Social communities and spatiotemporal dynamics of association patterns in estuarine bottlenose dolphins

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Abstract

Network analysis has recently been used to delve into the dynamics of cetacean sociality. Few studies, however, have addressed how habitat shape influences sociality, specifically how linear water bodies constrain the space where individuals might interact. We utilized network and spatiotemporal analyses to investigate association patterns and community structure in a bottlenose dolphin population in a linear estuarine system, the Indian River Lagoon (IRL), Florida. Using sighting histories from a multiyear photo-identification study we examined association patterns for 185 individuals collected over a 6.5 yr period (2002–2008). The population was highly differentiated ($S = 0.723$) and organized into six distinct social communities ($Q = 0.544$), spread in an overlapping pattern along the linear system. Social organization differed between communities, with some displaying highly interconnected networks and others comprising loosely affiliated individuals with more ephemeral associations. Temporal patterns indicated short-term associations were a significant feature of the fission-fusion dynamics of this population. Spatial analyses revealed that social structure was shaped by an individual’s ranging patterns and by social processes including preference and avoidance behavior. Finally, we found that habitat “narrowness” may be a major driving force behind the sociality observed.

Key words: social network, social structure, community structure, association patterns, bottlenose dolphin, *Tursiops truncatus*.

The foundation of many studies of social structure involve assessments of the stability and form of individual association patterns as they can be informative measures of dyadic interactions and patterns of social preference and avoidance over time (Whitehead 1997, Mann 2000). Grouping behavior, however, is ultimately driven by ecological factors such as food dispersion and vegetation type, and by adaptive behavioral traits including feeding, predator avoidance, reproductive strategies and inclusive fitness (Hamilton 1964, Jarman 1974, Trivers 1985). Thus, ranging patterns and space preference as well as social preference are behaviors that must also be taken into consideration when investigating the dynamics of group membership over space and time (Best et al. 2014, Shizuka et al. 2014). A challenge therefore is how to disentangle space use from social preference when assessing social structure (Shizuka et al. 2014). A third element that can potentially influence grouping patterns is the configuration of the physical environment itself where, for example, the shape

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and dispersion of optimal habitat may affect association patterns by simply influencing encounter rates among conspecifics.

Network analysis has become a powerful tool in the study of sociality of multiple taxa including primates (Henzi et al. 2009, Ramos-Fernandez et al. 2009), fish (Croft et al. 2006, Mourier et al. 2012), birds (Shizuka et al. 2014), carnivores (Wolf et al. 2007) and cetaceans (Lusseau and Newman 2004, Cantor et al. 2012, Mann et al. 2012) and can be particularly useful in determining the spatiotemporal dynamics of fission-fusion populations (James et al. 2009). Network theory can be used to study all hierarchical levels of social organization from the individual to the population and thus provides a better understanding of the structure and function of complex social structures (Pinter-Wollman et al. 2014). Network approaches can provide particularly powerful insight when combined with assessments of ranging behavior and space use and, we argue, with investigations on the influence of habitat configuration on association patterns.

Previous studies of bottlenose dolphins, *Tursiops truncatus*, have found that populations tend to live in fission-fusion societies (e.g., Wells et al. 1987, Connor et al. 2000). A fission-fusion society is defined by casual groups of varying size and composition, which associate, disassociate, and reassociate at frequent intervals (Conradt and Roper 2005). Fission-fusion societies are by definition highly dynamic, and studies of *Tursiops* sociality are increasingly focused on the spatiotemporal dynamics of their social organization (Connor et al. 2000, Lusseau et al. 2006, Mann et al. 2012).

Interactions between individuals establish the social structure of a population, which in turn can affect individual fitness, information flow, the etiology of disease transmission, and the genetic structure and viability of populations (Trivers 1985, Lee 1994, Lusseau et al. 2006). Therefore, determining why and how animals are social can be of great importance to understanding their ecology and fitness (Krebs and Davies 1987, Dunbar 1988). Sociality can be driven by any number of factors including sex (Connor et al. 2000, Wolf et al. 2007), age (Lusseau and Newman 2004, Mourier et al. 2012), kinship (Frère et al. 2010a, Wiszniewski et al. 2010), and behavior (Krutzen et al. 2005), and by foraging type (Daura-Jorge et al. 2012, Mann et al. 2012) and habitat preferences (Lusseau et al. 2006, Wiszniewski et al. 2009). This sociality, defined by the nature of interactions among individuals, is most obviously manifest by the size, composition and temporal dynamics of social units.

Bottlenose dolphins have been known to form communities within populations, and these communities have been defined as “associated individuals with long-term site fidelity to a specific area” (Wells 1986, Urian et al. 2009, Elliser and Herzing 2012). This definition is based on Goodall’s (1986) studies of chimpanzee communities where animals associated in temporary subgroups, varying in size and composition, and shared a geographically defined area. In this study, we use the Croft et al. (2008) definition of a community as a group of individuals that are more associated amongst each other than with the rest of the society. Croft’s use of Newman’s modularity clustering technique to determine community structure provides a quantitative way to determine true community structure within a population.

Changes in an individual’s ranging behavior can affect its association behavior, so it is crucial that spatial dynamics be examined in relation to the social structure of a population (Pinter-Wollman et al. 2014). Few dolphin studies have explored the influence of ranging patterns on social processes (Lusseau et al. 2006, Cantor et al. 2012, Mann et al. 2012). Our study area is a uniquely linear habitat and, to our knowledge, no dolphin studies to date have investigated how habitat shape might influence the social organization, and specifically the community structure, of a
population. Spatial segregation of communities could arise from individual preferences to specific habitats (Wiszniewski et al. 2009) or simply be driven by the social preferences of individuals. The linear shape of our study area likely promotes spatial segregation, which could potentially cause an asocial effect by limiting opportunities for individuals at the extreme ends of the habitat to associate and interact, and needs to be taken into account when examining the social patterns within the population.

We investigated community structure and the spatiotemporal dynamics of association patterns in a population of bottlenose dolphins residing in a shallow and uniquely linear estuarine system: the Indian River Lagoon (IRL) along Florida’s Atlantic coast. Sighting histories and telemetry have revealed that most dolphin movements are confined to a long, narrow band of habitat stretching 250 km from north to south (Durden et al. 2011; Mazzoil et al. 2005, 2008a; Fig. 1), and that social affiliations are not random (Kent et al. 2008). Spatial heterogeneity in habitat along the north-south axis of this system suggests local differences in dolphin ecology may exist, while regional differences observed in dolphin health (Reif et al. 2006, Greig et al. 2007, Murdoch et al. 2008) and in habitat quality (Sime 2005, Landsberg et al. 2006, Provanca and Van den Ende 2006) indicate nonuniform impacts on and/or response across this population. A detailed understanding of how dolphins organize themselves and what factors influence social affiliation patterns within this population has thus both applied and fundamental implications. We used network, spatial and temporal analyses to resolve community structure and determine how ranging patterns, space preference, and the unusual habitat shape may influence association patterns in this population.

**Methods**

*Field Sampling and Data Analysis*

Boat-based photo-identification surveys were conducted in the IRL from July 2002 to December 2008. The intracoastal IRL system runs 250 linear kilometers along the east coast of Florida, covering 876 km². It is comprised of four water bodies: the St. Lucie River, the Indian River, the Banana River, and Mosquito Lagoon (Fig. 1). This study area is unique when compared to other similar cetacean study sites in its linear shape, allowing the animals to move essentially only along a north-south axis. Ingress and egress to the Atlantic Ocean is possible via four inlets and one set of locks (Fig. 1), although a recent study (Mazzoil et al. 2011) found that there was a high level of residency within the IRL dolphin population. Currently the entire IRL dolphin population is designated as one estuarine stock (Waring et al. 2011).

Each dolphin survey of the entire lagoon system was completed within a single month and conducted over consecutive days when possible. From July 2002 through August 2005, monthly surveys were conducted. In 2006, only one survey of the entire study area was completed. During 2007 and 2008, four seasonal (winter, spring, summer, and fall) surveys of the entire system were conducted. A group was defined as an aggregation of dolphins within 100 m of each other that were engaging in similar behavior. Details of survey design, data collection, and analyses of digital images have been described previously (Mazzoil et al. 2004, 2005, 2008b). Individuals were identified by markings on the dorsal fin using standard photo-identification procedures and only animals considered to be distinct were included in the analysis (Hammond et al. 1990). To standardize the data and minimize demographic effects,
Figure 1. Map of the Indian River Lagoon (IRL), Florida showing core areas for each community, calculated using a 50% fixed kernel density home range for each individual.
analyses were limited to animals that were available to be seen during the entire study period (i.e., were seen in the first and last years of the study period, or prior to or after, respectively, using a larger data set available for this population (1999–2009)). The purpose of this was to eliminate bias created by including any animals that may have died, permanently emigrated, or were recruited into the catalogue during the study period.

Over the entire study period, we sighted 2,966 groups over 358 surveys (total days = 319, on some days there were multiple boats surveying different areas of the lagoon) (Table 1). Ninety-nine percent of the sightings had complete photographic coverage of all animals in each group. Of these sightings, 1,086 individuals were identified and 670 of those individuals were considered distinct (nondistinct animals were not included in the analyses.) One hundred and eighty-five distinct animals fit our constraints, i.e., they were sighted five or more times (the mean number of sightings was 14.11 ± 5.66) and were available to be seen for the duration of the study period, and were used in the analyses.

Association Patterns

All of the individuals in the same group were considered to be associated, according to Whitehead’s (2008a) “gambit of the group” hypothesis. The strength of the relationship between dyads was calculated using the half-weight association index

\[ \text{HWI} = X \left[ \frac{X}{X + Y_{ab} + \frac{1}{2}(Y_a + Y_b)} \right] \]

where \( X \) is the number of times dolphins \( a \) and \( b \) were observed together, \( Y_{ab} \) is the total number of times dolphins \( a \) and \( b \) were identified in separate groups, \( Y_a \) is the number of times dolphin \( a \) was identified and \( Y_b \) is the number of times dolphin \( b \) was identified (Cairns and Schwager 1987) in SOCPROG 2.4 (Whitehead 2009). Analyses were restricted to distinct individuals seen at least five times during the study period to eliminate transient individuals and avoid spurious associations. Our sampling interval was defined as one day (Whitehead 2008a) and in rare cases where an animal was sighted multiple times in one day, only the first sighting was used in the analyses (Cantor et al. 2012).

We calculated the coefficient of variation of the HWI (\( S \)) and the correlation coefficient of the true and estimated association matrices (\( r \)) using maximum likelihood procedures (Whitehead 2008b) with SOCPROG 2.4 (Whitehead 2009). \( S \) is a measure of social differentiation in a population, with values <0.3 indicating low social differentiation and values >0.5 indicating a well-differentiated society; \( r \) is a measure of the power of the analysis to detect the true pattern of social structure, with values

### Table 1. Summary of the sampling effort of the long-term photo-identification study of bottlenose dolphins in the Indian River Lagoon, Florida.

<table>
<thead>
<tr>
<th>Year</th>
<th>Sampling effort (h)</th>
<th>Total observation (h)</th>
<th>Sampling periods (d)</th>
<th>Observed groups</th>
<th>Group size (mean ± SD)</th>
</tr>
</thead>
<tbody>
<tr>
<td>2002</td>
<td>215.2</td>
<td>68.7</td>
<td>33</td>
<td>265</td>
<td>4.17 ± 3.4</td>
</tr>
<tr>
<td>2003</td>
<td>534.8</td>
<td>165.9</td>
<td>81</td>
<td>627</td>
<td>4.33 ± 4.03</td>
</tr>
<tr>
<td>2004</td>
<td>574</td>
<td>164</td>
<td>95</td>
<td>688</td>
<td>4.24 ± 4.03</td>
</tr>
<tr>
<td>2005</td>
<td>426.1</td>
<td>141.5</td>
<td>68</td>
<td>479</td>
<td>4.87 ± 4.73</td>
</tr>
<tr>
<td>2006</td>
<td>40.3</td>
<td>9.8</td>
<td>6</td>
<td>68</td>
<td>3.24 ± 2.74</td>
</tr>
<tr>
<td>2007</td>
<td>235</td>
<td>74</td>
<td>34</td>
<td>389</td>
<td>4.25 ± 3.79</td>
</tr>
<tr>
<td>2008</td>
<td>234</td>
<td>71.6</td>
<td>41</td>
<td>450</td>
<td>3.48 ± 3.26</td>
</tr>
</tbody>
</table>
close to 0.4 indicating a moderate representation of a true pattern and values close to 1 indicating an excellent representation (Whitehead 2008b).

A Monte Carlo permutation test was performed using the methods of Bejder et al. (1998) to determine if the observed association indices were higher than expected by chance. The association matrix was randomized 10,000 times with 100 flips per permutation, at which point the P-values stabilized. A significantly higher CV (coefficient of variation) of observed association indices vs. permuted data indicates that preferred companions are present in the population, while a lower proportion of non-zero association indices in the observed versus the expected association indices suggests social avoidance is occurring (Whitehead 2008a). Gregariousness was tested using the same procedure (implemented in SOCPROG) to determine if any individuals were consistently found in large or small groups.

**Spatial Patterns**

We examined the relationship between dyadic association indices and dyadic home range overlap to determine the influence of an individuals’ ranging behavior on social interactions. First, an individual’s fixed kernel density home range (Worton 1989) was estimated (bandwidth = ad hoc method, grid = 500). The entire home range was defined as the 95% contour, and the 50% contour defined the core area. Ideally, for marine organisms, land should be excluded as nonhabitat from any spatial analyses. New methods that account for hard boundaries, including the local convex hull approach (Getz and Wilmers 2004, Getz et al. 2007), have recently emerged, but require large numbers of locations to account for complex coastlines. Furthermore, attempting to account for land manually resulted in an extreme loss of resolution (i.e., individual dots around each sighting as opposed to a more fluid utilization distribution). Considering that the habitat’s linear dimensions dominated its general shape, nonclipped home ranges (i.e., kernel densities which overlapped land as well as water) were used in all overlap analyses.

Ideal sample size for home range estimation has been widely debated, and most suggest anywhere from 30–50 (Seaman et al. 1999) to 100–300 observations per individual (Girard et al. 2002) for highly precise representations of space use. However, in recent social network studies of cetaceans smaller sample sizes (n = 3–5 sightings) were used to estimate individual range and/or spatial overlap (Lusseau et al. 2006, Cantor et al. 2012). Resights of individuals from our study (n = 5–29 sightings) fall within this range.

To estimate spatial overlap, we used both the utilization distribution overlap index (UDOI) and a probabilistic measure of space sharing (PHR) (Fieberg and Kochanny 2005). UDOI is a modification of Hurlbert’s (1978) index of niche overlap and measures the amount of overlap relative to two individuals using the same space uniformly, while PHR is the probability of dolphin b being found in dolphin a’s home range (Fieberg and Kochanny 2005). UDOI and PHR were calculated for both the entire home range and the 50% core area for each dyad.

To test the relationship between association and spatial overlap, we used Mantel tests (Mantel 1967) with 1,000 permutations to examine the correlation between both overlap measures and the HWI association for each dyad. Due to the size and linear nature of our study area, we were concerned that the above correlations might be skewed (i.e., animals in the northern-most part of the lagoon were less likely to travel to the southern-most part and therefore, less likely to overlap and/or associate with animals in the south). Therefore, we ran the above analyses within each
community (identified by the network analysis) in addition to the overall population overlap. Animals were grouped based upon their community. Then correlations between the UDOI/PHR (of both the entire home range and the core area) and the HWI were examined for each community (Mantel tests, 1,000 permutations). All spatial overlap and home range analyses were completed using the adehabitatHR package (Calenge 2006) in R (R Development Core Team). All Mantel tests were performed in R using the ade4 package (Dray and Dufour 2007).

Temporal Patterns of Association

Temporal variability in associations can be measured using lagged association rate (LAR) analysis (Whitehead 1995). The population LAR is an estimate of the probability that previously associated pairs will still be associated after a given time lag. The LAR was compared to the null association rate, which is the expected value of the LAR if the population is associating at random. Standard errors were calculated using a jackknife procedure over 30 d periods (Whitehead 1995). Seven theoretical models were fitted to the temporal pattern to characterize how the relationships changed over time. The models are based on combinations of three components of fission-fusion societies: constant companionships (individuals associating for long periods of time), casual acquaintances (individuals associate for some time and then disassociate, possibly reassociating again), and rapid dissociation (associates disassociate in a short time). The model that minimized the Quasi-Akaike Information Criterion (QAIC) (Whitehead 2007) was selected as the most parsimonious. Models differing by only two units from the model with the lowest QAIC were also considered good representations of the data. All individuals (including those with less than five sightings) were included in these analyses to avoid a positive bias (Whitehead 2008a).

Community Structure

To determine whether the population was divided into clusters of individuals, or communities, based on social affiliation we used Newman’s (2006) modularity clustering technique. The best partitioning of the network is one that maximizes the modularity value; to define this partitioning, the network is iteratively split into clusters until a peak in the modularity is attained (Newman and Girvan 2004, Newman 2006). Modularity coefficient ($Q$) values of 0.3 or higher indicate strong community divisions in the population (Newman 2004). To conduct the modularity analyses we used Newman’s (2006) eigenvector method implemented in SOCPROG 2.4 (Whitehead 2009). We used Gephi 0.8.2 (Gephi Consortium, 13 Rue de l’Université, Paris, France) to illustrate the community structure within the network. To best visualize the network structure, node positions were arranged using the Force Atlas algorithm within Gephi which interprets small-world, scale-free networks with the fewest biases possible by attracting and repulsing nodes in proportion to the distance between them (Bastian and Heymann 2010).

Community Dynamics

To explore the variations in social organization within and between the communities, we analyzed association indices, network metrics, and temporal patterns (e.g., Wiszniewski et al. 2009). Mean and maximum HWI association indices were calculated within and between each community. Network measures of strength,
eigenvector centrality, reach, and clustering coefficient were calculated to examine differences between and within communities. Strength equals the sum of the association indices for each individual; high strength indicates that an individual is strongly associated with others in the population. Eigenvector centrality is the weighted sum of both direct and indirect connections, thereby measuring the influence of an individual in the network. Reach is a measure of indirect connectedness, or how far an individual’s influence can be transmitted along the network paths, and includes individuals two or fewer steps away. The clustering coefficient, which was calculated for weighted networks in SOCPROG using the matrix definition described by Holme et al. (2007), is a measure of how well an individual’s associates are themselves associated. We also evaluated the network’s clustering coefficient with the subsequent removal of individuals seen less frequently by restricting the data to individuals with a minimum of 10 (n = 145), 15 (n = 86), and 20 (n = 38) sightings. LAR analysis was used to compare temporal patterns within and between the resulting communities. LARs for each community were compared to the null association rate and estimated using jackknifing over 30 d periods (Whitehead 1995).

Habitat Shape and Sociality

To investigate the potential relationship between habitat shape and dolphin social structure we regressed network metrics and association indices for each community against habitat “narrowness.” Narrowness was defined as the mean (±SD) linear shore-to-shore width (in km) of a community’s core area. Width measurements were taken every km along the primary axis of the core area using ArcGIS software version 10.1 (Environmental Systems Research Institute Inc., Redlands, CA).

Results

Association Patterns

The overall mean HWI was 0.010 ± 0.006 (dyadic HWI range of 0.001–0.025) and the overall maximum HWI for the population was 0.270 ± 0.196 (individual HWI maximum range of 0.069–0.923); n = 1,843 pairs. The CV of true association indices was $S \pm SE = 0.723 \pm 0.028$, which indicates a well-differentiated population. A high $S$ value was expected considering the low spatial overlap amongst individuals inhabiting the northern and southern ends of the linear study area. The correlation between true and estimated association indices for the entire study population was low with $r \pm SE = 0.192 \pm 0.011$, which normally reveals an inaccurate representation of the data (Table 2). However, as noted earlier, the population has a linear distribution and we observed that the lowest association indices were among individuals at the study site’s northern and southern boundaries. Thus the low overall $r$ value could be due to a negligible chance of interaction between animals at opposite ends of the study area. We ran this analysis within each community and found moderate-high values of $r$ (average $r = 0.479$) indicating that our analysis is representative of the true pattern at the appropriate scale (Table 2).

A significantly higher CV of observed vs. expected association indices (HWI_{observed} CV = 3.718, HWI_{expected} CV = 3.204, P > 0.95) indicates that long-term preferred companions are present in the population. The proportion of nonzero association indices was lower (though not significant) in the observed vs. the expected association
indices (observed = 0.108, expected = 0.117, P < 0.0005) indicating avoidance may be occurring in the population. The test for gregariousness determined that there are few gregarious and antisocial animals (observed = 10, expected = 9.25), which further emphasizes the presence of preference and avoidance amongst individuals in the population.

Temporal Patterns of Association

The lagged association rate remained higher than the null association rates throughout the study, indicating nonrandom associations of individuals (Fig. 2). LAR decreased during the length of the study, demonstrating a time-dependence for the associations of individuals throughout the study period. The most parsimonious model (based on the QAIC values, see Table S1) was characterized by “rapid disassociation and casual acquaintances,” which suggests that most associations were brief and not stable, and re-associations were common. The model suggests that

\[ g(d) = 0.12674 \times e^{-(d/2.74 \times 10^{-4})} \]

the probability of associations was estimated to decline by half after approximately 6.93 yr (2,530 d).

Community Structure and Dynamics

The modularity coefficient (Q = 0.544) indicated significant divisions in the population, resulting in six distinct clusters, or communities (Fig. 3). Indeed, mean and maximum association indices were significantly higher within (HWI mean = 0.032 ± 0.031, maximum = 0.327 ± 0.213) than among (HWI mean = 0.003 ± 0.004, maximum = 0.177 ± 0.163) communities as expected. Mean and maximum levels of association were highest in comA (mean = 0.163 ± 0.054, maximum = 0.574 ± 0.325), the community at the northern end of the study area. These data is most likely artificially inflated due to the incomplete assessment of all associations within that community, whose animals are known to range further north and

<table>
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<th></th>
<th>n</th>
<th>HWI</th>
<th>S</th>
<th>r</th>
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<tbody>
<tr>
<td>Overall</td>
<td>185</td>
<td>0.010 (0.006)</td>
<td>0.727</td>
<td>0.195</td>
</tr>
<tr>
<td>comA</td>
<td>7</td>
<td>0.163 (0.054)</td>
<td>1.002</td>
<td>0.676</td>
</tr>
<tr>
<td>comB</td>
<td>38</td>
<td>0.045 (0.029)</td>
<td>0.859</td>
<td>0.510</td>
</tr>
<tr>
<td>comC</td>
<td>27</td>
<td>0.019 (0.007)</td>
<td>0.641</td>
<td>0.266</td>
</tr>
<tr>
<td>comD</td>
<td>41</td>
<td>0.026 (0.015)</td>
<td>0.719</td>
<td>0.342</td>
</tr>
<tr>
<td>comE</td>
<td>45</td>
<td>0.036 (0.015)</td>
<td>0.776</td>
<td>0.457</td>
</tr>
<tr>
<td>comF</td>
<td>27</td>
<td>0.094 (0.036)</td>
<td>0.660</td>
<td>0.644</td>
</tr>
<tr>
<td>Within</td>
<td></td>
<td>0.032 (0.031)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Between</td>
<td></td>
<td>0.003 (0.004)</td>
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interact with individuals outside of our study area. ComF had the next highest mean and maximum HWI (0.094 ± 0.036; 0.352 ± 0.177). The community with the lowest mean and maximum HWI was comC (0.019 ± 0.007; 0.170 ± 0.056). Preference and avoidance occurred within all communities, with all CVs of association indices being higher and all proportions of nonzero indices being lower in the observed vs. the expected values.

Figure 2. Lagged association rates (LAR) for (A) all individuals, the best-fitting model of rapid disassociation and casual acquaintances, and the null association rate; and (B) within the communities, showing the null association rate. Standard errors of all LARs were calculated by jackknifing over 30 d periods.

2Personal communication from George Biedenbach, Georgia Aquarium’s Dolphin Conservation Field Station, 9509 Oceanshore Boulevard, St. Augustine, FL 32080, 22 March 2013.
ComC had much lower values for all network measures than the other communities, which, coupled with a low mean association rate, suggests a loosely connected social structure (Table 3). ComB, comE and comF had higher strength and reach than the other communities, as well as relatively high association rates, indicating that individuals are well connected to each other in these communities. However, comF was the only community in which the reach value was higher than expected in a random network. ComA had the highest eigenvector centrality and clustering coefficient, which is likely due to the limited sampling of this community (as discussed above) which may bias the small number of individuals ($n = 7$) toward seeming more connected than they actually are. ComF had the next highest clustering coefficient,
indicating a dense network of individuals in that community. All communities, with the exception of comA, had clustering coefficients lower than random, signifying that an individual’s associates are less likely to be connected to each other than in a random network. This may be a result of the linear nature of the habitat restricting animals from associating, e.g., individuals at the northern and southern reaches of a community’s habitat may never interact. The network clustering coefficient did increase upon removal of more sporadically seen individuals (see Table S2).

Lagged association rate analysis indicated that associations within each community were relatively stable and were higher than the null association rate for the duration of the study period, thereby supporting the separation of the communities (Fig. 2). The exception was in comF, which after an initial time period began to decrease over the length of the study, increasing only slightly at the end. Models were then fitted to each of the community LARs: comA, comB and comC all showed rapid disassociation and constant companions; comD and comF showed rapid disassociation and casual acquaintances; comE showed constant companions and casual acquaintances. All communities had several additional models that were supported ($\Delta$QAIC $\leq 2$, Whitehead 2008); the one model that all six communities had in common was that of rapid disassociation and casual acquaintances, which was the best model for the entire population. ComD and comF were the only communities that did not have a model that included constant companions.

**Spatial Patterns of Dyads and Communities**

Overall, a weak positive correlation was observed between the home range overlap of individuals and dyadic association within the population (Fig. 4). The weak correlation between HWI and PHR (95%) was statistically significant (Mantel test: $r = 0.28, P < 0.001$); however, the correlation between HWI and UDOI (95%) was not significant (Mantel test: $r = -0.007, P = 0.346$). Spatial overlap and HWI were also very weakly correlated for individual 50% core area (Mantel test: PHR 50%: $r = 0.193, P < 0.001$; UDOI 50%: $r = 0.345, P < 0.001$). This consistently weak correlation could be driven by the constraints of the linear habitat and by preference and/or avoidance behavior towards other individuals.

When separated by community, the correlation between HWI and spatial overlap (both PHR 95% and UDOI 95%) remained extremely weak (Mantel $r$ ranged from $-0.012$ to $0.435$, $0.001 < P < 0.498$), with the exception of animals within the comA community (Mantel test: PHR 95%: $r = 0.566, P = 0.013$; UDOI 95%:

### Table 3. The network measures of strength, eigenvector centrality, reach, and clustering coefficient for the overall population and its communities. Standard deviation is shown in parentheses. An asterisk indicates significant $P$-values.

<table>
<thead>
<tr>
<th></th>
<th>Strength</th>
<th>Eigenvector centrality</th>
<th>Reach</th>
<th>Clustering coefficient</th>
</tr>
</thead>
<tbody>
<tr>
<td>Overall</td>
<td>1.876 (1.111)*</td>
<td>0.040 (0.062)*</td>
<td>4.749 (3.829)</td>
<td>0.065 (0.038)*</td>
</tr>
<tr>
<td>comA</td>
<td>0.977 (0.325)*</td>
<td>0.310 (0.233)*</td>
<td>1.045 (0.424)*</td>
<td>0.236 (0.109)</td>
</tr>
<tr>
<td>comB</td>
<td>1.673 (1.075)*</td>
<td>0.130 (0.098)*</td>
<td>3.925 (2.849)*</td>
<td>0.108 (0.042)*</td>
</tr>
<tr>
<td>comC</td>
<td>0.485 (0.181)</td>
<td>0.166 (0.100)*</td>
<td>0.267 (0.100)</td>
<td>0.145 (0.129)</td>
</tr>
<tr>
<td>comD</td>
<td>1.043 (0.597)</td>
<td>0.125 (0.095)</td>
<td>1.435 (0.988)</td>
<td>0.115 (0.047)</td>
</tr>
<tr>
<td>comE</td>
<td>1.599 (0.653)</td>
<td>0.133 (0.069)*</td>
<td>2.973 (1.401)</td>
<td>0.063 (0.016)*</td>
</tr>
<tr>
<td>comF</td>
<td>2.454 (0.938)*</td>
<td>0.177 (0.077)*</td>
<td>6.867 (2.899)*</td>
<td>0.163 (0.021)*</td>
</tr>
</tbody>
</table>
As the study area likely only covers part of this community’s range, these results may be positively skewed by over estimating a strong relationship between spatial overlap and social affiliation. Analysis of the individual 50% core areas yielded similar results.

Core areas of each community were fairly discrete (Fig. 1), with the largest overlap between comD and comE (UDOI = 0.094; PHR\textsubscript{comD, ComE} = 0.314; PHR\textsubscript{comE, comD} = 0.305). However, the 95% community home ranges overlapped considerably (UDOI = 0–0.639; PHR = 0–0.917) with only the northern-most and southern-most communities not overlapping, suggesting community structure was not based exclusively on spatial segregation.

**Habitat Shape and Sociality**

For the five communities for which we had complete core areas a strong negative relationship was observed between the mean width of a community’s core area and mean network strength ($r^2 = 0.72$, $P < 0.05$) and reach ($r^2 = 0.66$, $P < 0.05$). There was no significant relationship between mean HWI ($r^2 = 0.35$, $P > 0.05$) and centrality ($r^2 = 0.14$, $P > 0.05$) and core area narrowness. No relationship was observed between narrowness and mean clustering coefficient ($r^2 = 0.001$, $P > 0.05$).

**Discussion**

The estuarine population of bottlenose dolphins in the Indian River and Mosquito Lagoon system exhibited a wide range of association patterns, comprising both weak and strong affiliations among dyads and preferred and avoided companionships over the 6.5 yr study. Time lag analysis revealed fission-fusion dynamics to these associations best characterized as casual acquaintances that rapidly disassociate and often re-associate. Network analysis revealed individuals clustered into six distinct
social communities; spatial analyses found these communities occupying relatively discrete core areas along the north-south axis of the lagoon system. Patterns of social organization and dynamics differed between communities. As expected, association indices were higher within communities than between, while measures of social cohesion varied between communities. This variation combined with weak correlations between estimates of spatial overlap and association patterns indicate interrelated factors influencing the structure, dynamics, and location of bottlenose dolphin communities within the study area.

Similar to a number of other studies of coastal, estuarine and embayment populations of this species, the IRL population is characterized by fluid association patterns and yet comprised of distinct social communities with discrete, minimally overlapping core ranges. Populations in Sarasota Bay and Tampa Bay along Florida’s Gulf coast were found to have discrete communities with little to no overlap of core areas (Wells 1991, Urian et al. 2009). Similarly, embayment populations of Indo-Pacific bottlenose dolphins, *T. aduncus*, in southeastern Australia comprised communities that occupied spatially discrete core areas (Wiszniowski et al. 2009). This contrasts with populations in Queensland, Australia (Chilvers and Corkeron 2001) and the east coast of Scotland (Lusseau et al. 2006), where communities exhibited substantial core area overlap. Such comparisons between populations are hampered somewhat by differing definitions of a dolphin community, which have been based on observed patterns of movement and residency (Litz 2007, Mazzoil et al. 2008b, Laska et al. 2011), social affiliations (Chilvers and Corkeron 2001, Lusseau et al. 2006, Wiszniowski et al. 2009) or some combination of the two (Wells 1986, Wells et al. 1987, Urian et al. 2009). Here individual ranging patterns exerted a substantial influence on patterns of association and social structure at the population level. Dolphins whose utilization distributions were centered in the southern end of the study area never ranged to the study area’s northern end. Similarly, the most northerly dolphins did not range as far south as the southern end, thus corroborating our earlier findings (Mazzoil et al. 2008b). These two areas comprised discrete social communities with no range overlap. Between these two areas, however, individual ranging patterns appear to comprise a continuum of overlapping ranges (Fig. 5). And yet we identified a number of distinct social communities. Further, while these communities’ entire ranges overlapped substantially they tended to occupy relatively exclusive core areas (Fig. 1). Thus, individuals that cluster into discrete social communities have core UDs that also cluster around relatively discrete regions of the estuarine system suggesting that at these spatial scales it is the shared use of a common area that shapes community structure.

Interestingly, range overlap did not predict dyadic association strength within those communities. The finding of preferred and avoided companionships and the relatively poor relationship between dyadic range overlap and the strength of dyadic associations within communities indicate that social processes play a major role in association patterns and social structure in the Indian River and Mosquito Lagoon subbasins. The influence of limits to ranging distance and the shared use of common core areas on dolphin community structure, and the poor correlation between individual home range overlap and associations within those communities that was observed in this study exemplify the complex mutual relationship between association patterns and space use in many social species as well as the difficulties associated with disentangling this relationship (Shizuka et al. 2014, Best et al. 2014).

Both intrinsic and extrinsic forces likely drive social patterns in this population. Intrinsic drivers include preferred associations which may arise among closely related
or unrelated individuals, depending on the role of kin selection (Hamilton 1963) in the evolution of social behavior in this species. Kin-based societies have been documented in many species including lions (Packer et al. 1991), wolves (Pilot et al. 2010, Stenglein et al. 2011) and pilot whales (Amos et al. 1993). Kin-based associations have also been recorded in some bottlenose dolphin populations (Krützen et al. 2003, Parsons et al. 2003, Frère et al. 2010b) but not others (Möller et al. 2001) highlighting the behavioral ecological plasticity of this species. A recent study revealed genetic differentiation between dolphins in the Mosquito Lagoon and Indian River-proper (Rodgers 2013). By contrast, limited heterogeneity was found within the Indian River-proper (Rodgers 2013) and it did not correlate with the community structure reported here, indicating that a more thorough genetic investigation is required to comprehensively assess the role of kinship in social affiliations.

Such intrinsic factors are ultimately shaped by extrinsic drivers including the physical environment, resource dispersion, habitat complexity, predation risk, and interspecific competition. Wiszniewski et al. (2009) proposed that community segregation in a population of Indo-Pacific bottlenose dolphins in southeastern Australia was shaped largely by individual adaptation to local environmental conditions. Chilvers and Corkeron (2001) found that two sympatric communities of the same species in Queensland, Australia could be distinguished primarily by foraging specializations but also by habitat preferences, while Rossbach and Herzing (1999) observed environmental differences and differences in foraging strategies among bottlenose dolphin communities in shelf waters off the Bahamas. In Florida Bay, Torres and Read (2009) found dolphins appeared to be segregated based upon preferred foraging strategy, rarely seeing dolphins from each strategy together. The 250 km long IRL system is one of the most ecologically diverse estuarine systems in North America (FDER 1989) and spans a major biogeographic boundary between the subtropics and temperate zones (EPA-NEP 1996). The latitudinal range, underlying bathymetry, location and size of rivers and ocean inlets, and presence of an

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**Figure 5.** Utilization distributions (UD) for all individuals. Vertical bars represent north-south extent of the 50% core UD for each dolphin. Individuals are grouped by community; community designations are represented by colors (red = comA, orange = comB, yellow = comC, green = comD, blue = comE, purple = comF). Units along the y-axis are degrees latitude using the Universal Transverse Mercator (UTM) system.
extensive canal system that drains into the IRL all contribute to extensive spatial and
temporal variation in water temperature, depth, salinity, and currents (Woodward-
Clyde Consultants 1994), tidal range and levels of flushing (Smith 1993), and the
extent of fresh water and marine influence along the north-south axis of this ecosystem
(Seward et al. 1994, Sigua et al. 2000, USACE and SFWMD 2001). There is
also substantial spatio-temporal variation in the species composition and dyna-
mics of primary production (Gilmore 1985), in fish biodiversity (Gilmore 1995, Tre-
main and Adams 1995), and in the distribution and abundance of other apex
predators including sharks (Curtis et al. 2011).

This heterogeneity directly influences prey availability, predation risk and com-
petition for dolphins and likely reflects variation in dolphin ecology, including social
ecology, across the system. That dolphin communities occupy discrete core areas sug-
gests there are likely ecological differences among communities. Variation in sociality
is evident in the differences in the various network measures of social cohesion across
communities.

Few studies have investigated the role of habitat dimensions as an extrinsic factor
shaping the social environment. Habitat fragmentation has been found to affect ele-
ments of song sharing in birds (Briefer et al. 2009). Similarly, habitat structure and
fragmentation are thought to drive social structure in spinner dolphins (Karczmarski
et al. 2005). This study revealed that habitat shape may also influence both associa-
tion and ranging patterns and thus community structure in bottlenose dolphins. Habitat dimensions may exert an indirect effect by influencing the distribution of
resources (e.g., food, nursery areas), or by influencing the distribution of predators and
thus the level of predation risk. Habitat shape may also have a more direct effect by
influencing dolphin movement patterns and conspecific encounter rates. Linear habi-
tats, for instance, confine individuals to narrow corridors of habitat when moving
between habitat patches thus increasing conspecific encounter probabilities. The IRL
is a uniquely narrow, linear habitat for coastal bottlenose dolphins. It may be signifi-
cant that the least cohesive of all the communities, comC, has a core range in the wid-
est part of the IRL system (Fig. 3, Table 3). Similarly, another community
occupying the relatively wide habitat of Mosquito Lagoon and part of the northern
section of the IRL, comB, has a low density network with low network measures of
connectivity. Conversely, the more dense community networks are found in the nar-
rower regions at the southern end of the study area. The most interconnected commu-
nity, comF, occupies the relatively narrow habitat of the St. Lucie River estuary
and the southern IRL where available habitat rarely exceeds 2.5 km in breadth and typi-
cally is between 1 and 2 km wide. Whether directly or indirectly, this area confines
dolphins to a narrow, linear habitat where individuals likely encounter each other at a
higher rate than in the broader reaches of the northern Indian River, Banana River,
and Mosquito Lagoon. Tellingly, the scale of mean range overlap among individual
dolphins (PHR and UDOI) was also found to correlate with habitat narrowness across
communities (see Table S3) further underscoring the complex relationship between
ranging patterns, space preference, habitat shape, and association patterns in this
species.

Detailed information on the social and community structure of a population is
necessary to accurately describe stocks which are used for species management. There
could be important management implications if a large population is treated
uniformly, rather than with respect to distinct substructures within the population,
risking failure to accurately assess impacts of local stressors and mortality factors.
Subregions within this estuarine system differ greatly in habitat characteristics and
display spatial and seasonal variation in anthropogenic impacts such as fisheries interactions (Stolen et al. 2012), environmental pollutants (Sime 2005), and boat traffic (Bechdel et al. 2009). Regions of the lagoon have been subject to localized and temporally sporadic harmful algal blooms and biotoxins (Landsberg et al. 2006, Provancha and Van den Ende 2006), sea grass die-offs (Steward et al. 1994, Sigua et al. 2000, Garland 2014), and fish kills (Provancha et al. 1992, EPA-NEP 1996). In diverse habitat areas, such as the IRL, an understanding of the spatiotemporal dynamics of the social structure would be advantageous in determining the possible effects of localized environmental and anthropogenic events.

Spatial variation has been observed in the prevalence of the infectious disease, lobomycosis, in dolphins (Murdoch et al. 2008), and other infectious diseases such as orogenital papillomas (Bossart et al. 2005) and morbillivirus (Bossart et al. 2010, NOAA Fisheries 2014) have been confirmed in this population. The presence of multiple organic pollutants (Fair et al. 2007a, 2007b, 2010) and heavy metals (Stavros et al. 2011), as well as antibiotic-resistant bacteria (Greig et al. 2007) have been detected in individuals during capture-release health assessments. Three localized NOAA-declared unusual mortality events have occurred in the IRL in recent years including one ongoing event at time of writing (2001, 2008, and 2013–2014); the suspected cause of the 2001 event was the biotoxin saxitoxin, but it was not confirmed, and the cause of the 2008 and 2013–2014 events may be cetacean morbillivirus (NOAA Fisheries 2008, 2014). The ability to identify the location of point source contaminants, to determine disease origins, and to track and predict patterns of disease amongst individuals is of great importance in assessing the risk and scale of local impacts.

This study provides a more realistic and biologically meaningful framework to assess such risks and impacts and formulate effective responses. Dolphins are social species where information transfer and disease transmission rely on the pattern of social interactions among individuals. Network analysis can help us understand the social implications affecting overall health trends, epidemiological events, and gene flow. Knowledge of social affiliations and ranging patterns combined with genetic structure could be an extremely useful tool when modeling the patterns and spread of disease and behavioral response throughout the population. The combined approach of assessing individual dolphin ranging patterns and social affiliations using association strength, lagged association rates, and network analysis in relation to home range overlap and then utilizing this data to determine spatial proximity and disease transfer potentials could be invaluable to the management of the population during the occurrence of an epidemiological or environmental event.

**Future Directions**

Individual social preferences, resource dispersion, competition, predation pressure, anthropogenic effects, relatedness, and habitat shape likely influence social variability in this estuarine population of bottlenose dolphins. Genetic analyses of this population are ongoing and will hopefully resolve how sex and kinship relate to individual associations, ranging behavior and social organization. Genetic structure might indicate that social structure within the population is quite ephemeral and social affiliations and community membership may change over the course of an individual’s life. Social networks are incredibly dynamic and future studies of this population should increase the temporal span of the study to understand how the social structure evolves over time. It will be important to explore the relationship between ranging and
association patterns compared to foraging ecology and habitat use in order to be prepared for potential environmental impacts that could affect prey resources and critical habitat areas. Using social networks as a quantitative way to model and monitor the spread of contagion may become a standard tool in examining past and on-going epidemiological events. The combined use of social structure, genetic structure, and ranging patterns make for a more effective management tool that could be key to preserving animal populations.

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Wells, R. S. 1986. Structural aspects of dolphin societies. University of California, Santa Cruz, CA.


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Supporting Information

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Table S1. Exponential decay models ranked by lowest quasi-Akaike Information Criterion (QAICc) for lagged association rates (LAR) of IRL dolphins from 2002 to 2008. Association rates between individuals ($g$), as a function of time lag ($d$), were related to the proportion of constant companions ($P_{cc}$) and the proportion of casual acquaintances ($P_{cas}$) that lasted for time period $\tau_{cas}$ (but were not permanent), and to the proportion of casual associations ($P_{perm}$) that had more permanent associations ($\tau_{perm}$) (see Whitehead 1995).

Table S2. The network’s clustering coefficient measured with removal of individuals with fewer sightings.

Table S3. Narrowness of each community’s habitat compared to the average home range overlap of all dyads in the community. Home range overlap is measured by a probabilistic measure of space sharing (PHR) and a utilization distribution overlap index (UDOI). Both PHR and UDOI were calculated for the entire home range (95%) and the core area (50%) for each dyad. ComA was excluded since complete home range areas were not available for these individuals.