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**O uso do espaço influencia as relações do boto-cinza,
Sotalia guianensis?**

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O uso do espaço influencia as relações sociais do boto-cinza, *Sotalia guianensis*?

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Para minha família

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“Em todas as coisas da natureza existe algo de maravilhoso.”

(Aristóteles)

RESUMO

As relações sociais entre os indivíduos de uma população são parte essencial da vida de animais extremamente sociais como os golfinhos. Recentemente, muita atenção tem sido dada às forças formadoras da estrutura social em animais. No entanto, o quadro geral ainda não é claro, e longe de ser trivial. Os sistemas sociais são complexos, amarrados a uma história evolutiva e moldado por várias forças ecológicas e de variação individual. No presente trabalho, foram investigados os padrões sociais da maior população conhecida do boto-cinza (*Sotalia guianensis*), que reside na Baía de Sepetiba, Rio de Janeiro, Brasil. Foram analisados dados de foto-identificação coletados ao longo de um período de seis anos (2005-2011). Os padrões sociais foram descritos utilizando uma gama de análises. Em primeiro lugar, foi descrito o padrão social geral explorando a estrutura da rede social. Em segundo lugar, foi testada se as associações entre indivíduos foram diferentes do esperado ao acaso. Terceiro, foi avaliado como estas associações mudaram ao longo do tempo. Quarto, foi avaliado se o comportamento e uso do espaço varia entre os indivíduos, mediante densidades de Kernel. Finalmente, o uso do espaço foi comparado com a estrutura em larga escala da rede, através do cálculo da sobreposição espacial dos módulos sociais usando um índice generalizado para a distribuição de utilização. Foram identificados 647 indivíduos da população durante o período de pesquisa. Analisamos a rede social formada por 67 indivíduos, todos avistados mais que 5 vezes, divididos em quatro módulos sociais distintos ($Q = 0.13$, 95% CI = 0.06-0.08). Estes módulos foram compostos por indivíduos densamente associados aos outros presentes dentro do mesmo módulo, mas menos ligado ao resto da população (HWI médio observado = 0.211, aleatório = 0.204, $p = 0.020$; CV observado HWI = 1.159, aleatório = 1.117, $p = 0.043$). Foram encontradas evidências de associações de longo prazo na população (SLAR= null > 1000 dias), com associações entre pares durando em média, alguns dias (dyadic LAR = 10,63). Foi encontrado o uso do espaço altamente sobreposto para os indivíduos de todos os módulos para kernel 95% (PHR = 0.72-0.99) e pouco sobreposto para kernel 50% (PHR = 0.19-0.76). Esta sobreposição espacial sugere que há uma preferência por áreas da Baía de Sepetiba, sendo comum para a maior parte da população, mas que cada módulo apresenta um uso de áreas nucleares diferenciado. Foi encontrada para a população de *Sotalia guianensis* da Baía de Sepetiba uma estrutura social com módulos

sociais distintos que sofrem pouca influência do espaço e de mudanças demográficas temporais. A população apresentou um claro padrão de fissão-fusão com associações duradouras e outras rápidas, semelhante ao encontrado em outras populações de delfínídeos, residentes, próximos da costa. O presente trabalho colabora com o entendimento das estruturas sociais de golfinhos e principalmente nas relações sociais dos botos-cinza.

Palavras-chave: Ecologia comportamental, Boto-cinza, *Sotalia guianensis*, estrutura social, Baía de Sepetiba, uso do espaço

ABSTRACT

Social relationships among individuals of a population are an essential part of the lives of extremely social animals such as dolphins. Recently, much attention has been given to the drivers of social structure in animals. However, the overall picture is still not clear, and far from trivial. Social systems are complex, tied to an evolutionary history and shaped by several ecological forces and individual variation. In this study, social patterns have been investigated for the largest known population of Guiana dolphin (*Sotalia guianensis*), resident of Sepetiba Bay, Rio de Janeiro, Brazil. Photo-identification data was collected over a period of six years (2005-2011). The social patterns were described using a range of analyzes. First, the overall social pattern was described by exploring the structure of the social network. Second, it was tested whether the association between individuals were different than would be expected by chance. Third, it was evaluated how social associations may change over time. Fourth, the ranging behavior and space use were estimated using Kernel densities. Finally, space use was compared with the large-scale structure of the network, by calculating the spatial overlap of social modules using a generalized index for the distribution operation. 647 individuals were identified in the population during the studied period. The social network formed by the best-known 67 individuals (observed more than 5 times) was divided into four distinct social modules ($Q = 0.13$, 95% CI = 0.06 - 0.08). These modules were composed of densely connected individuals, which were themselves less connected to the rest of the population (mean HWI: observed = 0.211, random = 0.204, $p = 0.020$; CV HWI: observed = 1.159, random = 1.117, $p = 0.043$). Long-term associations were found in the population, with associations between pairs lasting on average a few days (dyadic LAR = 10.63d). Highly overlapped space use was found for individuals of all modules for Kernel 95% (PHR = 0.72-0.99) and little overlapping for Kernel 50% (PHR = 0.19-0.76). This pattern suggests there are some preferred areas in Sepetiba Bay, which are commonly used by most of the population, but also that each module has slightly more discrete core areas. The social structure found for the population of *Sotalia guianensis* in Sepetiba Bay has distinct social modules, with little influence of space and demographic changes. The population showed a pattern of fission-fusion with both short and lasting associations, similar to that found in other coastal populations of Delphinidae. This study

contributes to the understanding of forces acting on the societies of dolphins and especially in social relations of the Guiana dolphin.

Key-words: Behavioral Ecology, Guiana dolphin, *Sotalia guianensis*, social structure, Sepetiba Bay, social network, space use

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INTRODUÇÃO GERAL

O estudo de redes sociais e suas métricas vêm sendo cada vez mais aplicados com a finalidade de elucidar diversos padrões na estrutura social de populações de mamíferos (e.g. Nishida & Hiraiwa-Hasegawa 1987, Whitehead 2003, Lusseau et al. 2006, Best et al. 2013), aves (Ryder et al. 2008, Shizuka et al. 2014), anfíbios (Venezuela-Sánchez et al. 2014), peixes (Croft et al. 2004) e insetos (Nandi et al. 2014). A teoria de redes é uma abordagem plausível para representar relacionamentos sociais de uma população (e.g. Croft et al. 2008). Recentemente aplicadas às sociedades animais, as redes sociais são representações gráficas das interações sociais entre indivíduos, em geral heterogêneas, dentro de uma população. O estudo da estrutura de uma rede revela o comportamento social de indivíduos de uma população e nos permite inferir os mecanismos que a geram (Krause et al. 2009). Além disso, a posição de um indivíduo em uma rede de interações sociais pode ter importante repercussão na sua aptidão (Krause et al. 2007).

Para entender melhor o comportamento animal é preciso levar em conta múltiplos fatores (Timberg 1963). As redes sociais podem ser aplicadas para responder perguntas a respeito de uma população de animais. Um esforço científico vem sendo feito para entender os mecanismos por trás do padrão de associações e interações sociais (Sih et al. 2009, Pinter-Wollman et al. 2013). Os padrões de interação social interferem em vários aspectos da biologia e ecologia dos organismos, como reprodução, obtenção de recursos, área de vida, transmissão de informação, genes e patógenos (Whitehead 2008). De maneira análoga, a variação individual no comportamento social, o ambiente, o tempo e/ou transmissão de informação entre indivíduos podem igualmente influenciar a estrutura social de uma população (Cantor & Whitehead 2013). Uma pergunta-chave ainda requer resposta: a proximidade física e o uso do espaço definem a estrutura social de uma população?

Essa dúvida está em pauta desde a década de 1980. Madison (1980) encontrou uma relação entre a formação de território do roedor *Microtus pennsylvanicus* e suas associações sociais, na qual fêmeas são extremamente territoriais e mantêm seu grupo social coeso, e próximo ao seu território. Uetz e Cangialosi (1986) encontraram influência de fatores genéticos e ambientais no uso do espaço, escolha de local de teia e

comportamento social de aranhas *Metepeira spinipes*. Recentemente, estas perguntas têm sido abordadas com técnicas estatísticas de análise de rede, por exemplo com andorinhas *Zonotrichia atricapilla* (Shizuka et al. 2014), cangurus *Macropus giganteus* (Best et al. 2014), esquilos-voadores *Glaucomys volans* (Garroway et al. 2012), javalis *Sus scrofa* (Podgorski et al. 2014) e sapos *Rhinoderma darwinii* (Venezuela-Sánchez et al. 2014). Esses trabalhos encontraram relações significativas entre a escolha e o uso do espaço com as escolhas sociais dos indivíduos.

Para cetáceos, trabalhos mais recentes que tratam de estrutura social vem tentando, cada vez mais, explorar a relação do ambiente, demografia, genética e características individuais com os padrões sociais encontrados. Entre eles, podemos citar estudos com golfinho-nariz-de-garrafa *Tursiops spp.* (e.g., Gero et al. 2005, Frére et al. 2010, Randic et al. 2012, Blasi & Boitani 2014, Kopps et al. 2014) nos quais encontramos alto grau de filopatria, uso de áreas sobrepostas, relações sociais fortes e fracas, com vários níveis de associações e até hierarquia entre os diferentes grupos sociais de golfinhos (Blasi & Boitani 2014), mas sem uma relação clara entre a estrutura social e o uso do espaço. Para orcas *Orcinus orca*, que apresentam estruturas sociais matrilineares e clãs distintos, o uso do espaço é fracamente compartilhado, podendo ocorrer inclusive aversão entre grupos diferentes, como ao redor da Ilha de Vancouver (Baird & Dill 1995, Foster et al. 2012). No caso do golfinho-rotador *Stenella longirostris*, estudos nas ilhas do Hawai'i demonstraram a formação de agrupamentos mais fortes e mais ligados às ilhas e locais específicos do arquipélago do que se esperava (Karczmarski et al. 2005). Da mesma forma, também as falsas-orcas *Pseudorca crassidens*, apresentaram preferências pelos arredores de determinadas ilhas e localidades das ilhas havaianas, o que refletiu diretamente na suas relações sociais (Baird et al. 2008).

Uma das populações de cetáceos melhor estudada, a população de *Tursiops aduncus* de Shark Bay, na Austrália, é de imensa importância para o entendimento das sociedades de golfinhos. Em 30 anos de estudos com essa população, descobriu-se que os indivíduos, principalmente machos, formam diversos níveis de alianças sociais, variando na intensidade de associação e interação, de maneira similar apenas às sociedades humanas (Connor & Krützen 2015). Essas associações e a falta delas acontecem mesmo sem a distinção clara de áreas separadas e grande sobreposição do uso do espaço para as “coesões” de machos (Randic et al. 2012) e para os grupos de fêmeas (Frére et al. 2010).

O uso do espaço é uma característica fundamental dos seres vivos, determinado por múltiplos processos que atuam em escalas espaciais e temporais. Ele influencia a estrutura e dinâmica de populações, comunidades e ecossistemas; a evolução e diversidade da vida (Stenseth & Lidicker 1992, Nathan et al. 2008). Muitas populações biológicas ocupam ambientes heterogêneos (Bullock et al. 2002). Para cetáceos, a vida em um ambiente tridimensional com distribuição de alimentos e predadores incertos, sem locais típicos de refúgio, pode influenciar muito na relação entre o uso do hábitat e suas escolhas sociais (Gowans et al. 2008).

As diferentes espécies de cetáceos variam enormemente com relação aos ambientes em que habitam, podendo viver em rios, estuários, ao redor de ilhas, mar aberto; de regiões tropicais aos mares gelados das região polares. Ambientes diferentes influenciam diretamente na evolução de diferentes comportamentos sociais (Gowans et al. 2008). Apesar do aumento considerável de estudos sociais de cetáceos nos últimos dez anos, a relação entre o ambiente e o comportamento social, de forrageamento e pressão de predadores ainda precisa ser avaliada para que possamos entender melhor as forças formadoras das sociedades dos cetáceos (e.g. Connor et al. 2000, Cantor & Whitehead 2013). Estudos sobre estrutura social demandam grande número de reavistagens dos indivíduos (e.g. Whitehead 2008), impossibilitando pesquisas pontuais e impondo desafios logísticos ao estudo de populações não residentes e que vivem longe da costa.

Golfinhos de hábitos costeiros costumam apresentar sistemas sociais com dinâmica de fissão-fusão (Norris et al. 1994, Connor et al. 2000, Lusseau 2006). A dinâmica de fissão-fusão, como revista por Aureli et al. (2008), se refere à variação na coesão social e espacial de um grupo ao longo do tempo. Como esperado para indivíduos com grande mobilidade que habitam um ambiente tridimensional e imprevisível no tempo e espaço (Gowans et al. 2008), botos-cinza *Sotalia guianensis* também apresentam um sistema social com dinâmica de fissão-fusão (Santos & Rosso 2008, Cantor et al. 2012, Lunardi & Ferreira 2013, 2014). Populações com dinâmica de fissão-fusão são socialmente flexíveis: os indivíduos agregam-se por um período de tempo no qual os benefícios da sociabilidade são altos (Connor et al. 2001) ao mesmo tempo em que formam grupos menores, governados por pressões ecológicas e sociais (Dunbar 2003). Essa dinâmica social pode influenciar em muitos aspectos a ecologia dessa espécie. Espera-se que o uso do hábitat, governado pelas

características ambientais e biológicas, influencie diretamente nas escolhas sociais dos indivíduos de boto-cinza. Em uma população residente com grande número de indivíduos (Nery et al. 2008), a divisão em grupos e a dinâmica de fissão-fusão pode ser essencial para minimizar as desvantagens de se viver em grupos nessa área.

No presente trabalho tentamos elucidar a influência do uso do espaço nas escolhas sociais dos botos-cinza da Baía de Sepetiba. O boto-cinza (*Sotalia guianensis*) é uma espécie de golfinho encontrada tipicamente em baías e estuários (Simões-Lopes 1998). Locais com grande produtividade, protegidos de ventos e predadores, de pouca profundidade, com menor salinidade, mas que sofrem grandes mudanças e grandes impactos antrópicos, como é o caso da Baía de Sepetiba (Lopes 2013). A Baía de Sepetiba se localiza a 60km da cidade do Rio de Janeiro (Fig.1), uma das maiores e mais populosas regiões metropolitanas do Brasil, com mais de 12 milhões de habitantes (IBGE, 2014). Ela é uma Baía semi-protégida, grande (560km²), com pouca profundidade (em média, 8 metros). Nela encontramos diversos habitats como mangue, restinga, costão rochoso, praias, ilhas, estuários (Araújo 2004).

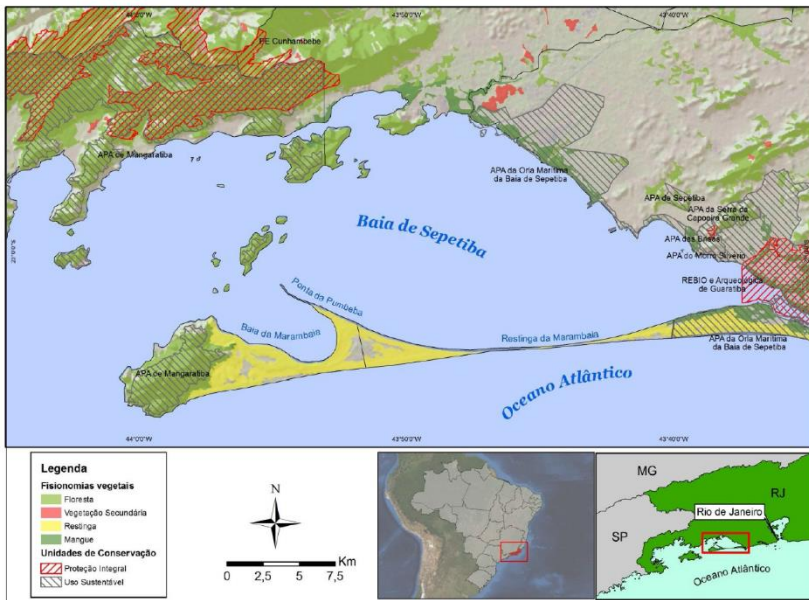


Figura 1: Baía de Sepetiba, sua localização em relação ao Brasil e ao estado do Rio

de Janeiro. Também em destaque suas fisionomias vegetais e Unidades de Conservação (Lopes 2013).

Em Sepetiba, encontramos a maior população conhecida de *Sotalia guianensis*, com mais de mil indivíduos (Flach et al. 2008, Nery & Simão 2012), um extremo para a espécie. Esse fator por si só, demonstra a importância de se estudar essa população e suas particularidades, que provavelmente influenciam tanto sua relação com o espaço quanto suas relações sociais.

Padrões de fissão-fusão são encontrados em diferentes populações de golfinhos (Connor & Krutzen 2015). Esses padrões não devem ser diferenciados de maneira categórica, mas entendidos como uma escala contínua (Gowans et al. 2008; Aureli et al. 2008). Acreditamos que este trabalho contribui com a compreensão dos padrões sociais de pequenos cetáceos de forma analítica, excluindo possível viés espacial e demográfico, a ser comparado com outras populações costeiras de cetáceos, principalmente outras populações de boto-cinza.

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Does Space Use Influence Social Relationships of Guiana Dolphins?

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Abstract

While social relationships of highly social species are generally the products of individual trade-offs of group living, the emergent social structure can be, at least partially, a byproduct of non-social factors, such as the spatio-temporal opportunities for individuals to interact. We investigate if space use influence the social relationships of the individuals of the largest population of Guiana dolphins (*Sotalia guianensis*), which inhabits an estuarine habitat in a protected bay. We explored social patterns of dolphins—from dyadic interactions to the large scale structure of their social network—bearing in mind the use of the bay during six years. We found a society displaying fission-fusion dynamics (with many brief social interactions to long-lasting association across years) and structured into four social modules. The social relationships and modules were unlikely determined by space use, which suggests that they are not simple aggregation of individuals due to local resource availability. While other ecological forces, such as predator avoidance, resources distribution and environmental characteristic may be influencing the associations, our findings add to the recent efforts of accounting for alternative, non-social drivers of social structure in animals.

Keywords: *Sotalia guianensis*, social network, space use, social structure, Sepetiba bay

1. Introduction

How animals explore and navigate the habitat they live in is a central question in ecology (Horne et al. 2008). The space use influence and is influenced by many of behavioral and life-history traits, such as foraging strategies, predator avoidance, group-living, mating systems, social structures and communication (Geist 1974, Emlen & Oring 1977, Macdonald 1983, Ostfeld 1990).

Individual space use is thought to be an output of resource availability (Ford et al. 2000, Steban et al. 2014) and the distribution of others animals (e.g. competitors, predators and social companions) (Campbell 1992, Ford et al. 2000, Connor 2007, Passadore et al. 2014). Competition and social grouping can define space use. Being in the same area can even mean a measure of social interaction for strongly territorial animals with kinship-based social structures such as wolves (Rutledge et al. 2010). For species with high site fidelity, the social context greatly correlates with the use of the habitat (Best et al. 2013, Shizuka et al. 2013, Podorski et al. 2014, Venezuela-Sánchez et al. 2014). Social relationships and space use can be tied and influence each other. Individuals with overlapping home ranges can have more opportunities to interact and so are expected to associate with each other more often than if individuals whose overlap of home ranges are more discrete (Best et al. 2014).

Social structure studies aim to quantify social interactions among individuals to understand how social relationships scale up to large-scale social patterns (Whitehead 2008, Croft et al. 2008). Relationship, in this context, accounts for a succession of associations between two individuals quantitatively and qualitatively, and how this associations acts in respect of both space utilization and time (Hinde 1976). For most social studies on cetaceans, identifying individuals in groups is the most common working proxy for inferring social relationships. Individuals identified in the same social group for a given period are considered socially associated (the 'gambit of group' hypothesis, Whitehead & Dufault 1999). It is very hard to observe and quantify social interactions between individuals of cetaceans simply because they spend most of the time and perform most behaviors underwater. Additionally, cetaceans are highly mobile, they cover many nautical miles in a short period of time, most species inhabit offshore waters and some can dive for very long time (Mann 1999).

Despite such logistical constraints, cetaceans have served as important models for social systems, due to high cognitive capability and behavioral flexibility that confer complexity to their social systems (e.g. Connor et al. 2001, Whitehead 2003, Lusseau et al. 2006, Rendell & Whitehead 2001, Gero et al. 2014). However, many species still lack better knowledge on its social behavior, how to really quantify sociality and the forces acting on it (Gowans et al. 2008, Pinter-Wollman et al. 2013). To better understand how social choices influence on habitat selection and if space use choices influences on social structure we studied a Guiana dolphin (*Sotalia guianensis*) population on southeastern Brazil for 6 consecutive years.

Sotalia guianensis (Van Benéden 1864) is a small coastal dolphin that inhabits estuarine areas on western Atlantic Ocean, from Honduras (Flores & da Silva 2009) to south coast of Brazil (Simões-Lopes 1988). Guiana dolphins are typically found in groups ranging from 2 to 13 individuals (Di Benedetto et al. 2001, Edwards & Schnell 2001, Azevedo et al. 2005, Santos & Rosso 2008). However, in southeastern Brazil, the average group size is higher, from 29 to 32 individuals (Lodi & Hetzel 1998, Lodi 2003, Daura-Jorge et al. 2005, Flach et al. 2008). Flores & Fontoura (2006) reported in southern Brazil even larger group sizes, with most *Sotalia guianensis* encounters ranging from 60 to 80 individuals. The largest population of *Sotalia guianensis* is found on Sepetiba Bay, our study site, with estimations of over one thousand individuals (1,269 individuals Flach et al. 2008; 1,099 individuals Nery & Simão 2012), where large groups with more than a hundred individuals are found consistently (Flach et al. 2008). These large groups tend to merge and split along the day, showing fission-fusion-like dynamics (Aureli et al. 2008) as found in others populations for this species (Santos & Rosso 2008, Cantor et al. 2012).

Here we combine social network analysis with spatial and temporal analysis to evaluate whether the social dynamics of Guiana dolphins is influenced by patterns of space use and demographic effects. The population of Sepetiba is the largest of all known populations of this species, representing a distinctive case. The present work aims for a detailed understanding of the social relationships of Guiana dolphins and the elements influencing on their social structure. We first explored the overall social pattern *via* network, then we tested whether the association between individuals were different than would be expected by chance. Later we evaluated how associations changed over time. Finally, we estimated the use of space and compared with the large-scale

structure of the network, by calculating the spatial overlap of modules using a generalized social index for the distribution.

2. Methods

2.1. Study area

The Sepetiba Bay is a large (526km²) and shallow (average depth of 8m) coastal bay located in Rio de Janeiro state, southeastern Brazil (22°54' - 23°04'S, 43°34' - 44°10'W) (Fig. 1). Although average depth is 8m, there are three dredged channels with profundity of more than 30m. Additionally, between islands, there are few areas that can reach 47m deep, in which there is an influx of cooler waters (Fig. 2) (Simão & Poletto 2002).

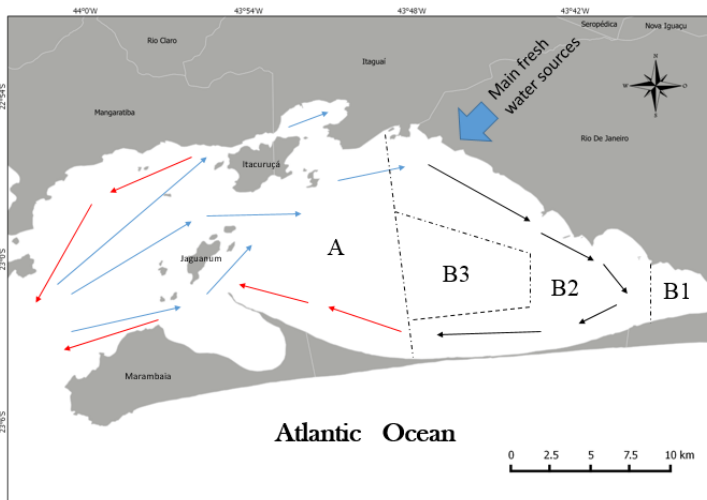


Figura 2: Oceanographic process on Sepetiba Bay, southeastern Brazil. Arrows indicates oceanographic currents: blue arrows indicates lower temperature currents, red arrows indicates higher temperature currents, black transforming currents (Signori 1980). A, B1, B2 and B3 represents different levels of salinity; “A” being the area with the highest salinity (Barcellos 1995).

The bay includes different ecosystems like beaches, islands, rocky cliffs, mangrove and intertidal swamp (Muehe & Valentini 1998). The west part is connected with the Atlantic Ocean, having a predominantly coarse and sandy substratum with presence of many rocky islands. The east area is estuarine, has dominantly muddy substratum with beaches that are rocky, sandy, muddy, and in places, fringed with mangrove vegetation (Fig. 3) (Albiere & Araújo 2010). It is under the influence of nine rivers which are responsible for almost the totality of freshwater inputs, reaching an annual flow of 7.6 million m³ (Lacerda et al. 2001).

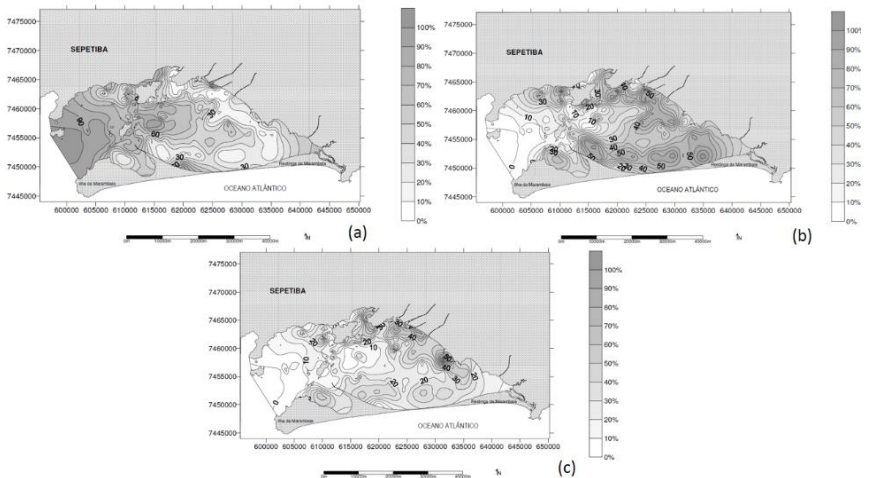


Figura 3: Distribution in percentage of sediments on the sea bottom of Sepetiba Bay, Rio de Janeiro, southeastern Brazil. Darker colors represents higher proportion in the sediment, lighter colors represents lower proportions. From left top to bottom: (a) sand distribution, (b) clay distribution and (c) silt (Souza 2004).

Due to the variety of ecosystems, Sepetiba Bay encompasses great biodiversity and historically has been an important source of fisheries, also nursery and reproduction sites for a number of species (Francioni et al. 2004). For the last 30 years, mostly the northeastern region of Sepetiba Bay, closer to the city of Rio de Janeiro, suffered from fast and unplanned development, augmentation of tourism, overfishing, demographic expansion, implementation of ports and over four hundred industries in the area (Molisani et al. 2004). This led to some environmental issues, including high levels of heavy metals (Lima Junior et al. 2002), fishing stocks extremely reduced, water and air pollution, biodiversity and top

predators loss, eutrophication, oil contamination, deforestation and soil erosion (Neto et al. 2006).

2.2. Data Collection

From August 2005 to July 2011, we carried out 130 boat surveys evenly distributed throughout the years and seasons (Table 1). Four predefined routes were designed to cover the bay; and for each survey a route was arbitrarily chosen. When a group of Guiana dolphin was sighted, we approached slowly and followed the group until we believed all individuals were photographed or for as long as the weather permitted. During the followings, the number of individuals in the group was estimated by experienced researches and geographical position was recorded with a GPS when the group was first approached. We attempted to photograph the dorsal fins of all individuals, with no individual preferences, using a SLR Camera equipped with 100-400mm lenses (more about survey protocols in Flach 2008). Groups were defined as two or more individuals, in close proximity (100m radius) (Irvine et al. 1981).

Tabela 1: Number of group sightings throughout the study period used for social analysis. Only the first sightings in each day of survey was utilized for network and space analysis.

Period	Number of sightings used	Total sightings
06/2005 - 12/2005	9	27
01/2006 – 06/2006	14	49
07/2006 – 12/2006	13	28
01/2007 – 06/2006	15	42
07/2007 – 12/2007	9	30
01/2008 – 06/2008	16	38
07/2008 – 12/2008	3	5
01/2009 – 06/2009	6	11
07/2009 – 12/2009	11	18
01/2010 – 06/2010	12	21
07/2010 – 12/2010	7	23
01/2011 – 06/2011	15	42

2.3. Analysis

2.3.1. Photo-identification

We minimized the probability of recording spurious interactions by analyzing only groups with less than 50 individuals, considering that in large groups individuals are less likely to interact with all members of the group. In most surveys we found more than one group on the same day, but to ensure sampling independence we analyzed only the first group encountered in each day. We photographed 131 groups of dolphins between August 2005 and July 2011. The mean group size was 31 ± 16 individuals.

Photo-identification effort at the sea was 72.5 hours. Individuals were first identified following standard photo-identification protocols (Würsig & Jefferson 1990) followed by an independent analysis with assistance of Darwin fin-recognition software (Stanley 1995). To avoid misidentifications, individuals without distinctive marks were not included in the analysis (Hammond et al. 1990). Over 10,000 photos were analyzed, from which we identified 647 different dolphins.

2.3.2. Social Analysis

We considered all individuals identified in the same group as in association, according to the ‘gambit-of-the-group hypothesis’ (Whitehead and Dufault 1999, Whitehead 2008). We used the half-weight index (HWI) to calculate associations between pairs of dolphins, which ranges from 0 (two individuals never located together) to 1 (two individuals always located together) (e.g. Whitehead 2008).

$$HWI = \frac{x}{\frac{1}{2}(n_a + n_b)} = \frac{x}{x + \frac{1}{2}(y_a + y_b)}$$

In which:

x = numbers of groups in which individual a was seen with b
 y_a = numbers of groups in which individual a was seen but not b
 y_b = numbers of groups in which individual b was seen but not a

A social network is a graphic representation of the associations and relationships of individuals. It contains nodes representing individuals, and links or edges connecting these nodes, representing associations or interactions recorded empirically (e.g. Croft et al. 2008). In our case, the HWI association matrix served as the adjacency matrix of the Guiana dolphin social network: in the network, we represented photo-identified individuals as nodes connected by links whose thicknesses were proportional to the HWI weights.

We tested whether the social network was structured in modules — subsets of nodes that are highly internally connected but weakly connected with the rest of the network — using an algorithm that maximized the modularity metric Q (Newman 2006). A modular structure would represent sets of individuals that interact more often within each other, potentially delineating a ‘social community’ within the population (e.g. Scott 2000, Newman & Girvan 2004). To test the significance of the modularity, we designed a null model that generated a set of 1,000 of theoretical networks of same number of nodes and links, by randomly assigning the HWI among dyads (see Opsahl et al. 2008). For each theoretical network, we calculate the same Q -value to build a benchmark distribution to which the observed Q -value was compared. We considered the empirical network to present a reliable division into modules if empirical Q -value lays outside of the 95% confidential interval of the benchmark distribution (e.g. Manly 1997).

To further describe the network structure, we also calculated three other global network metrics — Cluster Coefficient, Connectance, and Diameter (e.g. Whitehead 1997, Scott 2000, Boccaletti et al. 2006) — that indirectly describe grouping patterns. Cluster Coefficient calculates the probability that two nodes A and B which are connected to a same third node C are themselves connected. In other social networks, this means that “friend of a friend is also a friend” (Newman 2003). Social networks with high Cluster Coefficient contain more triads, are denser. Cluster Coefficients vary between 0.1 - 1.0 and can be a comparative measure between social networks (Liben-Nowell et al. 2005). Connectance measures the proportion of realized links given the total number of possible links in the network. Higher Connectance describes denser network, with shorter paths between the individuals, which is a favorable condition for spread of

quantities in the network, such as information, culture, diseases (Petchey et al. 2009). The Diameter is the length (in number of edges) of the longest path between any two nodes in the network. It measures the distance between two furthest individuals in a network (Newman 2003).

To avoid spurious associations we filtered off the network all individuals that were sighted less than 5 times (Whitehead 2008) during the 6 years of survey. Therefore, we analyzed 67 out of the 647 individuals photo-identified. This represents the social core of the population (Ottensmeyer & Whitehead 2003, Silk et al. 2015). The network was drawn in Gephi software (Bastian et al. 2009).

To test the null hypothesis that individuals associate randomly (e.g. Lusseau et al. 2006; Whitehead 2009), we performed a permutation test. We permuted individuals into groups (20,000 iterations) observed during the same 100-day period (20,000 iterations, 1,000 flips each) constraining observed group size and individual capture frequency, using the swap algorithm adapted by Bejder et al. (1998) and Whitehead (1999). We constrained the permutation within 100-day periods to increase the statistical power of the test and minimize demographic effects, i.e., to avoid that individuals that never used the area at the same time were analyzed. Within this sampling period is reasonable to assume population closure and allowed that the permutation algorithm performed well on our sparse data set. We also applied the same permutation test to individuals assigned to the four social modules we found on the network (see results). The test allowed us to compare associations within and between social modules. In all cases, the presence of long-term preferred associations is suggested by higher standard deviation (SD) and coefficient of variation (CV) of association indices than expected by chance, while short-term 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 with package {igraph} (Csárdi & Nepusz 2006).

2.3.3. Spatial Analysis

We analyzed the ranging behavior of the photo-identified dolphins using the Quantum GIS 2.4. Software (QGis Development Team, 2014). The geographical position of each individual of each of the four social modules

we found on the network (see results) was 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 (minimum 5), we were unable to estimate individual space use with a reliable accuracy. Therefore, we estimated the home range of each social module, lumping 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 et al. 1989). We estimated the core area of a module as the 50% density volume contour, while the 95% volume contours represented the home range.

2.3.4. Home Range effects on Social Network

Gregarious behavior can influence more on the use of space than social preferences if communities are largely spatially segregated (Lusseau et al. 2006, Wiszniewski et al. 2009). 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. To test whether social preferences influenced in the individual's choice of habitat selection we calculated the overlap of space use among social modules.

We used the Utilization Distribution Overlap Index (UDOI) and PHR for the core and home range areas (Fieberg & Kochanny 2005). The first is a generalization of a niche overlap measure and gives the overlap of areas utilized by the groups of dolphins. Values of $UDOI < 1$ indicates less overlap relative to uniform space use, whereas $UDOI > 1$ indicate higher than normal overlap relative to uniform space use (Fieberg & Kochanny 2005). The second estimates the volume under the utilization distribution of a given 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 use a specific, separate region on the studied area.

Different utilization of the bay by different social communities would be expected for the *Sotalia guianensis* population of Sepetiba Bay since, there are daily formation of two groups of over one hundred individuals of dolphins in two different parts of the bay; one normally located on the entrance of the bay and other on the interior (Flach et al. 2008; Dias et al. 2009). Furthermore, individuals, while on these large groups, showed preference for either the bay interior or entrance while, having been recorded continuously in only one of the areas (Flach unpublished data, pers. comm. 2014).

2.3.5. Temporal Patterns

An important aspect of social structure is the temporal patterns of relationships and if the social structure encountered is stable along the survey period. Whitehead (1995) introduced a series of analysis to describe how associations change over time. Temporal context offers good insight on how the social relationships of individuals are structured. Relationships are time-dependent and can change during different periods of time, normally decreasing in strength over time. To evaluate temporal stability of associations we calculated Standardized Lagged Association Rate (SLAR) including all individuals. Standardized Lagged Association Rate accounts for the case when not all true associates of an individual are recorded during a sampling period (Whitehead 2008), what is probably the case for this large *S. guianensis* population. 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).

We compared the observed SLAR with the null expectancy in which individuals associate randomly. The standardized null association rate is the inverse of the population size minus one, which does not change with time lag (Whitehead 2008). Null association rates happen when there is no relationship between two associations; therefore, the time taken to relationships on the population to decay and be equal the null association rate is a good measure of the combination of social and temporal patterns of the social network. Moreover, different patterns of fission-fusion dynamics of the population can be inferred by temporal analysis (Whitehead, 2008). SLAR (and null and intermediate rates) were plotted

continuously against time lag, using a moving average method to improve visualization (Whitehead 2008). Different moving average of potential associations over the lagged association were tried to smooth the curve. Spatial analyses were performed on Socprog 2.5. (Whitehead 2009).

We fitted theoretical exponential decay models to the observed SLAR, selecting the most parsimonious with quasi-Akaike Information Criterion (QAIC, Whitehead 2007), to account for the over dispersion of the data (Burnham & Anderson 2002). The fitted models were the following. SLAR1: $g' = a$. No change in association rate with lags of one sampling period or more. This could represent the “closed, non-interacting units” pattern, in which association persists throughout the study. SLAR2: $g' = a.e^{-bt}$. This indicates casual acquaintances in a large population, possibly including rapid disassociation. The duration of association is of the order of $1/b$, and may re-associate later. SLAR3: $g' = a + c.e^{-bt}$. Associations rates fall with time lag and then level off; the duration of associations is of the order of $1/b$, and if there is no rapid disassociation, then the gregariousness is $1/(a + c)$, and, in the case of permanent units that temporally group, the typical size units is about $1 + a/(a + c)^2$. In this model, associations typically endure for longer periods. SLAR4: $g' = a.e^{-bt} + c.e^{-dt}$. There are two levels of disassociation, perhaps the fission/fusion of nearly permanent social associations forming and segregating, into and out of groups, or leaving the area/dying.

In open populations, individuals can migrate and immigrate, so population composition can change over time and influence social dynamics. To test if there were many changes in our population during the period of the study a turnover analysis was made based on Whittaker’s community turnover. We split the survey period in smaller periods of 36, 18, 9, 6 and 4 months and compared the average turnover of the population for each period with the null expectancy (Cantor et al. 2012).

3. Results

3.1. Social Analysis

We found a differentiated and highly connected social network with four social modules (Figure 2) ($Q = 0.13$, 95% CI = 0.06 - 0.08). The weighted clustering coefficient ($CC_w = 0.589$) and connectance ($d = 0.466$) which varies from 0.1-1.0 were high. Overall, the mean and coefficient of variation (CV) of the empirical association indices was higher than expected by chance (Mean observed HWI = 0.211, random = 0.204, $p = 0.020$; CV observed HWI = 1.159, random = 1.117, $p = 0.043$).

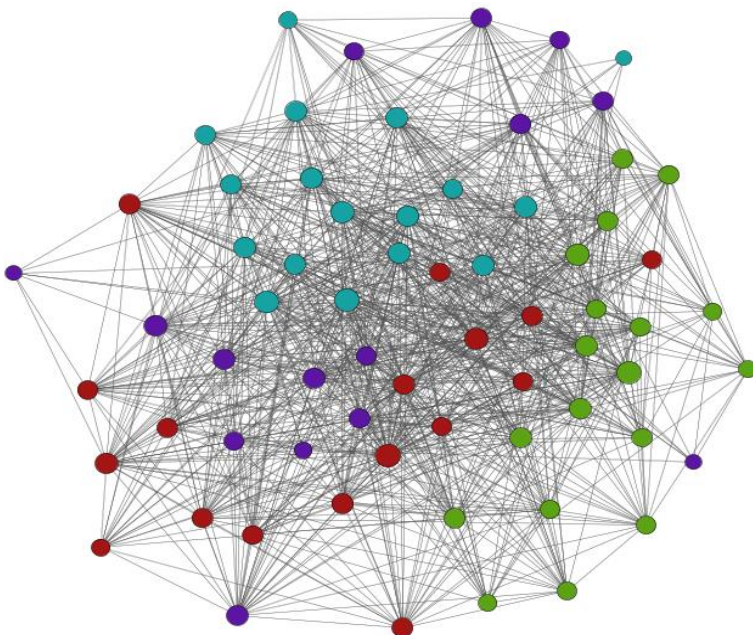


Figura 4: Social network of Guiana dolphins *Sotalia guianensis* from Sepetiba Bay. Nodes represent individuals, edges represent associations. Size of the nodes represents their *degree*: larger nodes represents individuals with higher *degree*, and smaller nodes with lower *degree*. Social modules were represented in different colors: module 1 (red), module 2 (green), module 3 (blue), module 4 (purple).

The permutation test within each social module suggested short-term associations within the module 1, since the observed mean associations (HWI) were significantly lower than the expected by chance for module 1 (Module 1: mean HWI = 0.10309 < 0.10746, $p = 0.0359$; module 2: mean observed HWI = 0.11267, random = 0.11287, $p = 0.4582$; module 3: mean

observed HWI = 0.06949, random = 0.07147, $p = 0.1310$; module 4: mean observed HWI = 0.12274, random = 0.12242, $p = 0.5655$).

3.2. Space Use *versus* Social Preferences

There was great overlap in the 95% Kernel Density Estimations among all four communities and variable overlap in the 50% KDEs core areas (Fig. 3). The total ranging of the social modules was highly overlapped (PHR 95% varying from 0.72 – 0.99, UDOI 95% varying from 0.95 - 1.59) (table 2 and table 4), while there were less overlap of core areas (PHR 50% varying from 0.19 – 0.76, UDOI 50% varying from 0.16 – 0.36) (table 3 and table 5). This pattern can also be observed on the map plotting with the kernel densities (Figure 3).

Tabela 2: Volume under the Utilization Distribution of all individuals of a giving module i that is inside the home range of another module j (i.e., the probability to find an animal of the module i in the home range of j). Numbers 1 to 4 represents the social modules found for the social network of *Sotalia guianensis*.

PHR 95%			
Module	1	2	3
2	0.7703		
3	0.8207	0.9506	
4	0.9661	0.9923	0.9910

Tabela 3: Volume under the Utilization Distribution of all individuals of a giving module i that is inside the core are of the module j (i.e., the probability to find an animal of the module i in the core are of the module j). Numbers 1 to 4 represents the social modules for the social network of *Sotalia guianensis*

PHR 50%			
Module	1	2	3
2	0.2177		
3	0.2895	0.5701	
4	0.5235	0.7649	0.7127

Tabela 4: Utilization Distribution Overlap Index 95%, a measure similar to the Hurlbert index of niche overlap that represents the overlap of home range. Numbers 1 to 4 represents the social modules for the social network of *Sotalia guianensis*. Values of $UDOI < 1$ indicates less overlap relative to uniform space use, whereas $UDOI > 1$ indicate higher than normal overlap relative to uniform space use

UDOI 95%			
Module	1	2	3
2	0.9891		
3	1.0624	1.4885	
4	1.2939	0.9118	0.9637

Tabela 5: Utilization Distribution Overlap Index 50%, a measure similar to the Hurlbert index of niche overlap that represents the overlap of core area. Numbers 1 to 4 represents the social modules (Newman Q) for the social network of *Sotalia guianensis*. Values of $UDOI < 1$ indicates less overlap relative to uniform space use, whereas $UDOI > 1$ indicate higher than normal overlap relative to uniform space use.

UDOI 50%			
Module	1	2	3
2	0.1799		
3	0.2354	0.2773	
4	0.3049	0.1667	0.2163



Figura 5: Kernell densities for each of the four social modules in Sepetiba Bay. Dots on maps represents the locations of each group of animals recorded, colors of

the dots are the same from the social network: module 1 (red), module 2 (green), module 3 (blue) and module 4 (purple) (from up left to right: module 1, module 2, module 3, module 4). 50% kernel is shown in red, representing the core distribution of the modules. 90% kernel is shown in blue.

3.3. Temporal Patterns

The standardized lagged association rates were significantly higher than expected by chance, for at least a period of 1,000 days. The overall probability of association was low and clearly decay over time (Fig. 4). The most parsimonious model describing this decay was the SLAR 2, suggesting that the duration of association is of the order of 10.36 days ($1/b = 0.1036$). The associations are brief, dubbed as “casual acquaintances” and “rapid dissociations”, No other model provided strong support to the observed SLAR, as shown by the Δ QAIC and QAIC weights in Table 6.

Tabela 6: Theoretical exponential decay models fitted to empirical Standardized Lagged Association Rates (SLAR) found for individuals of *Sotalia guianensis* in Sepetiba Bay from 2005-2011, ranked by the lowest Akaike Information Criteria (QAIC) values. The Δ QAIC, the QAIC weight and model likelihood indicate the relative support for each model.

Model type	QAIC	Δ QAIC	QAIC weight	likelihood
$g' = 0.0042219 \cdot e^{-0.0042219t}$	6477.97	0.00	0.99	1.00
$g' = 0.0034546$	6488.09	10.12	0.01	0.01
$g' = 0.0034437 + 111.647 \cdot e^{-9.64888t}$	6490.18	12.21	0.00	0.00
$g' = 0.0042655 \cdot e^{-0.00035412t} + (-0.24558) \cdot e^{-1.0871t}$	6543.95	65.98	0.00	0.00

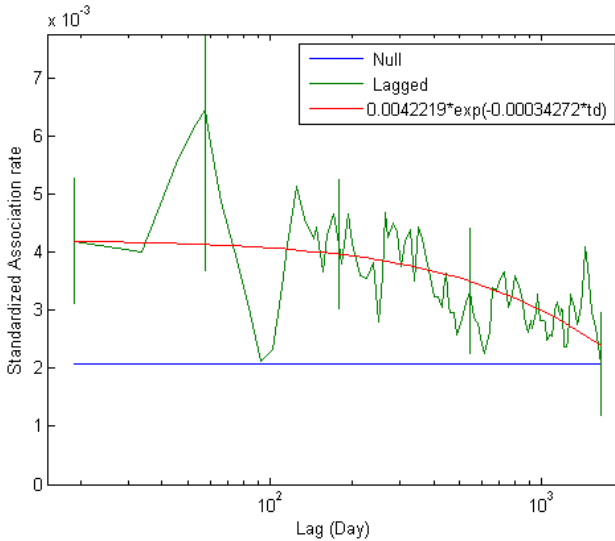


Figure 6: Lagged association rates. Best fitted model was Casual Acquaintances (SLAR2, Table 4). The blue line represents the Null association rates, green line represents the empirical lagged association rates, with vertical lines representing standard errors estimated by a jackknife procedure, and red line represents the fitted model.

We performed a measure of turnover based on Whittaker's community turnover and obtained changes of the population composition among subunits of the dataset (Fig.5). We found that on average the population composition changed significantly less than expected by chance, especially in short periods of time. This is clear for periods of as long as 18 months, but probably holds true for the entire study, since the turnover for 36 months is still very low. Therefore, Guiana dolphins used the study area for long periods and theoretically all individuals in the population had the opportunity to associate with each other. If all individuals were part of the population during the entire study, it is very unlikely that demographic effects like migration, emigration, deaths and births could explain the large-scale structure of the social network.

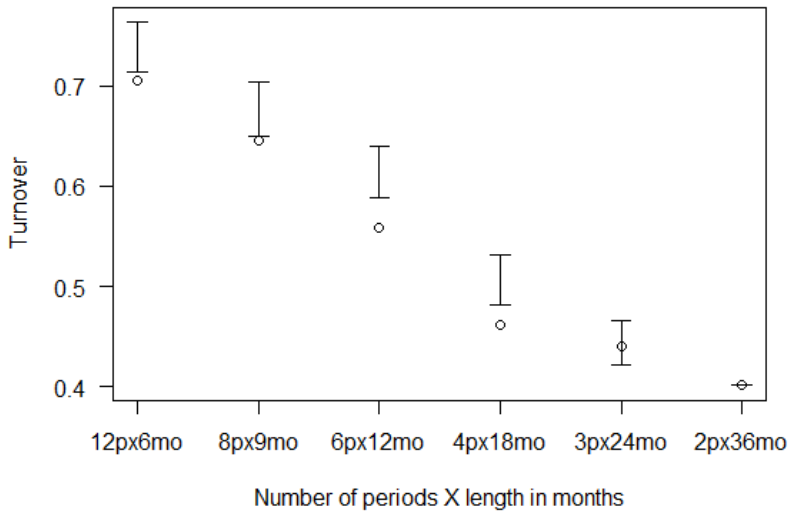


Figura 7: Population turnover for different periods and subsections of time. The full survey period (72 months/ 6 years) were divided in smaller subsections (12 periods of 6 months, 8 periods of 9 months, 6 periods of 12 months, 4 periods of 18 months, 3 periods of 24 months and 2 periods of 36 months) to evaluate demographic changes on the population.

4. Discussion

Understanding the impact of ecological patterns on animal social choices and behavior is essential in order to identify factors that may have influenced on the formation and evolution of sociality. Our findings suggest that space use may not have such a strong impact and fails to explain most social aspects of populations of dolphins, highly mobile and social animals, which experience a tridimensional environment. We found a socially differentiated population of Guiana dolphins in Sepetiba Bay, southeastern Brazil, in spite of environmental and demographics effects.

Our findings show that the Guiana dolphin population in Sepetiba Bay lives in a society with fission-fusion dynamics in which the associations are brief, dubbed as “casual acquaintances” and “rapid dissociations”, which are usually characteristic of larger populations and highly dynamic social systems (Whitehead 2008). We found a highly connected society in comparison to other dolphin populations (Lusseau et al. 2006; Wisznieksi et al. 2009), further structured into four distinct social modules. This suggests that despite the peculiarities of this population, socially it is similar to other resident, estuarine and coastal populations of small cetaceans, with preferred and avoided associations composing a system with fission-fusion dynamics (Connor 2007; Randic et al. 2012; Yi-Jiun et al. 2013).

A highly overlapped space use for the *Sotalia guianensis* population in Sepetiba Bay is similar to other populations of this species (Babitonga Bay: Schulze, 2012; Norte Bay: Wedekin, 2007). Even in such large bays, Guiana dolphins utilize the space in a heterogeneous way. Indeed, the population of Sepetiba Bay has some preferred areas, mostly close to the islands. Even though the Bay is very shallow with eight meters of depth on average, these areas are 10 meters deep or more (Simão & Poletto 2002). *Sotalia guianensis* feeds on many different fish species and different types of prey, such as squid and shrimps (Lopes et al. 2012). Nonetheless, diet preferences have been shown favoring demersal fish species (di Benedetto 2000; Rossi-Santos & Wedekin 2006; Cremer et al. 2012) which could explain their constant presence in deeper areas of Sepetiba Bay and their preference for those areas. Additionally, it has been observed this species around islands with rocky coast as a barrier for herding fish schools (Cremer 2000, Rossi-Santos & Flores 2009, Santos 2010), thus these can be important areas for the dolphins. Furthermore, deeper areas have influx of cooler water by cooler currents (Fig. 2). These areas can represent channels for fish entrance in the bay, since Sepetiba Bay is an important area for fish reproduction (Francioni et al. 2004) and cooler water can also be important for dolphin's thermoregulation (Yeates & Houser, 2008).

Fully aquatic marine vertebrates that feed on ephemeral resources have sensory detection ranges limited by seawater and experience extreme variability in food supply (Sims et al. 2008). We suggest that frequent large patchy schools of fish inside the bay (Araújo et al. 2004) could support the formation of large groups. Also, in fission-fusion societies experiencing

patchy environments, foraging together can be more advantageous and efficient (Ramos-Fernández et al. 2006). On the other hand, if groups have a larger number of possible foraging patches, then it would always split when social connections are weak. In our study we recorded only smaller groups that represent a fission from large aggregations; this stage could inform about the fission mechanisms (Gowans et al. 2008). The dynamic system between social network and patterns of fission-fusion could explain why in the same population the lag over which groups split can last from hours to days. Fission and fusion duration differences between dyads is expected. Individuals have different social needs influencing on the strength of social relationships. Some other factors such as recognition and memory of social relationships may also be important in the fission-fusion patterns. Indeed, species such as cetaceans and primates display stable and complex relationships combined with a large neocortex size (Marino et al. 2007). Fission-fusion dynamics found for Guiana dolphins in Sepetiba bay is similar to what is found for Dusky dolphins (*Lagenorhynchus obscurus*) in Argentina's coast in which large groups are found for maximize predation, while smaller groups are also found most of the daytime period (Würsig & Würsig, 1980).

Wells et al. (1987) suggests that habitats protected from open oceans may be composed of small populations of dolphins with site fidelity and limited movement patterns. This does not necessarily mean that all members of the population are present in the area all times (Würsig and Harris 1990). Dolphins may roam, most commonly sub adults (Wilson et al. 1999) and males (Wells et al. 1987), and there can be varying degrees of site fidelity, resulting in resident and transient animals (Weller and Würsig 2004). Our turnover analysis suggest that for smaller periods than 18 months the population did not varied much in its composition. That lack of continued individual's exchange in Sepetiba population for its closest, almost contiguous population, in Ilha Grade's Bay, Rio de Janeiro state has already been noted genetically (Hollatz et al 2011) and has also shown significant differences for diet (Bisi et al. 2013), feeding tactics (Oliveira et al. 2013), contaminants (Bisi et al. 2012) and whistles characteristics (Andrade et al. 2014). Combined with the clear spatial overlap, we suggest that all individuals in the population had the possibility of associate with all other individuals in the population (although there were probably transient individuals, we restricted our analyses to only individuals seen more than 5 times to minimize their effect in the social pattern). Moreover, our temporal analysis and permutation tests corroborate the expected fission-

fusion dynamics, with mostly brief associations but some lasting for longer periods. Despite the clear spatio-temporal overlap of opportunities to interact, there seem to be a distinct substructure within this population, with individuals associating more often with subsets of the population. Since non-social demographic effects are unlikely explanation for the large-scale structure of this population (e.g. Cantor et al. 2012), we suggest that other social drivers can be at play.

Personality can be a social driver and influence in social relationships (Sih et al. 2009; Wilson et al. 2013). Namely, Croft et al. (2003) have found that personality of guppy fishes (i.e. being shy or not) affected their associations. Familiarity can also account for some social preferences. It is logical to think that individuals that associate and interact more often will continue to do so constantly if it reflects fitness benefits (Kurvers et al. 2013). Further, female bottlenose dolphin (*Tursiops aduncus*) population in Shark Bay has been investigated in the account of home range, kinship and sociality (Frère et al. 2010). Although home range and sociality influenced on social relationships, they found individuals that did not associate at all, even having 100% home range overlapped. That shows that social advantages and kinship can have a more meaningful effect on social preferences than shared space use. We suggest that future studies should always take into consideration not only the influence of space use, but also temporal aspects of social relationships, particularly in the case of societies that experiment group splitting/joining events in a fission-fusion-manner, on multiple time scales.

CONCLUSÃO GERAL

Golfinhos vivem em grupos sociais fluidos, com uma grande variedade de estratégias sociais. No presente trabalho encontramos na maior população de botos-cinza conhecida, uma sociedade com dinâmicas de fissão-fusão, em que há preferências sociais, formando quatro grupos sociais distintos, com associações duradouras para grande parte do período de pesquisa, mas que também forma associações fluídas e não tão fortes, em períodos de tempo mais curtos, constantemente.

Não foi encontrada uma relação da estrutura social e o uso do hábitat, quando se tratando das áreas mais utilizadas pela população de botos da Baía de Sepetiba, uma vez que, a área utilizada pelos grupos sociais se sobrepôs quase que completamente. Essa sobreposição de hábitat está muito relacionada às preferências claras de uso de habitat pelos botos-cinza. Apesar da Baía de Sepetiba ter mais de 500 km², os *Sotalia guianensis* não a utilizam homogeneamente, apresentando preferência por áreas mais profundas e mais próximas das ilhas, o que também é verdade para outros locais, com outras populações da espécie, como a Baía de Paraty (Lodi 2003), Baía de Babitonga (Cremer 2000) e Baía de Norte de Florianópolis (Wedekin et al. 2007). Talvez as diferenças de uso do espaço pelos módulos sociais sejam mais importante nos núcleos de suas áreas de vida, aquelas mais utilizadas pelos grupos. Sugerimos mais investigações sobre as preferências espaciais dos indivíduos da Baía de Sepetiba, com mais dados geoespaciais, para um melhor esclarecimento sobre essa relação.

De maneira geral, as relações sociais dos botos-cinza *Sotalia guianensis* encontradas não são um simples reflexo de questões de uso do espaço ou demográficas. Provavelmente, as relações sociais para essa espécie, como para outras espécies de golfinhos, são um fator fundamental e de extrema importância para a sobrevivência e aptidão individual. As fortes relações e comportamentos sociais são importantes para encontrar e capturar presas, além da proteção contra predadores e transmissão de conhecimentos. Dessa maneira, as vantagens em se manter associações a longo prazo, pode influenciar diretamente em vantagens individuais, sobrepondo simples questões geográficas ou demográficas.

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