of sex and age composition, residency patterns and interaction with trammel nets on this social organization. Association data for 23 regularly sighted individuals were obtained from summer photoidentification surveys collected from 2005–2012. Using a combined cluster and social network analysis approach, we found associations between dolphins were hierarchically structured, where two mixed-sex social units were subdivided into smaller temporarily dynamic groups. We found non-random and long-term preferred associations in the population; however, the degree of social cohesion, residence pattern and interaction with trammel nets differed considerably between the two social units. Six of eight females occurred in the more resident social unit-1; in addition, social unit-1 individuals had significantly stronger associations, higher preferred associates, lived in larger groups and occurred less frequently with trammel nets. Nine of eleven males were clustered in social unit-2 and five of these males, interacting with trammel nets, formed small groups and preferred associations. We propose that female and male groups associate in the study area during the breeding season and that some males choose to interact with reproductive females forming a distinct but interrelated social unit. Other males may be associating in a larger fission-fusion network, which consists of dolphins that appear to temporarily join the network from the coastal population. We cannot exclude that some males specialized in trammel net foraging, suggesting that this foraging technique may favor a solitary lifestyle. Large group sizes and high degree of social cohesion for females could be an indication



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of greater protection and more efficiency in detecting, deterring or repelling anthropogenic pressures. Most likely dolphins' social organization depends on a combination of socio-ecological, demographic and anthropogenic factors.

Introduction

Bottlenose dolphins (*Tursiops truncatus*), like many mammal species [1], [2], [3], live in fission–fusion societies where individuals join and leave groups on a flexible basis, with group composition and size changing frequently on small spatial and temporal scales [4]. High rates of group composition changes in *fission–fusion* societies are thought to be an adaptive response to the dynamic interaction of ecological variables [5].

Several factors potentially affect the social structure of bottlenose dolphins, including predation risk [6], habitat structure [7], [8], [9], prey distribution [6], [10], cultural transmission [11], [12], [13], breeding success [14], male competition [15], [16], [17], [18], and risk of infanticide [19], [20], [21]. The stability of social relationships in a population, however, is expected to increase when the benefits of stable, cooperative relationships balance the costs, such as increased resource competition and socially transmitted parasites [22]. Sexual segregation is believed to be the basic social framework of some bottlenose dolphin populations (e.g. *T. aduncus* in eastern Australia) where grouping patterns reflect sex-specific behavioural strategies [23]. In some wild populations, sexually mature male bottlenose dolphins form first-order alliances in pairs, trios, and second-order super-alliances, which cooperate by pursuing distinct alliance strategies to monopolize females in reproductive condition [15], [16], [17], [18]. However, other studies have shown that male alliances may not occur in all bottlenose dolphin populations and the degree of sexual segregation and the proportion of mixed-sex groups can be geographically very variable [24], [25], [26], [27]. Females may be highly social or even solitary (e.g. at Sarasota Bay and Shark Bay), associating with related and unrelated females [14], [28], [29], [30], [31]; their associates being mostly dependent upon their reproductive status [5], [14]. For example, in Sarasota Bay (Florida), female strategies appear to be driven by calf protection (from predators and/or conspecifics) with adult females and their calves forming strongly bonded bands [4], [28].

Many studies have shown that bottlenose dolphins have a varied diet and their feeding behaviour may be very flexible [32], [33], [34]. Specializations in the diet [33], [34], [35] and the techniques used to capture prey [11], [12], [13], may also have a role in shaping social structure. However, human activities can have a substantial impact on the social organizations of dolphin groups, for example through changes in the distribution of food resources, which may affect the costs of feeding competition [36]. Anthropogenic food patches in the marine environment, such as aquaculture farms [37] and active trawlers [38], [39] may

change the behaviour of bottlenose dolphins through the modification of habitats, changes in predation pressure, and variations of food distribution and availability, which may affect the social interactions and the demography of the dolphin population.

In the Mediterranean, the bottlenose dolphin occurs in coastal habitats [36], [40], [41], [42] and its diet includes several commercial fish species [43]. As fish stocks are generally declining [36], [44] bottlenose dolphins are increasingly in conflict with coastal artisanal fishing [36], [37], [39], including trammel nets, and serious injuries are quite common [45], [46]. At present, the social structure of resident bottlenose dolphin populations in the Mediterranean is poorly understood. The limited information available, however, suggests that aquaculture farms [37], and active trawlers [39], may play an important role in shaping social arrangements.

We began a study on a small population of Mediterranean bottlenose dolphins (Aeolian Archipelago, Southern Italy) in 2005 [47], [48]. In this area the inshore occurrence of the species is related to the complex geomorphology of the volcanic islands [47]. However, the ecology and behaviour of the bottlenose dolphins are likely to be extensively influenced by the food resources found in trammel nets [48]. Dolphin groups are generally smaller in habitats where trawlers operate and foraging groups are smaller than groups of dolphins engaged in other behavioural activities [48].

The purpose of this study is to evaluate the socio-ecological, demographic, and anthropogenic factors that influence the social structure of bottlenose dolphins in the Aeolian Archipelago (2005–2012). Specifically we assessed the role of sex and age composition, individual residency patterns and the temporal stability of association in driving the social organization. We also tested the hypothesis that trammel nets may affect such social patterns, given that dolphin groups were known to interact with this opportunistic food resource [48]. We used measures of association between pairs of individuals (i.e. half-weight association index) [49] to evaluate the social unit composition and cohesion, and statistical methods [50], [51], as well as temporal analysis to describe the temporal stability of dolphins' social structure [52]. As reproductive success is known to have an important role in the sociality of gregarious animals [4], [14], [15], [31] we expect that differences in patterns of associations would occur between males and females. We also expect that dolphins sighted more or less frequently near trammel nets may be socially differentiated, considering that specializations in the diet [32], [34], [35] and techniques used in capturing prey [11], [12], [13] are already known to shape association patterns.

Our results represent the first documentation on the association patterns and social structure for this small bottlenose dolphin population. As the bottlenose dolphin encounter rate and group sizes have been decreasing in recent years, understanding the social structure of this population and how anthropogenic modifications of the environment impact social organizations, may be critical for future conservation efforts.

Materials and Methods

Study site and data collection

The study area covered 280 km² of coastal waters in Filicudi, one of the seven islands of the Aeolian Archipelago located at 38° 35' N, 14° 34' E in the Southern Tyrrhenian Sea (Sicily, Italy) ([Fig. 1](#)).

Data on dolphin group sightings covered eight summer periods (2005–2012). Dolphins were sampled from a boat during daily surveys [[47](#)]. Surveys were conducted in the morning (from 6.00 a.m. to 14.00 pm), in good light conditions (visibility was more than 300 m) and calm waters (mean = 1.1; sea state based on Beaufort scale was less than 3), with sea state which did not change between early (mean = 0.8, SD = ± 0.5, n = 298) and late summer (mean = 1.7, SD = ± 1.9, n = 159) (Student t, $P=0.1$) or variations from year to year (Kruskal-Wallis, $F=4.6$, $P=0.2$).

Bottlenose dolphins were sampled using a combination of group follows [[53](#)] and photoidentification techniques [[54](#)], [[55](#)]. The study did not require any permit to observe animals as it was carried out without handling or close contact with animals in the study area. Once sighted, the dolphin groups were slowly approached in order to minimize disturbance and their positions recorded using a hand-held global positioning system (GPS). The first position was recorded only when the boat reached ≤ 30 m distance from the focal group. For each three-minute period of sighting, the location of the focal group, its size and the behavioural activity were recorded. We also recorded the position of trammel fishing nets when they were within 100 m of the focal group [[48](#)]. Group size was visually determined *in situ*, and later verified by standard photo-id techniques and videos taken during each sighting. Assuming that clustered animals were also interacting [[56](#)], we defined associations by membership to the same group, i.e. animals photographed in the same group and moving in the same general direction, interacting or engaged in similar activities were considered to be associated [[32](#)]. We included as group members any individuals within 10 m of at least one other dolphin in the group. When more than one group of dolphins was encountered in the same survey, each group was recorded as an independent sighting [[57](#)]. When a group split, one of the sub-groups was followed, the choice of group being random and independent of group size and/or activity [[57](#)].

Each group member was classified according to its relative size: (1) adults, larger and robust animals, with darker skin color and many marks on the dorsal fin and the body, and often accompanied by a calf [[58](#)]; (2) juveniles, less-robust and smaller animals (at least two-thirds the length of adults), usually with less-distinctive nicks, or without nicks in their dorsal fins and not obviously associated with an adult, and (3) calves, smaller animals in close association with an adult and usually without nicks in their dorsal fins. Calves were also identified by behavioural patterns such as surfacing behaviour and swimming in an infant position (in contact underneath the mother) [[59](#)].

The sex of the individuals was determined primarily by opportunistic views of the genital region and were later verified by standard photo-id techniques and

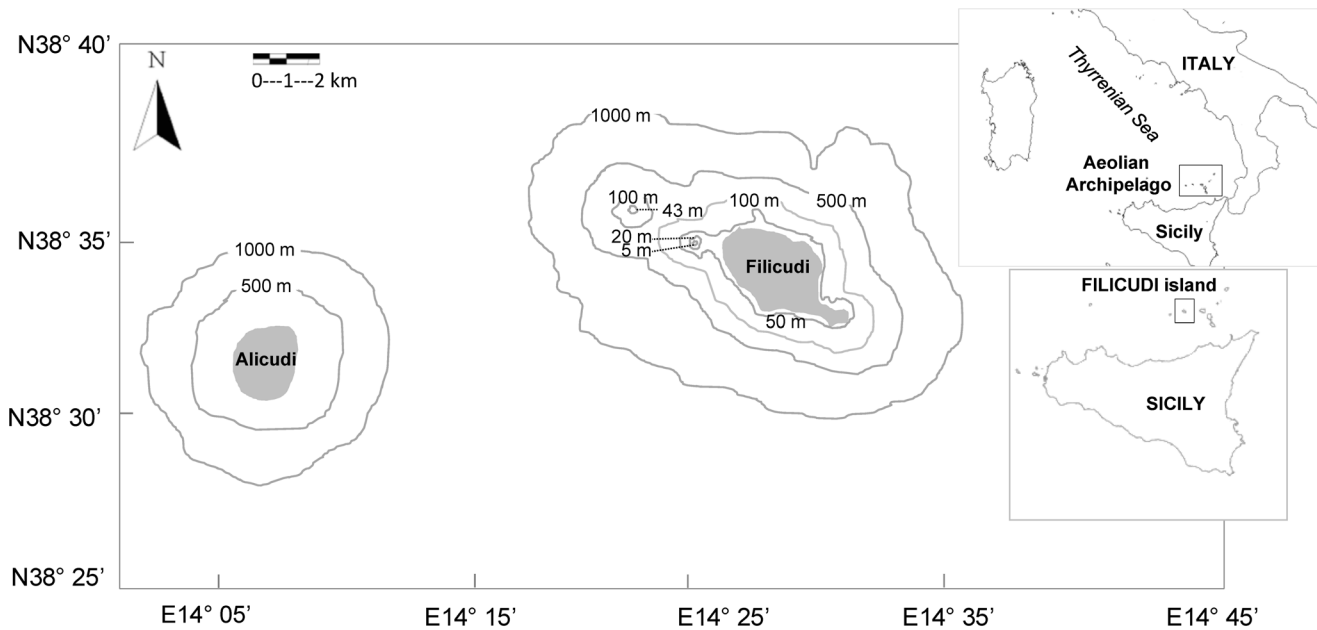


Fig. 1. Map of the study area (Filicudi and Alicudi islands, Aeolian Archipelago, Sicily, Italy).

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videos taken during each sighting. Although genetic data are not available to distinguish univocally the sex, the animals showed high site fidelity to the area permitting to collect several photographs for sex determination. Females were sexed when they maintained a close and durable relationship with a calf and were presumed to be mothers. Although bottlenose dolphins show a slight morphometric sexual dimorphism, adult males are known to show a significantly higher number of scars on their dorsal fins than juveniles [60]. Although this feature has not been confirmed for our population, the adult animals with heavy scarring and multiple fin nicks which were never observed in close contact with a calf were classified ‘estimated male’ [30].

Data organizing

Photographs of dorsal fins were sorted according to standard protocols, using nicks, notches, or scars [55]. We compared good/optimal quality images of distinctive fins with a photo-identification catalog of known individuals. The photographic capture rate was calculated as relative proportion of scarce, good and optimal quality pictures. We calculated the cumulative number of newly-sighted dolphins per survey and the yearly encounter rate (expressed in groups per km) as n/L with n the number of sighted groups and L the effort in km each year [61]. The annual group size was calculated as the mean (\pm SD) group size each year. We also calculated the mean number (\pm SD) of dolphins that were not photo-identified each year during the focal follows (not-identified dolphins). We defined residence classes based on the number of sighting of each dolphin. We

also calculated the annual residence of each dolphin as the number of individual's sightings each year divided by the total number of sightings each year. Each year, we calculated the percentage of males, females and dolphins of unknown sex and the percentage of calves, juveniles and adults. At the end of the study, all individuals were assigned to an age class according to data acquired from their last sighting. As all dolphins were associated at least once to trammel nets during the study, we calculated the percentage of sightings with and without trammel nets for each dolphin. For each individual, we also calculated the percentage of sightings (1) in early (June–July) and late (August–September) summer, (2) in early (from 6.00 a.m. to 10.00 a.m.) and late (from 10.00 a.m. to 14.00 p.m.) morning and (3) in good (Beaufort scale 0–1) and worse (Beaufort scale 2–3) sea weather conditions. We used the mean group size computed on pooled sightings as cut off value to define small and large groups; for each dolphin we calculated the percentage of sightings within groups with size more and less than this cut off value.

Quantifying social associations

Coefficients of association were calculated using the half-weight index (HWI), which is defined by the equation $2N/(N_{PHDA}+N_{PHDB})$, where N is the number of times that individual PHDA and PHDB were seen together, and N_{PHDA} and N_{PHDB} are the total number of sightings of each individual [49], [62]. A zero value of HWIs indicates that the pair had never been observed together in the same group while a score of 1 indicates that the animals were always observed in the same group. The HWI accounts for bias from pairs being more likely to be scored when separate than together [62]. We chose the HWI because it allows for comparison with many other studies on bottlenose dolphins [63], [64], [65]. To ensure independence of sampling and avoid serial autocorrelation of sightings, we only used the first sighting when an individual dolphin was sighted more than once in a day [66]. Pooled HWIs (years combined from 2005 to 2012) and one for each combination of sex were calculated for pairs of individuals that were sighted six or more times in the study period. Calves were excluded because of their unique dependent relationship with their mothers [67]. The HWI may be underestimated when not all individuals of a group are identified. For large groups (>8 individuals) only the observations in which at least 80% of the individuals were photo-identified were included in the analysis. We used group membership samples to obtain an association matrix of all individuals [56]. Mean, maximum and minimum HWIs were calculated for each individual.

Testing for non-random association patterns

Determining whether or not associations are non-random is essential to assess the significance of individual HWIs. We used a permutation test, according to Bejder *et al.* (1998), with modifications following Whitehead *et al.* [68] to test for non-random associations in all data combined against the null hypotheses that

dolphins associate randomly [66], [68]. Associations between individuals were tested by randomly permuting groups within sampling periods. In this case the null hypothesis is that there are no preferred or avoided companions (individuals who preferentially group together or avoid one another) given the number of groups each animal is seen in during each sampling period. This method accounts for individuals that are not present in each sampling period due to birth, death and migration, a fact that may occur during the longer time frame of the pooled datasets. If some individuals preferentially associate with other individuals, then the standard deviation (SD) of HWIs should be higher in the real data set than the random data sets. Low means of HWIs, produced by short-term preferences, tended to lower the SD of HWIs and thus mask the presence of long-term preferences. To compensate for this effect, we used the coefficient of variation (CV) of the HWIs as a test for long-term preferences [56], [69]. A significantly higher CV of real HWIs compared to randomized data indicates the presence of long-term preferred companions in the population [56], [69]. The number of random permutations was determined increasing the number of permutations until the p value stabilizes [66]. The resulting p values of permutations were not considered as a formal statistical threshold but rather an indication of the strength of evidence for non-random associations; thus, a Bonferroni adjustment was not required. We permuted the associations within daily sampling intervals to remove possible demographic effects [56]. We identified a dyad as having a preferred association when the association index was twice the mean index, including zero values [61]. We chose this arbitrary threshold value because it is approximately twice the expected value when associations were completely random [69]. A Mantel test, using 1,000 permutations, was applied to assess differences in association depending on sex [70]. In addition, a Chi-square test was applied to determine whether the number of dyads on different HWIs classes (selected according to the range and distribution of the HWIs values) significantly differed between sexes.

The calculation of HWI, the permutation test, and the Mantel test were computed using the compiled version of SOCPROG 2.3 [71].

Network metrics

We calculated three network statistics from the association matrix of individuals using SOCPROG 2.3 [71]. These included (1) the strength, a measure of individuals' gregariousness obtained from the sum of association indices for each individual [72], (2) the clustering coefficient, which represents individual sociality and the proportion of an individual's neighbors that are themselves neighbors [73], and (3) affinity, which represents the weighted mean strength of neighbors and indicates whether individuals strongly connect to individuals that also have strong connections [72]. The variation of the social system was measured using the coefficient of variation of true association indexes (social differentiation), which is an estimate of whether the data reflect a homogeneous society or a socially differentiated population [71].

We used SOCPROG 2.3 [71] to calculate the network statistics for pooled data and obtained mean values and standard errors through the bootstrap method with 1,000 replicates.

Network analysis

The social organization of the population was graphically represented by a sociogram using SOCPROG 2.3 [71], which does not assume that the society is hierarchically structured.

We also applied a Hierarchical Clustering analysis (average linkage method) to the association coefficients for the entire study period. We obtained a dendrogram where the individuals were arranged on one axis and their degree of association on another [69]. Cluster analysis assumes that the society is structured in a hierarchical fashion with different groups of dolphins clustered together (social units). The relevance of the dendrogram was assessed by means of the correlation coefficient, which is the correlation between the dyads in the association matrix and the level at which the pairs are joined in the dendrogram [69]. A correlation coefficient ≥ 0.80 indicates a good match and, although it does not indicate a truly hierarchically structured society, it suggests that the model is reasonably consistent with the data [69]. The average-linkage method of clustering was used because it gave the highest correlation coefficient [69] and because very small or large similarities (caused by random error, measurement error or unusual relationships) have less impact on the results than other linkage methods [56]. The association index corresponding to the maximum modularity was used to define community division by clusters [69], [74], [75].

We also explored the factors affecting changes in the association pattern by Principal Component Analysis (PCA) and MANOVA. Specifically we assessed the role of sex and age composition, individual residency patterns and interaction with trammel nets on social organization. The PCA was applied to the HWIs matrix, and the scores on principal components (PC_{HWI}) (i.e. the transformed variable values) used as a smaller set of new predictors [47], [76]. The loadings on the PC_{HWI} were used to find the correlation coefficients between HWIs and PC_{HWI} . A Student *t* was applied to test if the PC_{HWI} scores (explaining 80% of variance) were significantly different between sexes and age classes. We also tested the differences between dolphins with mean HWIs larger and smaller than the cut off value for preferred associations. MANOVA was applied to the PC_{HWI} scores with different dependent variables: residence pattern, group size, summer period, sighting time, sea weather conditions and number of sightings with trammel nets. We used the SAS 8.1 software to examine these relationships [77], [78].

Temporal patterns of association

We calculated the changes in association rates over time within the population using the lagged association rate (LAR; [52]) in relation to time for all relationships (all dyads). The LAR was compared to the null association rate

initially to determine whether nonrandom patterns of associations occurred over the entire study period. We developed models of temporal stability [52] using exponential decay and constants to mimic the dynamics of association patterns between pairs of individuals and we fitted the models to the observed data to characterize the social components of the society. The models comprised different combinations of three components, i.e. constant companions (CC, permanent relationships), rapid disassociations (RD) and casual acquaintances (CA; nonpermanent relationships which decay over various time lags), that can last from a few days to several years. For this latter component, the duration of the acquaintances was approximated from the exponent of the exponential function (in days). We tested eight social structure models ranging from societies composed only of constant companionships (in which the association rate in days remains constant through time) to models considering two levels of casual acquaintances and some rapid disassociation, where the constants express the proportion of animals with which an individual associates at rates given by the exponential functions. The model that best described the temporal dynamics of the association patterns was indicated by the smallest quasi-Akaike information criterion (QAIC; [79]). Standard errors for the LAR and parameter estimates were obtained by jackknifing (displayed as 1 standard error interval around the mean).

Annual residence

We applied a PCA to the annual residence (variable) of each dolphin (statistical unit) to investigate whether association patterns differed significantly among years. Independent principal components (PC_y) were extracted from the variables and the leading of them, i.e. those which explained more than 80% of variance, loaded by the residence pattern [47], [76]. We used MANOVA to test whether association patterns differed significantly among years; the scores on PC_{1y} and PC_{2y} were applied as independent variables and those on PC_{1HWI} and PC_{2HWI} as dependent variables in the analysis. We used the SAS 8.1 software to examine these relationships [77], [78].

Results

Marking, recapturing and residence pattern

A total of 146 sightings were obtained from 2005 to 2012 corresponding to 98.75 hours spent with the dolphins (for sighting: mean = 36.9 minutes, SD = 35.2 minutes, range 12–190 minutes). The data used in this paper are based on 100 dolphin sightings that were examined and confirmed by photo-identification. The photographic capture rate was not correlated to the number of newly-sighted dolphins each year ($R^2=0.33$, $P=.13$). Thirty-four individuals, excluding calves, were well marked and recaptured at least once from 2005 to 2012 (Table 1). The total number of sighted (mean = 14.25, SD = ± 5.09), newly-sighted (mean = 4.25, SD = ± 4.37) and re-sighted (mean = 10.0, SD

Table 1. Encounter rate (N/km²) (± SD), mean group size (± SD), number of sighted, newly-sighted and re-sighted dolphins and mean not-identified dolphins (± SD) each year.

	2005	2006	2007	2008	2009	2010	2011	2012	Kruskal Wallis test
Mean encounter rate (SD)	0.0256 (0.0052)	0.0256 (0.0061)	0.0265 (0.0053)	0.0052 (0.0042)	0.0065 (0.0033)	0.0045 (0.0043)	0.0036 (0.0018)	0.0006 (0.0013)	$P < 0.0001$
Mean group size (SD)	6.20 (2.19)	4.85 (1.37)	5.44 (2.21)	4.58 (3.06)	6.50 (3.72)	6.27 (3.46)	3.93 (1.65)	4.00 (0.81)	$P = 0.004$
Sighted dolphins	10	12	24	14	16	17	14	7	-
Newly-sighted dolphins	10	7	11	2	1	1	1	1	-
Re-sighted dolphins	0	5	13	12	15	16	13	6	-
Mean not-identified (SD)	1.0 (1.7)	2.3 (2.1)	0.5 (0.8)	0.8 (0.7)	0.4 (0.8)	0.2 (1.4)	0	0	$P = 0.02$
Adults (%) (n=20)	70	100	75	79	75	76	71	43	-
Juveniles (%) (n=11)	20	0	21	14	19	24	14	57	-
Calves (%) (n=3)	10	0	4	7	6	0	14	0	-
Females (%) (n=9)	50	42	33	50	33	45	37	17	-
Males (%) (n=12)	0	42	38	29	50	35	42	67	-
Unknown sex (%) (n=13)	50	16	29	21	17	20	21	16	-

In the first column, the percentage of adults, juveniles and calves and the percentage of females, males and dolphins with unknown sex sighted each year. In the last column the results of the test of significance among years for the mean encounter rate, group size and number of not-identified dolphins.

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= ± 5.6) dolphins each year are given in [Table 1](#). We calculated the mean group size computed on pooled sightings (mean = 5.22, SD = ± 2.21).

Both the encounter rate and group size decreased from 2005 to 2012 ([Table 1](#)). At the end of the study, 59% of dolphins were classified as adults, 32% as juveniles and only 9% as calves ([Table 1](#)). Group size was higher with (mean = 7.91, SD = ± 3.75, range 3–18 individuals) than without (mean = 3.8, SD = ± 3.1, range 1–12) calves (Student t, $P < 0.0001$) in the focal groups. Sex was determined or “estimated” for 61.8% of the photo-identified dolphins: 53% of adult and 9% of juvenile dolphins. Of these, 43% were female and 57% male. Seven females were strongly associated to calves during 25 sightings and the number of calves per group ranged from 1 to 3 with a mean number of calves of 1.2 ± 0.8 when calves were present. The mean number of sightings for individual was 12.2 (SD = ± 9.2, range 1–37). Four residence classes were established according to the number of sightings for each individual: very frequent (>21 times; n=7), frequent (14–20 times; n=7), low frequent (10–13 times; n=5), rare (4–9 times; n=8) and occasional (1–3 times, n=7) dolphins. Excluding one male (PHD1), sighted 37 times (the highest value), males (mean = 14.1, SD = ± 3.9) were sighted less frequently than females (mean = 21.3, SD = ± 7.9) (Student t, $P < 0.0001$). All dolphins, excluding calves, were sighted more frequently in early than in late summer (Student t, $P < 0.0001$) with no differences between sexes (Chi-square,

$P=0.2$). Finally, males were sighted more frequently with trammel nets (mean = 45.4, SD = ± 11.3) than females (mean = 28.8, SD = ± 8.0) (Student *t*, $P < 0.0001$).

Social associations

Twenty-three dolphins, 8 females, 11 males and 4 of unknown sex, were used to analyse the association patterns. Two “estimated” males (PHD2 and PHD8) were classified as dolphins of unknown sex in the association analyses, since their high preference for female and calf groups. Pooled HWIs (all years 2005–2012) were calculated for pairs ($n=529$, mean = 0.28, SD = ± 0.16) and one for each combination of sex: male-male ($n=122$, mean = 0.29, SD = ± 0.13 , range 0–0.51), female-female ($n=64$, mean = 0.44, SD = ± 0.18 , range 0–0.71) and female-male ($n=88$, mean = 0.21, SD = ± 0.12 , range 0–0.63).

The observed association matrix of pooled HWIs was randomized 10,000 times with 1,000 flips per permutation with a two-sided significant level of 0.03. Significantly higher SD levels of association (SD = 0.16268, random SD = 0.11041, $p > 0.9999$) and CV of association indices (CV = 0.70667, random CV = 0.47131, $p > 0.9999$) indicates that long-term preferred and avoided companions are present in the population. Fifty-eight preferred associations (11.5%) were identified, i.e. they had association indices which were twice the mean index calculated including zero values. Out of the possible 22, the average individual was observed associated with 21.26 (SD = ± 1.91) individuals. All 23 individuals formed at least one preferred association (i.e. HWI greater than twice the mean) and for each individual, a mean number of 4.57 (SD = ± 2.84 , range 1–10) associations was preferred. Seven dolphins had $>26\%$ of their associations preferred (6–10 individuals preferred), while only 3 individuals formed one preferred association. The association levels were significantly higher for females than males (Mantel test with 1,000 permutations: $P < 0.001$). The number of dyads on 6 classes (selected according to association coefficients values) were significantly higher for females than males (Chi-square test, $n=6$, $\chi^2=5.14$, $P < 0.0001$). The maximum HWI was significantly different between females (mean = 0.59 ± 0.13) and males (mean = 0.49, SD = ± 0.09) (Student *t*, $P=0.02$). Associations between pairs were categorized as low (<0.3), moderate (0.3–0.5) and high (>0.5) for pooled data and one for each combination of sex. Of all female-female dyads, 25% ($n=12$) had high, 32% ($n=9$) moderate and 25% ($n=7$) low HWIs. On the contrary, 75% ($n=41$) of male-male dyads had low, 22% ($n=12$) moderate and only 2 dyads had high HWIs. Only four female-male dyads (4%) had high HWIs, while 19% ($n=17$) had moderate and 76% ($n=67$) low HWIs. Of all female-UN dyads, 25% ($n=8$) had high, 50% ($n=16$) moderate and 25% ($n=8$) low HWIs. Finally, 7% ($n=3$) of male-UN dyads ($n=44$) had high, 11% ($n=5$) moderate and 81% ($n=36$) low HWIs. Two females (PHD3–PHD5) and 3 males (PHD7, PHD11 and PHD17) were sighted at least once with any of the other dolphins (min. HWI >0). The highest HWIs (0.71) were observed for 2 female-female dyads: PHD3–PHD6 and PHD6–PHD16. Fifty

avoided associations (9.9%) were identified, i.e. they had association indices with zero value. The number of avoided individuals was smaller for females (mean = 1.8 ± 1.4 ; range 1–4) than males (mean = 2.4 ± 2.6 ; range 1–9) (Student *t*, $P=0.0007$) and 1 juvenile male (PHD13) had the highest number of avoided associations (39.1%).

Network analysis

Social differentiation was estimated as 0.814 (SD = ± 0.092), indicating a socially well differentiated population (>0.5) [69]. Significant differences in individuals' clustering coefficient, strength and affinity from a random network were assessed using 1,000 permutations. An individual's direct associates were less likely to be connected than expected in a random network (measured by the clustering coefficient: mean = 0.39, SD = ± 0.05 ; random mean = 0.48, random SD = ± 0.02 ; $P<0.0001$). The individuals had a significantly lower strength (mean = 5.29, SD = ± 1.56 ; random mean = 5.40, random SD = ± 1.25 ; $P<0.0001$) and higher affinity (mean = 5.70, SD = ± 0.40 ; random mean = 5.68, random SD = ± 0.11 ; $P<0.0001$) than expected by chance. We found that the dolphins with high degree of strength also have high affinity ($r=0.63$, $P<0.001$), therefore the individuals preferentially associated with others with similar numbers of associates [69].

Sociogram (Fig. 2) illustrate the relationships between individuals in all groups (individual dolphins are identified by their ID codes, known sex and age class).

The Clustering eigenvector method applied to the association coefficients divided the population into 2 principal clusters (clustering using average linkage; correlation coefficient = 0.833). Modularity 1 (for gregariousness) was not high enough to represent useful community divisions (modularity = 0.265) (Fig. 3) [75]. A primary division specifically corresponded to a mixed-sex cluster of 11 animals (social unit-1): 6 females, 2 males and 3 dolphins of unknown sex. Two secondary sub-divisions of this cluster better separated one female (PHD10) and two juveniles from other adult individuals ($n=8$). The second cluster corresponded to 12 dolphins (social unit-2) and it was composed of 8 adult males, 2 adult females and 2 juveniles of unknown sex. Four secondary sub-divisions of this cluster better separated 5 males (1 juvenile and 4 adults) from 3 adult males and transitory pairs of male-female dolphins (Fig. 3). Social unit-1 individuals showed higher HWIs (mean = 0.50, SD = ± 0.12) than those in social unit-2 (mean = 0.26, SD = ± 0.10) (Student *t*, $P<0.0001$). In addition, social unit-1 individuals had higher maximum HWIs (mean = 0.65, SD = ± 0.06) compared to those within social unit-2 (mean = 0.45, SD = ± 0.06) (Student *t*, $P<0.0001$). Social unit-2 individuals had a higher number of avoided dolphins (mean = 3.1, SD = ± 2.2) compared to those in social unit-1 (mean = 1.8, SD = ± 1.1) (Student *t*, $P<0.0001$). In general, dolphins in social unit-1 showed higher number of sightings (mean = 21.4, SD = ± 8.3) than those in social unit-2 (mean = 13.6, SD = ± 4.7) (Student *t*, $P<0.0001$). Dolphins in social unit-1 had higher mean number of sightings within groups with size >5.22 (mean = 74.1, SD = ± 8.7 ,

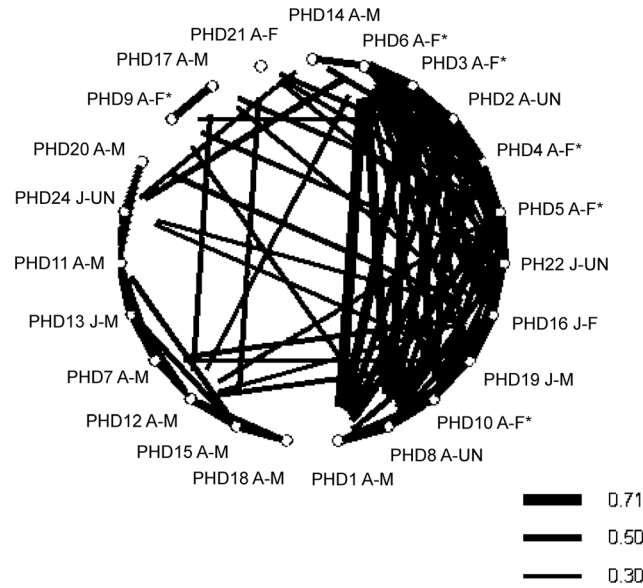


Fig. 2. Sociogram showing the associations with HWIs ≥ 0.30 . Lines of increasing thickness correspond to increasing pairwise associations. Study animals are identified by their ID codes (PHDn, n=1–23), age class (A= adult, J= juvenile and C= calf) and sex (F= female, M= male and UN= unknown sex). Females with calves are marked (F*).

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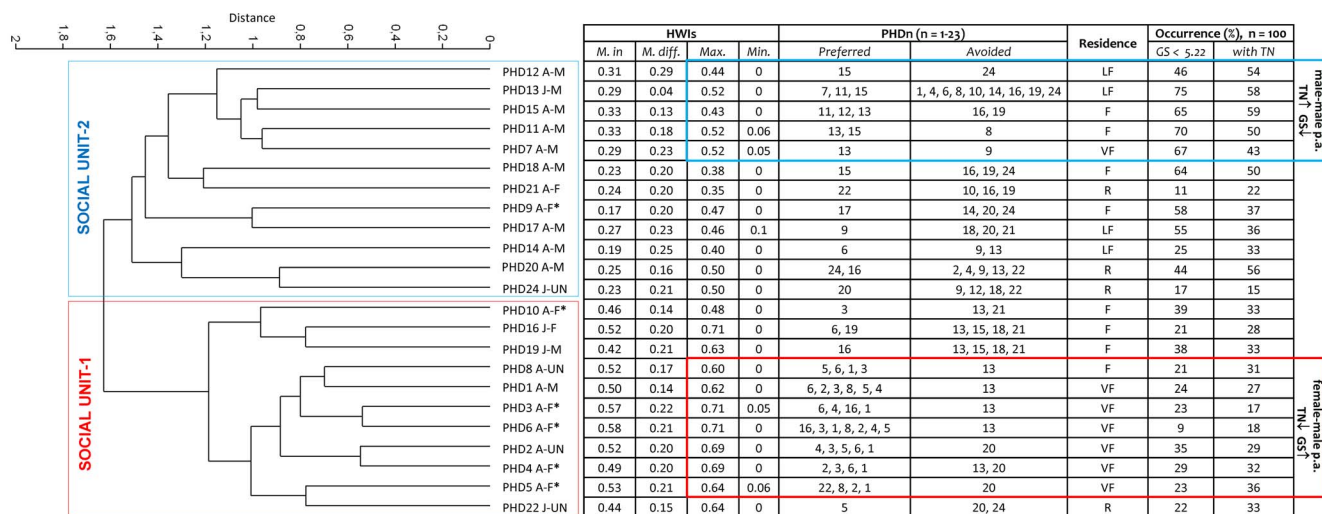


Fig. 3. Grouping patterns of 23 individuals. The Clustering eigenvector method identified 2 principal clusters: social units-1 and -2. Dolphin are identified by their ID code (PHDn, n=1–23), age class (A= adult, J= juvenile and C= calf), and sex (F= female, F*= females with calves, M= male, UN= unknown sex). Each dolphin is shown with (1) mean HWIs calculated within (M.in) and (2) between (M.diff.) social units, (3) maximum HWI and (4) minimum HWI, (5) preferred and (6) avoided dolphins (min. HWIs), (7) residence pattern (VF: Very frequent, F: Frequent and R: Rare), (8) occurrence (%) in groups with size lower than the mean group size (GS < 5.22), (9) occurrence (%) with trammel nets (TN). Male-male and female-male preferred associations (p. a.) are also shown.

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$P < 0.0001$) than those in social unit-2 (mean = 50.3, SD = ± 21.5 ; $P = 0.4$). Finally, dolphins in social unit-2 had higher mean number of sightings with trammel nets (mean = 42.6, SD = ± 14.1 , $P = 0.01$) than those in social unit-1 (mean = 29.2, SD = ± 6.8 , $P < 0.0001$) (Fig. 3).

Eight principal components described 89% of variance with PC1_{HWI} 39% and PC2_{HWI} 17% (Fig. 4). The scores on PC1_{HWI} (Student *t*, $P < 0.0001$) but not on PC2_{HWI} (Student *t*, $P = 0.46$) were significantly different between dolphins with mean maximum HWI higher and lower than the cut off value for preferred associations (Fig. 4). The annual presence of dolphins was significant on PC1_{HWI} in 2008 (Student *t*, $P = 0.007$) and on PC2_{HWI} in 2007 (Student *t*, $P = 0.008$) and 2009 (Student *t*, $P = 0.006$). The scores on PC1_{HWI} were significantly different between females and males (Student *t*, $P < 0.0001$) and between calves/juveniles and adults (Student *t*, $P < 0.0001$). Both the scores on PC1_{HWI} (Student *t*, $P < 0.001$) and PC2_{HWI} (Student *t*, $P = 0.04$) were significant in showing differences between females with calves and males with juveniles. On the PC4_{HWI}, a different pattern of association which was not dependent on any of the treated variables was identified for the individuals PHD9, PHD14, PHD17, PHD20 and PHD24 (data not shown).

MANOVA model

The residence pattern was significantly selected by the model (overall MANOVA) ($F = 2.64$, $P = 0.006$) with the highest values on the PC1_{HWI} ($R^2 = 0.26$, $P = 0.001$). No significant difference was observed between summer periods ($F = 1.3$, $P = 0.31$). A significant difference was observed for group size ($F = 18.1$, $P < 0.0001$) and PC1_{HWI} had the highest values ($R^2 = 0.60$, $P < 0.0001$), but also PC3_{HWI} ($R^2 = 0.2$, $P = 0.04$). The PC2_{HWI} ($R^2 = 0.25$, $P = 0.014$) and PC4_{HWI} ($R^2 = 0.14$, $P = 0.06$) were significant for the weather conditions ($F = 3.4$, $P = 0.03$) while the PC2_{HWI} ($R^2 = 0.29$, $P = 0.006$) and PC3_{HWI} ($R^2 = 0.41$, $P = 0.0009$) for the sighting time ($F = 1.3$, $P < 0.0001$). Finally, the percentage of interaction with trammel nets ($F = 10.9$, $P = 0.0001$) was significantly selected on the PC1_{HWI} ($R^2 = 0.56$, $P < 0.00001$). All these data are graphically represented on Fig. 4.

Temporal pattern of association

LAR analysis indicated that nonrandom associations within individuals persisted over the entire study period (plot not shown). The LAR appeared to stabilize above the null association rate (i.e., the rate if animals were randomly associating) as time increases, indicating that after group formation, the population maintains stable relationships for multiple days. The lagged association rate of individuals in the population was best explained by a model including three levels of associates (lowest QAIC = 4311.6252), represented by the equation $a_2 + a_{3a} \exp^{-(a_1 * td)}$ consisting of CC (long-term, a_2), CA (short-term, a_3 ; individuals associate for a certain length of time and then disassociate) and rapid dissociations (RD; some associates leave very quickly). Associations between dolphins were temporally

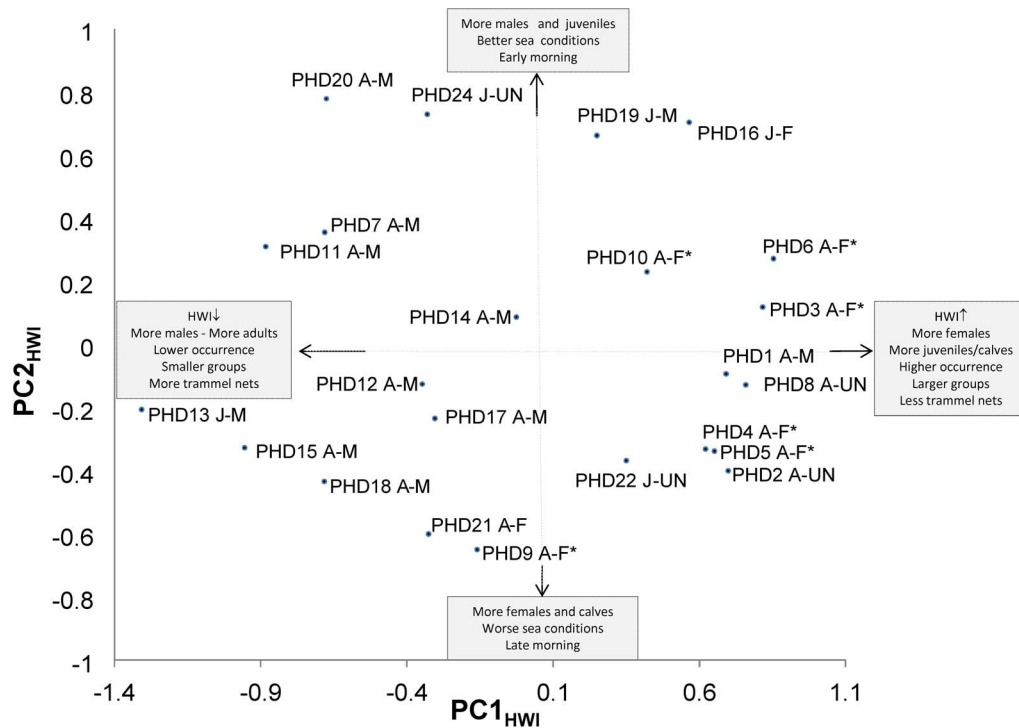


Fig. 4. Plot of scores on the principal components, PC1_{HWI} and PC2_{HWI}. On the plot, different groups of dolphins are separated according to the explaining variables (age, sex, weather conditions, sighting time, group size and trammel nets). Dolphins with higher (HWI ↑) and lower (HWI ↓) HWIs than the cut off value for preferred associations are also indicated. Each dolphin is identified by ID code (PHDn, n=1–23), age class (A= adult, J= juvenile and C= calf) and sex (F= female, M= male and UN= unknown sex). Females with calves are marked (F*).

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stable, where individuals had constant companions ($a_2=0.38$) and casual acquaintances ($a_3=0.30$) that lasted few days (length of casual acquaintances is $a_1=0.33$). This suggests that typically individuals remained with a set of associates over periods of days (a mix of CA and CC) and at the end of these days, they rapidly disassociated from all individuals except a moderate number of CC, which share more stable and stronger associations lasting several years. As the smallest difference in QAIC was $\Delta QAIC = 6.8$, there was no support for any of the other models [79].

Annual degree of residency

Four independent principal components, the PC1y (39.7%), PC2y (21.3%), PC3y (15.2%) and PC4y (9.4%) were calculated, explaining 85.7% of variance. Within a common trend of association pattern, different groups of dolphins were preferentially sighted in particular years (Fig. 5). Using the loading values, we found the annual residence particularly significant in 2005, 2008, 2010 and 2012 on the PC1y while in 2005, 2006, 2009 and 2012 on the PC2y (Fig. 5).

The more frequently sighted dolphins had positive scores on the PC1y and PC2y (Student t, $P<0.0001$). On the contrary, the dolphins with an increasing

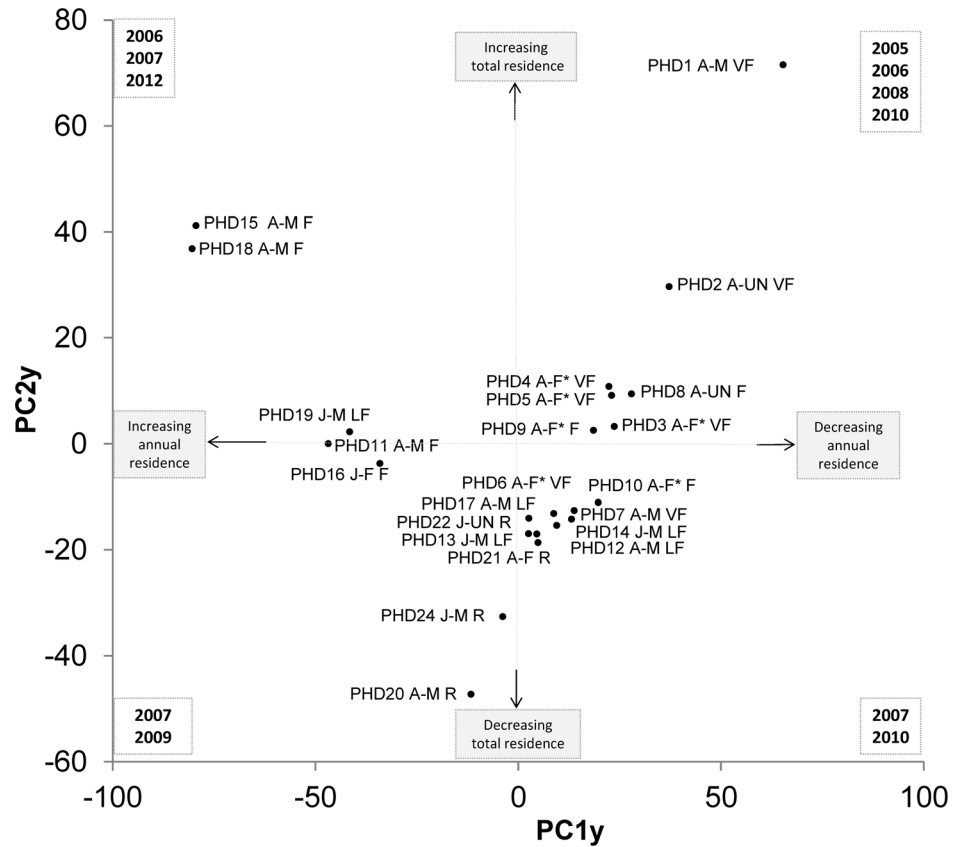


Fig. 5. Plot of the principal component scores on PC1y and PC2y representing the annual residence of each dolphin. The dolphins are shown in the plot according to the significant years, i.e. their highest loading values. The residence and association patterns of dolphins are shown in each quarter of the plot according to the test of significance.

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annual residence pattern had positive scores on the PC1y and negative on the PC2y (Student t, $P < 0.0001$). As according to the MANOVA model ($F = 2.6$, $P = 0.05$), the dolphins with preferred association were represented on the PC1y, with the highest part of information provided by the PC1_{HWI} on the PC1y ($R^2 = 0.25$, $P = 0.01$).

Discussion

Residence pattern and social structure

Many bottlenose dolphin populations show long-term site fidelity and those in the Aeolian Archipelago appear to be no exception, [28], [65], [80], [81]. Of the 34 dolphins identified in our study, only 2 were sighted once and five < 3 times. Seven dolphins were re-sighted repeatedly (21–37 times) in summer months. Three dolphins (PHD1, PHD3, PHD5) were absent for only one year of this study and one (PHD2) for two years. The occurrence of some dolphins (males PHD14

and PHD18, and females PHD10 and PHD21) fluctuated between years and few individuals were not observed for several subsequent years before returning to the study area. At least one dolphin group was sighted each month between 2005 and 2012 suggesting that a core group of animals was permanently resident while several others were passing irregularly to temporarily visit the area from the coastal population. The social organization of the bottlenose dolphin in the Aeolian Archipelago is different to that observed in other populations [4], [5], [24], [26]. We found that the association patterns between dolphins were hierarchically structured, where two mixed-sex social units were subdivided into smaller, temporarily dynamic social groups. The association index, and therefore the partition of clusters, was based on maximum modularity, which was not high enough (modularity = 0.27) to represent useful community divisions [74], [75], [82]. Furthermore, the cophenetic correlation coefficient value of 0.83 ensured that the hierarchical average linkage cluster analysis of the association data reflects the matrix of interaction rates [82]. Both social units were composed of long-term preferred companions, as observed in previously studied bottlenose dolphin populations [4], [5], [18], [83]; however, the degree of social cohesion, residence pattern and interaction with trammel nets differed considerably between the two social units. The population's society proved to be well differentiated (social differentiation = 0.814), therefore presenting weak as well as strong relationships between certain individuals. Additionally, we found that the dolphins with high degree of strength also have high affinity. As a result, the important individuals are preferentially linked with each other [69], therefore suggesting the presence of mixing in the population.

Patterns of association of reproductive females

Females seemed to play an important role in the formation and maintenance of the community social arrangement. In our study, associations between individuals were considerably stronger and temporally more stable in the more resident social unit-1. Six of 8 females (PHD3, PHD4, PHD5, PHD6, PHD10 and PHD16) were clustered within this social unit showing significantly stronger associations (max. HWIs from 0.48–0.71) and high number of preferred companions (from 1–7).

In some bottlenose dolphin populations, females tend to associate more closely with those in a similar reproductive conditions [14], [30], [31]. For example, in Sarasota Bay (Florida) adult females with their calves show stable and high level associations with other females within social clusters named “bands” [4], [65]. Seven females were strongly associated to 8 calves during the study years. Five of these females were clustered in social unit-1 (PHD3, PHD4, PHD5, PHD6 and PHD10), while only one in social unit-2 (PHD9). One calf was strongly associated to a juvenile female (PHD27) sighted only 3 times with social unit-1 individuals, and therefore not used in the analysis. During the study years, 3 calves probably became juveniles (calves of females PHD5, PHD6 and PHD9) while 3 are still calves (calves of females PHD3, PHD4, and PHD27). Two calves probably died (one in 2005 and one in 2009) as they were never re-sighted with their mother

(PHD10) in the months after their first sighting. Females in social unit-1 may constitute a small network of mature females with similar reproductive state (i.e. pregnant females or those with similar-aged calves).

The strength of associations between females may be likely to change over years as a result of variable interbirth intervals [31]. Although the same association pattern between females was observed among years, some females were preferentially sighted in particular years. We cannot completely exclude that reproductive females temporarily left the study area to give birth in safer areas. In Shark Bay (Australia), females bottlenose dolphins remained in their natal area and continued to associate with their mothers after conceiving calves [30]. In Sarasota Bay (Florida), females returned to their natal band when their first calf was born, suggesting that bands may be largely composed of maternal relatives [4]. The fluctuations in the annual residence of females with calves, suggest that females may temporarily separate from the other females, returning to the study area after a segregation period.

Potential advantages of group living for female bottlenose dolphins in a similar reproductive status include protection from predators [84], [85] and defense against sexual coercion and infanticide by males [19], [20], [86], [87]. In our study, female bottlenose dolphins had significantly higher preferred associates and lived in larger groups compared to males. As already observed in other bottlenose dolphin populations [4], [30], [81], the group size increased when calves were present and females with calves preferred larger groups than adults only [48]. An interesting result of both the Shark Bay and Sarasota studies is the variation among females' 'sociability' with more solitary individuals while others are found in groups [4], [30], [88]. In this study only 2 females (PHD9 and PHD21) showed a more "solitary" behaviour: one female (PHD21) preferred being associated to a mother-juvenile couple (PHD5-PHD22), while the other (PHD9) was strongly associated with 1 adult male (PHD17) but moderately with the other females (mean HWI =0.3) and weakly with the other males (mean HWI =0.068). The mother-calf bond is the strongest association found in most dolphin communities [4], [30] and kinship may play an important role in determining associations within female bands and band membership [89]. Of 5 juveniles, 3 were clustered within social unit-1 showing higher associations to females (maximum HWI =0.71) than males (maximum HWI =0.52), while only 2 formed preferred associations with adult males. Preferred associations between female-juvenile pairs were observed in 2 cases (PHD5-PHD22 and PHD6-PHD16) with these juveniles (PHD16 was a female and PHD19 a male) that also showed preferred associations between them (maximum HWI =0.63) within social unit-1. Although genetic data are not available to reveal kinship relations, we cannot exclude that some dolphins may arrange associations in relation to kinship and relatives [89], [90].

Patterns of association of males

The 11 males recorded in this study exhibited striking differences in association pattern and companion preferences suggesting a complex internal structure [4],

[15], [18], [91], [92], [93]. We found adult males occurring into 4 general classes: males (PHD1) that formed preferred associations with both males and females; males (PHD7, PHD11, PHD12 and PHD15) that formed preferred associations with 1–3 males but weaker associations with other males and females; males (PHD18) that were solitary or associated for only a short period of time with other males; males (PHD14 and PHD17) that formed preferred male–female pairs only. Our findings differ from those of Shark Bay bottlenose dolphins in which association coefficients of male–male dyads (maximum HWI = 0.58) match those seen for mother and calf pairs (maximum HWIs = 0.71) [15], [18]. In general we found male–male associations weaker than most female–female associations (maximum HWIs = 0.71) but also preferred male–female associations (maximum HWIs = 0.69). Clustering analysis revealed that males that formed preferred associations with males (from 1–3), generally do not associate or associate weakly with the others. In contrast, “solitary” males were connected for only a short period of time to other males or females. Males that formed preferred associations were consistently observed in the largest groups within social unit-1 and in small groups within social unit-2. On the contrary, males with weaker associations were sighted more frequently in larger groups within social unit-2.

Strong associations may be forced by socio-ecological and demographic factors such as age and sex composition [23], [30], female reproductive status [14] and male–male competition for females [18]. It could be costly for females to frequent mixed-sex groups, except throughout the breeding season [31]. We can suppose that female and male groups associate in the study area during the breeding season and that some male choose to interact with reproductive females forming a distinct but interrelated community. Bottlenose dolphins have a 12-month gestation [88], [94] and, in the Aeolian Archipelago, newborn calves and pregnant females have been observed mainly in spring and early summer, a time that partially coincides with the sightings of the largest mixed-sex groups. As already observed for other bottlenose dolphin populations, we found association of one or more female (single or mother/calf pairs) with one or more males lasting for several days [18], [83], [90], [92]. Most likely, not all the males have the same access to reproductive females. One male (PHD1) clustered in the more resident social unit-1, showed higher access to reproductive females compared to the other males (maximum HWI = 0.62). Presumably the adult dolphins, PHD2 and PHD8, were males as well; in addition, these dolphins formed preferred associations with at least 1 female (maximum HWIs = 0.69) but weaker associations with other males, with the exception of PHD1 (maximum HWI = 0.58).

Some males showed markedly lower residence pattern compared to the other males. This result suggest that these dolphins may be associating in a larger fission–fusion network, which consists of dolphins that appear to temporarily join the network from the coastal population, during the breeding season, and then disappear from the study area [95], [96]. For example, some males (PHD14, PHD17 and PHD20) with a more “solitary” behaviour, formed preferred associations with at least 1 female. These dolphins may not be residents of the

area, missing in several years, or have larger home ranges, showing a more irregular residence pattern compared to the other males [95], [96].

Trammel nets interactions

As bottlenose dolphins are generally believed to have a varied diet [32], [35], [43] specializations in the diet [33], [34], and the techniques used to capture prey [11], [12], [13], might be related to the observed association patterns.

Our results showed that small groups are formed when dolphins forage and feed in the proximity of trammel nets [48]. In addition, the significantly high density of dolphins in the proximity of trammel nets [48] may indicate an adaptation to exploit spatially and temporally variable anthropogenic food resources. We cannot exclude that these dolphins specialized in trammel net foraging, suggesting that this foraging technique may favor a solitary lifestyle, probably because it is easier for dolphins to forage alone and consume small fish while avoiding intraspecific competition [37], [38].

In Sardinia (Italy) the strength of association among preferred associate dolphins was considerably lower when individuals were opportunistically feeding near fish farms [37]. Apparently, the Aeolian population showed a different pattern, where some males (PHD7, PHD11, PHD12, PHD13 and PHD15) interacting with trammel nets formed preferred associations. This structure seems to be similar to that observed in other bottlenose dolphin populations, where individuals showed a more complex social structure composed of distinct communities differently influenced by fishing activities [38], [39], [97], [98]. Intensive trawlers operations and lack of protection of dolphins' habitats in the study area [48] may have changed the distribution of resources required by the dolphins (for food and defense) which may affect the costs of feeding competition and the social organizations of dolphin groups [36], [44], [46]. The *Tursiops truncatus* population in Aeolian Archipelago may be relatively small (only 34 individuals classified based on photoidentification between 2005 and 2012). In addition, the encounter rate and group size are decreasing in the last years and only a core group of animals is resident in the study area; as a result, preferred associations among males may occur as an adaptive response to survive with relatively few associates [7].

We found that 1 juvenile male (PHD13) formed more regularly preferred associations with some males (PHD7, PHD11, PHD15), but avoided many other dolphins. In addition, this male was more frequently sighted with trammel nets and in small groups than the other dolphins. Bottlenose dolphin populations have already been shown to evolve and transmit foraging methods via social learning and local tradition or culture [11], [12], [13]. However, the high bottlenose dolphin feeding requirements [34], may promote the formation of social associations that increases the feeding efficiency via information exchanges. In complex habitats, like the shallow waters of Filicudi island [47], individuals that follow may also benefit from the experience of those that lead them in searching food resources [99]. We cannot exclude that juveniles may attain substantial

benefits by cooperating with individuals that have similar foraging preferences [37], [39] or lead them during the foraging activities [99], [100].

The hypotheses that all individuals are gradually shifting to a foraging behaviour associated to trammel nets or that some of them choose not to interact with trammel nets forming a distinct but interrelated social unit cannot be excluded. Behavioural constraints may be essential in driving the development and maintenance of cooperation in this dolphin community [23], [30], [32]. We previously demonstrated a certain degree of spatial segregation between groups of dolphins with different sizes and involved in different activities [48]. We found that female bottlenose dolphins decreased their use of trammel nets habitats and preferred larger groups as they provided more opportunities for resting (defense from predators/disturbance), socializing, and calf care/learning [48]. Large group sizes and high degree of social cohesion for females clustered in social unit-1 could be an indication of greater protection and more efficiency in detecting, deterring or repelling anthropogenic pressures. Given that the local fishermen are known to frighten the dolphins using harpoons or guns in this as in other Mediterranean areas [45], [46], variations in the behavioural patterns between females and males may also create differences in group dynamics between the two social units. Risk of predation has been found to change according to habitat type in other bottlenose dolphin populations [6], [101]. Increasing levels of anthropogenic activities, such as dolphin-watching may also affect group dynamics to some degree [102]. However, as we have no data on the dolphins' social structure prior to the beginning of this study, we cannot unequivocally demonstrate that trammel nets have been the major cause of the existing social structure in the Aeolian Archipelago.

Conclusions

Our results represent the first documentation on the association patterns and social structure for this endangered bottlenose dolphin population. These findings should be incorporated into population viability analyses in order to contribute to the designing and implementation of appropriate conservation initiatives in the area. Future investigations are required with a larger data set to better understand the primary mechanisms involved during the development and maintenance of these associations. Of particular interest will be to determine the factors, such leadership and dominance, affecting dolphin associations, in addition to the benefits and costs that dolphins incur in cooperating with other dolphins over long periods of time. Our results also improve the current socio-ecological framework around the complex interaction of factors driving *fission–fusion* societies in general.

We confirm that all data underlying the findings in this study are available without restrictions upon request at blasimf@yahoo.com for researchers who meet the criteria for access to confidential data.

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Author Contributions

Conceived and designed the experiments: MFB. Performed the experiments: MFB. Analyzed the data: MFB. Wrote the paper: MFB LB.

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