Anthropogenic food patches and association patterns of Tursiops truncatus at Lampedusa island, Italy

Daniela Silvia Pace,a Marina Pulcini,b and Francesca Triossia
aOceanomare Delphis Onlus, Via Gino Marinuzzi 74, 00124 Rome, Italy and bIstituto Superiore per la Protezione e la Ricerca Ambientale, via di Casalotti 300, 00166 Rome, Italy

Anthropogenic food patches in the marine environment, such as aquaculture farms and active trawlers, may impact on the behavior of marine mammals through modification of habitats, changes in predation pressure, or alterations in food distribution, availability, and predictability, affecting related social interactions and population demographics. This study examined patterns of association of a population of common bottlenose dolphins (Tursiops truncatus) around Lampedusa Island (Italy) during 1996–2006 and tested the hypothesis that the trawl fishery and the presence of an aquaculture farm could affect such patterns. Here, we used measures of association between pairs of individuals to assess this impact on social unit composition/cohesion and some analytical techniques to describe the structure of dolphin social networks and temporal stability of associations. Association information for 71 regularly sighted individuals was obtained from photo-identification surveys within groups observed or not at “feeding stations.” We found association patterns between dolphins were nonrandom. The Lampedusa population seems to be arranged into 6 clusters and organized in communities composed of animals that were either never in association with feeding stations (N individuals) or those that are (Y individuals), although mixed assemblages were also recorded. Both communities showed long-term preferred companions, with different degrees of social cohesion—as resulted by network measures and temporal analysis. Delineating community structure at Lampedusa Island has offered basic information for further investigations in the area, also providing novel evidences on how disparities in association patterns between bottlenose dolphin individuals may have resulted from a combination of ecological and anthropogenic factors. Key words: aquaculture, bottlenose dolphin, feeding, Mediterranean Sea, social structure, trawling fishery, Tursiops truncatus. [Behav Ecol]

INTRODUCTION

The social structure of many species is plastic; such intraspecific variation is thought to be adaptive (Lott 1991), but it raises the possibility that anthropogenic alteration can modify social structure and behavior, possibly changing the nature of social relationships (Blumstein 2010). Human activities can affect the behavior of mammals through the modification of habitats, changes in predation pressure, or alterations in food distribution, availability (Chilvers and Corkeron 2001), and predictability. This type of changes in food resources via human impact may modify feeding patterns, strategies, and behavior, by influencing also individuals’ use of either personal information on resources derived from their own previous experience or social information obtained vicariously (Danchin et al. 2004; Dall et al. 2005), therefore affecting related social interactions as well as population demographics (see Bronikowski and Altman 1996 for baboons, Papio cynocephalus).

Bottlenose dolphins (Tursiops spp.) are among the best-known cetaceans. Everywhere they have been studied, bottle-nose dolphins live in fission–fusion contexts where animals, as a result of individual movements (van Schaik 1999), frequently join and split from parties (e.g., Smolker et al. 1992; Chapman et al. 1993), therefore forming unstable schools in size and composition, often on a daily or hourly basis (Connor et al. 2000). Yet despite this fluidity, individuals form long-lasting, individually specific association preferences (Möller et al. 2006). Groups with this kind of highly flexible yet complex form of social relationship and degrees of “fission–fusion dynamics” (Aureli et al. 2008) possibly evolved in response to patchy and ephemeral food sources and perhaps to social and predator pressures too (e.g., van Schaik and van Hooff 1983). The association patterns of individuals can vary dramatically both among populations and within the same population over time (Aureli et al. 2008), being affected by a number of ecological factors and environmental variables that may have a role in shaping social structure, that is, resource acquisition, care of calves, etc (Wrangham and Rubenstein 1986) as well as population density (Connor et al. 2000; Wiszniewski et al. 2009). For example, anthropogenic food patches in the marine environment, such as aquaculture farms and trawlers, concentrate prey items and can be exploited by bottlenose dolphins presumably because it is energetically favorable to do so (Fertl and Leatherwood 1997; Karpouzli and Leaper 2004); thus, they can impact on their populations by causing changes in the spatial use of an area and by altering behavior or social structure and organization (Fertl and Leatherwood 1997; Chilvers and Corkeron 2001, 2003; Díaz López and Shirai 2008). Under this framework, the opportunity to look at patterns of association in nearshore bottlenose dolphin populations affected by human use of coastal waters, especially by fisheries activities and habitat modification (Fertl and Leatherwood 1997; Díaz López 2006a, 2006b), can...
provide insight into the impact of such activities on fission–fusion dynamics.

The purpose of this study is to examine patterns of association for common bottlenose dolphins (Tursiops truncatus) around the island of Lampedusa (Italy) during the period 1996–2006 and test the hypothesis that the trawl fishery and the presence of a fish farm could affect such patterns, considering that some individuals are already known to interact with these human “feeding stations” in order to exploit them as opportunistic food sources (Pace et al. 1999, 2003). We expected that the social structure of groups seen with or without trawls/fish farm would reflect nonrandom associations occurring within them. Here, we used measures of association between pairs of individuals (i.e., half-weight association index; Cairns and Schwager 1987) to assess this impact on social unit composition and cohesion and analytical techniques to describe the structure of dolphin social networks (Lusseau et al. 2006) as well as temporal and spatial stability of associations (e.g., lagged association rates [LARs]; Whitehead 1995; Owen et al. 2002; Karczmarski et al. 2005). As many species with complex social lives are threatened by human influence, understanding the social behavior of these species, and how anthropogenic modifications of the environment impact social organizations, may prove critical for future conservation efforts (Couzin 2006).

MATERIALS AND METHODS

Study site

Bottlenose dolphins were observed around Lampedusa, a small Italian island included in the Pelagian Archipelago (lat 35°20′–35°52′N, long 012°20′–012°53′E) and located on the African continental shelf, at about 150 km from the Tunisian coast, in the Sicily Channel (Western Mediterranean basin) (Figure 1). Lampedusa is a geographically isolated low populated island, without great coastal impacts and human pressure. However, its waters are exploited by different kind of fisheries, with a significant impact of trawlers (n = 27 during the study period, with an additional undefined number of other trawling boats coming from the Sicilian coasts) operating principally in the South-Eastern and Western part of the Island (Pace et al. 1999, 2003). Moreover, an aquaculture inshore cage (containing greater amberjacks Seriola dumerilii) was placed at about 35 m depth off the eastern part of the island, between 1997 and 1999, causing a local temporary ecological change around the island (these structures are known to produce considerable amounts of nutrient waste in dissolved form—i.e., ammonia and urea—and in particulate form—i.e., uneaten food and feces, therefore triggering trophic enrichment; see Bergheim and Asgård 1996; Karakassis et al. 2000). The fish farm was destroyed by a storm in 1999 and never reestablished.

The coast and sea bottom of Lampedusa vary from south to north. The southern coast consists of a series of canyons forming a succession of high promontories and small sandy beaches in deep inlets. The bottom slopes softly reaching a maximum depth of 120 m down to the western coast of Tunisia and of 300 m on the eastern coast of Lampedusa. The northern coast consists of high steep cliffs; there are no beaches and the bottom drops off, reaching 300 m depth approximately 1 km off the coast.

Field techniques

Dedicated daily photo-identification surveys were conducted between 1996 and 2006 summer seasons (July–September each year) during daylight hours in calm seas (Beaufort sea state ≤ 3). The distribution of effort varied only according to weather conditions, trying to equally cover the study area (about 500 km², within 6 nautical miles from the coast) each year, without specific effort at trawls/fish farm. The research platform changed over time: in 1996–1997, it was carried out with a 4 m inflatable boat; in 1998–2001, with two 4.5 and 5.2 m rigid hull inflatable boats and a 12 m sailing vessel (2001 only); and in 2002–2006 with a 4.7 m rigid hull inflatable boat and a 12 m sailing vessel. A code of conduct was established for the observing vessels to minimize their effects on the focal schools (Lusseau 2003a). Observations ended when the weather deteriorated, the focal school was lost or the day ended. During each encounter with dolphins, Beaufort sea state, location (by estimating initial position obtained through triangulation with landmarks in the earlier years and by GPS in later years), behavior, and the total number as well as age class of dolphins in the group were estimated. Information on gender was collected whenever possible.

Once a school was detected, weather or not associated with trawls/fish farm, the identity of individuals in the group was determined using standard photo-identification techniques on the distinctive characteristics (e.g., size, shape, and markings) of their dorsal fins and body markings (Würsig and Jefferson 1990). Photographs were taken throughout the duration of each encounter in an attempt to photograph each individual in the group. During 1996–2001, slide film was used to obtain photographs of dolphin dorsal fins with a Nikon D50 and Canon EOS cameras equipped with 70–210 and 100–300 mm lenses. The slides were later digitized for analysis. During 2002–2006, digital images were obtained using a D70 Nikon camera with 80–300 mm lenses.

Association analysis

Photographs of dorsal fins were sorted according to standard protocols, using nicks, notches, or scars (Würsig and Jefferson 1990). Good quality images of distinctive fins were compared with a photo-identification catalog of known individuals. Unidentified animals were not used in analyses.

For this study, associations were defined using the “gambit of the group,” which assumes that animals that are clustered are interacting with one another (Whitehead and Dufault 1999). Therefore, association was defined by membership in the same group, that is, animals photographed in the same group and moving in the same general direction, interacting or engaged in similar activities were considered to be associated (Owen et al. 2002; Rogers et al. 2004; Möller et al. 2006). Focal group follows (Whitehead 2004) were used to collect associations and behavioral data.

A common problem in studies of social association is determining the minimum number of sightings required to include an individual in the analysis. There is no consensus in the literature on the appropriate threshold of sightings required, ranging from 2 (Slooten et al. 1993) or 3 (Rogers et al. 2004) sightings per individual to 10 (Quintana-Rizzo and Wells 2001) or 30 (Gero et al. 2005) sightings per individual. Chivers and Corkeron (2002) discussed the trade-off between ensuring that data are representative (by including individual animals with low resighting frequencies) while also making sure that data are reliable (by having fewer individuals that were sighted more frequently). Many (n = 50) of the total identified animals (n = 148) in this study were present in Lampedusa area only during one survey season, compounding the problem of low sighting rates for individuals. Thus, in the absence of a consensus threshold, a commonly employed cutoff of 3 sightings was used. We chose 3 as our limit because it permitted enough individuals to be included in the analysis while allowing the results to be comparable with other studies. To ensure independence of sampling and avoid serial
autocorrelation of sightings, only the first sighting of an individual animal was used if an individual dolphin was sighted more than once in a day (Béjder et al. 1998; Chilvers and Corkeron 2002).

It has become common in animal behavior studies to define an association index as a helpful tool that uses the frequency of specific interactions and behaviors to indicate the strength of a social relationship. An association matrix of all individuals may then be obtained from the group membership samples (Whitehead and Dufault 1999). Coefficients of association are estimates of the proportion of time that particular individuals spend together, and rates may range from 0, for animals that are never seen together, to 1, for animals that are always seen together. The half-weight index (HWI) (Cairns and Schwager 1987; Bräger et al. 1994) was used in this study to compute coefficients of association between the pairs of dolphins. HWI is calculated as: 
\[
HWI = \frac{2N}{n_1 n_2},
\]
where 2N is the total number of joint sightings counted once for every appearance of the 2 individuals together, n1 is the total number of sightings for one individual and n2 is the total for the other individual.

The HWI accounts for bias from pairs being more likely to be scored when separate than when together (Cairns and Schwager 1987). Therefore, the HWI was employed because it can be used in instances where not all individuals in a group are photographed and because it allows for comparison with many other studies on bottlenose dolphins (Wells et al. 1987; Smolker et al. 1992; Bräger et al. 1994; Quintana-Rizzo and Wells 2001; Chilvers and Corkeron 2002; Lusseau 2003b; Möller et al. 2006; Wiszniewski et al. 2009).

HWI was calculated for 71 (of a total of 148) individuals in 1) all encountered groups (ALL; n = 151), 2) only groups encountered at human feeding stations (GFS; n = 56). Individuals were divided into 2 classes: 1) those that were observed following trawls and/or near the fish farm at least once during the study (Y; n = 55) and 2) those that were never sighted following trawls and/or near the fish farm in any time during the study (N; n = 16). Understandably, GHF groups, that is those not encountered at feeding stations, may include Y individuals as these animals were not exclusively observed following trawls and/or near the fish farm. This was true for 54 of the 55 Y individuals.

We ran analyses on 3 levels to examine potential differences in association patterns of bottlenose dolphin at Lampedusa island: 1) association levels, 2) network metrics, and 3) temporal stability of associations. Given that these analysis are influenced by the number of times animals have been observed, the following aspects were evaluated to understand if sighted groups (and their memberships) were influenced by the higher possibility to encounter animals at human feeding stations: 1) relative abundance index (RAI, expressed in individuals per km; Laran and Drouot-Dulau 2007) in GFS calculated as \(\frac{n}{L} \times s\), with n: the number of sighted groups, L: the effort in km (n/L represents the encounter rate), and s: the mean school size; 2) photographic capture rate by Y and N individuals in GHS and GFS groups; and 3) average time (in minutes) spent by Y and N individuals in GHS and GFS groups.

**Association levels**

The possibility that bottlenose dolphins at Lampedusa island could be divided into clusters, such that association indices are generally high among individuals in the same cluster.computational note: the HWI was used to calculate coefficients of association between the pairs of dolphins. HWI is calculated as: HWI = 2N/(n1 + n2), where 2N is the total number of joint sightings counted once for every appearance of the 2 individuals together, n1 is the total number of sightings for one individual and n2 is the total for the other individual.

The HWI accounts for bias from pairs being more likely to be scored when separate than when together (Cairns and Schwager 1987). Therefore, the HWI was employed because it can be used in instances where not all individuals in a group are photographed and because it allows for comparison with many other studies on bottlenose dolphins (Wells et al. 1987; Smolker et al. 1992; Bräger et al. 1994; Quintana-Rizzo and Wells 2001; Chilvers and Corkeron 2002; Lusseau 2003b; Möller et al. 2006; Wiszniewski et al. 2009).

HWI was calculated for 71 (of a total of 148) individuals in 1) all encountered groups (ALL; n = 151), 2) only groups encountered at human feeding stations (GFS; n = 56). Individuals were divided into 2 classes: 1) those that were observed following trawls and/or near the fish farm at least once during the study (Y; n = 55) and 2) those that were never sighted following trawls and/or near the fish farm in any time during the study (N; n = 16). Understandably, GHF groups, that is those not encountered at feeding stations, may include Y individuals as these animals were not exclusively observed following trawls and/or near the fish farm. This was true for 54 of the 55 Y individuals.

We ran analyses on 3 levels to examine potential differences in association patterns of bottlenose dolphin at Lampedusa island: 1) association levels, 2) network metrics, and 3) temporal stability of associations. Given that these analysis are influenced by the number of times animals have been observed, the following aspects were evaluated to understand if sighted groups (and their memberships) were influenced by the higher possibility to encounter animals at human feeding stations: 1) relative abundance index (RAI, expressed in individuals per km; Laran and Drouot-Dulau 2007) in GHS and GFS calculated as \(\frac{n}{L} \times s\), with n: the number of sighted groups, L: the effort in km (n/L represents the encounter rate), and s: the mean school size; 2) photographic capture rate by Y and N individuals in GHS and GFS groups; and 3) average time (in minutes) spent by Y and N individuals in GHS and GFS groups.

**Association levels**

The possibility that bottlenose dolphins at Lampedusa island could be divided into clusters, such that association indices are generally high among individuals in the same cluster.
and low among individuals in different clusters, was assessed by modularity (Newman 2004). The difference between the proportion of the total association within clusters and the expected proportion, if pairwise association coefficients were randomly distributed, given the summed associations of the different individuals (Whitehead 2008b). To find the best delineation, which could be defined as that with the highest modularity, the eigenvector-based method suggested by Newman (2006) was used.

Then, mean (i.e., the mean proportion of time an individual is sighted with each individual in the sampled population) and maximum (i.e., how affiliative an individual is with its closest associate) levels of individual’s associations were calculated. The mean association index, calculated as the mean association of all possible dyads in each group, is an estimate of the probability that a randomly chosen member of one class (Y or N) was associated with another randomly chosen individual of the same class or with a randomly chosen member of the opposite class during any sampling period (Whitehead 1997, 1999), and the estimates are insensitive to different numbers of Y and N. The maximum association index represents the mean of the association indices between maximum associates (individuals that shared the highest association rate) within and between classes.

Dyads occurring more often than expected by chance were defined using the Manly and Bejder permutation technique (Manly 1995; Bejder et al. 1998), with modifications introduced in Whitehead (1999, 2008a) and Whitehead et al. (2005), which sequentially inverts the intersection of 2 rows and 2 columns in a 1:0 data matrix, a “flip.” This technique tests the significance of these associations by randomly permuting groups within sampling, keeping constant the group size and the number of times each individual was seen. We permuted groups within samples to test the null hypothesis that there are no preferred or avoided companions given the summed associations of all possible dyads in each group, is an estimate of the probability that a randomly chosen member of one class (Y or N) was associated with another randomly chosen individual of the same class or with a randomly chosen member of the opposite class during any sampling period (Whitehead 1997, 1999), and the estimates are insensitive to different numbers of Y and N. The maximum association index represents the mean of the association indices between maximum associates (individuals that shared the highest association rate) within and between classes.

Furthermore, because we have entered a class variable (Y and N), a Mantel permutation test (see Schnell et al. 1985) to investigate for correlations between 2 association matrices was carried out on the null hypothesis that “associations/interactions rates between and within classes were similar” (i.e., whether the dyadic values of one association measure are significantly correlated with those on another). Results were expressed as the t value (with infinite degrees of freedom), P value (for one-tailed test) for the analytical approximation, and matrix correlation coefficient. If within class associations/interactions were higher, t is positive, P large (>0.95), and the matrix correlation is positive (Whitehead 2008b).

The calculation of HI, the modularity, the permutation test, and the Mantel test were carried out using SOCPROG 2.3 compiled version (Whitehead 2008b).

Network metrics
Three individual-based network statistics calculated from the weighted (association matrix) network were averaged over and within individuals. These included the strength, which represents a measure of individual’s gregariousness and is the sum of the association indices for each individual (Barthelemy et al. 2005), the clustering coefficient, which represents a measure of individual sociality and is the proportion of an individual’s neighbors who are themselves neighbors (a measure of “cliquishness” as calculated by Holme et al. 2007), and affinity, which represents weighted mean strength of neighbors, that is, determines whether individuals strongly connect to individuals who also have strong connections (Barthelemy et al. 2005). To test whether network structure was influenced by individual association preferences and whether association patterns differ significantly between classes of individuals within sightings, network metrics (Lusseau et al. 2008; Krause et al. 2009) calculated for each class of individual within different groups (ALL, GFH, and GFS) were compared with those of an expected network based on 1000 permutations (until the P value stabilized; see Bejder et al. 1998; Whitehead 2008b). All network analysis was also run in SOCPROG 2.3 (Whitehead 2008b).

Temporal stability of associations
Finally, temporal patterning in social relationships, that is, changes in association rates over time, was calculated for all groups of individuals using the LAR (Whitehead 1995). LAR for any time lag t represents an estimate of the probability that 2 individuals associated at a particular time are still associated t time units later. LAR was initially compared with the null association rate to determine whether nonrandom patterns of associations occurred over the entire study period. The null association rate indicates the expected value of the LAR if there are no preferred associations; in other words, if the associations are random. Mathematical models proposed and used by Whitehead (1995) describing different rates of exponential decay, that is, models of temporal stability, were then fitted to the observed data, to assess the probability of 2 animals remaining associated after various time lags. The components constituting the models tested included (sensu Whitehead 1995): constant companions (CC; stable associations over time, i.e., who stay together permanently), casual acquaintances (CA; nonpermanent relationships, which decay over various time lags but may reassociate at a later time point, i.e., who associate for some time, disassociate, and may reassociate), and rapid disassociations (RD; some associates disassociate very quickly, within one time period). The model best describing the temporal dynamics of association patterns was indicated by the smallest quasi-Akaike information criterion (QAIC; Whitehead 2007). Jackknife standard errors for the LAR were calculated by sequentially omitting data from 30-day periods (Whitehead 1995).
Temporal stability analysis was also run in SOCPROG 2.3 (Whitehead 2008b). All other statistical analysis were performed by SYSTAT 12.

RESULTS

A total of 151 groups was selected for this study of 576 observed between July and September each year (Table 1), with a number of 95 (defined as GHF) not encountered at human feeding stations and a number of 56 (defined as GFS) encountered at human feeding stations. All selected groups met the photo-identification standards (only good quality images of distinctive fins; see MATERIALS AND METHODS).

Seventy-one individuals (of a total of 148) were used in this association study based on the condition that each was seen at least 3 times between 1996 and 2006, with a number of 55 (defined as Y individuals) observed at feeding stations at least once during the study (25 at trawls, 4 at fish farm, and 26 at both) and 16 (defined as N individuals) never seen in association with either anthropogenic activity. GHF groups, that is, those not encountered at feeding stations, may include not only 16 Y individuals but also 54 Y individuals because they were not exclusively observed following trawls and/or near the fish farm.

No detectable differences were found in the average group size between GHF (mean = 5.9 ± 3.3, median = 5, range 1–17) and GFS (mean = 5.39 ± 2.75, median = 5, range 1–20) groups (Mann–Whitney U test: U = 2280, P = 0.134), with an overall value of 5.74 ± 3.21. Observed group size from 1996 to 2006 changed significantly between years (Mann–Whitney U test: U = 1127, P < 0.001), with a lowest yearly mean of 3.5 ± 2.06 in 2000 ranging up to 6.82 ± 3.87 in 2006, though a distribution over the 11 years ranged from pairs of animals to 20 individuals (Table 1).

As for measurements estimated to understand if sighted groups (and their memberships) were influenced by the higher possibility to encounter animals at human feeding stations, no detectable differences between GHF and GFS groups were observed in RAI values (0.22 and 0.20, respectively) and in both capture rate and average time spent in GHF groups for Y and N individuals (capture rate: Y = 3.62, N = 3.57; average time: Y = 332.4 min, N = 328.3 min). However, Y animals were located with higher rate in GHF than in GFS groups (GHF: mean = 3.62 ± 0.19, median = 4, range 0–12; GFS: mean = 2.81 ± 0.24, median = 2, range 0–6; Mann–Whitney U test: U = 876, P < 0.001), with higher amount of time spent in GHF groups (GHF: mean = 332.4 ± 0.37, median = 300; GFS: mean = 279.9 ± 0.18, median = 240; Mann–Whitney U test: U = 986, P < 0.001).

Association levels

The eigenvector method of Newman and Modularity 1 (from gregariousness) divided the Lampedusa population into 6 clusters (clustering using average linkage; cophenetic correlation coefficient = 0.8037), with 3 individuals showing ties near zero. This division specifically corresponds to differences in the interaction with human activities of the individuals, with one group of 4 animals exclusively composed by N dolphins, one group of 8 animals mostly composed by N individuals (n = 6), 3 clusters including a total number of 44 Y individuals only and one mixed group of 15 individuals (10 Y and 5 N). With a value of 0.289, modularity of this arrangement was close to the suggested 0.3 value, which represents a good division (Newman 2006). Sociograms (Figure 2) illustrate relationships between individuals in ALL (a), GHF (b), and GFS (c) groups (study animals are represented by their ID codes; codes without parentheses indicate N individuals).
Within (a), 2 N-N dyads and 4 Y-Y dyads had the highest association, with maximum values of 0.67, while among (b), 2 N-N dyads, 8 Y-Y, and 2 N-Y dyads had stronger HWIs, and 16 Y-Y within (c). No remarkable changes in the interactions between pairs of individuals were observed after the removal of the fish farm, with only one dyad no longer seen associated again.

Overall association indices were quite low, with a mean association rate of 0.06 (SD = 0.3) (Table 2a). However, max levels of individual’s associations, with values of 0.41, 0.44, and 0.55 in ALL, GHF, and GFS groups, respectively (Table 2b), indicate that some individuals formed strong bonds. Significantly, higher mean levels of association (mean = 0.0634, random = 0.060; \( P < 0.001 \)) and CV of association indices (CV = 1.69042; random CV = 1.16075; \( P < 0.001 \)) in ALL groups indicate that long-term preferred companions between periods are present in the population (Whitehead et al. 2005). A total of 628 preferred associations (25.2%) were identified out of a possible 2485 dyads, that is, they had HWIs above twice the mean index including all zero values (see MATERIALS AND METHODS). All 71 individuals formed at least one preferred association.

Mantel tests (Table 3) demonstrated significantly higher association values among and between classes for different class of individuals seen in ALL and GHF groups. As expected, no differences were seen in GFS groups. The null hypothesis is that associations between classes and within classes are similar; the null hypothesis can be rejected if it does not fall between 0.025 and 0.975 (Whitehead 2003). Interclass associations (N-N) were less strong than intraclass association, with a significant tendency for Y-Y associations to be strongest.

The CV of true association indices using maximum likelihood was 0.69 \( (SE = 0.051) \), indicating a well-differentiated population. With a mean of 0.45 associations per dyad, the correlation between true and estimated association indices was moderate at 0.57 \( (SE = 0.039) \), showing that the data set has reasonable power to provide a good representation of social structure (Whitehead 2008b).

Network metrics

The 3 selected network measures showed differences in social behavior between class of individuals and from random expectations. Strength and affinity were always related, meaning that the “important” individuals were preferentially linked with each other, which is known as assortative mixing, a situation that seems generally characterized of social networks (Newman 2002). Y individuals had higher values of strength and affinity in ALL and GHF groups than N, whereas values significantly lower than expected were observed in GFS (Table 4a). The clustering coefficient remains rather constant at low level (individuals only associate with neighbors); however, an individual’s direct associates were less likely to be connected than expected in a random network in ALL and GHF groups for Y animals (Table 4a). Within-classes comparisons showed distinctly different patterns between Y and N individuals, with N individuals having a significantly lower strength and affinity than expected by chance, whereas higher significant departure from random was detected in each measure in Y animals (Table 4b). The clustering coefficient revealed a denser structure in N individuals, although significant lower values than expected in ALL and GHF groups were observed for Y animals.

Temporal stability of associations

LAR analysis first indicated that nonrandom associations persisted over the entire study within individuals (Figure 3). LAR for bottlenose dolphins in Lampedusa island showed a decrease in dyads being sighted together again after more than a few weeks. However, the LAR appeared to stabilize above the null association rate (i.e., the rate if animals were randomly associating) as time increases, indicating that the population contains and maintains stable relationships for multiple years. The best fitting model curve (lowest QAIC; Table 5), represented by the equation \( a_2 + a_3 \exp(-a_1 \times t) \) of SOCPROG, indicates 3 levels of associates found in this population, consisting of CC (long-term), CA (short-term; individuals associate for a certain length of time and then disassociate), and rapid disassociations (RD; some associates leave very quickly)
Table 2
Mean (a) and max (b) level of associations between and within classes of individuals ($Y = $ individuals seen at anthropogenic feeding stations; $N = $ individuals never seen at anthropogenic feeding stations)

<table>
<thead>
<tr>
<th>Class of individuals</th>
<th>Groups</th>
<th>$n$</th>
<th>$i$</th>
<th>$Y$</th>
<th>$N$</th>
<th>$N-N$</th>
<th>$Y-Y$</th>
<th>$F$-within</th>
<th>$F$-between</th>
<th>Overall</th>
</tr>
</thead>
<tbody>
<tr>
<td>(a) Mean</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>ALL</td>
<td>151</td>
<td>71</td>
<td>0.04 (0.02)</td>
<td>0.07 (0.03)</td>
<td>0.05 (0.05)</td>
<td>0.04 (0.02)</td>
<td>0.08 (0.03)</td>
<td>0.07 (0.05)</td>
<td>0.04 (0.02)</td>
<td>0.06 (0.03)</td>
</tr>
<tr>
<td>GHF</td>
<td>95</td>
<td>70</td>
<td>0.04 (0.02)</td>
<td>0.06 (0.03)</td>
<td>0.05 (0.05)</td>
<td>0.04 (0.03)</td>
<td>0.07 (0.04)</td>
<td>0.06 (0.04)</td>
<td>0.04 (0.03)</td>
<td>0.06 (0.03)</td>
</tr>
<tr>
<td>GFS</td>
<td>56</td>
<td>55</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>0.06 (0.03)</td>
</tr>
<tr>
<td>(b) Max</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>ALL</td>
<td>151</td>
<td>71</td>
<td>0.48 (0.16)</td>
<td>0.39 (0.08)</td>
<td>0.47 (0.17)</td>
<td>0.23 (0.11)</td>
<td>0.38 (0.08)</td>
<td>0.40 (0.11)</td>
<td>0.25 (0.11)</td>
<td>0.41 (0.11)</td>
</tr>
<tr>
<td>GHF</td>
<td>95</td>
<td>70</td>
<td>0.45 (0.13)</td>
<td>0.44 (0.16)</td>
<td>0.37 (0.18)</td>
<td>0.28 (0.14)</td>
<td>0.45 (0.16)</td>
<td>0.41 (0.15)</td>
<td>0.30 (0.14)</td>
<td>0.44 (0.15)</td>
</tr>
<tr>
<td>GFS</td>
<td>56</td>
<td>55</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>0.55 (0.16)</td>
</tr>
</tbody>
</table>

The table shows groups (ALL groups, groups not observed at feeding stations [GHF], and groups observed at feeding stations [GFS]), sample size ($n$), and total number of individuals ($i$) seen in groups. SDs are given in parentheses.

Table 3
Differences in HWI association

<table>
<thead>
<tr>
<th>Groups</th>
<th>$n$</th>
<th>$t$</th>
<th>$r$</th>
<th>$P$</th>
</tr>
</thead>
<tbody>
<tr>
<td>ALL</td>
<td>151</td>
<td>5.3981</td>
<td>0.1878</td>
<td>0.999</td>
</tr>
<tr>
<td>GHF</td>
<td>95</td>
<td>2.7932</td>
<td>0.1018</td>
<td>0.989*</td>
</tr>
<tr>
<td>GFS</td>
<td>56</td>
<td>0.9332</td>
<td>0.0410</td>
<td>0.759</td>
</tr>
</tbody>
</table>

The table shows groups (ALL groups, not observed at feeding stations [GHF], and groups observed at feeding stations [GFS]), sample size ($n$), results of Mantel tests ($t$), matrix correlations ($r$), and $P$ values ($P$) ($H_0$: associations between and within classes of individuals are similar).

*Significant differences ($P > 0.95$).
in maximizing overall fitness of the population. However, Mantel tests demonstrated that interclass associations (N-Y) were significantly less strong than intraclass association, with a considerable tendency for Y-Y associations to be strongest. Since individuals were observed without any association with anthropogenic structures in GHF groups and it is possible that the population existed around Lampedusa island prior to the start of the trawl fishery in the 1960s, the opportunistic nature of the interaction and the possible display of cultural differences (Rendell and Whitehead 2001) have to be considered. The hypotheses that all individuals are gradually shifting to a complete “trawler dolphin” population or that some of them choose to not interact with human activities forming a distinct but interrelate community cannot be excluded. As we have no data on the dolphins’ social structure prior to the start of the trawl fishery and prior to the beginning of this study, we cannot unequivocally demonstrate that trawling has caused the existing social structure in Lampedusa Island. However, as social interactions provide the opportunity for cultural transmission and social learning (Rendell and Whitehead 2001), with constantly changing school composition, information could have been shared rapidly throughout the population. Bottlenose dolphin populations have been already shown to evolve and transmit foraging methods via social learning and local tradition or culture (Rigley 1983; Pryor et al. 1990; Whiten and van Schaik 2007). Thus, the feeding opportunities for Y dolphins created by trawls, and aquaculture facilities may have become part of their foraging strategies, although these animals are capable of consuming other food sources as demonstrated by their presence in feeding GHF groups. Both human activities concentrate prey items; as a result, bottlenose dolphins have been observed to 1) forage in association with trawls, during which dolphins either feed on the target species or on species that are ancillary to the catch (Fertl and Leatherwood 1997; Chilvers and Corkeron 2001; Pace et al. 2003) and 2) visit fish farm, occasionally or regularly, in search of prey potentially attracted by the cages trigger trophic enrichment (Karakassis et al. 2000; Würsig and Gailey 2002; Dempster et al. 2004; Díaz Lópe and Shirai 2008). At Lampedusa Island, where the feeding preferences of bottlenose dolphins are not known, the catch of the trawl fishery during summer consists of numerous demersal species, including some primarily targeted by bottlenose dolphin in other Mediterranean coastal waters (Bearzi et al.

Table 4

<table>
<thead>
<tr>
<th>Strength</th>
<th>N</th>
<th>GHF</th>
<th>GFS</th>
<th>Clustering coefficient</th>
<th>ALL</th>
<th>GHF</th>
<th>GFS</th>
<th>P</th>
<th>P</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>(a) Class of individuals</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Random</td>
<td>2.98 (1.47)</td>
<td>3.32 (1.55)</td>
<td>3.51 (1.58)</td>
<td>0.001</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Y</td>
<td>3.94 (1.12)</td>
<td>3.31 (1.58)</td>
<td>3.51 (1.58)</td>
<td>&lt;0.001</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Random</td>
<td>4.12 (1.81)</td>
<td>3.45 (2.11)</td>
<td>3.18 (1.74)</td>
<td>&lt;0.001</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Y</td>
<td>4.69 (0.89)</td>
<td>5.05 (0.90)</td>
<td>4.03 (0.82)</td>
<td>0.001</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(b) Within classes</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Random</td>
<td>1.03 (0.43)</td>
<td>1.38 (0.61)</td>
<td>3.51 (1.58)</td>
<td>&lt;0.001</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Y</td>
<td>1.30 (0.58)</td>
<td>1.86 (0.81)</td>
<td>3.51 (1.58)</td>
<td>&lt;0.001</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Random</td>
<td>3.45 (1.97)</td>
<td>3.21 (2.06)</td>
<td>3.51 (1.58)</td>
<td>&lt;0.001</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Y</td>
<td>3.45 (1.97)</td>
<td>3.21 (2.06)</td>
<td>3.51 (1.58)</td>
<td>&lt;0.001</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Significant differences from a random network were assessed using 1000 permutations. SDs are given in parentheses. ns, not significant.

Figure 3

LAR (solid line) compared with the best fitting model (broken line) and null association rate (dotted line) in pooled sightings for all individuals. The plot shows the probability of associations persisting after increasing time lags.
and ghf sightings were observed for $Y$ animals, whereas a denser structure emerged in $N$ individuals (each dolphin had fewer associates). Combining the fact that each $Y$ dolphin had more preferred associates than $N$ with significantly lower levels of clustering and higher levels of gregariousness, it is likely that $Y$ individuals change partners more regularly. These dolphins may preferentially associate with different individuals during different sightings, whereas the choice of associates for $N$ individuals may be more constrained as a result of socioecological and demographic factors. These differences within network measures could be related to the subtle social strategies that individuals employ in maintaining the cohesion of the group, with social costs and benefits probably playing an influential role in determining social unit composition in such a society (i.e., splitting and then resume the cohesion when the costs of aggregating are low or benefits of sociability are high).

The pattern of temporal association between individuals in Lampedusa Island indicated that some associations persisted over the entire study. The best-fit model predicted a general decline in the number of dyads remaining associated over time, with some dyads disassociating quickly (RD) and other individuals that associate for a certain length of time and then disassociate (CA). Nonetheless, some associations persisted throughout time, therefore maintaining stable relationships for multiple years (CC). These results are consistent with the previous findings of this study and sound with the assumption that individuals increase their fitness by choosing behavioral strategies that reduce social conflict with other members of the same population (Bergermüller and Taborsky 2010).

Delineating community structure at Lampedusa Island has offered basic information for further investigations in the area, also providing novel evidences on how disparities in association patterns between bottlenose dolphin individuals may have resulted from a combination of ecological and anthropogenic factors. The feeding opportunities for dolphins created by the constant operation of trawling fishery and by the presence of the aquaculture cage (even if limited in time and space) have become part of their “way of life,” therefore directly affecting such top predators population as well as indirectly producing complex social responses.

**FUNDING**

The study was funded by Oceanomare Delphis Onlus and CTS Environmental Department.

The authors would like to thank all institutions and colleagues who essentially sustained and contributed to this study. We are grateful to CTS Environmental Department (Gabriella La Manna and Simona Clò) for providing us with some photographic materials; to David Lusseau for his suggestions on the use of SOCPROG; to Stefano Duga, Giancarlo Giacomini, Giandomenico Ardizzone, and 2 anonymous referees for their constructive criticisms of earlier versions of the
manuscript; to Trevor Willis for his kind linguistic assistance and precious scientific support; and to María Berica Rasoto for her valuable inputs and constant encouragements over years.

REFERENCES


