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ORIGINAL ARTICLE

Guiana dolphins form social modules in a large population with high ranging overlap and small demographic changes

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Abstract
The number and strength of social relationships are generally the products of group living trade-offs. However, they can be at least partially influenced by asocial factors such as the spatiotemporal opportunities for individuals to interact. We explored the social patterns of the largest population of Guiana dolphins—from dyadic interactions to the large-scale structure of their social network—considering their use of space and demographic changes during 6 years. We found that their society displays fission-fusion dynamics, characterized mainly by brief associations among individuals, and is weakly structured into four social modules. Spatial use and temporal demographic changes had minor effects on the patterns of associations among individuals. This suggests that the social modules unlikely represented spatiotemporal aggregations of individuals due to resource availability but rather involved social preferences among individuals. We show that Guiana dolphins can form social modules even in a large population with high ranging overlap and few demographic changes over time, although these social boundaries are blurred by the dynamic nature of the social relationships. Our findings illustrate and support the recent claims for the need of taking asocial processes in account when studying social structure of any animal species.

Significance statement
Animal social relationships are dynamic, usually reflecting group living trade-offs. Simultaneously, they are influenced by the opportunities individuals have to interact. Group membership—co-occurrence in the same space and time—is the most used proxy for describing animal social relationships. Therefore, if the spatiotemporal context is not accounted for, the resultant social structure can be misrepresented. Here, we explore the social patterns of Guiana dolphins explicitly accounting for space use and temporal demographic changes. We show the largest population of Guiana dolphins displays fission-fusion dynamics, while it is structured into four distinctive sets of individuals. By accounting for asocial processes, we suggest such social modules were unlikely to result from unequal opportunities to interact but rather involved social preferences among individuals. Our findings highlight the importance of separating asocial from social processes while studying animal societies.

Keywords *Sotalia guianensis* · Social network · Space use · Social structure · Population turnover

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Introduction

Animal social relationships are dynamic, with individuals constantly responding to group living trade-offs (Krause and Ruxton 2002; Whitehead 2008). For most animal species, group formation is the fundamental requirement for social interactions (e.g., Whitehead and Dufault 1999). Such co-occurrence of conspecifics in close proximity at the same time is convenient when studying animal societies (e.g., Farine 2015). This is evident in studies of aquatic animals, where limitations of underwater observations make group membership the most common working proxy for social relationships (e.g., Whitehead 2008). The underlying assumption of this well-used method is that individuals identified in the same group have opportunities to socially interact (the "gambit of the group" hypothesis; Whitehead and Dufault 1999). So with a succession of recorded events in which individuals are observed in the same group, one can estimate the strength of their social relationships via association indices (e.g., Whitehead 2008).

In most cases, the proportion of time individuals observed together is the only information one can feed statistical methods to unravel the structure of their societies (e.g., Croft et al. 2008; Whitehead 2008). Despite imperfections (Castles et al. 2014), group membership holds the minimum requirements for social interactions (Hinde 1976; Farine 2015) since it reflects attractive/repulsive forces among conspecifics (Krause and Ruxton 2002). Yet, to be meaningful, such proximity-based measures need to account for the spatiotemporal context in which the social interactions take place (Cantor et al. 2012a; Pinter-Wollman et al. 2013). The social structure portrayal can be biased if not all individuals have had opportunities to be in close proximity. Spurious social patterns (e.g., social modules, preferences, avoidances) can emerge due to spatial or temporal segregation, such as when individuals have strong preferences for different areas or when they use a common area but at different times (Whitehead 1999; Wiszniewski et al. 2009; Cantor et al. 2012a). Therefore, spatial use and demographic changes should be investigated in parallel with social structure (Pinter-Wollman et al. 2013).

This is especially relevant for societies with high degrees of fission-fusion—i.e., with groups constantly varying in size, composition, and spatial cohesion (*cf.* Aureli et al. 2008). The forces driving group dynamics in such societies are many, including, but not limited to, environmental conditions and habitat complexity (e.g., temperature, topography), biological pressures (e.g., predation risk, competition for mates and food, prey availability), and individual assortativity (e.g., preference to interact with individuals of the same sex, kin-related, or who behave similarly) (e.g., Gowans et al. 2008; Whitehead and James 2015). We have only recently started to account for the effects of other asocial processes that can mask the interpretation of animal social structures, such as habitat structure (e.g., Leu et al. 2016), space use (e.g., Wiszniewski et al. 2009), movements, and demographic changes (e.g., Cantor et al. 2012a). However, the degree to which they drive the structure of specific animal societies, especially in aquatic environments, is relatively unknown.

A good example of animal societies influenced by such asocial processes are those of Guiana dolphins, *Sotalia guianensis* (Cantor et al. 2012a), whose populations display a marked variation of group size along the coastal and estuarine areas off the southwestern Atlantic Ocean. While typically found in groups of 2 to 13 individuals, they can form groups of about 30 members in some populations (e.g., Santos and Rosso 2007; Flach et al. 2008a). Guiana dolphin societies display fission-fusion dynamics (Santos and Rosso 2008; Lunardi and Ferreira 2014), but this evidence comes only from small populations with small groups. It is unclear if a similar social structure would emerge in populations were large aggregations and groups are frequently merging and splitting. The largest Guiana dolphin population inhabits the Sepetiba Bay, southeastern Brazil, where their numbers are estimated to be over a thousand (Flach et al. 2008b; Nery and Simão 2012), and the groups frequently consist of over hundreds of individuals (Dias et al. 2009; Nery and Simão 2012). We would expect the social structure of this population to be influenced by asocial processes for three reasons. First, large groupings may have lower spatial cohesion and lower rate of social interaction, since not all members can be in very close spatial proximity during all times. Second, a sizable population may experience more pronounced demographic changes. Finally, the large groupings of Guiana dolphins vary in their spatial use of the Sepetiba Bay following fine-scale conditions and resource availability (Dias et al. 2009).

Here, we evaluate the social patterns of the largest population of Guiana dolphins, in Sepetiba Bay, accounting for patterns of space use and potential demographic changes over a 6-year period. First, we explore the overall social pattern of this population by testing whether individuals associate at random or, alternatively, whether their social network is structured into modules. Second, we evaluate if the population composition, as well as the probability of individuals to associate, changes over time. Finally, we evaluate whether individuals from different social modules demonstrate differences in space use. In the spatiotemporal scale considered here, we found few demographic changes and a high overlap of ranging behavior, which suggests the social modules in this population are likely defined by social preferences among individuals. Combined, these findings emphasize that asocial processes must be taken into account to reveal a more realistic portray of animal social structures (see Pinter-Wollman et al. 2013).

Methods

Data sampling

From August 2005 to July 2011, we carried out 132 boat surveys evenly distributed throughout the years and seasons (ESM 1: Table S1) in the Sepetiba Bay, southeastern Brazil (22° 54′–23° 04′ S, 43° 34′–44° 10′ W). The Sepetiba Bay is a large (526 km^2) and shallow (8 m deep on average) coastal bay, with three dredged channels (>30 m). The western portion is connected with the Atlantic Ocean, with coarse sandy substratum and many rocky islands; the eastern area is estuarine, with muddy substratum, rocky and sandy beaches, and mangrove vegetation (Flach et al. 2008a). We designed four predefined routes to cover the bay (ESM 1: Figure S1); in each survey, we arbitrarily chose one route and attempted to sample all of them as equally as possible.

When a group of Guiana dolphins was sighted, we recorded their geographical position with a GPS, estimated the number of individuals in the group, and attempted to photograph the dorsal fins of all individuals, with no individual preferences, using a SLR camera equipped with a 100–400-mm lens. Individuals were identified based on the patterns of natural marks on their dorsal fins, using standard photo-identification protocols (Hammond et al. 1990), followed up by an independent, computer-assisted photographic matching analysis (Stanley 1995). These primary data for social analyses were recorded blindly because (a) it was not possible to identify individuals in the field and (b) the photo-identification was performed months later by independent researchers who did not participate in the data collection. To avoid misidentifications, individuals without distinctive marks were not included in the analysis (Hammond et al. 1990). We analyzed over 10,000 photos, and we identified 647 distinctive dolphins.

A group of Guiana dolphins was defined as two or more individuals in close proximity (within a circular area of 100 m of diameter) and engaged in similar behavior and usually in coordinated general movement (Irvine et al. 1981; Flach et al. 2008a). Dolphins from this population can form large groups (up to 90 dolphins, 71 % of the time) and aggregations of up to 450 dolphins (Dias et al. 2009). Since in large groups individuals are less likely to interact among all individuals with the same probability, we minimized the chance of recording spurious interactions by analyzing only groups with less than 50 individuals. This threshold excluded the aggregations of dolphins from our analyses (see Dias et al 2009), in which individuals cluster due to a third factor (e.g., an available resource), gain no benefit from each other, and are likely to compete (see Whitehead 2008). In total, we sampled 132 groups of dolphins (mean = 31 ± 16 standard deviation) that met these criteria. All the data used in this work are available from the authors upon request.

Social analyses

We considered all individuals identified in the same group to be in association (the "gambit of the group" hypothesis; Whitehead and Dufault 1999). In most surveys, we found more than one group on the same day. We only analyzed the photographic records of the first group encountered in each day to ensure sampling independence among such groups that change composition often and consequently reduce the long time involved in the photo-identification of the immense volume of photographs taken. To calculate associations between individual dolphins, we used the half-weight index (HWI, ESM 1: Table S2), which ranges from 0 (never seen together) to 1 (always seen together) (Whitehead 2008). To avoid spurious associations, we only calculated association indices among individuals sighted more than five times (Whitehead 2008) during the 6 years of survey. Therefore, our social analyses included 67 out of the 647 photo-identified individuals—the social core of the population (e.g., Silk et al. 2015).

We plotted the association matrix as a network of photo-identified individuals (nodes) connected by weighted links whose thicknesses were proportional to the HWI values. To test whether this social network was structured in modules—subsets of nodes that are highly internally connected but weakly connected with the rest of the network (ESM 1: Table S2)—we used an algorithm that maximized the binary modularity metric Q (Newman 2006). A modular structure would indicate that sets of individuals interact more often with each other, i.e., with more and stronger association indices, potentially delineating a "social community" within the population (e.g., Croft et al. 2008). To test the significance of the modularity, we designed a null model to generate a set of 1000 of theoretical networks of the same number of nodes and links, by randomly assigning HWI values among dyads (see Opsahl et al. 2008) and calculated Q for each network. We considered the empirical network to present a reliable division into modules if its Q-value was outside of the 95 % confidential interval of the theoretical Q-value benchmark distribution.

To further describe the network structure and grouping patterns, we calculated three other metrics (ESM 1: Table S2): weighted cluster coefficient, connectance (see Croft et al. 2008), and social differentiation (Whitehead 2008). Cluster coefficient (CC_w) is a global network metric that calculates the probability that two nodes, A and B, connected to a same third node, C, are themselves connected. Connectance (or density, d) represents the proportion of realized links in the network given the total number of possible links. High clustering and connectance describe denser networks, with many triads and short paths between individuals. Finally, social differentiation (S) is an estimate of the coefficient of variation of the true association indices, which informs how differentiate a society is ($S < 0.3$ homogeneous, $S > 0.5$ well-differentiated, $S > 2.0$ extremely differentiated societies) (Whitehead 2008).

Standard errors (SE) for S were calculated with bootstrap methods (100 iterations).

We tested the null hypothesis that individuals associate at random (Bejder et al. 1998) by permuting individuals into groups observed during the same 80-day sampling period, constraining observed group size and individual capture frequency. We performed 20,000 permutations (with 1000 flips each) using a swap algorithm (Bejder et al. 1998, adapted by Whitehead 1999). Performing the permutation test with an 80-day period was appropriate for two reasons. First, S is maximized at 80-day sampling periods (ESM 1: Figure S3). Since S informs how differentiated a society is, higher S-values provide more statistical power to test the null hypothesis of random associations (Whitehead 2008) and can be used as an indirect measure of effect size between empirical and permuted datasets. Second, within 80 days, it was reasonable to assume the population was closed, so we constrained the permutations within these periods to minimize demographic effects (i.e., avoid grouping together individuals who never used the area at the same time; Whitehead 1999). We also applied this permutation test to evaluate the associations among individuals within each of the four social modules found in the network (see the "Results" section). In all cases, the presence of long-term (i.e., between 80-day period) preferred associations is suggested by higher coefficient of variation (CV) of association indices than expected by chance, while short-term (i.e., within 80-day period) preferences are indicated by significantly lower mean HWIs (Bejder et al. 1998). All social analyses were performed with SOCPROG 2.5 (Whitehead 2009), except for modularity and null model analyzed in R environment (Development Core Team R 2008) with package *igraph* (Csárdi and Nepusz 2006).

Temporal analyses

Relationships are time-dependent, often decreasing in strength over time (Whitehead 1995). We calculated the standardized lagged association rates (SLAR) using the entire dataset with 647 individuals to evaluate temporal stability of associations. SLAR is an estimate of the probability that if two individuals are associated at any time, the second is a randomly chosen associate of the first after the specified lag (Whitehead 1995). It accounts for cases in which not all of the true associates of an individual are recorded during a sampling period (Whitehead 2008), what is probably the case for this large population. We compared the observed SLAR with the null expectancy in which individuals associate randomly (standardized null association rates; Whitehead 1995).

To describe the decay in the association probabilities over time, we fitted theoretical exponential decay models to the observed SLAR, selecting the most parsimonious with quasi-likelihood Akaike Information Criterion (QAIC, Whitehead 2008), which accounts for over dispersion of the data (Burnham and Anderson 2002). The fitted models were the following: SLAR1 ($g' = a$) represents no change in SLAR with lags of one sampling period or more, suggesting that associations are constant during the study. SLAR2 ($g'(t) = a.\, e^{-b \cdot t}$) represents briefer associations with possible re-associations, suggesting casual acquaintances and rapid disassociation in a large population. SLAR3 ($g'(t) = a + c.\, e^{-b \cdot t}$) represents associations which fall with time lag and then level off, suggesting many brief associations along with others that last for longer periods. SLAR4 ($g'(t)t(t) = a.\, e^{-b \cdot t} + c.\, e^{-d \cdot t}$) represents two levels of disassociations, perhaps the fission/fusion of nearly permanent social associations forming and segregating, into and out of groups, or leaving the area/dying. SLAR and model fitting were performed using SOCPROG 2.5 (Whitehead 2009).

Changes in population composition

In open populations, individuals can emigrate and immigrate, so population composition can change over time and potentially influence social structure. To test if there were pronounced changes in the population during the study period, we calculated the turnover of individuals across different subsections of study duration. We split the total survey period (72 months) in smaller periods of 36, 18, 9, 6, and 4 months and compared population turnover (i.e., the differences in the presence of individuals) between subsequent periods, with the Whittaker dissimilarity index (Cantor et al. 2012a). To test the significance of the observed turnover, we compared the averaged dissimilarity index with benchmark distributions generated by a null model that randomized individuals among periods of time (1000 iterations) but restricting the individual sighting frequency. Significantly high dissimilarity values (falling outside of the 97.5 % confidence interval) would represent high turnover of individuals, i.e., that the population composition changed pronouncedly; conversely, significantly low values (outside of the 2.5 % CI) would represent a rather stable population composition (e.g., Cantor et al. 2012a).

Spatial analyses

We analyzed the ranging behavior of dolphins that were photo-identified more than five times using the Quantum GIS 2.4 Software (QGIS Development Team 2014). The geographical positions of each individual from all four social modules found on the network (see the "Results" section) were plotted using a universal transverse Mercator projection with a WGS84 map datum. To avoid autocorrelation, a maximum of one sighting point per individual per day was used, thus enabling each sighting to be considered an independent data point.

Because the individual sighting frequency was highly variable and most of the individuals were sighted only a few times, we were unable to estimate individual space use with reliable accuracy. Therefore, we estimated the spatial range of each social module, combining the sightings of all individuals of a given social module. We used fixed kernel utilization density estimates (KDEs) with the "ad hoc" method for determining the optimal smoothing parameter (Worton 1998). We estimated the core area of a social module as the 50 % density volume contour, while the 95 % volume contours represented the home range.

Different spatial use of the bay could be expected for this Guiana dolphin population because daily formation of two groups or aggregations (over a hundred individuals) has been observed in two different parts of the bay: entrance and the interior (Flach et al. 2008a; Dias et al. 2009). To test whether social preferences influenced the individual's choice of habitat selection, we calculated the overlap of space use among social modules. We assessed whether within-module assortative mixing occurred by calculating the overlap among the core area (50 % KDEs), and home ranges (95 % KDEs) of the social modules, with the Utilization Distribution Overlap Index (UDOI) and the probability of overlap (PHR) (Fieberg and Kochanny 2005). UDOI is a generalization of a niche overlap measure and gives the overlap of areas utilized by the groups of dolphins; UDOI <1 indicates less overlap relative to uniform space use, whereas UDOI >1 indicates higher than normal overlap relative to uniform space use (Fieberg and Kochanny 2005). PHR estimates the volume under the utilization distribution of all individuals from a given social module that is inside the home range of another module (i.e., the probability to find an animal of a module within the home range of individuals of another module). Low overlap on each of these metrics would mean that each social module uses a specific, separate region on the studied area.

Results

Social patterns

The Guiana dolphin social network presented high clustering coefficient ($CC_w = 0.58$) and connectance ($d = 0.46$), indicating large number of associations among individuals. Yet, the network was modular ($Q = 0.133$, 95 % CI = 0.060–0.083), with four social modules of individuals that tended to associate more among themselves (Fig. 1). The overall association pattern was not random: the coefficient of variation (CV) of the observed association indices (HWI) was higher than expected by chance (Table 1) indicating there were long-term association preferences in the population. Within social modules, only module 1 contained such long-term associations (Table 1). The relatively low social differentiation ($S = 0.235 \pm 0.048$ SE) suggested a rather homogeneous society; thus, we note that the size of differences between the CVs of the empirical and random HWI is not particularly marked, despite statistical significance (Table 1).

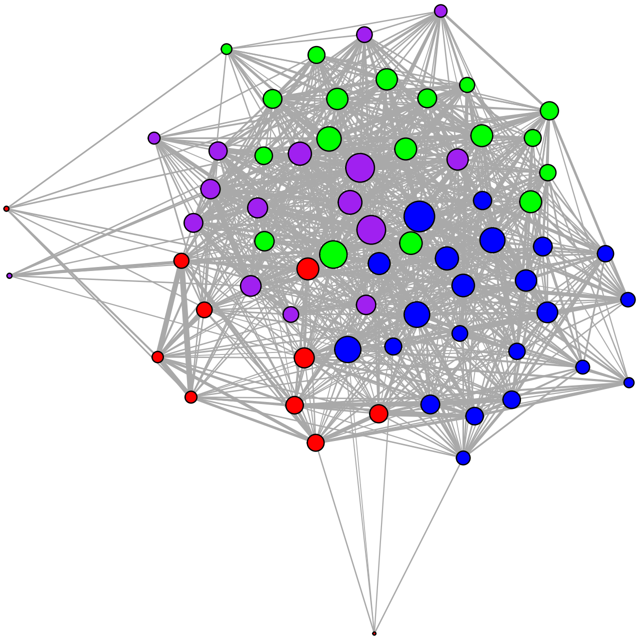

Fig. 1 Social network of Guiana dolphins from Sepetiba Bay. Nodes representing individuals (seen more than five times) which are connected by links whose thicknesses are proportional to their half-weight association indices. Node size is proportional to the number of associates (node degree), and color code indicates social modules: module 1 (*red*), module 2 (*green*), module 3 (*blue*), module 4 (*purple*)

Temporal patterns in associations

The SLAR were significantly higher than expected by chance, for at least a period of 1000 days (Fig. 2). The overall probability of association was low and clearly decayed over time. The most parsimonious model describing this decay was the SLAR2, suggesting that associations were brief (dubbed as "casual acquaintances"). No other model provided support for the observed SLAR, as shown by the ΔQAIC and QAIC weights (Table 2).

Changes in population composition

The turnover of individuals was significantly lower than expected by chance, especially in short periods of time, suggesting that the population composition did not change substantially during the study period (Fig. 3). This was clearer for periods of as long as 24 months and also applied for the turnover among periods of 36 months, which was very low. This showed that the social core of the population used the study area for the entire study period and, in theory, all individuals analyzed here had opportunities to associate with each other during the study period. This makes demographic changes via

Table 1 Summary of permutation test results for preferred associations among the entire Guiana dolphin network (all) and by social module (1–4), considering only individuals seen more than five times

Social module	*N*	Observed mean HWI	Random mean HWI	*p* value[a]	Observed CV HWI	Random CV HWI	*p* value[b]
All	67	0.095	0.934	0.793	1.23	1.236	0.007*
1	18	0.103	0.099	0.968	1.386	1.153	0.001*
2	17	0.107	0.106	0.698	1.042	1.113	0.918
3	15	0.068	0.069	0.149	1.646	1.583	0.186
4	17	0.121	0.12	0.655	1.067	1.053	0.337

N number of individuals, *Observed* empirical data, *Random* permuted data, *Mean HWI* mean half-weight association index, *CV HWI* coefficient of variation of HWI

*Significant difference between the summary statistic for the empirical and random data at the $p < 0.05$ level using 1000 iterations

[a] Significantly lower mean HWI for the observed data would suggest short-term (within the sampling period) preferred associations

[b] Significantly higher CV for the observed data suggests long-term (between the sampling period) preferred associations

immigration/birth and emigration/death unlikely drivers of the modular structure observed in the social network (Fig. 1).

Space use versus large-scale social structure

There was great overlap in the 95 % KDE among all four social modules and variable overlap in the 50 % KDE core areas (Fig. 4). The total ranging of the social modules was highly overlapped (PHR 95 % varying from 0.72 to 0.99, UDOI 95 % varying from 0.95 to 1.59), while there was less overlap of core areas (PHR 50 % varying from 0.19 to 0.76, UDOI 50 % varying from 0.16 to 0.36). All KDE overlap values are available in the ESM 1: Table S3. The spatial overlap of social modules also suggested that differences in space use are minor and an unlikely driver of the modular structure of the social network (Fig. 1).

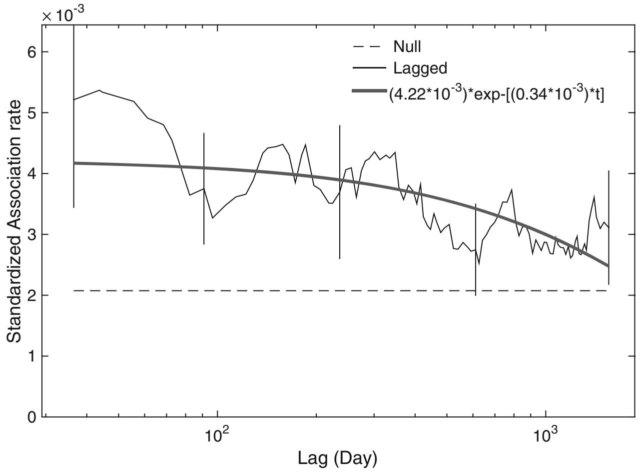

Fig. 2 Lagged association rates among all individuals of Guiana dolphin identified in Sepetiba Bay (*thin black line*). The best fitted model (*thick black line*) suggests associations are mainly brief (SLAR2, Table 2) and higher than the null association rates (*dashed line*). *Whiskers* represent standard errors estimated by a jackknife procedure

Discussion

Our findings agree that Guiana dolphins form societies with fission-fusion dynamics (Cantor et al. 2012a; Lunardi and Ferreira 2014), but more importantly, they show that the largest population of Guiana dolphins is structured into social modules. Although not entirely distinctive, these modules emerge in a population with high ranging overlap and little demographic changes. By accounting for these asocial processes, our results suggest that social choices and individual preferences play an important role shaping the large-scale social structure of this population. Our study illustrates and supports the importance of separating asocial from social processes while studying animal societies.

The Guiana dolphins of Sepetiba Bay are organized in a highly fluid, yet structured, society. Their social network is highly connected and includes clustered relationships, meaning that most of the individuals tend to interact (or form groups) at some point. In comparison to other dolphin populations (e.g., Lusseau et al. 2006; Wiszniewski et al. 2009; Cantor et al. 2012a), the social network of Guiana dolphins from Sepetiba is denser, with overall briefer associations, which is characteristic of large populations and highly dynamic social systems (Whitehead 2008). In fact, among Guiana dolphins, the group size and composition tend to change rapidly—about every 20 min (Lunardi and Ferreira 2014)—in agreement with the common fission-fusion dynamics found in coastal small cetaceans (e.g., Wells et al. 1987; Wiszniewski et al. 2009). We suspected the larger groupings observed in Sepetiba Bay could be even more dynamic, since the actual rate of interaction among members would be smaller due to lower spatial cohesion in such large groups (Flach et al. 2008a; Dias et al. 2009). Despite the general brevity of associations, the population contains non-random associations, suggesting that pairs of individuals display social preferences over longer time periods. This combination of social

Table 2 Theoretical exponential decay models fitted to empirical standardized lagged association rates (SLAR) found for individuals of Guiana dolphin in Sepetiba Bay from 2005 to 2011, ranked by the lowest Quasi-likelihood Akaike Information Criterion (QAIC) values. The ΔQAIC, the QAIC weight, and model likelihood indicate the relative support for each model

Models	Formulae	QAIC	ΔQAIC	QAIC weight	Likelihood
SLAR2	$g'(t) = \left(4.22 \times 10^{-3}\right) \cdot e^{-\left[\left(0.34 \times 10^{-3}\right) \cdot t\right]}$	6477.97	0.00	0.99	0.99
SLAR1	$g'(t) = 3.45 \times 10^{-3}$	6488.09	10.12	0.01	0.01
SLAR3	$g'(t) = (3.44 \times 10^{-3}) + 111.64 \cdot e^{(-9.65 \cdot t)}$	6490.18	12.21	0.00	0.00
SLAR4	$g'(t) = \left(4.27 \times 10^{-3}\right) \cdot e^{-\left[\left(0.35 \times 10^{-3}\right) \cdot t\right]} - 0.25 \cdot e^{-(1.09 \cdot t)}$	6543.95	65.98	0.00	0.00

fluidity with individual social preferences leads to a social network structured into weakly marked social modules.

Societies structured into modules (or "social communities," "social units") are recurrent across vertebrates (e.g., Lusseau et al. 2006; Gero et al. 2015). Such modular structure reflects the heterogeneity in social contact among individuals. Time and space are basic factors affecting the emergence of social modules, especially in very dynamic societies (Cantor et al. 2012a). Indeed, social modules in dolphin societies characterized by fission-fusion dynamics can result from spatially (e.g., Wiszniewski et al. 2009; Titcomb et al. 2015) or temporally segregated individuals (e.g., Cantor et al. 2012a). Our findings suggest that the modular structure of the Sepetiba Guiana dolphin population reflects social processes, rather than temporal demographic changes or variation in spatial use.

First, we considered the possibility of demographic effects, namely whether the population composition changed over the study period. Since our study span (6 years) is a short window in the life span of Guiana dolphins (about 30 years, Rosas et al. 2003), we would not expect pronounced demographic changes due to mortality or births. However, movements of individuals—temporary and permanent immigration and emigration—can yield significant population turnover in a population with high survival and/or low mortality (Cantor et al. 2012a, b). Although bounded habitats (e.g., bays protected from open oceans) often contain dolphin populations with high site fidelity and limited dispersal (Wells et al. 1987), not all members of the population are necessarily present in the area at all times (e.g., Cantor et al. 2012a). Dolphins, notably the sub-adults and males, may roam over larger areas (Wells et al. 1987). Thus, the degree of site fidelity may vary within the same population, with some individuals being resident and others more transient (i.e., leaving or passing through the study area; Cantor et al. 2012b). The turnover of Guiana dolphin individuals in Sepetiba Bay is apparently small, seen during this study through the lack of pronounced changes in composition of the social core of the population (i.e., the more resident and frequently re-sighted individuals). This fact corroborates the lack of individual exchange between Sepetiba Bay and the closest, almost contiguous, population of Ilha Grande's Bay, in which individuals differ genetically (Hollatz et al. 2011), in diet preferences (Bisi et al. 2013), feeding tactics (Oliveira et al. 2013), and whistle characteristics (Andrade et al. 2014). We highlight that by focusing on the social core, we reduced spurious relationships and population changes due to individual movement of individuals; but still, we can yield a significant portray of the Guiana dolphin social system since partial social networks based on fluid associations are robust to unknown individuals (e.g., Silk et al. 2015).

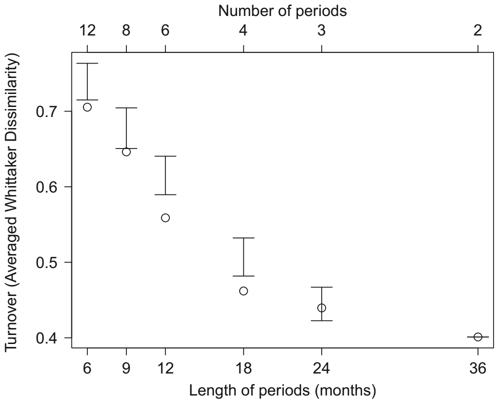

Fig. 3 Population turnover in different periods of time. The total survey period (72 months in 6 years) was divided in smaller sections (12 periods of 6 months, 8 periods of 9 months, 6 periods of 12 months, 4 periods of 18 months, 3 periods of 24 months, and 2 periods of 36 months) to evaluate possible changes in composition of the population. *Top axis* gives the number periods in which the total study was divided into; *x*-axis gives the length of such periods; *y*-axis gives our measure of population turnover, the average Whittaker dissimilarity index between subsequent periods (*white circles*); and *whiskers* represent 95 % confidence interval of a benchmark distribution generated by a null model

Second, while the social core of the population used the Sepetiba Bay during the same time, we further considered whether individuals from different social modules had preferred areas within the bay. Guiana dolphin groups could use the entire bay in Sepetiba, but the spatial use is heterogeneous (Dias et al. 2009) as seen in other populations (e.g., Wedekin et al. 2007). In Sepetiba Bay, Guiana dolphins prefer areas close to the natural channels and rocky islands, which are

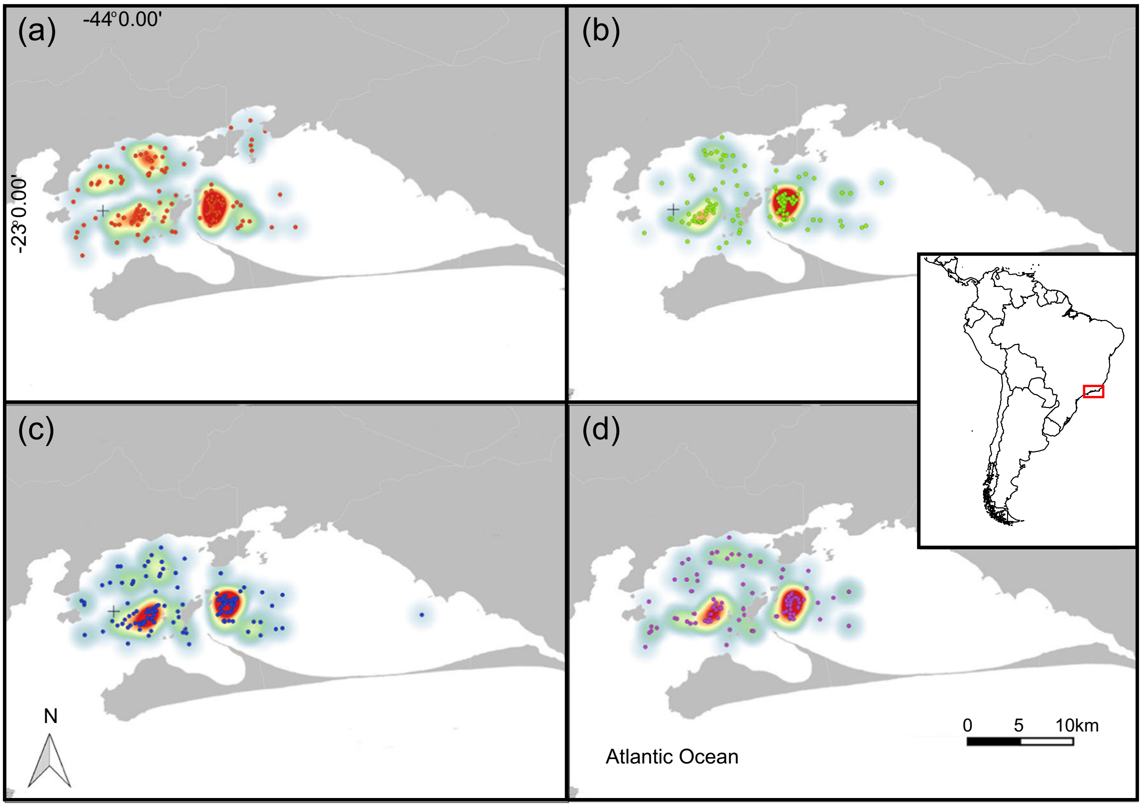

Fig. 4 Kernel density estimate (KDE) for each of the four social modules in Sepetiba Bay. *Dots* represent distinct group of animals, with color code following the social network: **a** module 1, **b** module 2, **c** module 3, and **d** module 4. The *red shades* represent the core area (50 % KDE), and the *blue shades* represent the distribution area (95 % KDE) of the social module

deeper (10–47 m; Flach et al. 2008a; Dias et al. 2009) and may be used as a barrier for herding fish schools (e.g., Rossi-Santos and Flores 2009). Furthermore, deeper areas have influx of cooler water from cold currents. These areas may represent channels for fish entrance in the bay, since Sepetiba Bay is an important area for fish reproduction and cold water can also be important for dolphin's thermoregulation (Yeates and Houser 2008). While the core areas of the social modules were slightly more discrete (perhaps due to some degree of spatial preference or attempt to reduce competition), the overall ranging area of all social modules within the bay clearly overlapped.

Combined, the high spatial overlap and small demographic changes over time suggest that all individuals had, at least theoretically, the possibility to associate with one another. Therefore, the modular structure suggests the influence of social or ecological drivers. In the marine environment, modular social structure is evident in multilevel societies, such as in orca and sperm whales, in which natal philopatry lead to matrilineal social units or modules (e.g., Ford et al. 2000; Gero et al. 2015). But social modules in societies with fission-fusion dynamics (e.g., Lusseau et al. 2006) may emerge due to simpler processes. For instance, prey availability or predator risk might aggregate or disperse individuals (Stanford 1995), as well as biological traits (such as sex, age, kinship, behavioral similarity) may make a subset of individuals more prone to interact within each other than with the rest of the population (e.g., Daura-Jorge et al. 2012). Moreover, individual behavioral variation (e.g., personality; Croft et al. 2003) and social preferences (e.g., familiarity; Kurvers et al. 2013) can influence these relationships. We found some individual social preferences among the Guiana dolphins in Sepetiba, but the overall dynamic nature of their social relationships complicated the identification of boundaries among social modules. At the moment, we can speculate that individual preferences and avoidances underlay, in the broadest sense, the formation of social modules. As more detailed data at the individual level becomes available, one will be able to sort out the contribution of these biological traits in social preferences (e.g., Whitehead and James 2015) that ultimately shape the modular structure of this society.

Conclusions

Our study reinforces that Guiana dolphin societies are dynamic, especially in the largest population where individuals form the largest group. However, we also show that this society is organized into social modules. By weighing the influence of asocial processes, we suggest that social modules are not simply a product of unequal opportunities for individuals to interact but rather that they are formed through social choices. Nevertheless, we acknowledge that the low social differentiation and highly dynamic association characteristics of Guiana dolphins blur the boundaries among social modules, and therefore, it remains unclear to what extent the modular social structure is delineated by individual social preferences. A more comprehensive portrayal of this dolphin society would include individual information, such as variation in sociability and gregariousness or assortativity based on biological traits. In addition, comparisons with other Guiana dolphin populations—which vary markedly in basic social metrics such as group size (e.g., Santos and Rosso 2007)—and other ecologically equivalent species—such as humpback dolphins *Sousa* spp.—would be very informative in the search of common underlying mechanisms shaping societies of delphinids. In all cases, we emphasize the need to take into account the influence of the spatiotemporal contexts in which social relationships take place (Pinter-Wollman et al. 2013)—an ever-changing feature in societies characterized by fission-fusion dynamics.

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Compliance with ethical standards

Ethical statement All procedures performed in studies involving animals were in accordance with the ethical standards of the institution or practice at which the studies were conducted.

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Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

Informed consent Not applicable.

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