UNIVERSIDADE FEDERAL DE SANTA CATARINA
CENTRO DE CIÊNCIAS BIOLÓGICAS
DEPARTAMENTO DE ECOLOGIA E ZOOLOGIA
PROGRAMA DE PÓS GRADUAÇÃO EM ECOLOGIA

MAURICIO NEVES CANTOR MAGNANI

MODELAGEM DA DINÂMICA POPULACIONAL E SOCIAL DE *SOTALIA GUIANENSIS* (CETACEA: DELPHINIDAE)

Florianópolis, SC, Brasil

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“Modelagem da dinâmica populacional e social de Sotalia guianensis (Cetacea: Delphinidae)”

por

Maurício Neves Cantor Magnani

Dissertação julgada e aprovada em sua forma final pelos membros titulares da Banca Examinadora (Port. 07/PPGECO/2011) do Programa de Pós-Graduação em Ecologia - UFSC, composta pelos Professores Doutores:

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“A curva é o caminho mais agradável entre dois pontos”

Mario Quintana

RESUMO

Sistemas complexos têm fascinado cientistas com sua auto-organização e propriedades emergentes. Este é um estudo em longo prazo de dois aspectos de um sistema biológico auto-organizado: a dinâmica populacional e social de *Sotalia guianensis*, um delfinídeo endêmico do oeste do Oceano Atlântico. A população de boto-cinza que habita o Banco dos Abrolhos, costa leste do Brasil, oferece-se como uma boa oportunidade para modelagem de tais dinâmicas, através do tempo e espaço. Isso porque (1) o monitoramento sistemático estende-se por mais de oito anos (2002-2009), tornando evidentes mudanças demográficas de uma população aberta; e (2) porque a área de estudo abrange um hábitat altamente heterogêneo, em um gradiente de águas estuarinas internas a recifes de coral distantes da costa, o que torna a estratificação do uso do hábitat uma hipótese plausível. Em suma, este estudo tem um objetivo duplo: abordar como a população muda ao longo do tempo, fornecendo uma série de estimativas de parâmetros demográficos; e como estas mudanças afetam a estrutura social, do nível individual aos padrões da rede de interações da população. Primeiramente, o experimento de longo-prazo de marcação-recaptura (Cormack-Jolly-Seber e Desenho Robusto de Pollock) revelou uma população pequena, composta por indivíduos residentes e que temporariamente deixam ou passam pela área de estudo. Taxas de sobrevivência foram altas e constantes, o que é esperado para animais cuja expectativa de vida é muito maior que a duração do estudo. Estimativas de abundância flutuaram, possivelmente devido ao balanço entrada-saída de indivíduos, mas nenhuma tendência foi detectada. O esforço de amostragem atual apresentou alta probabilidade de detecção de declínios abruptos, uma situação mais confortável que a muitas outras populações de cetáceos. Embora ainda não sensível a variações sutis, o monitoramento poderá identificá-las com esforço adicional plausível (mais três anos). Estas mudanças populacionais encontraram-se refletidas no padrão de interações sociais. A partir da sugestão de um modelo conceitual de topologia de redes sociais de delfinídeos, uma abordagem espaço-temporal testou a estrutura da rede social de *S. guianensis*. Esta foi organizada em subconjuntos de indivíduos densamente conectados. O uso do espaço não pode ser atribuído à emergência destes três módulos. Por outro lado, o *turnover* de indivíduos na população foi o fator determinante da separação temporal das interações sociais em módulos. Dentro da escala temporal do *turnover*, a população seguiu uma dinâmica de fissão-fusão, caracterizada pela maioria das interações casuais e poucas associações preferidas. Os principais produtos do trabalho são como seguem: (1) Foi atestado um corpo analítico robusto, baseado em modelos de população aberta e fechada, para estimativa de diversos parâmetros demográficos baseado em dados de foto-identificação; (2) Fica salientado que fatores não-sociais podem afetar consideravelmente redes sociais não-humanas, portanto, devem ser levadas em consideração para um retrato fidedigno de sociedades com dinâmica de fissão-fusão. Tais resultados se baseam no tempo como maior fator de causa de mudança e auto-organização deste sistema complexo. Os mesmos podem inspirar pesquisa adicional, que terá implicações tanto aplicadas quanto teóricas. No primeiro caso, as análises demográficas podem ser aplicadas às demais populações de *S. guianensis*, para permitir comparação padronizada futura. Tal esforço conjunto permitirá uma definição adequada do *status* da espécie e, portanto, aperfeiçoamento dos esforços de conservação. Por fim, o modelo conceitual de redes sociais pode gerar novas hipóteses testáveis. Reconhecer os determinantes da topologia das redes sociais é um importante passo na identificação dos mecanismos atuando nos sistemas sociais. Este esforço contribui, em última instância, para abordar como características ambientais e biológicas têm interagido, moldando as diversas estruturas e dinâmicas sociais encontradas em Delphinidae.

Palavras-chave: dinâmica populacional, marcação-recaptura, tendência populacional, redes sociais, organização social, sociedades não-humanas, *Sotalia guianensis*, Banco dos Abrolhos.

ABSTRACT

Complex systems have fascinated researchers for their self-organization and emergent properties. Here, I present a long-term study of two aspects of a biological self-organizing system: the population and social dynamics of *Sotalia guianensis,* an endemic delphinid of western Atlantic Ocean. The population of Guiana dolphins in the Abrolhos Bank, eastern Brazil, offers a fine opportunity for modeling such dynamics through the time and space. This is because (1) the systematic monitoring spanned for eight years (2002–2009) making demographic changes of an open population evident; and (2) the studied area encompassed a highly heterogenic habitat, in a gradient from protected inner river to offshore coral reefs, which makes a stratification of the habitat use a plausible hypothesis. In summary, this study has a twofold aim: to address how the population changes, providing a set of demographic parameter estimates, and how such changes affect the social structure, from pairwise association level to the whole population network patterns. Firstly, the long-term mark-recapture experiment (Cormack-Jolly-Seber and Pollock's Robust Design) revealed a small population, comprised of resident dolphins and individuals that temporarily leave or pass through the study area. Survival rates were high and constant, expected for animals whose life spans extend the study duration. Abundance estimates fluctuated, possibly due to balance of additions and deletions, but were no trend was detected. The current monitoring effort had high probability of detect abrupt population declines, which is a better situation than that for many other monitored cetacean stocks. Although not sensitive yet to subtle declines, the monitoring would identify such trends with feasible additional effort (additional three years). These population changes were found reflected in the patterns of social interaction. A conceptual framework for social network topology of delphinids was suggested, and had predictions tested by combining spatial, temporal and demographic approaches. The social network of Guiana dolphins was structured into a modular architecture as predicted, and the individuals' space use overlap could not be assigned as a major force driven such topology. However, the turnover of individuals in the population has temporally split the associations into the three network modules. Within the turnover temporal scale, the population followed a fission-fusion dynamics, as characterized by most fluid acquaintances and few preferred associations. Therefore, the principal outcomes of this study are as follows: (1) a robust baseline, based on open and closed population modeling, for estimating several demographic parameters was further attested to photo identification data; (2) It was highlighted that non-social factors can greatly affect non-human association networks, and should be accounted for an apposite portrayal of societies with different degrees of fission-fusion dynamics. Such results pointed the time as one of the major factors affecting the self-organization of our studied complex system. They also might inspire further research, which has both applied and theoretical implications. On the former, the suggested demographic analytical guideline may be applied to other *S. guianensis* populations to allow further comparisons. Such synergistic efforts will allow a reliable definition of conservation status of this species, and optimize conservation efforts. Finally, the theoretical framework of social networks may encourage new working hypothesis. Recognizing determinants of network topology is an important step towards the identification of mechanisms driving social systems. This effort, ultimately, contributes to address how environmental and biological characteristics have interacted and shaped the diversified social structure and dynamics of Delphinidae.

Key words: population dynamics, mark-recapture models, social network, social organization, non-human societies, *Sotalia guianensis*, Abrolhos Bank.

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INTRODUÇÃO GERAL

Os sistemas complexos, tanto físicos quanto biológicos, têm fascinado cientistas por sua auto-organização e propriedades emergentes (Amaral & Ottino 2004). Seu estudo é intrigante, seja pelo entendimento das forças internas que conduzem à formação de padrões no sistema (Camazine *et al.* 2001) ou pelos mecanismos externos a que eles se adaptam (Amaral & Ottino 2004).

Uma população animal é um exemplo de sistema biológico complexo, moldado por diferentes forças interagindo ao longo do tempo. Entender a estrutura deste sistema requer respostas a duas questões básicas: quantos elementos compõem o sistema; e como eles interagem e se organizam. Estes questionamentos nos levam à descrição da estrutura populacional e social, respectivamente. Um dos caminhos para tal descrição é partir de um modelo, um processo inerente ao pensamento científico e comum a toda inferência feita em ecologia (Kéry 2010).

Experimentos de marcação-recaptura têm sido comumente utilizados para descrever a estrutura e dinâmica populacional de diversos *taxa* (*e.g.*, Schaub *et al.* 2001, Bjorndal *et al.* 2003, Bradshaw *et al.* 2003, Bailey *et al.* 2004). Classicamente, abundância tem sido estimada mediante modelos de população fechada (Otis *et al.* 1978), que assumem uma situação estática. A abordagem mais realista dos modelos de populações abertas leva em consideração mudanças temporais no tamanho populacional, como o balanço entre entrada (nascimento, imigração) e saída de indivíduos (morte, emigração) (Lebreton *et al.* 1992), principalmente para estimar taxas de sobrevivência. Ao combinar as duas abordagens, é possível estimar abundância de maneira acurada a partir de modelos de população fechada e assim como a sobrevivência, a partir de modelos de população aberta (Pollock 1982). Além disso, probabilidades de emigração temporária podem ser obtidas baseando-se no fato de que indivíduos da população podem estar indiponíveis para captura em qualquer momento do estudo (Kendall *et al.* 1997).

Já o estudo da organização social tem se beneficiado da teoria de redes complexas como uma das promissoras ferramentas de descrição e quantificação precisa de padrões (veja revisões: Krause *et al.* 2007, Croft *et al.* 2008, Wey *et al.* 2008). Alavancado por avanços na mecânica estatística (Albert & Barabási 2002), a teoria de redes têm guiado uma recente e extensiva busca por padrões em redes ecológicas, tanto de comunidades (*e.g.* Bascompte 2009) quanto de populações (*e.g.*

Araújo *et al.* 2010). Formalizando a ligação entre comportamento individual e processos populacionais, explorar a estrutura de redes sociais permite, portanto, extrair detalhes da estrutura social de sistemas altamente dinâmicos e heterogêneos (*e.g.* Lusseau 2003, Croft *et al.* 2004).

O conhecimento detalhado das dinânicas populacional e social da maioria das espécies de mamíferos marinhos continua incompleto. Isto se dá em especial devido às dificuldades logísticas que tornam seu estudo em ambiente natural desafiador, custoso e lento (Taylor & Gerrodete 1993). Embora a dinâmica de algumas populações de cetáceos tenha sido extensivamente estudada, estas se restringem principalmente à ambientes costeiros (*e.g.* Verborgh *et al.* 2009, Ramp *et al.* 2010) e apenas recentemente têm sido aplicados métodos aperfeiçoados que levam em conta uma série de variações naturais (*e.g.* Currey *et al.* 2009, Silva *et al.* 2009). Consequentemente, muito das informações demográficas disponíveis apresentam baixa precisão, o que interfere no poder de detecção de tendências populacionais (Taylor *et al.* 2007). Pelo mesmo motivo, a organização social é um tema que tem sido explorado mais recentemente, após o acúmulo de dados de estudos em longo prazo. Estes revelam a ordem Cetacea como altamente heterogênea em relação a este aspecto (veja Connor *et al*. 1998, Mann *et al*. 2000). As interações sociais nesta Ordem oscilam entre o instável e o estável; as estruturas sociais compartilham características com mamíferos de alta complexidade cerebral (primatas, e.g. Würsig 1978, Wrangham 1980; e proboscídeos, e.g. Weilgart *et al*. 1996), e estão sujeitas às restrições ecológicas experimentadas por alguns mamíferos terrestres (artiodáctilos, e.g. Jarman 1974; e carnívoros, e.g. Packer *et al*. 2000).

Sotalia guianensis P.J. Van Bénedèn é uma das espécies de delfinídeos que permanece como uma lacuna no conhecimento das dinâmicas populacional e social de cetáceos. Ocorre principalmente em águas rasas e costeiras e em estuários da costa Atlântica da América do Sul, a partir do sul do Brasil (27º35'S: Simões-Lopes 1988) ao nordeste da Nicarágua (Carr & Bonde 2000) e possivelmente Honduras (15°58'N, 79°54'W: Flores & da Silva 2009), costa Atlântica da América Central, provavelmente de maneira descontínua (Borobia *et al.* 1991), como sugerem as áreas de vida relativamente pequenas (*e.g.* Flores & Bazzalo 2004). Estudos sobre a espécie focam-se predominantemente na biologia geral (*e.g.*, Santos *et al.* 2001, Azevedo *et al.* 2004, Wedekin *et al.* 2007) e comportamento (*e.g.*, Daura-Jorge *et al.* 2005, Filla & Monteiro-Filho 2009).

Alguns destes aspectos, como comportamento alimentar e reprodutivo, fornecem subsídios para inferência de possíveis mecanismos responsáveis por flutuações naturais nos parâmetros demográficos e na determinação de padrões de sociabilidade. Eles podem, em última instância, influenciar o balanço entrada-saída de indivíduos da população e o balanço custo-benefício da formação de grupos. Por exemplo, sabe-se que *S. guianensis* consome principalmente espécies de peixes demersais e pelágicos, tanto de ambientes costeiros estuarinos quanto marinhos, além cefalópodes (*e.g.* Di Beneditto & Ramos 2004, Daura-Jorge *et al.* 2011, Pansard *et al. in press*) e alguns crustáceos (Santos *et al.* 2002). O forrageio em diferentes habitats pode interferir na presença de indivíduos nas áreas de estudo, que geralmente estão mais restritas a águas costeiro-estuarinas por questões logísticas. Já o efeito combinado da maturação tardia (machos: sete anos, fêmeas: cinco a oito, Di Beneditto & Ramos 2004), recrutamento ao longo do ano com período de 11-12 meses de gestação (Rosas & Monteiro-Filho 2002), e ciclo reprodutivo estimado em dois anos (Santos *et al.* 2001, Rosas & Monteiro-Filho 2002, Di Beneditto & Ramos 2004) sugere que, em condições normais, a entrada-saída demográfica da população tenha um influência reduzida, uma vez que os estudos tem duração muito menor que a expectativa de vida. Em uma perspectiva social, o forrageio ocorre tanto individualmente quanto em grupos de diversos tamanhos; e o sistema de acasalamento é considerado promíscuo (Rosas & Monteiro-Filho 2002). Estas características, somadas a particularidades de exposição do hábitat e disponibilidade de presas da área de estudo (*e.g.* Santos & Rosso 2007), poderiam conferir diferentes graus de dinamismo na formação de grupos.

Contudo, esforços de estimativa de abundância ou densidade são pontuais, e demais parâmetros populacionais, como sobrevivência, taxa de emigração e tendência populacional, são desconhecidos para a espécie. Portanto, um monitoramento efetivo que ofereça estimativas robustas de uma série de parâmetros populacionais é uma necessidade imediata. Constitui o primeiro passo na definição do *status* de conservação da espécie (classificado como *Deficiente em dados*, Secchi 2009), um conceito que norteia os esforços de conservação.

Já a maioria das informações disponíveis sobre natureza e duração das relações sociais da espécie restringe-se à composição e tamanho de grupo e suas correlações com comportamentos e variáveis ambientais (e.g. Azevedo *et al.* 2005, Daura-Jorge *et al.* 2005, Santos & Rosso 2007). As tentativas de esclarecimento da organização social são ainda mais escassas e restritas à mesma população (Estuário de

Cananéia, Sudeste do Brasil: Monteiro-Filho 2000, Santos & Rosso 2008). Embora conduzidas com a mesma população, obtiveram conclusões contrastantes, possivelmente devido às disparidades metodológicas. Enquanto um propõe três diferentes graus de estabilidade social (“família”, a mais freqüente, caracterizada pelo relacionamento e coesão entre alguns indivíduos e potencialmente estável por algum tempo; “grupo”, ou associação entre famílias; e indivíduos solitários, raros e que posteriormente tornavam-se membros de famílias) (Monteiro-Filho 2000), outros contestam sugerindo que associações estáveis não são características desta população e que relações sociais fluidas podem ser o padrão para a *S. guianensis* (Santos & Rosso 2008). Este impasse evidencia a necessidade de ampliar esforços para esclarecer a questão. Embora indivíduos sejam freqüentemente vistos em pequenos grupos (*e.g.* Geise 1991, Geise *et al.* 1999, Edwards & Schnell 2001, Daura-Jorge *et al.* 2005), outras configurações de grupo ocorrem ao longo da sua área de ocorrência. Diferenças latitudinais nas condições ambientais, abundância de presas e proteção do ambiente (batimetria e exposição ao mar aberto), promovem variações no agrupamento intraespecífico (Lodi & Hetzel 1998, Lodi 2003, Santos & Rosso 2007) e no uso do hábitat (e.g. Wedekin *et al.* 2007, Rossi-Santos *et al.* 2007). Esta variação resultante da disponibilidade e uso de recursos e do risco de predação também é bem documentada para outros delfinídeos (Wells *et al.* 1987, Connor *et al.* 2000, Gygax 2002). Portanto, são contribuições relevantes para a discussão da estrutura social: a inclusão de dados de outra população, que habita estuário diferente e pode estar sujeito a distintas condições ambientais; e a utilização de abordagens metodológicas mais recentes.

Este é um estudo em longo-prazo que consiste em um experimento descritivo e que testa hipóteses sobre ecologia populacional e social de *S. guianensis*. A população do Estuário do Rio Caravelas (BA), situado no Banco dos Abrolhos, costa leste do Brasil, oferece-se como uma boa oportunidade para modelagem da dinâmica de um sistema biológico auto-organizado, através do tempo e espaço. Isso porque (1) o monitoramento sistemático estende-se por oito anos (2002-2009), tornando evidentes mudanças demográficas de uma população aberta; e (2) porque a área de estudo abrange um hábitat altamente heterogêneo, em um gradiente de águas estuarinas internas até recifes de coral distantes da costa, o que torna a estratificação do uso do hábitat uma possibilidade. O objetivo deste trabalho é, portanto, duplo: investigar as mudanças demográficas ao longo do tempo; e como elas afetam a estrutura social, do nível individual à rede de interações da população.

No primeiro capítulo, apresenta-se a descrição da dinâmica populacional, mediante a estimativa de uma série de parâmetros demográficos, como sobrevivência e abundância, de uma população composta por indivíduos residentes e emigrantes temporários. Por fim, testa-se a hipótese da existência de tendência populacional. O segundo capítulo sugere um modelo conceitual para previsão de topologias de redes sociais de delfinídeos e testa-o investigando a organização social da população em estudo. Especificamente, descreve-se a estrutura das associações entre indivíduos, prevendo a emergência de uma estrutura modular na rede social, devido às esperadas relações interindividuais fluidas (veja Santos & Rosso 2008). Sabendo que fatores espaço-temporais podem influenciar a oportunidade dos indivíduos interagirem (Kappeler & van Schaik 2002, Aureli *et al.* 2008), o estudo testa potenciais mecanismos não-sociais que poderiam resultar em uma rede estruturada em módulos. Devido à alta complexidade de hábitat que a área de estudo abrange, primeiramente foi investigado se diferenças no uso do espaço poderiam corresponder às associações preferenciais. Em seguida, padrões temporais de associação entre indivíduos foram investigadas, baseada na dinâmica prevista para uma população aberta, revelando novos *insights* sobre influência de fatores não-sociais nos padrões de sociabilidade não-humana.

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CAPÍTULO 1

ASSESSING POPULATION PARAMETERS AND TRENDS OF GUIANA DOLPHINS (*SOTALIA GUIANENSIS*): AN EIGTH-YEAR MARK-RECAPTURE STUDY

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Assessing Population Parameters and Trends of Guiana Dolphins (*Sotalia guianensis*): an Eight-Year Mark-Recapture Study

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Abstract

This study represents the first attempt to study the population dynamics of Guiana dolphins (*Sotalia guianensis*), by evaluating a set of demographic parameters. The population of the Caravelas River Estuary, eastern Brazil, was systematically monitored through a long-term mark-recapture experiment (2002-2009). Abundance estimates revealed a small population (57 to 124 dolphins), comprised of resident dolphins and individuals that temporarily leave or pass through the study area. Temporary emigration from the estuary to adjacencies ($\gamma''=0.33\pm0.07$ SE) and return rate ($1-\gamma'=0.67$) were moderate and constant, indicating that some dolphins use larger areas. Survival rate ($\varphi=0.88\pm0.07$ SE) and abundance were constant throughout the study period. Power analysis showed that the current monitoring effort have high probability of detecting abrupt population declines ($1-\beta=0.9$). Although the monitoring is not yet sensitive to subtle population trends, sufficient time to identify them is feasible (additional three years). Despite such apparent stability, this population, as many others, inhabits waters exposed to multiple human-related threats. Open and closed population modeling applied to photo identification data provides a robust baseline for estimating several demographic parameters and can be applied to other populations to allow further comparisons. Such synergistic efforts will allow a reliable definition of conservation status of this species.

Key words: population dynamics, mark-recapture models, temporary emigration, survival, abundance, population trends, robust design, *Sotalia guianensis*, Abrolhos Bank.

Introduction

Mark-recapture surveys are commonly used to estimate demographic parameters of several vertebrate taxa, including marine mammals (*e.g.*, Schaub *et al.* 2001, Bjorndal *et al.* 2003, Bradshaw *et al.* 2003, 2007, Bailey *et al.* 2004, Converse *et al.* 2006). Classically, abundance has been estimated through closed population modeling (Otis *et al.* 1978), which assumes a static population. The more realistic open population models account for temporal changes in population size as a balance between birth-immigration and death-emigration (Lebreton *et al.* 1992), chiefly to estimate survival rates. By using a combination of both approaches, it is possible to accurately estimate abundance from closed models and survival rate from open models (Pollock 1982). Additionally, the probability of temporary emigration can be addressed based on the fact that a given individual could be unavailable for capture at any time during the study (Kendall *et al.* 1997).

Detailed knowledge of the dynamics of most marine mammal populations is still incomplete. Logistical constraints mean that studying free-ranging cetaceans can be challenging, expensive, and time-consuming (see Taylor and Gerrodette 1993). As a consequence, assessment of population parameters has concentrated on populations of large migratory baleen whales (*e.g.*, Chaloupka *et al.* 1999, Mizroch *et al.* 2004, Ramp *et al.* 2006, Ramp *et al.* 2010) or cetaceans that inhabit coastal areas (*e.g.*, Verborgh *et al.* 2009). For the same reason, much of the available information has low precision, which leads to low power to detect trends in the stocks (see Taylor *et al.* 2007).

Coastal dolphin populations have been the subject of some of these studies (*e.g.*, Cameron *et al.* 1999, Parra *et al.* 2006, Lukoschek and Chilvers 2008, Reisinger and Karczmarski 2010). However, even for the well-studied cosmopolitan bottlenose dolphin (*Tursiops* spp.), we lack vital information for most populations. For instance, few studies have reported population-specific survival rates (but see Currey *et al.* 2009). Recently, however, such estimation procedures have been improved by including the effects of transience and temporary emigration (Silva *et al.* 2009).

Guiana dolphins (*Sotalia guianensis*) occur exclusively in shallow and coastal waters of the western Atlantic Ocean (15°N to 27°S, Silva and Best 1996). Recent studies have primarily addressed general biology (*e.g.*, Santos *et al.* 2001, Azevedo *et al.* 2004, Wedekin *et al.* 2007) and behavior (*e.g.*, Daura-Jorge *et al.* 2005, Filla and Monteiro-Filho 2009). There are few instantaneous estimates of Guiana dolphin abundance or density, and both survival rates and population trends are unknown. This central theme in ecology highlights one of the main gaps in the body of knowledge about this species. Moreover, as anthropogenic disturbances increase, population dynamics receives increased emphasis, as it supplies appropriate analytical tools for conservation purposes.

Guiana dolphin populations are frequently exposed to human activities because they inhabit coastal areas (Borobia *et al.* 1991). Mortality due to accidental (*e.g.*, Di Beneditto, 2003) and intentional catches (Sholl *et al.* 2008), boat strikes (*e.g.*, Van Bressem *et al.* 2007), behavioral disturbances due to boat traffic (*e.g.*, Araújo *et al.* 2008), skin diseases (*e.g.*, Van Bressen *et al.* 2009), and high levels of persistent contaminants in tissues (*e.g.*, Yogui *et al.* 2003) are known threats to this species. Effective monitoring efforts that provide robust estimates of a set of population parameters are therefore a necessity. More importantly, these studies will fill the data and knowledge gaps that currently preclude a definition of conservation status for this species (*Data deficient* – Reeves *et al.* 2008).

We conducted a long-term mark-recapture experiment on the eastern Brazilian coast to study the population dynamics of Guiana dolphins. Our main objective was to estimate key population parameters such as survival and abundance of a population composed of resident and transient individuals in a heterogeneous habitat. To investigate possible changes in population size, a further aim of this study was to assess our likelihood of detecting a population decline.

Materials and Methods

Study area

This study encompassed the Caravelas River Estuary (17°30'S - 39°30'W) and adjacent coastal areas, spanning more than 700 km^2. It is located on the Abrolhos Bank, an extension of the continental shelf on the eastern coast of Brazil (Fig. 1). The region is highly heterogeneous, characterized by a mosaic of open waters protected by coral reef barriers, mangrove forests with channels, sandy beaches, and banks of shallow waters.

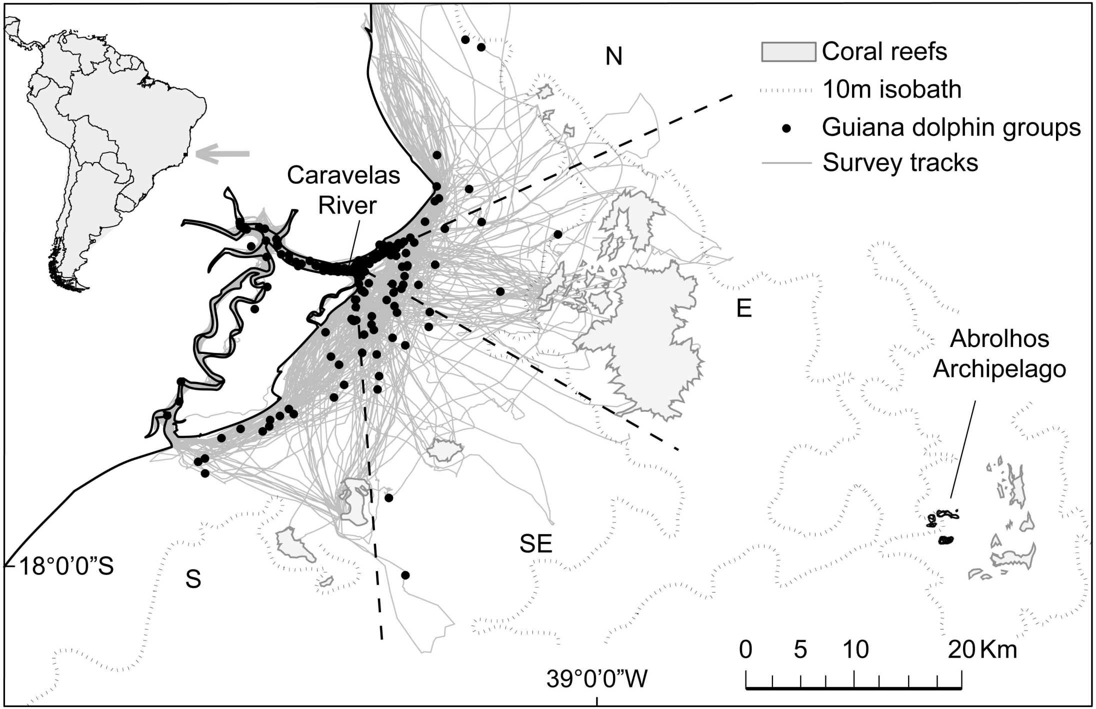

Figure 1. Caravelas River Estuary, coastal adjacent waters and coral reefs in the Abrolhos Bank, eastern coast of Brazil. Black dots indicate groups with identified Guiana dolphins.

Data collection and sampling design

A mark-recapture experiment was conducted using individual recognition through photo identification. For each animal a capture history was created, where a capture event in a sampling occasion was denoted as 1 (here a photographic record) and a not capture as 0. From maximum likelihood estimation procedures, we derived the population parameters that maximize the likelihood of observe our capture histories frequencies (Lebreton *et al.* 1992).

Data collection was carried out during surveys using a 5 m inflatable boat (50 hp outboard engine) between 2002 and 2005, and using a 12 m wooden vessel (33 hp inboard engine) from 2006 to 2009. Routes aimed to cover the study area homogeneously: each covered an average of 30 nmi (56.6 km), including departing and arriving at the estuary, and aimed to sequentially sample four different sub-regions within the study area (North, East, Southeast, and South – Fig. 1). Given the period required to cover the whole area, four consecutive sampling days were pooled and treated as a capture occasion.

Groups of dolphins were searched at slow speed (up to 5 kn) by two to five observers, alternating in three positions to cover 180^0 of the visual field. For all sightings, we recorded geographic coordinates, time, and the number of individuals. We attempted to photograph the dorsal fin of all dolphins in the group, taking as many photos as possible of both sides and without individual preferences. Because individuals cannot be recognized during the data collection, the capture effort was assumed equal for all animals. From April 2002 to July 2004, photographs were taken using a SLR camera (Nikon N-90), equipped with 300, 70-300, and 120-400 mm lenses. In August 2004, we switched to digital SLR cameras (Nikon D70 and more recently D80) and the same lenses.

Photo identification

Guiana dolphins were identified by natural markings on the dorsal fin, a technique widely used for individual recognition of cetacean species (Hammond *et al.* 1990), including Guiana dolphins (*e.g.*, Flores, 1999). During 2002 and 2004, the slide films were projected onto a white surface to produce profile drawings of each marked dorsal fin (adapted from Defran *et al.* 1990; see Rossi-Santos *et al.* 2007). The digital catalogue with photos from the entire period was periodically reviewed and included only high quality photographs (good focus and perpendicular angle). To minimize misidentification, the photo analysis was restricted to individuals with a very distinctive dorsal fin (at least one long-lasting notch on the trailing edge, Hammond *et al.* 1990). Calves and non-identifiable individuals (intact or indistinctive dorsal fin, or captured only on low quality photographs) were not included in our analyses.

Discovery curves

To visualize differences in sampling effort among years and to provide a valid comparison of the number of identified individuals under varying sampling effort, discovery curves were generated using the same method as for sample-based rarefaction curves (Gotelli and Colwell 2001). These are more robust surrogates of the traditional cumulative curves, representing the means of repeated re-sampling of the capture occasions at random and plotting the average number of marked individuals (Gotelli and Colwell 2001). Re-sampling was done by Monte Carlo methods, setting 1000 iterations and the expected curves were developed as a function of number of samples (Mao Tau) in the software EstimateS (Colwell RK, http://purl.oclc.org/estimates).

Mark-recapture analysis

Mark-recapture analyses were conducted using Program MARK (White and Burnham 1999). We used Cormack-Jolly-Seber (CJS) models for open populations (Cormack 1964, Jolly 1965, Seber 1965) to estimate apparent survival (φ) and capture probability (p). Departing from the full time varying CJS model, a set of candidate models were developed to test different effects on the estimated parameters: no variation (.), time-dependence (*t*); time-since marking, *i.e.*, age-dependence (*a2*); and the set of dolphins identified in a given occasion (*cohort*) (Lebreton *et al.* 1992). Because sampling effort varied during the study, we also introduced a *period* effect in the models, representing the variation of effort among the first three years and the last four years. The first three years were characterized by broader sampling efforts with analogue cameras, whereas in the later years, effort was reduced and digital cameras were used.

Mark-recapture models make the following assumptions (see Amstrup *et al.* 2005): (1) marks are not lost during the study; (2) marks are correctly recognized on recapture; (3) individuals are instantly released after being marked; (4) intervals between sampling occasions are longer than the duration of the sample; (5) all individuals observed during a given sampling occasion have the same probability of surviving to the next one; (6) study area does not vary; and (7) marked and unmarked animals have equal capturability. We relied on the validation of open population assumptions for dolphins discussed by Silva *et al.* (2009). In addition, we validated the assumptions of equal probabilities of capture and survival by the goodness-of-fit test using program RELEASE (Lebreton et al. 1992). Even if one or more assumptions failed, the occurrence and magnitude of the resulting extra-binomial variation (*overdispersion*, see Anderson *et al.* 1994) was evaluated and accounted for. We estimated the variance inflation factor ($\hat{c}$) through the Median $\hat{c}$ and bootstrap approaches, available in Program MARK (White and Burnham 1999), and used the highest value to adjust the lack of fit of the models.

Pollock’s Robust Design (RD) (Pollock 1982; Kendall *et al.* 1995, 1997) was applied to assess population size and emigration pattern. A year was considered as the primary period and used to estimate apparent survival. The 4-day pooled capture occasions within each year were set as the secondary periods and used to estimate abundance through closed-population models. The modifications on RD by Kendall *et al.* (1997), which allow for an animal in the population to be unavailable for capture at a given time, were used to estimate temporary emigration.

The models based on the RD were composed of the following parameters: φ_t = the apparent survival probability from primary period t to (t + 1); p_{st}, c_{st} = the probability that an individual available for capture in period t would be recaptured in the secondary sample s of the primary period t; γ'_t γ''_t = the probability that an individual would be unavailable for capture during primary period t given that it was unavailable or available (respectively) in the previous period (*i.e.*, the probability of temporary emigration). Population size ($\hat{N}$) was estimated using the full parameterization of maximum likelihood available in MARK (White and Burnham 1999). The following models were designed using the notation provided by Kendall *et al.* (1997): Markovian emigration models (γ' γ''), where the probability of availability depends on whether the animal was available for capture; random emigration models (γ' = γ"), where the probability of availability is completely random; and models with no emigration (γ' = γ" = 0).

The eight classical closed population models (Otis *et al.* 1978) used in the RD (Kendall *et al.* 1995) have other specific assumptions for the secondary period (for assessment of assumptions to cetacean data, see Wilson *et al.* 1999, Bearzi *et al.* 2008): (1) demographic closure; (2) lack of behavioral responses to capture procedure, *i.e.*, animals do not respond to being captured in a way that affects their subsequent probability of recapture; and (3) homogeneity of capture probabilities, *i.e.*, within a sampling occasion, all animals in the population have equal probability of being captured. Behavioral response models were discarded because we assumed *a priori* there were no reactions to the capture procedure involving photo identification (*trap dependence*). Thus, the capture probability (p) was considered equal to the recapture probability (*c*). Individual heterogeneity was included using the Pledger's mixture models, with two mixtures of capture probabilities (2-pi) (Pledger 2000). However, heterogeneity in capture probabilities was included only in those models with no emigration. The influence of time was tested for all parameters, both in primary periods (*t*) and secondary periods (*s*).

For the CJS approach, the most appropriate model was selected through the Quasi-Akaike Information Criterion ($QAIC_c$, Anderson *et al.* 1994), while the Akaike Information Criterion (AIC_c) was used for RD models. In all cases, specific biological hypotheses between nested models were tested using likelihood ratio tests (LRT, Burnham and Anderson 2002). Normalized $QAIC_c$ weights – or AIC_c weights for RD models – were used to measure the support for a given model relative to the others. Parameter estimates were averaged across all models based on QAICc – or AICc – weights (Burnham and Anderson, 2002).

Trends in abundance

Because the abundance estimates $(\hat{N})$ refer exclusively to the well-marked animals in the population, we corrected this to include the unmarked individuals in the total abundance estimates ($\hat{N}_\theta$). For each year, the proportion of identifiable individuals within the population (θ) was estimated as the number of well marked individuals divided by the total number of individuals observed in each group, averaged over all groups (*cf* Silva et al. 2009). Other similar methods for theta estimation are available (*e.g.*, Williams et al. 1993), but particularities of this population make our approach feasible. Since Guiana dolphins usually form small groups in the Caravelas River Estuary (Table 1), and generally a single group was sighted in each day ($\overline{X}$ = 1.26 ± 0.33 SD), the number of marked individuals in each group could be estimated with precision.

The total abundance estimates were obtained by $\hat{N}_{\theta} = \frac{\hat{N}}{\theta}$, and the variances of total population size were estimated using the delta method (Seber 1982) as:

$$\mathrm{var}\left(\hat{N}_{\theta}\right) = \hat{N}_{\theta}^{\,2}\left(\frac{\mathrm{var}\left(\hat{N}\right)}{\hat{N}^{2}} + \frac{1-\theta}{n\theta}\right)$$

where n is the total number of individuals from which $\hat{N}$ was estimated. Log-normal confidence intervals for total population size (see Burnham *et al.* 1987) were calculated as:

$$C = \exp\left[z_{\frac{\alpha}{2}} \times \sqrt{\ln\left(1 + \left[CV\left(\hat{N}_{\theta}\right)\right]^{2}\right)}\right]$$

where z is the normal deviate, α = 0.05, and CV is the coefficient of variation.

To determine the probability of detecting a linear population trend in the corrected abundance estimates, we performed a statistical power analysis (Fairweather 1991). By definition, a trend exists when the regression has a slope significantly different from zero (see Gerrodette 1987). Power analysis provides the probability of correctly rejecting the null hypothesis of constant population when it is actually increasing or decreasing (1 - β, where β is the probability of Type 2 error).

To explore the monitoring efficiency, we simulated two kinds of changes in the population: a precipitous decline of 50% in the abundance during the entire monitoring period (*e.g.*, Taylor *et al.* 2007) and a modest decline of 5% per year (*e.g.*, Lukoschek and Chilvers 2008). We analyzed the effort necessary to detect these changes with an acceptable power of 80% certainty (see Taylor *et al.* 2007).

Analyses were conducted using the software TRENDS (Gerrodette 1987, 1993), setting the parameters as follows: the significance criterion $\alpha = 0.05$; one-tailed test (because we are only concerned with a decrease); equal intervals between sampling occasions and exponential type of change. Corrected abundance estimates ($\hat{N}_\theta$) were transformed to the natural logarithm before performing the regression. Variance usually fluctuates according to some function of the abundance (Gerrodette 1993), and for mark-recapture estimates, the coefficient of variation (CV) on abundance is expected to be proportional to the square root of abundance (Gerrodette 1987). However, it can also vary due to the species and the method used. To test this, we plotted CVs of each year against $\sqrt{\hat{N}_\theta}$ and $\left(\sqrt{\hat{N}_\theta}\right)^{-1}$ (*cf* Gerrodette 1987). Since no clear relationship arose, we assumed CVs were constant with respect to abundance and thus calculated the overall CV of the monitoring period by averaging the annual CVs (Gerrodette 1993).

Results

Sampling effort

From 2002 to 2009, sampling was performed on 389 days and covered more than 13,425 nmi. We recorded 380 groups, totaling 1,702 sighted dolphins (10% calves) (Table 1). A total of 108 individuals were identified with good-quality photographs, and 12 were resighted in all years. Greater sampling effort was employed between 2002 and 2004 than in the later years. The number of individuals with long-lasting marks included in the analysis varied among years (Table 1). The rarefaction curves for 2002 to 2004 tended to stabilize with narrower confidence intervals (Fig. 2A, B). The opposite was found for surveys from 2005 on, when all confidence intervals were wider, and the curves were non-asymptotic (Fig. 2B, C, D). The number of new photo identified individuals per year fluctuated from 15 (2004) to 40 (2007), while the recapture rate varied from 55% (2007) to 86% (2004). From 30% to 64% of photo identified dolphins in one year were recaptured in the subsequent year (Table 2).

Table 1. Summary of annual sampling effort and basic results of the long-term mark-recapture experiment with Guiana dolphins (*Sotalia guianensis*) carried out in the Caravelas River Estuary, eastern Brazil.

Year	Sampling effort (mni)	Sampling effort (h)	Total observation (h)	4-day capture occasions	Sighted groups	Mean group size ± SD	Total sighted dolphins (calves)
2002	2,340.6	327.0	60.7	11	72	4.2 ± 2.1	316 (39)
2003	2,784.4	465.3	58.3	19	78	5.2 ± 3.1	385 (34)
2004	2,214.1	280.7	27.5	14	53	4.0 ± 1.8	201 (13)
2005	1,529.4	258.8	44.9	12	40	5.6 ± 4.1	217 (29)
2006	668.6	122.1	22.1	6	22	4.2 ± 1.2	100 (15)
2007	1,035.7	217.6	16.7	8	37	5.4 ± 2.8	165 (17)
2008	1,518.3	297.8	21.7	11	46	4.5 ± 2.5	177 (15)
2009	1,333.4	266.0	16.1	11	32	4.6 ± 2.2	141 (8)

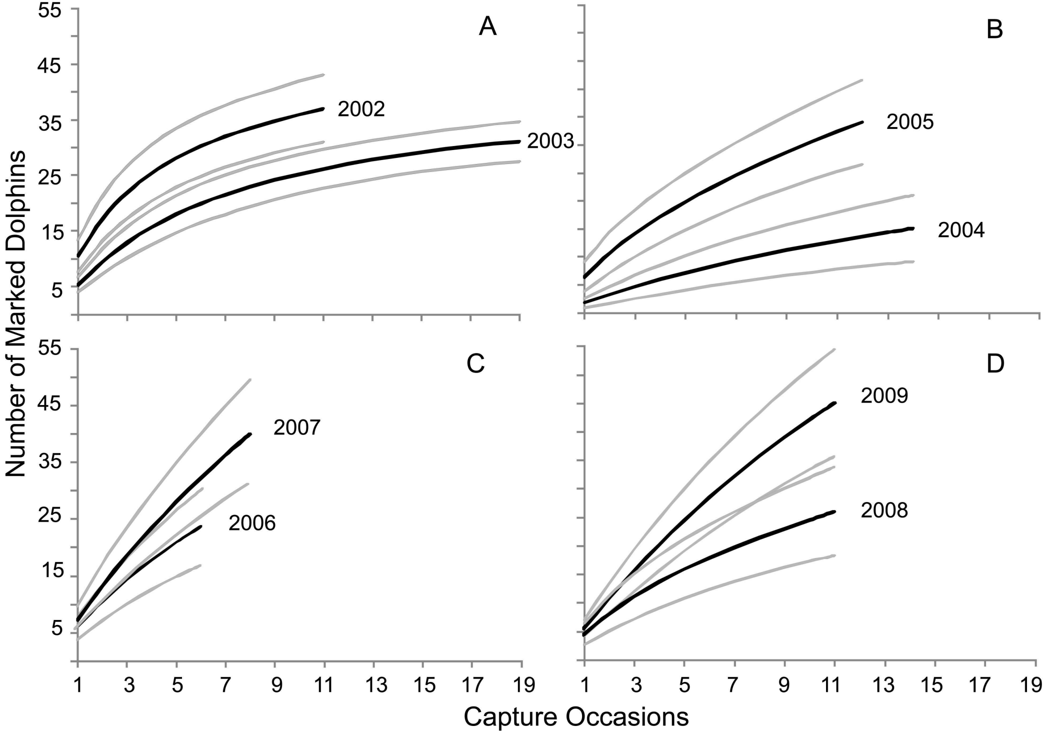

Figure 2. Sample-based rarefaction curves of cumulative photo identified Guiana dolphins in the Caravelas River Estuary from 2002 to 2009. Black curves represent the Mao Tau estimates and grey curves are the respective 95% confidence intervals.

Table 2. M-array of capture-recapture data used for open-population models. R(*i*) = Number of individuals marked (photo identified for the first time) for each occasion *i*; m(*i*,*j*) = number of individuals marked in occasion *i* and recapture for the first time in a capture occasion *j*; r(*i*) = total of individuals marked in occasion *i* and recaptured throughout the subsequent occasions.

Occasions	**R(*i*)**	**m(*i*,*j*)**							**r(*i*)**
		2003	**2004**	**2005**	**2006**	**2007**	**2008**	**2009**	
2002	37	24	1	0	1	3	1	0	30
2003	31		10	10	4	2	0	0	26
2004	15			9	3	1	0	0	13
2005	34				10	7	1	2	20
2006	24					12	4	2	18
2007	40						12	10	22
2008	26							15	15

Model selection for estimating population parameters

From the results of all components of the goodness-of-fit test, we did not violate the assumptions of equal probabilities of capture (TEST 2; p = 0.778) and survival (TEST 3; p = 0.522). The most parameterized CJS model fitted our data satisfactorily. The bootstrap approach estimated the highest variation inflation factor, which was marginally above 1 and indicated no substantial overdispersion ($\hat{c}$= 1.25). It may be caused by the presence of temporary emigrants in the population, or other source of heterogeneity of capture probability (see below). Despite the lack of evidence for such an effect, we adjusted the models with $\hat{c}$ to correct any potential violation of assumptions or intrinsic variations in the population.

In general, the CJS models with time (Table 3: models 15, 13, 12) or age-dependence (models 6, 3) of survival and models that allowed this parameter to vary with sampling effort (models 14, 9, 5) poorly fit the data or were not parsimonious. Similarly, models with capture probability dependent on time (models 12, 5, 4, 3), *period* (models 15, 10) or both (models 16, 14, 11, 7) also provided a poor fit to the data. Thus, the best CJS model had constant survival and capture probability varying in relation to cohort (model 1). The LRT agreed with the best model selected by $QAIC_c$, when comparing nested models. Moreover, there were no additional effects of *period* (model 2; P = 0.282) or time (model 11; P = 0.333) on capture probability.

RD models not accounting for temporary emigration poorly fit the data (Table 4: models 9-12), and emigration probabilities seemed to follow a Random Movement Model (model 1). In general, those models in which survival was time-dependent (models 6-8 and 10-12) and which allowed capture probability to vary between secondary periods (model 12) were not parsimonious or poorly fit the data. Thus, the best RD model had random and constant emigration probabilities, constant survival and time-dependent capture probability between and within primary periods (model 1). When comparing nested models, the LRT corroborated a constant survival (model 4, P = 0.205) and random emigration pattern (model 2, P = 0.165), but it suggested a temporal effect on the probability of an individual be unavailable for capture (γ; model 3, P = 0.012).

Table 3. Cormack-Jolly-Seber models for survival (φ) and capture probability (p) ranked by the lowest $QAIC_c$. $QAIC_c$ weight indicates the strength of evidence for a given model. Model notation: constant parameter (.), time (*t*), age (*a2*), *cohort* or *period* dependence.

	Model	**QAICc**	**ΔQAICc**	**QAICc Weights**	**Likelihood**	**No. Parameters**
1	{φ(.) p(*cohort*)}	411.621	0	0.468	1	8
2	{φ (.) p(*cohort* × *period*)}	413.487	1.87	0.184	0.393	10
3	{φ (*a2*) p(*t*)}	413.487	1.87	0.184	0.393	9
4	{φ (.) p(*t*)}	415.639	4.02	0.063	0.134	8
5	{φ (*period*) p(*t*)}	417.302	5.68	0.027	0.058	9
6	{φ (*a2*) p(.)}	417.414	5.79	0.026	0.055	3
7	{φ (.) p(*t* + *period*)}	417.825	6.21	0.021	0.045	9
8	{φ (.) p(.)}	419.019	7.40	0.012	0.025	2
9	{φ (*period*) p(.)}	420.802	9.18	0.005	0.010	3
10	{φ (.) p(*period*)}	420.929	9.31	0.005	0.010	3
11	{φ (.) p(*t* × *period*)}	422.266	10.64	0.002	0.005	11
12	{φ (*t*) p(*t*)}	423.331	11.71	0.001	0.003	14
13	{φ (*t*) p(.)}	423.561	11.94	0.001	0.003	8
14	{φ (*period*) p(*t* × *period*)}	423.996	12.38	0.001	0.002	12
15	{φ (*t*) p(*period*)}	425.732	14.11	0	0.001	9
16	{φ (.) p(*cohort* × t)}	439.523	27.90	0	0	29

Table 4. Pollock’s Robust Design models for survival (φ), temporary emigration (γ), capture (p) and recapture probabilities (c) ranked by the lowest AIC$_c$. AIC$_c$ weight indicates the strength of evidence for a given model. Model notation: no emigration ($\gamma'' = \gamma' = 0$); Markovian emigration ($\gamma'(x)\ \gamma''(x)$); random emigration ($\gamma'(x) = \gamma''(x)$); mixture proportion (pi); no behavior effect (p(x) = c(x)); constant parameter (.) or time-dependence (t, s).

	Model	**AIC$_c$**	**ΔAIC$_c$**	**AIC$_c$ Weights**	**Likelihood**	**No. Parameters**
1	$\{\varphi(.)\ \gamma''(.) = \gamma'(.)\ p(st) = c(st)\}$	1,717.222	0	0.540	1.000	102
2	$\{\varphi(.)\ \gamma''(.)\ \gamma'(.)\ p(st) = c(st)\}$	1,718.401	1.180	0.300	0.555	103
3	$\{\varphi(.)\ \gamma''(t) = \gamma'(t)\ p(st) = c(st)\}$	1,719.735	2.510	0.154	0.285	108
4	$\{\varphi(t)\ \gamma''(.) = \gamma'(.)\ p(st) = c(st)\}$	1,727.640	10.420	0.003	0.006	108
5	$\{\varphi(.)\ \gamma''(t)\ \gamma'(t)\ p(st) = c(st)\}$	1,728.688	11.470	0.002	0.003	114
6	$\{\varphi(t)\ \gamma''(.)\ \gamma'(.)\ p(st) = c(st)\}$	1,729.797	12.580	0.001	0.002	109
7	$\{\varphi(t)\ \gamma''(t) = \gamma'(t)\ p(st) = c(st)\}$	1,731.990	14.770	0.000	0.001	114
8	$\{\varphi(t)\ \gamma''(t)\ \gamma'(t)\ p(st) = c(st)\}$	1,744.131	26.910	0	0	120
9	$\{\varphi(.)\ \gamma''= \gamma'=0\ p(st) = c(st)\}$	1,764.346	47.120	0	0	101
10	$\{\varphi(t)\ \gamma''= \gamma'=0\ pi(.)\ p(s)\}$	1,768.690	51.470	0	0	32
11	$\{\varphi(t)\ \gamma''= \gamma'=0\ p(st) = c(st)\}$	1,772.300	55.080	0	0	107
12	$\{\varphi(t)\ \gamma''= \gamma'=0\ p(s) = c(s)\}$	1,880.055	162.830	0	0	23

Survival and capture probability

Apparent survival rates were high and stable during the study. The model-averaged estimates of both approaches provided similar results: CJS: φ = 0.88 ± 0.07 SE, 95% CI = 0.67 – 0.96; RD: φ = 0.89 ± 0.03 SE, 95% CI = 0.82 – 0.94.

CJS models detected fluctuations in recapture probabilities between cohorts throughout the monitoring (Fig. 3). Capturability was lower for the 2004 cohort (p = 0.215 ± 0.143 SE) and reached maximum values in 2003 (p = 0.629 ± 0.124) and 2009 (p = 0.633 ± 0.186).

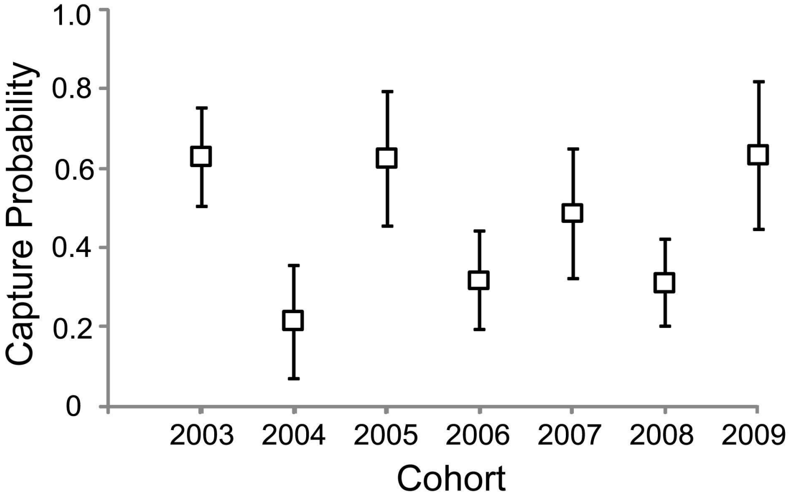

Figure 3. Capture probability estimates for the seven cohorts of Guiana dolphins in the Caravelas River Estuary, based on the averaged Cormack-Jolly-Seber model. Whiskers represent standard error.

Emigration probability

We used model-averaged results from the RD models to investigate individual movements. Specifically, we estimated the probability that an individual available for capture on previous occasions temporarily emigrated from the study area (γ”), and the probability that an individual that was outside the study area on a previous occasion remained outside it (γ’). Under a Random Movement model, temporary individual emigration from the sampled area to neighboring regions was the same for a given emigrant remaining outside of the study area ($\gamma'' = \gamma' = 0.33 \pm 0.07$ SE; 95% CI = 0.20 – 0.49). Thus, the probability of dolphins remaining in the study area between capture occasions ($1- \gamma''$) and the return rate of temporary emigrants to the study area were equal ($1- \gamma'' = 1- \gamma' = 0.67$). In addition, the probability that a given dolphin moved between the study area and the adjacent areas appeared not to depend on its location during the previous sampling occasion (see Kendall *et al.* 1997).

Abundance estimates

The number of dolphins using the study area varied among years, though not significantly. The averaged RD model yielded annual abundance estimates ranging from 25 to 69 marked dolphins, which were corrected to a total of 57 to 124 individuals (Table 5). Even with apparent peaks in the years 2004 and 2009, abundance was apparently constant across the years (Fig. 4).

Table 5. Abundance estimates ($\hat{N}$) of the Guiana dolphin population in the Caravelas River Estuary for each year from the averaged Robust Design model, with corrections ($\hat{N}_{\theta}$) to include the unmarked individuals.

	Proportion of marked dolphins		**RD Abundance Estimates**					
Year	**θ**	**SE (θ)**	$\hat{N}$	**CV**	**95%CI**	$\hat{N}_{\theta}$	**CV**	**95%CI**
2002	0.53	0.065	37	0.027	35 - 39	70	0.123	55 - 89
2003	0.39	0.055	31	0.031	29 - 33	79	0.143	60 - 105
2004	0.24	0.060	25	0.251	13 - 37	105	0.354	53 - 204
2005	0.54	0.059	37	0.061	32 - 41	67	0.117	55- 86
2006	0.59	0.091	34	0.163	23 - 44	57	0.215	38 - 87
2007	0.55	0.062	55	0.128	41 - 69	100	0.169	72 - 139
2008	0.38	0.079	34	0.144	25 - 43	89	0.246	56 - 144
2009	0.56	0.078	69	0.153	48 - 90	124	0.201	83 - 182

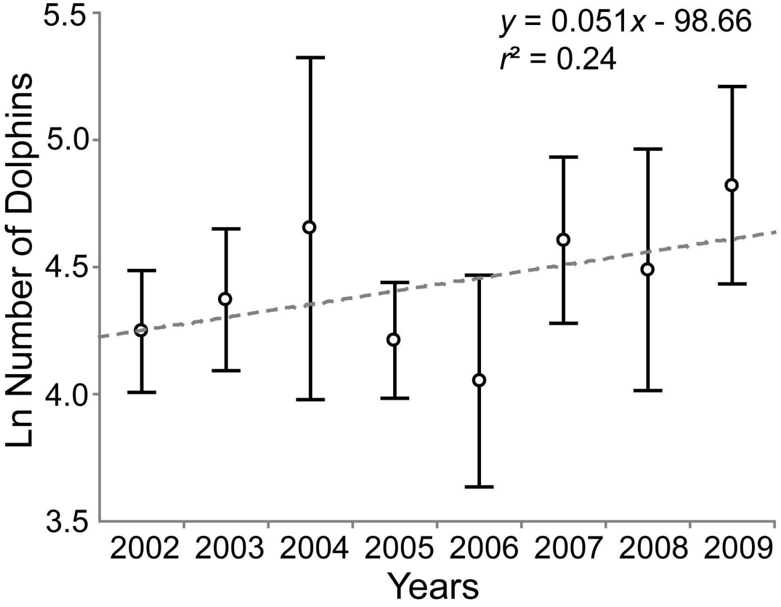

Figure 4. Regression line of ln-transformed annual abundance estimates (through averaged RD model and theta correction) of the Guiana dolphin population in the Caravelas River Estuary. Whiskers represent 95% confidence intervals.

Trends in abundance

The regression of the corrected abundance estimates ($\hat{N}_\theta$) throughout the monitoring period was not significant (t = 1.372, *P* = 0.219; Fig. 4). The precision of estimation was moderate (CV = 0.196; see Taylor *et al.* 2007), and the statistical power to detect the change indicated by the regression coefficient (b = 0.051) was reasonable (1 - β = 0.43).

The minimum rate of population decline detectable with acceptable statistical power (1 - β = 0.8) was an overall decrease of 45% or an annual decrease of 8%. Our monitoring showed sufficient power (1 – β = 0.90) to detect a precipitous decline of 50% in the population during the entire study. In order to detect a slight decrease of 5% per year (1 – β = 0.45), additional three years to our sampling effort to date would be required (eleven years of monitoring; Fig. 5).

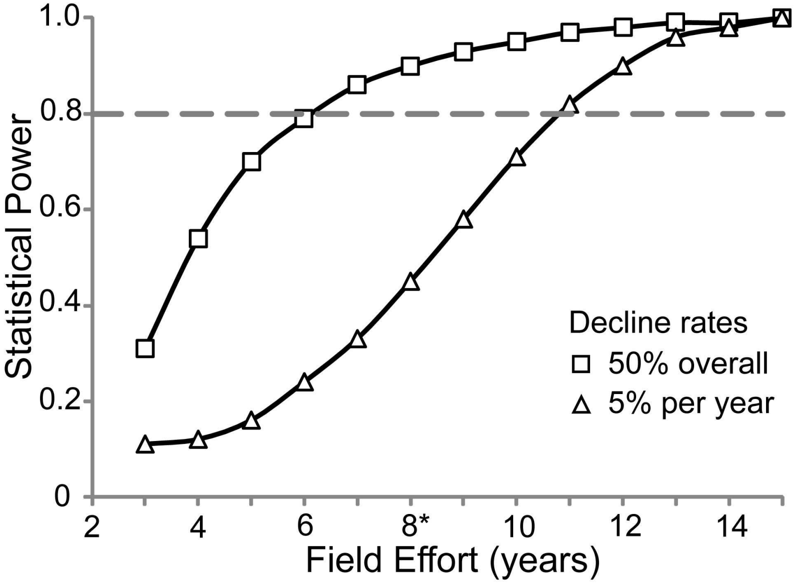

Figure 5. Statistical power to detect changes in the population of Guiana dolphins in the Caravelas River Estuary under two different scenarios: a decline of 50% during the entire monitoring period and a decline of 5% per year. The horizontal dashed line represents a probability of 80% of detecting a change. Asterisk represents the current monitoring period.

Discussion

There are three important outcomes of this study. From a local perspective, we have highlighted the importance of long-term monitoring in understanding the hitherto unknown population dynamics of Guiana dolphins within a highly heterogeneous habitat. From a regional view, the first estimates of several population parameters are provided for this species. Our work helps to fill the knowledge gaps that preclude definition of conservation status for Guiana dolphins, as anthropogenic disturbances threaten many populations. In a broader scale, our results confirm the feasibility of monitoring frameworks based on robust mark-recapture modeling of free-ranging cetacean data.

Survival

The most parsimonious models considered a constant and high apparent survival probability throughout the study period. High adult survival is expected for large and slowly reproducing mammals, whose life span is longer than the study duration (*e.g.*, Zeh *et al.* 2002). Although there is no other survival estimate available for Guiana dolphins, our survival rate is similar to that of bottlenose dolphins (*Tursiops truncatus*). Few studies have derived survival probabilities of small cetaceans from mark-recapture analyses (*e.g.*, Cameron *et al.* 1999, Currey *et al.* 2009, Silva *et al.* 2009), but other methodologies (*e.g.*, Wells and Scott 1990, Stolen and Barlow 2003) have also shown adults with relatively high survival probabilities.

Capturability

Capture probabilities fluctuated across cohorts, and indicated that individuals captured for the first time in each year showed different probabilities of being recaptured. This parameter is expected to be constant across cohorts only when recapture is similar among all individuals. Since it is a product of the probability of being detected and of being present in the sampled area (Lebreton *et al.* 1992), one may expect cohorts to differ due to differences in sampling effort and individual site fidelity.

We considered two potential explanations for variability in capture probabilities. First, differences in our monitoring scheme, especially the switch from analogical to digital photographic equipments, were expected to lead to variations in capturability. With less cost, more photographs were taken and laboratory tools for photo manipulation (*e.g.*, zoom, contrast) became more accessible. Thus, capture efficiency may be enhanced using digital photo identification techniques (Markowitz *et al.* 2003). However, models incorporating such sampling variation in capture probability poorly fit our data and actually failed to explain such fluctuations.

Alternatively, capture probability may have been influenced by variations in residence patterns. Since transient dolphins have high probability of being unavailable for capture on subsequent occasions (Pradel *et al.* 1997), a higher proportion of these individuals in a given year will result in a lower capture probability. In our case, fluctuations in capture probability matched the number of photographed dolphins in each year, which in turn reflected the relative proportion of non-resident individuals sampled annually (see Silva *et al.* 2009). This situation is corroborated by the existence of dolphins passing through our study area (Rossi-Santos *et al.* 2007) and by the evidence of an annual variation in emigration probabilities (based on LRT results).

Emigration patterns

Movements of animals can invalidate the assumption of homogeneous capture probabilities (Lebreton *et al.* 1992). Variation in site fidelity among individuals has been suggested for this species (*e.g.*, Santos *et al.* 2001, Azevedo *et al.* 2004) and for our studied population as well. The latter is composed of a core of year-round long-term resident individuals and many others that show low site fidelity to the Caravelas River Estuary (Rossi-Santos *et al.* 2007). This evidence indicates that dolphins temporarily emigrate from or immigrate to our study area. Therefore, by relying on RD general framework, it was possible to quantify such movements and presumably obtain unbiased estimates for other parameters (Pollock 1982, Kendall *et al.* 1997, Silva *et al.* 2009). Temporary emigration from the sampled area (33%) and return rates from neighboring regions (about 67%) were moderate during the monitoring period.

The incidence of temporary emigration combined with significant probabilities of remaining away from the area and varying site fidelity suggest that some individuals use other areas beyond the study area (see Fortuna 2006). Caravelas River Estuary and vicinity comprise one of the largest studied areas for this species (more than 700 km^2), and at the same time the area presents a patchy mosaic of habitats, encompassing closed and open waters. This pattern is different from other localities where the species has been studied: usually small areas where most sampling effort was restricted to protected bays (Flores 1999, Santos *et al.* 2001, Azevedo *et al.* 2004, Cremer 2007, Wedekin *et al.* 2007, Flach *et al.* 2008, Filla and Monteiro-Filho 2009). Guiana dolphins have been sighted in all regions adjacent to our study areas (Rossi-Santos *et al.* 2006), and habitats commonly used by the species in the Abrolhos Bank include estuarine systems, open coastal areas, shallow reef banks, and offshore islands (Rossi-Santos *et al.* 2006). It is reasonable to suppose that individual stratification of habitat use exists (see Wilson *et al.* 1997), given the small home ranges recorded for the species (Flores and Bazzalo 2004, Rossi-Santos *et al.* 2007, Wedekin *et* *al.* 2007) and the heterogeneity of habitats commonly used by the dolphins in the Abrolhos Bank.

Population size

Population size fluctuated during the monitoring, possibly because of interannual variation in the balance between additions (births or immigration) and deletions (deaths or emigration) in the population. For example, abundance reached its lowest level in 2006, but was much higher in 2004 and 2009. Such fluctuations in abundance, combined with the ranging patterns and residence levels, suggest the existence of a *super-population* (*sensu* Schwarz and Arnason 1996) using the study area (see Kendall 1999). The dolphins sighted at the beginning of the monitoring period were not the same individuals seen in later years. Some were resighted during the study, but many others may have left the area or the population.

Nevertheless, the Caravelas River Estuary holds a relatively small population of Guiana dolphins. As abundance estimates are only available for a few other populations, then opportunities for comparison are limited. Most of these estimates were obtained through strip or line transects sampling (Buckland *et al.* 2001). Few studies conducted mark-recapture analysis, and only through classical closed population models (see Chao and Huggins 2005 for a review). These models might include an unknown degree of bias (see Hammond 1990). Putting this possibility aside, it seems that most populations were estimated to consist of less than a hundred (Pizzorno 1999, Edward and Schnell 2001) or a few hundred individuals (Geise 1991, Geise *et al.* 1999, Acuña 2002, Cremer 2007). One large population of more than a thousand dolphins was studied in southeastern Brazil (Flach *et al.* 2008), but this is probably an exception for the species.

Population trends

Trends in abundance offer a clear indication of the health of a population (Williams *et al.* 2002). Assessment of such temporal changes is a priority recommendation for the species, from both local and global perspectives (IBAMA 2001, Reeves *et al.* 2008). The previous estimates of Guiana dolphin abundance provided only instantaneous information. This is the first study to provide a time-series of abundance estimates and is the first attempt to model population trends for the Guiana dolphin.

Despite annual fluctuations in abundance, the number of dolphins in the population of the Caravelas River Estuary was apparently stable. We could not reject the null hypothesis of constant population size suggested by the regression coefficient of the ln-transformed annual point estimates. Monitoring low rates of population change of highly mobile species in dynamic environments is truly difficult because such changes may be confounded with natural variability in abundance (Gerrodette 1987, Forney 2000). Our current effort is not yet sensitive to slight variations in population size. However, sufficient time to identify such variations is feasible (estimated to be eleven years of monitoring). This fact reinforces that long-term efforts are required to ensure reliability of conclusions about changes in population size.

The power to detect upward or downward trends is directly related to the precision of abundance estimates as well as to the rate of change in population size and to the monitoring duration (Gerrodette 1987, Fairweather 1991, Wilson *et al.* 1999, Taylor *et al.* 2007). Our study represents a case of relatively precise abundance estimates (see Taylor *et al.* 2007) and the monitoring scheme we have applied would be able to detect abrupt abundance changes with high certainty. This situation is much better than most other cetacean species. For example, the power to detect a precipitous decline (50% in 15 years) in this Guiana Dolphin population ($1 - \beta = 1.00$) is much higher than for the majority of studied stocks: over the same sampling period, power is between 0.00 and 0.50 for more than 85% of large whales and more than 95% of delphinid stocks (see Fig. 1 in Taylor *et al.* 2007).

Even with an apparently stable population of Guiana dolphins in the Caravelas River Estuary, the species is exposed to several long-term human-related threats in the area and throughout its distribution. Typically, many simultaneous threats affect populations' local persistence (Wedekin *et al.* 2005, Filla *et al.* 2008). While the cumulative effect of these impacts is not fully evident, a cautious and conservative interpretation should be maintained, especially because the species is a habitat specialist and small populations are scattered along the coast. Sustained monitoring effort is therefore required for effective management of this species and its habitats.

Conclusions

This study represents a first step towards understanding the population dynamics of Guiana dolphins. Our results shed light on the importance of long-term monitoring of the species, especially considering that anthropogenic pressures are expected to increase in coastal habitats in the future. A robust baseline for conducting population monitoring was based on open and closed population mark-recapture models applied to photo identification data. Reliable parameter estimates from other Guiana dolphin populations are urgently needed to allow further comparisons and to yield an adequate evaluation of the conservation status of the species.

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CAPÍTULO 2

TEMPORALLY SPLIT, SPATIALLY MERGED: THE FISSION-FUSION DYNAMICS OF A DELPHINID SOCIAL NETWORK

Temporally split, spatially merged: the fission-fusion dynamics of a delphinid social network

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Abstract

Resource predictability is among the key socioecological factors underpinning the complex matrix of trade-offs that rules the group patterns of animals. The individual decision on how long and with how many conspecifics an interaction is advantageous will ultimately determine the social organization, and shape their social network. Based on the strength and heterogeneity of social interactions, we provide a conceptual framework for predicting non-human social network topology. We tested the framework`s expectations using a combined spatial, temporal and demographic approach applied to a long-term dolphin association study. One *Sotalia guianensis* population from eastern Brazil offers a tempting system to examine whether non-social factors influence the social network topology in as much: 1) the studied area encompasses a highly heterogeneous habitat, with a possible stratification of habitat use; 2) the population dynamics is marked by deletion and addition of individuals, which offers an opportunity to evaluate the temporal-dependence of associations. We found that association patterns are structured into a modular social network. We discarded the individuals’ space use overlap as a major force driving this topology, however a demographic turnover is temporally splitting the interindividual associations into modules. Within the turnover temporal scale, the population followed a fission-fusion dynamics, as indicated by a majority of fluid acquaintances and few preferred associations. We highlighted that non-social factors can highly affect non-human association networks, and should be accounted for an apposite portrayal of societies with different degrees of fission-fusion dynamics. Our results may inspire new hypothesis on how intrinsic and extrinsic factors have shaped the structure and dynamics of delphinid social systems.

Keywords: modularity, social structure, population turnover, space use overlap, socioecology, group living, Guiana dolphins, *Sotalia guianensis*

Introduction

Social complexity emerges as individual efforts in creating mutual solutions to a basic problem: being alive. The challenges embedded can be roughly summarized as eating without being eaten, mating and rearing offspring. Departing from the evolutionary history of the species, particular contexts in which individuals perform these vital functions optimally give rise for different social structures (e.g. Eisenberg 1981). One solution to enhance individual survival and reproductive success is to live in groups, by supposedly reducing susceptibility to predation and increasing access to certain resources (e.g. Majolo et al. 2008). Benefits embrace enhanced foraging, vigilance and offspring rearing efficiency, while costs include increased competition, aggression, parasitism and disease spread (see Lee 1994, Connor 2000). Ecological (e.g. Crook 1970) and genetic factors (e.g. Hamilton 1964, Alexander 1974, but see Nowak et al. 2010), and phylogenetic inertia (Wilson 1975) are referred to the adaptive origin of group living and social behavior, not in a mutually exclusive manner (Slobodchikoff and Shields 1988).

Due to logistical difficulties in studying free-ranging aquatic animals, the social structure of mammals has been better explored in terrestrial habitats. However, even with the obvious differences imposed by both environments, animals face the same pressures related to sociability, and then may present similar social solutions (Wells et al. 1987, Wrangham 1987). Long-term efforts have revealed the Order Cetacea as a highly heterogeneous clade in relation to social systems (see Connor et al. 1998, Mann et al. 2000), sharing social features with independently evolved large brained mammals (primates, e.g. Würsig 1978, Wrangham 1980; and proboscideans, e.g. Weilgart et al. 1996), and ecological constraints of other terrestrial mammal orders (artiodactiles, e.g. Jarman 1974; and carnivores, e.g. Packer et al. 2000). The Sub-order Odontoceti shows a large range of social organizations, with interindividual relationships oscillating between unstable and quite stable, in contrast with the mainly ephemeral association found in the Sub-order Mysticeti (e.g. Clapham 1996, Connor 2000). Such social plasticity can even be found intraspecifically, for instance, between resident and transient killer whale populations (e.g. Bigg et al. 1990, Baird and Dill 1996), or bottlenose dolphins with different levels of relationship stability (e.g. Wells et al. 1987, Connor et al. 1999).

Through a socioecological perspective, the availability of resources is the primary factor shaping delphinid social structures. Spatio-temporal predictability of resources, such as food, mates, and safe habitats, may explain how the cost-benefit functions influence ranging behavior, intensity of competition, and optimal group size (Gowans et al. 2008). When resources are patchy and animals need to move large distances to find them, an unpredictable scenario is likely to occur. Therefore, grouping facilitates foraging and overcomes scramble competition. Large home ranges are generally observed in the open sea, which is characterized by low habitat complexity where the unique anti-predator strategy is to form a group. However, when resources are abundant and found locally, a more predictable situation arises, thus favoring small home ranges. Such condition is generally found in coastal and estuarine areas, i.e. more structurally complex habitats, where finding a suitable refuge may be more advantageous than grouping. Then, one could dichotomize that large groups could be expected when resources are unpredictable while smaller groups are a better social strategy at a predictable situation (see Gowans et al. 2008 framework).

The group size may ultimately affect the number and duration of the pairwise relationships (Table 1). Aggregations and large groups are generally comprised by many brief dyadic associates (e.g. Bel’kovitch 1991; Norris et al. 1994; Bräger et al. 1994), or temporarily unite more stable units (e.g. Östman 1994; Baird 2000). On the other hand, within smaller groups, there are fewer members to interact but they may have more opportunity of being engaged in closer associations (e.g. Scott et al. 1990; Whitehead et al. 1991; Connor et al. 2000, Baird et al. 2009, McSweeney et al. 2009; Hartman et al. 2008). Even though, this is not a trend without exceptions (e.g. Lusseau et al. 2003; Karczmarski et al. 2005; McSweeney et al. 2007, Cagnazzi et al. 2011).

Table 1. Theoretical dichotomic relationship between resource predictability and habitat and group features (from Gowans-Würsig-Karczmarski 2008) affecting interindividual interactions of delphinids. Complexity of habitat may influence ranging behavior and then group size and stability. At last, the number and duration of delphinid relationships may be affected, which here is polarized in several brief associations and a smaller number of lasting associations.

		Resource availability	
		Unpredictable	Predictable
Habitat	Complexity	high	low
	Range	low	high
Group	Size	large	small
	Stability	low	high
Interactions	Number	many	few
	Duration	short	long

Network theory derived from Euler's graph (Albert and Barabási 2002, Newman 2003) is one of the promising toolkits for description, analysis, and understanding of complex and self-organized systems (Amaral and Ottino 2004). Network thinking recently has drawn the public attention due to shared global and local properties among very distinct phenomena (e.g. Newman 2003, Bocatelli et al. 2006, Bascompte 2009). Advances in the field of mechanical statistics (Albert and Barabasi 2002) have driven an extensive search for patterns in biological networks, from fields such as community (see Bascompte 2009) and population ecology (e.g. Araújo et al. 2010). The study of animal behavior has greatly benefited from this implementation (reviewed by Krause et al. 2007; Croft et al. 2008, Wey et al. 2008). By formalizing the link between individual behavior and population processes, social patterns could be not only described, but have their deviations from randomness accurately quantified. The knowledge about animal society organization has its roots on the nature of dyadic associations (Hinde 1976, Whitehead and Dufault 1999). However, since social relationships rarely occur in isolation, a broader understanding of sociability requires perusing the network of such dyadic interactions. The social network potential for extracting details of the social structure is particularly functional for highly dynamic and heterogeneous interindividual interactions (e.g. Lusseau 2003, Croft et al. 2004).

Therefore, the topology of social networks encodes important information on differences in social organizations. Then, structural patterns of networks should help us to better understand the structure of an animal society (e.g. Croft et al. 2008). From the group size and stability dichotomization (Table 1) one may predict topological structure of the social networks, based on the strength of interactions (duration of relationships) and number of interactions (density of relationships) (Fig. 1). Aggregations may be engaged in numerous ephemeral associations, which could lead to a random social network. In this case no particular network structure may arise, since virtually all members of population can interact, at different levels, but mainly in short duration associations. On the other extreme, long-lasting and permanent associations can lead to a disconnected network (components), in which small parts of the population frequently interact only with each other. These intense relationships usually characterize the highly stable and hierarchically organized matrilineal social units (sperm whales, e.g. Whitehead et al. 1991, Lusseau et al. 2008; pilot whales, e.g. Amos et al. 1993; killer whales, e.g. Parsons et al. 2009). Between them are placed the fluid groups of intermediate sizes and composition, occurring at different levels in time and space, displaying different degrees of fission-fusion dynamics (cf. Aureli et al. 2008). This heterogeneous pattern may lead to a modular network topology, comprised of weakly interlinked groups of individuals which internally are strongly connected.

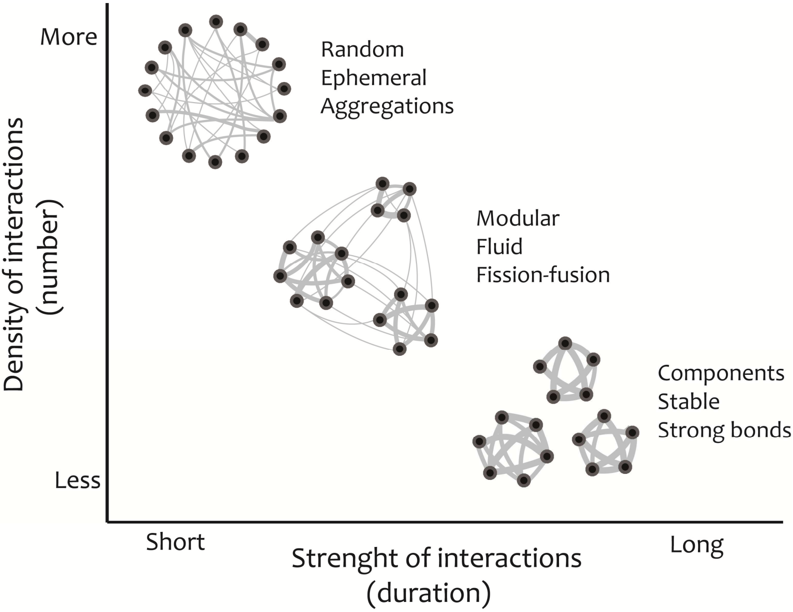

Figure 1. Hypothetical social networks depicting dyadic association patterns among delphinids based on density and strength of interactions. Stability of associations (ephemeral, fluid and stable) related to broad categories of social organization (aggregations, fission-fusion, and permanent pods) may theoretically shape the topology of delphinid social networks, here roughly represented by the extremes random, modular and disconnected components. In the network depiction, weighted edges connecting nodes represent the intensity of association between individuals.

Given that mammalian societies are complex systems (see Crook et al. 1976), grounded by distinct internal and external factors, one may be aware of varying patterns within this simplistic view. Several other mechanisms may contribute to generate modules (e.g. Lusseau and Newman 2004, Lusseau et al. 2008, Wiszniewski et al. 2009, Daura-Jorge 2011), thus varying levels of modularity may be expected (not included in the Fig. 1). An important source of variation relies on the spatiotemporal opportunities for individuals to interact with each other (Aureli et al. 2008). Non-social effects, such as those regarding space use patterns and temporal demographic changes, are known as important sources of variation in associations among individuals, limiting or favoring potential associates. Exit and entrance of individuals in the population, by death-emigration and birth-immigration, affect the likelihood of association along the time (e.g. Lehmann and Boesch 2004), as well as differences in home range or habitat preferences influence the association probability in a spatial scale (Clutton-Brock 1989).

Here, we tested this theoretical framework conducting a long-term experiment to assess the poorly known social organization of *Sotalia guianensis*, a delphinid endemic of the western Atlantic Ocean. Our main objective was to investigate the structure of relationships among dolphins and test the general hypothesis that their social network shows a modular structure. We suggest such hypothesis based in the proposed fluid social relationships for the species (Santos and Rosso 2008). Knowing that spatiotemporal factors can influence the opportunities for group members to interact (Kappeler and van Schaik 2002, Aureli et al. 2008), we further aimed to test candidate non-social mechanisms that could allow a modular structure to emerge. Due to the high complexity of habitat encompassed by our study area, we first investigate if individual differences in space use could lead to preferential associations. Second, we sought for a temporal pattern in dyadic association, based on the dynamics predicted for an open population. Finally, we evaluated a set of network metrics to examine if one of these mechanisms has driven the network structure observed. Thereby, this effort provides further insights into non-social determinants of non-human sociality patterns.

Material and Methods

Study area

The study covered the Caravelas River Estuary (17°30'S - 39°30'W) and its coastal adjacent areas, in the Abrolhos Bank, an extension of the continental shelf off eastern Brazilian coast (Fig. 2). The area encompasses a highly heterogeneous habitat, characterized by a mosaic of open waters protected by coral reef barriers, mangrove forests with channels, sandy beaches and banks of shallow and warm waters.

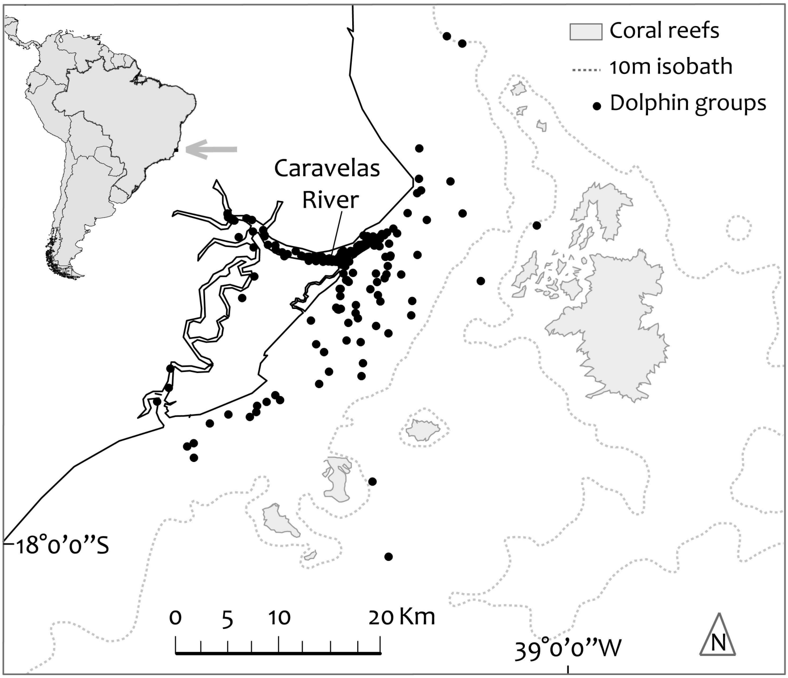

Figure 2. Caravelas River Estuary in the coast of Abrolhos Bank, eastern Brazil, and the Guiana dolphin (*Sotalia guianensis*) groups in which individuals were identified (black dots).

Sampling protocol

Data collection was carried out from April 2002 to March 2010, during boat surveys under routes planned to cover the study area homogeneously (see Cantor et al. *in press*). Visual search for groups of dolphins was done by at least three observers, covering 180 degrees of the visual field. For all group sightings, we recorded geographic coordinates (GPS) and group size and attempted to photograph the dorsal fin of all dolphins in the group, taking as many photos as possible of both sides and without individual preferences (for further details see Rossi-Santos et al. 2007).

Distinguishable individuals provide the basis for descriptions of social systems (Hinde 1976). Guiana dolphins were identified by natural markings on dorsal fin, a technique largely used for individual recognition of many cetacean species (Hammond et al. 1990). During 2002 and 2004, photographs were taken from SLR cameras (see Rossi-Santos et al. 2007), then digitalized and included in the digital catalogue with photos from 2005 to 2010. The catalogue was periodically reviewed and only high quality photographs were included for identification, i.e., those with good focus and a perpendicular angle of the dolphin in relation to the photographer.

Data filtering

To avoid misidentifications, calves and individuals without distinctive marks (i.e. at least one notch on the trailing edge) or those captured only in low quality photographs were not included in the analysis (see Hammond et al. 1990). Since there are significant individual movements across our study area (Cantor et al. *in press*) infrequently resighted individuals were relatively common. In order to reduce spurious association and also to increase precision of association indices and increase power of social analysis (Whitehead 2008a), we applied an observation threshold, keeping only individuals resighted at least three times (see also Croft et al. 2008). We also discarded groups in which only one individual was identified, but kept groups which only part of the individuals were identified. However, the average group size in the area was small ($\bar{\chi} = 4.7 \pm 0.61$ SD) and the proportion of identified individuals per group was relatively high for all studied years (see Cantor et al. *in press*).

Dyadic associations

To examine social relationships between Guiana dolphins, we considered all dolphins identified in the same group on the same day as being associated (*Gambit of group* hypothesis, Whitehead and Dufault 1999). To determine how often individuals grouped together, we calculated association indices for all pairs. These indices estimate the proportion of time a pair of individuals was observed in the same group, in relation to the amount of time they were observed in different groups (Cairns and Schwäger 1987, Ginsberg and Young 1992). Half-weight association index (HWI) is appropriate to this population because it compensates for bias when not all individuals in a group can be identified (see Whitehead 2008b). The index is defined as: $HWI = x/(x + yab + (ya + yb)\ /\ 2)$ where, x is the number of sampling periods with the dolphins a and b were observed in the same group; y_{ab} is the number of sampling periods with a and b identified but not in the same group; y_a is the number of sampling periods with only dolphin a identified, and y_b with only dolphin b.

The precision of the HWI, indicated by standard errors, was estimated through non-parametric bootstrap method with 1000 replicates (Whitehead 2008a). The variability of HWI (Social differentiation – *S*), which technically is the coefficient of variation of the real HWI, was evaluated by the maximum likelihood method (*cf.* Whitehead 2008a). It represents a heterogeneity measure of the relationship in the dolphin's society: *S*-values lower than 0.3 suggest a rather homogeneous society in relation to the association indexes; *S*-values greater than 0.5 suggest a well differentiated society; and *S*-values higher than 2.0 characterize extremely differentiated societies. To estimate the accuracy of the association matrix, we calculated the correlation coefficient between the true and the estimated association matrices, based on *S* estimated through the maximum likelihood method (*cf.* Whitehead 2008a). This is a measure of how well the association matrix reflected the real social structure. A correlation about 0.4 indicates a somewhat representative pattern, while values around 0.8 point out good representations.

Network topology

Interactions between individuals of Guiana dolphins were described as indirect weighted networks (e.g. Bocatelli et al. 2006). This social network is defined as an incidence matrix *A* describing the proportion of time that pairs of individuals were associated. Then, an element a_{ij} of the matrix A is the value of HWI for the individuals j and i. In the network representation, nodes representing individuals were connected by edges, whose thickness was proportional to the weight of association (HWI), whenever HWI was different of zero. The network was illustrated using Netdraw 2.091 software (Borgatti 2002, *NetDraw: Graph visualization software,* Harvard, Analytic Technologies), based on the spring-embedded layout, which arranges more similar individuals together.

Non-human social networks usually have their weight edges filtered (e.g. Lusseau 2003, Lusseau and Newman 2004, Lusseau et al. 2006, Croft et al. 2008), in an attempt to remove spurious associations, which supposedly biases conclusions (James et al. 2009). However, this arbitrary procedure could also remove important information encoded in the weak edges (e.g. Granovetter 1974). Thus, we evaluated unfiltered weighted networks (as suggested by, e.g. Lusseau et al. 2008, Opsahl et al. 2010), and challenged their features with null models (see below).

In order to describe the social network structure, we measured the following topological properties: (1) Density, (2) Weighted Clustering Coefficient, and (3) Modularity. (1) Density informs how connected the network is. It measures the proportion of observed interactions in relation to the possible interactions among all individuals (see Ydozis 1980). The equivalent for weighted networks was calculated by dividing the sum of all edge values (HWI) by the number of individuals. (2) Global clustering coefficient quantifies the degree to which nodes tend to cluster together. It is a social network's connectivity measure, representing the chance of the individual's associates being associated among themselves. Technically, the clustering coefficient is based on density of triplets, i.e. three nodes connected by either by two (open triplet) or three edges (closed triplet). Clustering coefficient is, then, defined by the number of closed triplets divided by the total triplets (e.g. Newman 2003). To take weights into account, we assigned the averaged weight for the edges of a triplet (*arithmetic mean method*; Barrat et al. 2004, Opsahl and Panzarasa 2009), with TNET package (Opsahl 2009) in the R environment (R 2010).

Finally, (3) Modularity quantifies the tendency of the nodes to cluster into cohesive sub graphs. A modular social network is composed by weakly interlinked groups of individuals which internally are strongly connected to each other. It complements the global clustering coefficient identifying the amount of modules and which individuals belong to each one. Modularity was calculated using Netcarto (Guimerá et al. 2004), that uses a stochastic optimization technique, the simulated annealing algorithm (Kirkpatric et al. 1983), to find the partition of the social network in modules that yields the highest difference between the actual density of connections among individuals inside the modules and the density of connections expected by chance (Guimerá and Amaral 2005a, 2005b). In order to explore how consistent the modularity was when taking weighted edges into account, we simulated an increasing cutoff scenario to define a binary interaction. We tested the modularity significance, and compared the number and similarity between new modules and the unfiltered modules. Significance was checked by generating 1000 random networks (see below) and compared with the empirical value for each HWI cutoff (that ranged from 0.1 to 1.0). To quantify how similar the new filtered modules were in relation to unfiltered ones, we applied the Sorensen index, which takes the double-presence of an individual into modules as reference of resemblance between two modules (Legendre and Legendre 1998).

Spatial patterns of dyadic associations

Mammalian social interactions are generally influenced by space use (Clutton-Brock 1989), because individual differences in home range or habitat preferences may affect the probability of individuals group together. Then, one would expect the strength of relationships to increase with the spatial overlap, i.e. that dolphins that use more similar areas tend to show higher probability of being in the same group. To test this hypothesis, we analyzed the relation between dyadic association and the averaged distance between pairs, with a Mantel correlation (1000 permutations) between association and distance matrices. To estimate how far in the space each dyad was, we calculated the mean Euclidean distance among all their geographic coordinates. For each individual, we used the first geographic coordinate of the group in which it was sighted. To ensure independence of samples we analyzed only the geographic position where individuals were separated, in different groups and days, because individuals in the same group were obviously using the same area.

To test if spatial patterns affected the network topology, we analyzed its relation with the emergence of modules, when lower intra and a higher inter-module distance of individuals is expected. Distances within and between modules were calculated by averaging the mean Euclidean distances between all pairs of individuals that composed a given module. The averaged distances were challenged with a null distribution generated by a null model (see below) to assess their significance. All analyses were programmed in the R environment (R 2010).

Temporal patterns of dyadic associations

Temporal stability of dyadic associations was evaluated through the Lagged Association Rates analysis (LAR, Whitehead 1995, 2008b). The population LAR (g) corresponds to the average probability of previously associated pairs being found together again after a given time lag *d*. For different time lags, the observed number of repeated associations was divided over the potential number of repeated associations and summed across all individuals. In a group with permanent companionships g(*d*) would be 1, while for groups in which members changes at high rates, this probability would fall exponentially with time lag to lower values (see Whitehead 1995). To determine occurrence of nonrandom associations, LAR were compared to the null association rates (NAR), in which all individuals could be randomly associated (Whitehead 1995). NAR were calculated considering the number of associates and the number of observations for each individual, but assigning the identity of its associates randomly.

To describe how relationships change over time, g(*d*) were plotted against time lags. Seven candidate exponential decay models were fitted in order to quantify structural parameters of the social organization (Whitehead 1995). They are based on the combination of three potential components of societies with fission-fusion dynamics: constant companionships (CC), i.e. individuals that are permanently associated; casual acquaintances (CA), representing individuals that associated further than a time lag *d*, but disassociate ; and rapid disassociation (RD), pairs that disassociate during a time lag *d*. The most parsimonious model was selected based on the quasi-Akaike Information Criterion (QAICc) (Burnham and Anderson 2002), due to the overdispersion adjustment and small sample size (Whitehead 2007). For a best display, LAR and NAR for lag increments of 1 day were averaged using a moving average window of 1000 days (Whitehead 1995, 2009). Standard errors for the LAR and NAR estimates were calculated by Jackknife procedure, sequentially omitting data from 30-

day periods, to overcome potential dependence among sampling periods (Whitehead 1995, 2009). These analyses were performed for all individuals, without the observation threshold filter, to avoid a positive bias of the LAR (*cf.* Whitehead 2008b). These analyses were calculated with the suite of Matlab (MATLAB7.1, release 14) programs SOCPROG2.4 (Whitehead, 2009).

Demographic effects

Other non-social effects on structure of interindividual associations were assessed by insights on population dynamics. Evaluating demographic effects helps to place patterns of association in perspective because, if one individual has left the population then it cannot associate with those that remained. Movement of individuals through the study area (i.e. immigration and emigration) was modeled by lagged identification rates (*LIR*, Whitehead 2001), which is the probability of identifying an individual in the study area at any time given its previous identification, comparing to a randomly chosen individual after a time lag. If the population is closed the LIR should be constant. If individuals are leaving the population (through emigration or mortality), a fall in the LIR is typically detected with a time lag. LIR that fall and then rise with time lag can be result of cyclical movements of individuals through the study area.

Exponential decay models were fitted to the observed LIR, based on a combination of several demographic parameters, such as the population size (N), mean residence time (a), mean time outside the study area (b), emigration (χ) and mortality rates (δ) (see Whitehead 2001). The quasi-Akaike Information Criterion (overdispersion corrected) informed the most parsimonious model (Burnham and Anderson 2002, Whitehead 2007). LIR confidence intervals were obtained by bootstrapping individuals with replacement to obtain replicates (*cf.* Whitehead 2007). LIR analyses were calculated with the suite of Matlab (MATLAB 7.1, release 14) programs SOCPROG 2.4 (Whitehead 2009).

A relation between association probabilities and absence of individuals in the study area (mortality, emigration) was sought by a linear regression of LAR and LIR for the same time lags (under a geometric progression). Based on the LAR and LIR best fitting models, we define the time lag in which the association and identification rates present lower probabilities (half) of continue existing. In order to relate the decayment of association probabilities with presence of individuals in the study area, we analysed the temporal scale of the turnover of individuals among different blocks of time. The total study length (96 months) was arbitrarily divided by numbers that only resulted in integer periods of months (6, 8, 12, 16, 32, 48 months). To quantity how different the blocks of time were in relation to the presence of individuals, we built a dissimilarity matrix of the blocks in relation to turnover of individuals with Whitakker's beta diversity index (Whittaker 1972). The averaged dissimilarity among the blocks of a given time cut-off was compared with the expected mean dissimilarity generated by a null model (see below).

Local network properties

To test if the observed network structure corresponds to the independent temporal classification of individuals, we calculated the (1) Average Weighted Shortest Path Length and the three Centrality Measures to each node of the network. To ensure that both the edge weights and the number of intermediary nodes (the base of Freeman's 1978 original metrics) affect the identification and length of paths and centrality metrics, we used the tuning parameter proposed by Opsahl et al. (2010). Values of $\alpha \epsilon [0,1]$ prioritize the number of intermediary nodes at the expense of the interactions' strength. Thus, a shorter path made of weak edges is favored over a longer path composed of stronger edges. By contrast, when $\alpha > 1$ additional intermediary nodes are less important than the strength, thus paths with less intermediaries and stronger interactions are favored. Finally, when $\alpha = 0$, metrics are binary, and with $\alpha = 1$ metrics are weighted.

(1) Shortest path length is the minimum distance between two individuals. We expected that individuals sighted within the same block of time present the shortest paths between them. Here, we exponentiated the edges weights to $\alpha = 2$ to focus on the stronger relationships. In a weigthed network, a path length is described by the lowest sum of edge weights between a pair of nodes, however in cases that edges represent "costs" (Dijkstra 1959). In social networks, the weight indicates the strength of the interaction, thus the small path length is better described by the lowest sum of the inverse of edge's weight (Brandes 2001, Newman 2001). Then we used the inverse of association index (1/HWI) as a measure of distance between two individuals (proportion of time

they were disassociated), in order to identify the “least costly” path (i.e. the path with stronger edges).

To select the most influential measure of centrality, we applied a Principal Component Analysis to (2) Weighted Closeness, (3) Weighted Betweenness, and (4) Strength, under four tuning parameter values (α=0, α=0.5, α=1, α=2). These are defined as follows: (2) Closeness centrality is the inverse of the sum of all shortest path length of a given node to every other node in the network (Freeman 1978). It represents the total distance of a given individual to the rest of individuals in the society. Central individuals are “closer” than peripheral individuals, which can reflect the individual influence on the flow through the network. (3) Betweenness centrality measures the number of shortest paths that passes through a focal node (Freeman 1978). It assesses the degree to which a node connects densely connected groups, and is able to funnel the flow in the network. (4) Strength is the weighted counterpart of the degree centrality of binary networks, i.e. the number of edges that a node has (Freeman 1978). It is usually quantified by summing the weights of all edges of a given node (Barrat et al. 2004). In a social context, both degree and strength represent the involvement of an individual in the network, explicitly through the number of individuals interacting with the focal node and the strength of its relationships. Then, both were combined by the tuning parameter, when α ϵ[0,1] favored the largest number of edges over the overall weight, whereas α>1 favored stronger edges over higher degrees (Opsahl et al. 2010).

Association patterns

We tested the hypothesis that Guiana dolphins have a random social structure, with no prefered or avoided associations of individuals. Animal association patterns are usually evaluated by Monte Carlo simulations (Bejder et al. 1998), in a similar fashion of methods used to address other ecological issues (Manly 1995). This widely applied pair-wise swapping algorithm was recently criticised, relying on an extensive debate in the ecology literature about methods of generating random binary matrices (Krause et al. 2009). Warned by this, we were inspired to utilize a different approach for testing the association indices significance. In order to avoid the supposed biases, here we relied on a null model (see first null model below) that randomize the raw group-individual matrix differently than the well-known permutation flips

(Bejder et al. 1998, Miklós and Podani 2004, Manly 2007). However, our randomization was done under the same constraints of that algorithm: the number of animals in each group and the number of groups in which each animal was identified (*cf.* Bejder et al. 1998). We also performed the recommended 20,000 randomizations to ensure independence of permuted matrices (Manly 1995, Bejder et al. 1998).

In a long term study, significant associations could occur as a bias from additions (births or immigration) and deletions (deaths or emigration) of individuals in the population, because some individuals shared time together in the study area and others did not. To rule out this non-social demographic effect from association indices, we first defined the maximum scale over which associations could be analysed, based on Lagged Association Rates and individual turnover analyses discussed earlier, separating the individuals sighted (at least once) in these period of time (32-months, see results). Then, each of these periods was split into sampling periods during which demographic effects were less likely to occur (*cf.* Whitehead 1999). Too short sampling periods decrease the power of the test, whereas long periods enhance the probability of type-1 error due to individual movements through the study area (*cf.* Whitehead 1999). We determined one-year period as a suitable length of sampling period, during which this population could be considered closed (Cantor et al. *in press*). At each iteration, one sampling period was chosen and the randomization procedure (see null models below) was carried out within it.

In order to further test the relation between emergence of modules in the social network of Guiana dolphins and the temporal effect we compare the average association indices (HWI) within and between both classes (modules; sighting periods of 32-months - see results). We expected individuals sighted in the same 32-month period to show association indices significant higher than individuals from different periods. The same pattern was expected for individuals composing the modules of the network. The comparison between and within classes was carried out through the Mantel test on the null hypothesis that association between and within classes were similar (Schnell et al. 1985).

Long-term preferred companionships (that persist across sampling periods) are indicated by a significantly high Coefficient of Variation of the real association indices. Short-term preferred companionships (within the sampling period) are indicated by a significantly low mean of the real association indices and an unexpectedly low proportion of non-zero of association indices (Whitehead 1999, 2005, 2008b). This procedure replace the summary statistics *S* used in Manly (1995) and Bejder et al. (1998). The p-value was calculated as the proportion of random values that was higher than real data, thus a significant difference, as an one-tailed test, was indicated large p-values ($p > 0.95$) (*cf.* Whitehead 1999, 2005, 2008b).

The test was extended for each dyad to test if the members associate preferentially, against the null hypothesis that there is no particularly strong or weak association (two-tailed test, *cf.* Bejder et al. 1998). This was done by considering a conservative cutoff on the random dyadic association distributions, to increase the probability of detecting real preferences (individuals seen together often) and avoidances (never seen together). Pairwise association estimates at or below the 2.5% percentile were considered as avoidance, and those at or above the 97.5% percentile were considered as preference. Within the percentiles, we defined the casual associations (*cf.* Frère et al. 2010a, 2010b). The number of expected significant dyads were calculate as the 5% of all possible pairs (*cf.* Whitehead 2008, *pers. comm.*). All analyses were programmed in the R environment (R 2010).

Null models

The observed levels of network structure and properties may emerge due to several mechanisms, even in random graphs (see Newman 2003, Bocatelli et al. 2006, James et al. 2009). To test if the observed patterns occurred at random, we compared empirical results with 1000 similar sized random networks. These networks were generated by null models that randomize the original matrix. To make them comparable, the degree distribution, number of nodes and edges were the original features constrained during the randomization process. To reject the null hypothesis, the observed result should not be a typical value from the random distribution taken as a benchmark, being out of the 95% confidence intervals (two-tailed test). Two null models were designed. The first checked the significance of network metrics (global average path length, clustering coefficient, modularity) and association indices. Departing from the raw Group x Individual matrix, individuals were resorted among groups. Every dolphin was assigned an interaction by randomly selecting another individual from the pool of possible partners. The probability of each cell being occupied is the average of the probabilities of occupancy of its row and column. This means that drawing an interaction is proportional to group sizes (marginal row totals) and individuals' capture frequency (columns). This procedure is structurally similar to null models used elsewhere (Bascompte et al. 2003, Vázquez et al. 2009). The second null model generates random values (mean Euclidian distances, turnover of individuals, and proportion of individuals) and local network properties to compare classes (modules, blocks of time, and sighting periods). For turnover analysis, the individuals were randomized into the blocks of time, retaining constant the number of times each individual was observed. For the rest, the classes were randomly assigned for the individuals. A mean random value within and between the classes were calculated to build the null distributions. All null models and analyses were programmed in the R environment (R 2010).

Results

From April 2002 to March 2010, sampling was performed on 401 days and covered more than 13,660 nmi, totaling 393 groups and 1,779 sighted dolphins. Within all the groups, 74.3% of individuals were identified and only 12% of groups had less than half of their individuals identified. From the 143 catalogued individuals, 36 undistinctive animals or captured in low quality photographs were not included in the analysis. By keeping only individuals recaptured at least three times, we focused our analyses on 49 individuals distributed in 158 groups. The Guiana dolphin population was organized as a well differentiated society (S = 0.87 ± 0.03 SE; maximum likelihood approximation), and the estimated association matrix was a moderate representation of the true pattern (r = 0.51 ± 0.03 SE).

Social network topology

The social network of Guiana dolphins was composed of n = 49 nodes, connected by 438 weighted edges (mean HWI = 0.167 ± 0.114 SD, range = 0.029 - 0.998). The number of realized interactions (density $\rho = 0.375$) and the weighted density ($\rho_w = 0.0622$) indicated a low connected network (mean degree $k = 18.0 \pm 8.7$) with relatively weak interactions (mean strength $s = 2.985 \pm 1.255$). The global clustering coefficient was higher than null expectance ($C_{w,am} = 0.665$, 95%CI =

0.586 – 0.659), suggesting a high tendency of nodes to cluster together. The social network was more modular than its random counter-parts (M_{obs} = 0.209, M_{random} = 0.119, 95%CI = 0.110 – 0.129). The network was divided into three modules, containing 21, 6 and 22 individuals, respectively. The modularity was relatively consistent under an increasing cutoff scenario for defining an interaction. The majority of association index cutoffs yielded higher modularity than expected by chance. Modularity remained consistent until a cutoff that was the double of the mean population association (cutoff = 0.3; Fig. 3A), when there were low qualitative changes between the new modules and the unfiltered network modules (similarity remained high, Fig. 3C). Moreover, only after such cutoff the network breaks into disconnected components (Fig. 3B).

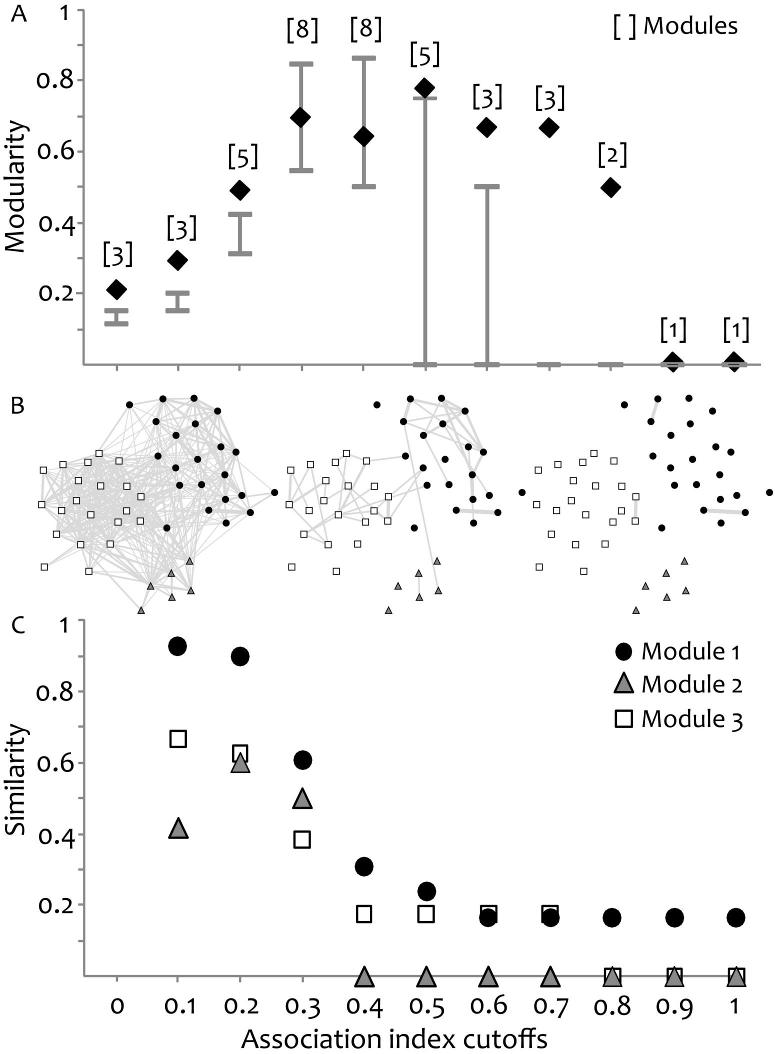

Figure 3. (A) Modularity of the social network of Guiana dolphins in the eastern Brazil under an increasing association index cutoff scenario for defining a binary dyadic association. Whiskers represent the 95%CI expectance generated by null model. Brackets indicate the number of modules in each cutoff. (B) Network breakdown due to HWI filtering: first graph (left) represents the unfiltered network, second graph was filtered at 0.3 HWI, and the third represents network filtered at 0.6 HWI or higher. (C) Similarity (Sorensen

index) between new filtered and the unfiltered modules: higher similarity was found until the 0.3 cutoff.

Spatial patterns and network topology

The spatial use of the study area has not influenced the probability of individuals to form groups. Individuals that use more similar areas did not tend to show higher association indices (Fig. 4). Dyadic half-weight association index was not correlated with the mean euclidian distance among all sightings of pairs of individuals (r = -0.0722, p = 0.923).

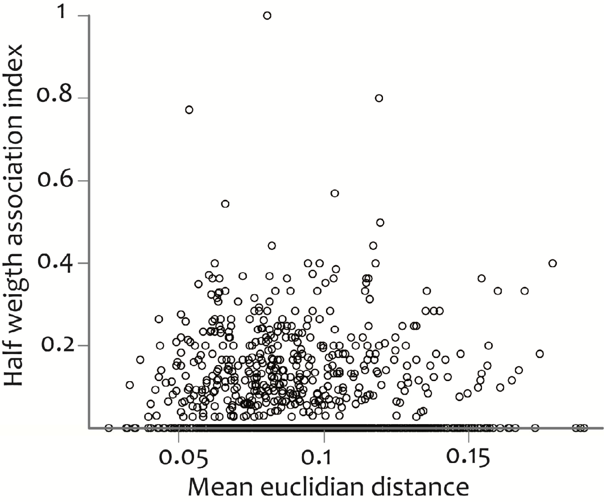

Figure 4. Correlation between association index and the mean Euclidian distance among all sightings of pairs of individuals of Guiana dolphins in eastern Brazil.

Moreover, the mean Euclidian distances between pairs of individuals within and between the three modules were not different from expected by chance (Fig. 5). As a result, the emergence of the modular network structure could not be explained by individuals' spatial use overlap.

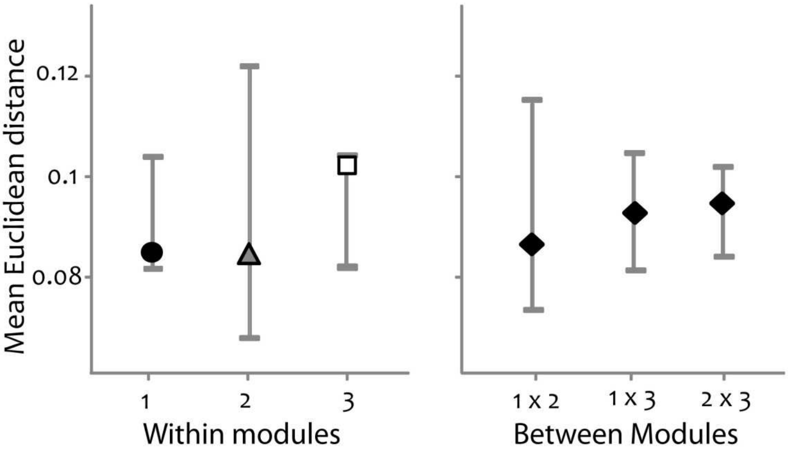

Figure 5. Mean Euclidean distance among pairs of Guiana dolphins within and between the three modules (1 = circle, 2 = triangle, 3 = square) of their social network. Whiskers represent 95%CI generated by null model.

Temporal patterns and network topology

The Lagged Association Rates (LAR) fell throughout the study, indicating time-dependence of association probabilities, and a significantly dissociation over the study. The LAR model with more support based on the QAICc consisted of rapid dissociations and casual acquaitances (Table 2), i.e. most associations were of short duration. Associations within the population were nonrandom, since the association rate remained higher than the null association model over the entire study period (Fig. 6a).

Time has also influenced the Lagged Identification Rates. Three exponential decay models for LIR were supported by the QAICc considering the set of candidate models (ΔQAICc ≤ 2; Table 3). The first two provided exactly the same fit and comprised parameters that indicate the occurrence of emigration and mortality. These models are mathematically equivalent to the best fit LAR model (Fig. 6b). The third model suggested the occurrence of reimmigration, in which temporary emigrants return to the population.

Lagged association and identification rates were highly positive correlated (observed values: $R^2 = 0.924$, $t = 9.85$, $p < 0.0001$; predicted by the best fitting models: $R^2 = 0.999$, $t = 237.01$, $p < 0.0001$) (Fig. 7).

This strong correlation between the average probabilities of association and individual re-identification made a combined interpretation feasible. Thus, from the best fit LAR model, it can be estimated that after about 975 days the likelihood of associations declined at half. At approximately the same time (about 964 days), the best fitting model yielded the same decrease in the Lagged Identification Rates (LIR). This time lag was exactly the same period in which the individuals turnover was higher than the null expectation (975 days ~ 32 months). The population showed significant differences in the composition of individuals only when the entire study was splitted in three periods (Fig. 8), consequently 32 months was the temporal scale of the population turnover.

Table 2. Candidate exponential decay models ranked by lowest QAICc for Lagged Association Rates (LAR) of Guiana dolphins from Caravelas Estuary between 2002 and 2010. The association rate between individuals (g) is given as a function of the time lag (d) and is related to the following parameters: proportion of constant companions (P_{cc}), casual acquaintance (P_{cas}) that last for a particular length of time (τ_{cas}) and a proportion of casual association (P_{perm}) that last for a longer period (τ_{perm}) (see Whitehead 1995).

LAR Models	**Explanation**	**QAICc**	**ΔQAICc**
$g(d) = P_{cas} \cdot e^{-d/\tau_{cas}}$	Rapid Dissociation + Casual Acquaitances	11482.1	0
$g(d) = P_{cas} \cdot e^{-d/\tau_{cas}} + P_{perm} \cdot e^{-d/\tau_{perm}}$	Rapid Dissociation + 2 levels of Casual Acquaitances	11484.61	2.51
$g(d) = P_{cas} \cdot e^{-d/\tau_{cas}} + (1 - P_{cas}) \cdot e^{-d/\tau_{perm}}$	2 levels of Casual Acquaitances	11530.3	48.2
$g(d) = P_{cc} + P_{cas} \cdot e^{-d/\tau_{cas}}$	Rapid Dissociation + Constant Companionship + Casual Acquaitances	11657.53	175.43
$g(d) = P_{cc} + (1 - P_{cas}) \cdot e^{-d/\tau_{cas}}$	Constant Companionship + Casual Acquaitances	11724.92	242.82
$g(d) = P_{cc}$	Rapid Dissociation + Constant Companionship	11733.32	251.22
$g(d) = e^{-d/\tau_{cas}}$	Casual Acquaitances	18919.66	7437.56

Table 3. Candidate exponential decay models ranked by lowest QAICc for Lagged Identification Rates (LIR) of Guiana dolphins from Caravelas Estuary between 2002 and 2010. Identification rates of individuals (R) as given as function of the time lag (d) and is related to the following parameters (see Whitehead 2001): Population size (N), Mean residence time in the study area (a), Mean time out of the study area (b), Emigration rate (χ), Mortality rate (δ); others (a_2, a_3) can be reparameterized as the proportion of the population in the study area at any time (a_2 /(a_2+a_3)).

LIR Models	Explanation	QAICc	ΔQAICc
$R(d) = N^{-1} \cdot e^{-\chi \cdot d}$	Emigration/Mortality	40430.69	0
$R(d) = N^{-1} \cdot e^{-d/a}$	Emigration/Mortality	40430.69	0
$R(d) = \dfrac{N^{-1} \cdot \left((b^{-1}) + (a^{-1}) \cdot e^{(-(b^{-1}+a^{-1}) \cdot d)}\right)}{(b^{-1} + a^{-1})}$	Emigration + Reimmigration	40432.69	2.00
$R(d) = \dfrac{\left(e^{-\left(\delta \cdot d/N\right)}\right) \cdot \left((b^{-1}) + (a^{-1}) \cdot e^{(-(b^{-1}+a^{-1}) \cdot d)}\right)}{(b^{-1} + a^{-1})}$	Emigration/Mortality + Reimmigration	40434.33	3.65
$R(d) = b \cdot e^{(-N \cdot d)} + \delta \cdot e^{(-a \cdot d)}$	Emigration/Mortality + Reimmigration	40434.58	3.90
$R(d) = a_2 + a_3 \cdot e^{(-\chi \cdot d)}$	Emigration+ Reimmigration	40838.41	407.72
$R(d) = 1/N$	Closed population	40846.70	416.01

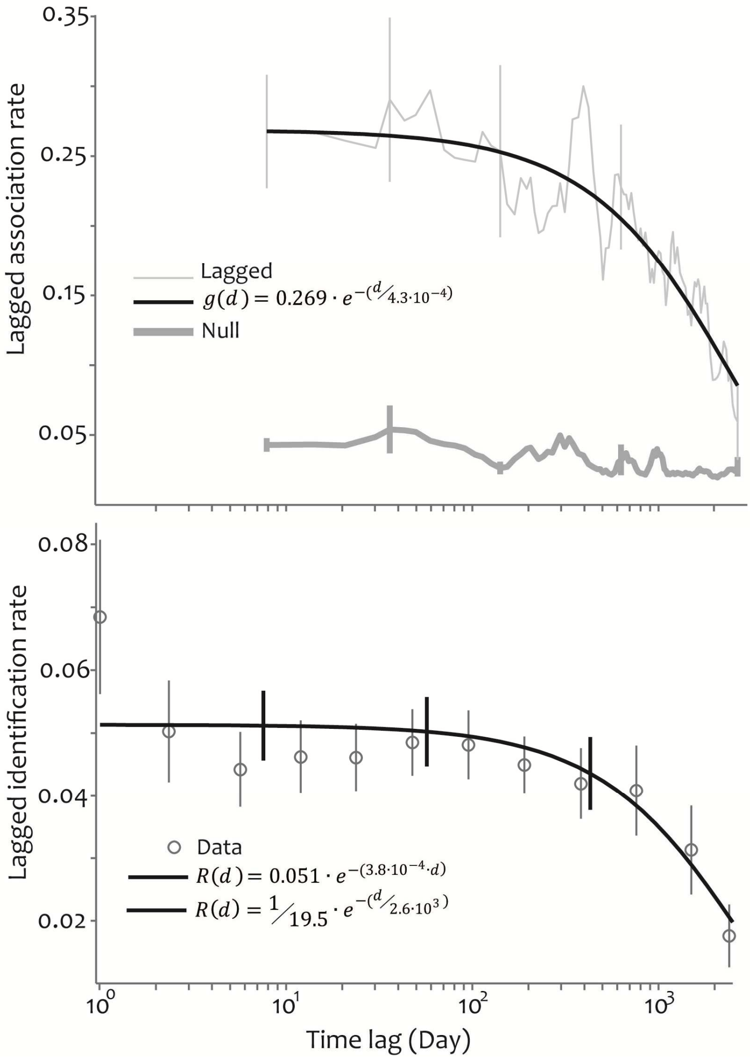

Figure 6. (a) Lagged Association Rates of the Guiana dolphin population from the east coast of Brazil fitted to a exponential decay model composed by rapid dissociations and casual acquaitances. Null association rates curve represents the case in which animals associated randomly; (b) Lagged Identification Rates were best described by two equivalent models that indicate occurrence of emigration and mortality. Error bars means 1 SE estimated by jackknifing procedure.

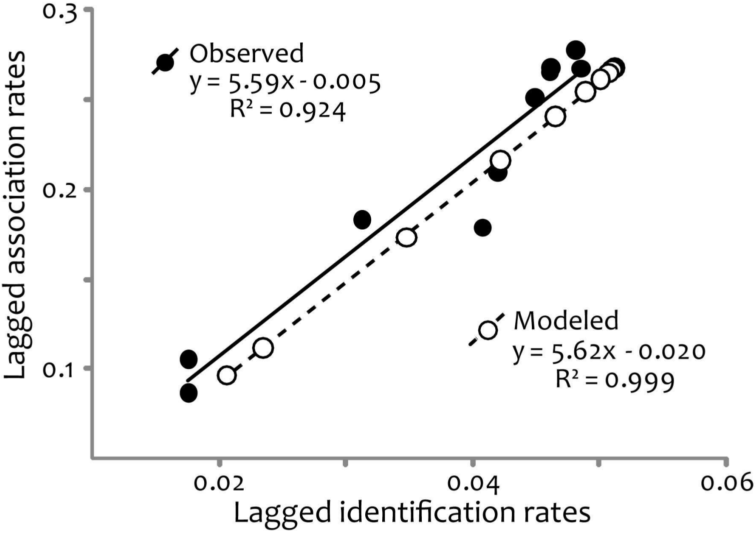

Figure 7. Linear regression of association probabilities over time (Lagged association rates) of Guiana dolphins in eastern Brazil and their identification probabilities in the study area (Lagged identification rates). Observed data (black dots, filled line) and data predicted by the best fitting LAR and LIR models (white dots, dashed line) (see Table 2 and 3) showed a high and significant positive relation.

The 32 months turnover periods reflected into the modular structure of the social network. The partition in three modules corresponds to a division formed by dolphins observed at one or more of the 32-month periods of the study (Fig. 9). From now on, individuals are treated according to three sighting period classes: the beginning of the experiment (individuals sighted exclusive from 1st 32-month period plus the individuals sighted both in the 1st and 2nd periods); the end (individuals exclusively from the 3rd period plus individuals recorded both in 2nd and 3rd periods); or during all the experiment (Individuals sighted in all three 32-month periods).

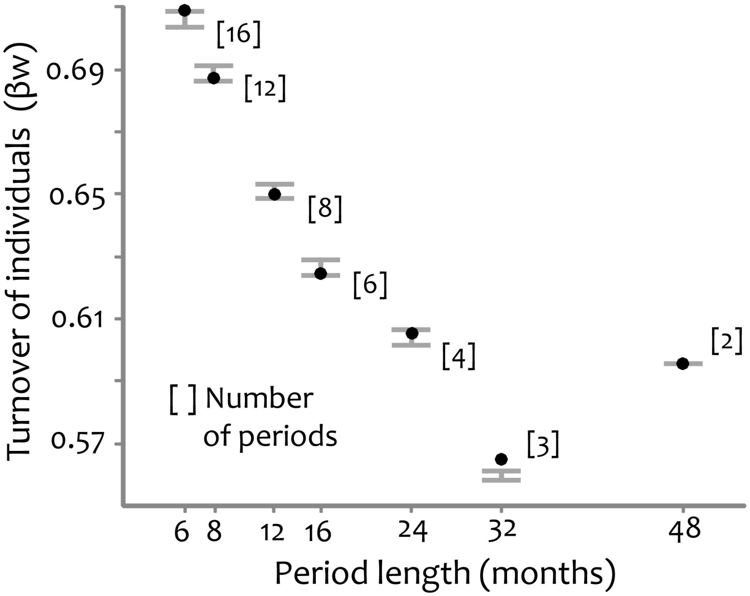

Figure 8. Differences in the composition of the Guiana dolphin population from the east coast of Brazilian coast as a function of different periods of time. Turnover of individuals (Whittaker's beta diversity) was higher than expected by chance between three periods of 32 months (~ 975 days). Brackets indicate the number of periods within the total study length. Whiskers represent the 95% CI generated by null model.

Therefore modules were defined by different individuals that composed the population during the study length. The proportion of dolphins sighted in the beginning of the experiment were significantly concentrated into the module 3. Individuals sighted in the end was found mainly in the module 1. Individuals sighted in periods of transition (1st and 2nd; 2nd and 3rd periods) followed the same patterns. A single individual sighted exclusively during the second period were find in the module 2. Dolphins recorded in the entire experiment were equally distributed across the modules (Fig. 10).

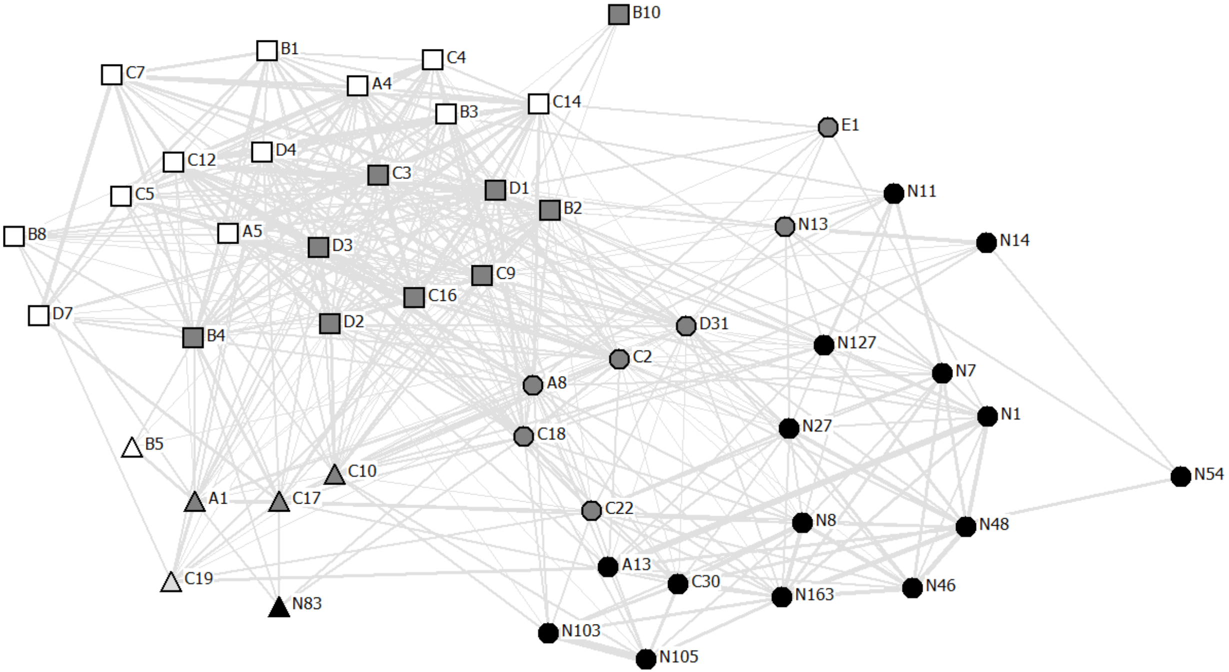

Figure 9. Social network of Guiana dolphins off eastern Brazil from 2002 to 2010 displaying three modules (1-circle, 2-triangle, 3-square), composed by individuals (nodes) from different periods of the study, connected by Half-weighted association indices (weighted edges). White nodes indicate dolphins sighted in the beginning (exclusive from 1st period and in the 1st and 2nd period of 32 months), while black nodes represents individuals sighted in the end of the experiment (only in the 3rd period and in the 2nd and 3rd periods). Grey nodes, equally distributed among modules, indicate individuals recorded in all three periods. The ligth-grey node (C19) represents the single individual sighted exclusively during the second period.

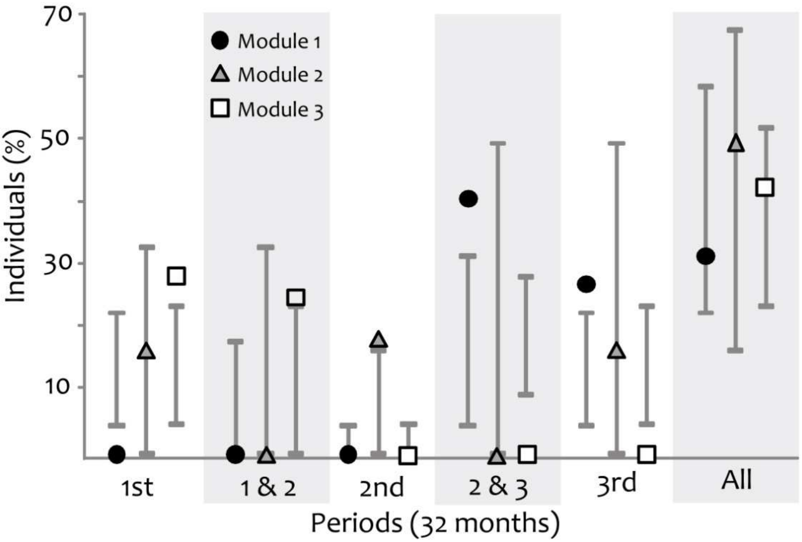

Figure 10. Proportion of dolphins from different 32-month sighting periods (1st, 2nd and 3rd) composing the three modules (1-circle, 2-triangle, 3-square) of the Guiana dolphin social network. Grey bands refer to the dolphins sighted in periods of transition (1&2 and 2&3) and recorded during the entire experiment (All). Whiskers represent 95%CI of proportions generated by null model.

Social network properties

The average shortest path length, favoring stronger edges in the whole network, was low and significant ($L_{w,\alpha=2}$ = 1.735, 95%CI = 1.078 – 1.543). On average, less edges separated two dolphins randomly selected within a class than between classes. The average shortest path length within individuals sighted during the first and during the last 32-month period was lower than expected by chance, whereas the average shortest path length between them was higher than null expectation (Fig. 11). It suggests a higher cohesion within individuals from the beginning and from the end of the study, which was reflected into the module division. Since equally distributed across the three modules, individuals sighted during all the study did not present path lenghts different from the null expectation, within and between other periods (Fig. 11).

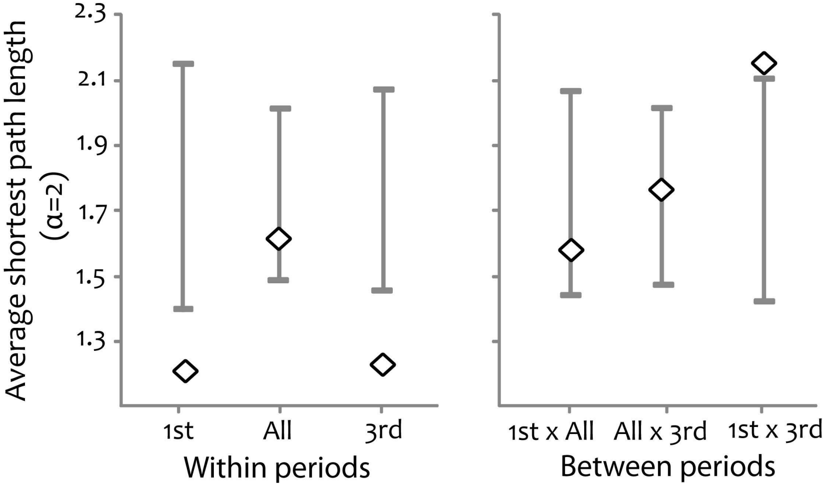

Figure 11. Average shortest path length (under tuning parameter α = 2) of Guiana dolphins in the social network within and between different periods of the study. Whiskers represent the 95%CI generated by null model.

PCA analysis pointed Closeness at α = 0.5 (eigenvector coordinates: Factor 1 = -0.951, Factor 2 = 0.081; PC 1 and 2 accounted for 80.7% of variation) as the most representative centrality metric from the 12 variables (Closeness, Betweeness, and Strength at α=0, α=0.5, α=1, and α=2). Those individuals sighted during all the study were more central in the network than the individuals from other periods (Fig. 12), i.e. more connected to the rest of individuals in the population, when prioritizing shorter paths with weak edges. It showed that individuals' centrality also varied between the classes of sighting period. Individuals in the beggining of the study showed closeness not different from the null expectation. Individuals exclusive from the end of the study were less central than expected (Fig. 12).

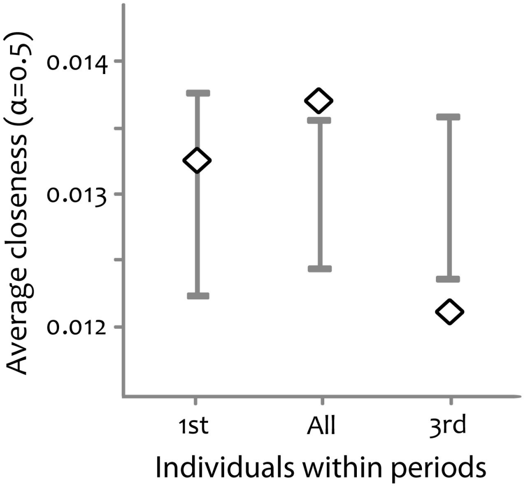

Figure 12. Social network centrality of the Guiana dolphins from different sighting periods measured by average weighted closeness (under tuning parameter α = 0.5). Whiskers represent the 95%CI generated by null models.

Association patterns

Association levels were higher than random values among individuals classified according to the period they were sighted (t = 7.555, p = 1, r = 0.248). Mean association among individuals sighted only in the *beginning* of the study, among individuals sighted only in the *end* of the study, and among individuals sighted during *all* the study were higher than null expectation. On the other hand, associations among individuals of different classes of sighting periods were lower than expected by chance (Fig 13). The same pattern was found for the association level of individuals classified by the modules of the network: mean associations were higher than expected within the modules, and lower between them (Mantel test, t = 13.3278, p = 1, r = 0.410) (Fig. 13). This results strengthen the relation between the differences in the presence of individuals in the population throughout the study and the emergence of modules.

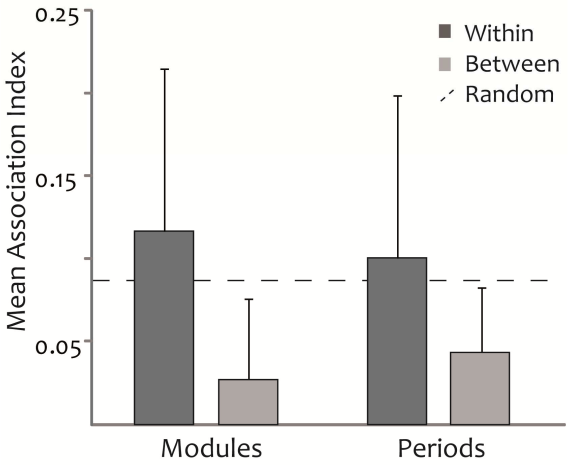

Figure 13. Mean association (Half-weight index) of Guiana dolphin dyads off eastern Brazil within and between classes: the three modules of the social network, and the three 32-month sighting periods (see text for further details). Random values represent the mean randomly HWI generated by null model. Whiskers represent 95%CI.

Relative to random expectations, the dyadic associations were low and variable. The occurence of few “preferred” and “avoided” companionships and absence of short-term companions may be the pattern of associations in this population. The maximum scale to analyze associations were determined by turnover and LAR-LIR analysis (975 dias ~ 32 months). Among all individuals that have inhabited the study area in the same 32-month period, the mean levels of association was not significantly different than expected by chance (Table 4). This indicated that short-term preferred companionships did not occur. The CVs of association indices were significantly higher within periods (Table 4). It suggested the occurrence of long-term companions within the population. Only few dyads were non-random associates: a low percentage of possible pairs showed levels of association lower ($p < 0.025$) and higher ($p> 0.975$) than expected, suggesting a “avoided” and “preferred” associations, respectively. The high mean association per individual ($H = 39.71$), combined with the social differentiation estimate (*S*), provided enough statistical power to reject the null hypothesis of no preferred associations in this dataset ($S^2 \times H = 30.06$; see Whitehead 2008a).

Table 4. Guiana dolphins' observed and expected association index (HWI) for all individuals sighted (at least once) in each 32-month period. Bold values indicate significant results (one-tailed test at α=0.05). Long-term preferred companionships are indicated by a significantly high Coefficient of Variation of the real association indices. Short-term preferred companionships would be indicated by a significantly low mean of the real association indices. Random HWI were estimated by 20,000 null model iterations. "Preferred"/"avoided" dyads showed higher/lower HWI than expected by chance (two-tailed test at α = 0.05); Percentage is based on expected number of significant dyads. SD = standard deviation, CV = coefficient of variation, Non-Zero = proportion of non-zero HWI.

	1st Period			**2nd Period**			**3rd Period**		
Groups	130			141			138		
Individuals	33			36			36		
Preferred	10 (37.9 %)			10 (31.7 %)			12 (38.1 %)		
Avoided	3 (11.4 %)			5 (15.9 %)			5 (15.9 %)		
HWI	**Real**	**Random**	***p***	**Real**	**Random**	***p***	**Real**	**Random**	***p***
Mean	0.094	0.098	0.748	0.066	0.071	0.889	0.067	0.069	0.622
SD	**0.110**	0.107	0.999	**0.107**	0.095	0.995	0.115	0.099	0.806
CV	**1.170**	1.083	0.972	**1.611**	1.339	1.000	**1.724**	1.438	0.999
Non-zero	0.580	0.600	0.236	0.433	0.469	0.061	0.394	0.439	0.023

Discussion

Focused on number and duration of relationships, we have proposed a theoretical framework to predict network topology for broad social organization classes of delphinids. The hypothesis of interindividual interactions' strength and density shaping the social network was corroborated by the long-term study of associations among Guiana dolphins. The intermediate number and duration of associations composing a fluid grouping pattern indicated that a social system with high fission-fusion dynamics can be architected in a modular network.

The relatively slightly connected network of Guiana dolphins represented a well differentiated society, in which the few strong and many weak ties depicted the fluidness of their social interactions. The tendency of dolphins to cluster together in the network indicates that not all dolphins have interacted with everyone. Such heterogeneous pattern of interactions was clearly structured into modules, and then placed within the range of our conceptual framework. The hierarchical organization of this population, structured in subgroups of tighter connected individuals, is comparable to those found in most real-world networks (e.g. Guimerá and Amaral 2005a, Newman 2006a, b), including the social ones (Newman and Park 2003). This division is one of the essentials of group-living organization (Krause and Ruxton 2002). Searching for such structures is a mean to unravel the intricate relation of selective socioecological forces responsible for the social patterns in a population.

Several populations of delphinids have presented a division into discrete social modules (e.g. Ford et al. 2000, Lusseau 2007, Lusseau et al. 2008, Wiszniewski et al. 2009), as well as other highly social mammals (e.g. elephants: Wittemyer et al. 2005, primates: e.g. Ramos-Fernández et al. 2006, Hill et al. 2008, pinnipeds: Wolf et al. 2007). A varied range of local determinants may lead a fluid social network to have their populations structured into modules. The Guiana dolphin population studied here offers an inviting case for examining if non-social sources affect association patterns and, ultimately, generate the modularity. This is because the studied area encompasses a mosaic of different habitats (see Rossi-Santos *et al.* 2006), which makes a population division based on home range segregation plausible. Moreover, the dynamics of this population is characterized by individuals entering and leaving the population (Cantor et al. *in press*), which bring us an opportunity to evaluate temporal effects in associations. Therefore, by putting such spatio-temporal effects into the social context, we present other insights in mechanisms generating modularity in non-human social networks. The population dynamics revealed that temporally separated individuals could drive the divisions in the network, within which the associations can be non-randomly organized.

In the same space at different times

Space use and ranging patterns of individuals may ultimately forestall or favor social interactions (Waser 1988). Home range overlap may involve costs of apportioning the habitat and its resources, which may lead to spatial avoidance of individuals (e.g. Hegner et al. 1982, Carpenter 1987; Maher and Lott 2000). On the other hand, shared space can increase encounters (Clutton-Brock 1989, Shier and Randall 2004, Chaverri et al. 2007, Cooper and Randall 2007), making social interactions seemingly more prone to occur between physically closed individuals (e.g. Kossinets and Watts 2006, McDonald 2009). Association patterns of some dolphin populations may be related to patterns of spatial overlap (e.g. Rosbach and Herzing 1999, Quintana-Rizzo and Wells 2001, Frère et al. 2010a, Cagnazzi 2011), but this is not always true in mammals (e.g. De Villiers and Kok 1997, Connor et al. 1999, Vonhof et al. 2004, Carter et al. 2009).

Non-random patterns of space use can turn out complex structures in fission-fusion networks (e.g. Ramos-Fernández et al. 2006, Fortuna et al. 2009). Then, at last, a modular network structure may emerge in either spatial segregation or overlapping. Dolphins from the same population can be found organized in different social units (e.g. Urian et al. 2009), sharing patterns of residency and associations. One of the causes is the combination of resource availability, pronounced habitat preferences and behavioral specializations (e.g. Lusseau et al. 2006, Wisziniewski et al. 2009). This pattern might be expected for Guiana dolphins in the Abrolhos Bank, considering the high heterogeneity of habitats used in a gradient from inner river to offshore coral reefs (Rossi-Santos et al. 2006), and relatively small individual spatial ranges (Rossi-Santos et al. 2007) possibly leading to a stratification of habitat use (Wilson et al. 1997). However it seems that all the analyzed individuals, at least in the study area (see Rossi-Santos et al. 2007, Cantor et al. *in press*), were "spatially merged", i.e. greatly overlapping their minimum spatial ranges. In contrast, if individuals use almost the same area but exhibit markedly social affinities, cohesive modules of interaction may arise due to strong preferred and avoided associations. We found no evidence of spatial use overlap being a major factor affecting the dyadic association, unlike some bottlenose dolphins (Frère et al. 2010a). This is in accordance with the relatively low relationship intensity among pairs in this population (see below). Consequently, space use is not the mechanism generating the observed modular structure in the Guiana dolphin social network.

This outcome reinforces that social matrices include more than ecological factors or social affinities, and many other factors could contribute to the shaping of a social organization (e.g. Wolf et al. 2007). Regarding delphinids social plasticity, particularities of some dolphin populations have driven the preferential assortment of individuals, such as sex and age class (Lusseau and Newman 2004), kinship (Frère et al. 2010a, Wiszniewski et al. 2010, Cagnazzi et al. 2011), foraging specializations (e.g. Bigg et al. 1990, Baird and Dill 1996, Chilvers and Corkeron 2001, Seargent et al. 2007, Daura-Jorge 2011), and habitat utilization (Wiszniewski et al. 2009, Rossbach and Herzing 1999), that when pronounced may have the potential to lead social divisions in the population. Even occasional natural disturbances can split a previously stable population into distinct social units (Elliser and Herzing 2011). Population dynamics is a less explored mechanism affecting associations (but see Carter et al. 2009, Parsons et al. 2009). Here we present a clear demographic effect shaping the social network of Guiana dolphins, which resulted in temporal modules. These subsets represent "temporally split" individuals.

A demographic effect

Social interactions are generally time-dependent (Whitehead 1995), and elucidating the temporal pattern is an essential step of social relationships studies (Hinde 1976). Moreover, considering the time factor is particularly important when dealing with fission-fusion social systems, due to the dynamism of interactions in different time scales (Whitehead 1995, Conradt and Roper 2005, Aureli et al. 2008). We showed the association probabilities of Guiana dolphins visibly dropping, an indication of significantly dissociation over time. Many reasons can lead to temporally dissociation of individuals (Whitehead 2008b). Environmental features, dispersion, physiology (see Whitehead 1995) or geographical traits (Lusseau et al. 2003) are among of the well-known. Interestingly, here the association rate drop was attributed to a population turnover.

Association probabilities among Guiana dolphins are strongly coupled with the likelihood of an individual recapture in the region. Emigration and mortality are relevant population parameters, which suggest that permanent departure and/or death have prevented some individuals of using the area at the same time. It should be highlighted that, combined with the occurrence of reimmigration (third LIR model), this pattern corresponds exactly to population dynamics obtained by more robust mark-recapture analysis: an open population comprised of a core of resident individuals and many other transient and temporary emigrants (Cantor et al. *in press*). Such additions and deletions of individuals make the population composition at the beginning of the study different from the end, then affecting the average likelihood of associations. The potential of individual removal to change the social dynamics of a population has been demonstrated in other fission-fusion systems, as decreasing the flexibility and increasing group size (Lehmann and Boesch 2004), and emerging distinct social units (Elisser and Herzing 2011).

In summary, we propose that this demographic effect is shaping the modular structure in three social subsets. Even sustaining a constant abundance (see Cantor et al. *in press*), this population has undergone a markedly population turnover. The temporal scale of these differences in the population composition was the same 32-month in which association and identification rates have matched their most prominent decay. Furthermore, individuals sighted within these periods were separated in the three modules: two containing dolphins of the extremes of the study, and a smaller mixed module. This fact adds an evidence of temporal influence on non-human social network topology to the recent growing debate of network dynamism, hitherto directed to ecological (e.g. Olesen et al. 2008, Díaz-Castelazo et al. 2010), metabolic, technological and human social networks (e.g. Palla et al. 2007, Bryden et al. 2010, Delvenne et al. 2010).

The temporal pattern in module formation was corroborated by local network metrics for individuals of different classes of sighting period. Individuals sighted exclusively in the extremes of the study were more closely and stronger connected, reflecting the division in modules. Shorter path lengths separated individuals from the beginning of the study and individuals sighted in other periods; individuals from the end were also closer to themselves. Since equally distributed across the three modules, resident individuals that were sighted along the entire study were less cohesive, with edges spread to dolphins in the whole network. On the other hand, it assigned these residents a more central position. Conversely, individuals present in the population either only in the beginning or in the last third of the monitoring occupied peripheral position in the network.

Identification of individuals with different positions in a network allows further inferences in transfer potential (of gene, diseases, parasites and information) through the society (reviewed in Krause et al. 2010). This arrangement points the resident individuals as the core of the population in the Caravelas Estuary. Being more frequent in the area, they are closer to transient individuals and may be in a key position in the society. More central individuals can influence leadership and decision-making processes in a group (Lusseau 2007, Lusseau and Conradt 2009, Lewis et al. 2010), and determine the network structure (Ramos-Fernández et al. 2009). Moreover, by reaching several others individuals, central individuals may also access information quickly or affect disease spread in the population (Lusseau 2003, Lusseau and Newman 2004, Guimarães et al. 2007, Fortuna et al. 2009, Salathé and Jones 2010).

From a static network structure to a fluid social structure

Despite a fixed representation, a graph encodes the dynamism of a system (see Bryden et al. 2010). At the lowest level of a static social network depiction are the time-varying pairwise interactions, the basis of a social structure characterization (Hinde 1976). The proximate means for maintenance and change of a social structure is the repetition of interactions between individuals (Lee 1994). Thus identifying and quantifying their deviation from randomness is a basic requirement to consider a population as socially structured (Whitehead et al. 2005). At the society level, nonrandomly fluidness in relationships across this Guiana dolphin population was earlier suggested by the temporal features of association probabilities. Grouping patterns were generalized as rapid associations (which last for less than a day) and casual acquaintances (last further than a day and then disassociate).

Testing association indices may be a tricky task (see Whitehead 1999, Miklós and Podani 2004, Whitehead et al. 2005). In order to dodge potential biases of popular permutation tests (Bejder et al. 1998, Krause et al. 2009), we relied on a different null model, based on established randomization procedures (e.g. Bascompte *et al.* 2003, Vázquez et al. 2009). Furthermore, the demographic effects could mask the real pattern if not accounted for, simply because individuals might not have the opportunity to encounter (Whitehead 1999). To overcome this, our experiment was split at the scale of the population turnover, and the randomization process constrained within periods which population closure was reasonable (see Cantor et al. *in press*). Thus, we propose this alternative as a reliable approach for testing dyadic associations.

Pairs of Guiana dolphins sighted within the same 32-month period on average showed higher association index than expected only by chance. Such trend was also found with the dolphins composing the network modules. Scaling down the search to the dyads, association degrees were mostly low and variable, but some non-random preferences and avoidances are noticed among many fluid associations. Some nonrandom partnerships between mammalian species that display dynamic grouping patterns are relatively common (e.g. Sundaresan et al. 2007, Ramos-Fernández et al. 2009). While delphinids generally exhibit short-duration associations (e.g. Wells et al. 1987, Connor et al. 1992, Slooten et al. 1993, Karczmarski 1999), within a population some adult females may form lasting associations (Frère et al. 2010a) and some males may be engaged in more stable long-term partnerships (e.g. Owen et al. 2002). This flexibility may suggest that relationships last as long as fitness benefits of sociality are high (e.g. Takahata et al. 1994; Wittemyer et al. 2005).

These outcomes, combined with the network properties, the temporal variation and spatial patterns, confer a fission-fusion dynamics to this Guiana dolphin population: high temporal variation in group size and composition, even with a moderate spatial cohesion among members (*cf.* Aureli’s et al. 2008 framework). Put together with the findings of lack of consistency in group membership in another population (Santos and Rosso 2008), the fission-fusion social organization may be a general pattern for this species. However, one must look to the latitudinal differences in this species average group size (e.g. Santos and Rosso 2007), a variation better documented for other delphinids (Gygax 2000). Systems with fission-fusion dynamics usually show pronounced group size variation as a response to the varying interaction of ecological variables (Wrangham 1982). Populations of Guiana dolphins spread along the latitudinal range of the species may experience significant differences in habitat protection (or predation risk) and food resources (prey abundance), which could affect individuals interactions (Gowans et al. 2008, Table 1). Therefore, a broader analysis should quantify the different degrees of fission-fusion dynamism in other Guiana dolphin populations. The combination of Aureli's et al. (2008) framework, the analytical outline presented here and the assessment of genetic factors (e.g. Frère et al. 2010b) and reproductive states (e.g. Möller and Harcourt 2008, Fischhoff et al. 2009, Patriquin et al. 2010) is a reliable starting point.

Concluding remarks

Recognizing determinants of network topology is an important step towards the identification of mechanisms driving social systems. This effort, in turn, contributes to address how environmental and biological characteristics have interacted over evolutionary time sculpting such systems (Crook et al. 1976, Wells et al. 1987). Here, the proposed reductionist framework of non-human social network architectures gave us insights of mechanisms affecting social organization. The Guiana dolphin society off eastern Brazil was modularly structured as predicted, and showed a population turnover as the major factor shaping the fluid dyadic associations. Therefore, we highlighted that non-social factors can greatly affect association networks, and should be accounted for an apposite portrayal of societies with fission-fusion dynamics.

Regarding the high complexity of social systems and the plasticity across different species and population, our framework may be simplistic and it still remains largely untested. But it is an opening for new working hypothesis. An accurate ethological modeling of social patterns is required to assess social processes (Whitehead 2008b) supporting next steps into more complex behavioral and ecological questions concerning cost-benefits of grouping (e.g. Majolo et al. 2008), individual fitness (e.g. Frère et al. 2010b), or genetic bases of social interaction (Fowler et al. 2011). Given our framework's socioecological basis, further studies may provide empirical data on intrinsic and extrinsic forces (e.g. predation, prey distribution) to strengthen the link between resource predictability and the social interactions (e.g. Ramos-Fernández et al. 2006; models suggested by Aureli et al. 2008). Moreover, one may ask whether the non-human societies evolve following a sequence of incremental increases in complexity, such the political evolution of societies of their living relatives (Currie et al.

2010). To these ends, the network formalism has been assigned as an auspicious beginning (Dorogovtsev and Mendes 2001, Amaral and Ottino 2004, Ohtsuki et al. 2006, Palla et al. 2007, Sih et al. 2009, Bryden et al. 2010).

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CONCLUSÃO GERAL

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Os frutos deste trabalho podem ser vistos em três diferentes escalas. Em uma perspectiva (1) local, a dinâmica populacional até então desconhecida de *Sotalia guianensis* no ambiente altamente heterogêneo do Banco dos Abrolhos teve diversos aspectos revelados. Trata-se de uma população pequena, composta por alguns indivíduos residentes e diversos outros que atravessam ou utilizam temporariamente a área. Sobrevivência e abundância anual são aparentemente constantes, porém a movimentação de indivíduos entre áreas adjacentes parece promover mudanças na população. Este efeito demográfico mostrou-se refletido no padrão de associações entre indivíduos. A taxa de substituição de indivíduos (*turnover*) parece separar temporalmente a população em dois principais conjuntos de interações sociais. Dentro da escala temporal do *turnover*, as associações mostram-se em sua maioria de curta duração; mas a presença de algumas associações não-aleatórias compõe um quadro heterogêneo.

Em uma escala (2) regional, este estudo oferece pela primeira vez uma série de parâmetros populacionais para a espécie. Reforça-se, assim, a importância de monitoramentos em longo prazo para obtenção de estimativas robustas e com boa precisão. Este trabalho contribui para o preenchecimento a lacuna de conhecimento que impede a avaliação adequada do *status* de conservação da espécie, enquanto uma série de pressões antropogênicas nos hábitats costeiros tende a crescer. O estudo oferece ainda, mais uma forte evidência da dinâmica de fissão-fusão como o padrão de interações sociais da espécie, tema ainda pouco explorado. Adiciona-se uma visão global do padrão de associações da população, até então restrita à análise entre pares de indivíduos. Mostra-se, assim, que uma rede social fluida pode ser arquitetada em módulos. Novamente, fica enfatizada a necessidade de larga escala temporal para levar em conta mecanismos não-sociais afetando o padrão de sociabilidade.

Por fim, com uma visão mais (3) ampla, este estudo confirma a viabilidade de modelagem de dados de foto-identificação de cetáceos de vida livre, obtidos em meio a diversos desafios logísticos, com experimentos de marcação-recaptura e de agrupamento de indivíduos. Dessa forma, se oferece como guia de conduta de análises populacionais e sociais, visando uma comparação padronizada futura. Esta comparação, se conduzida com outras populações de *S. guianensis*, apresenta uma aplicação prática imediata: a definição adequada do *status* da espécie, que deve aperfeiçoar esforços de conservação. Ao propor um modelo conceitual de previsão da topologia de redes sociais de classes de organizações encontradas em Delphinidae, o estudo arrisca-se, ainda, a inspirar novas hipóteses de trabalho. Mostrou-se que a inserção de efeitos espaço-temporais no contexto social pode oferecer novos *insights* sobre mecanismos que afetam a topologia de redes sociais. Portanto, estes devem ser levados em consideração para uma caracterização adequada de sociedades com dinâmica de fissão-fusão. Reconhecer determinantes da topologia de redes é um passo importante na identificação de como mecanismos biológicos e ambientais tem interagido ao longo do tempo evolutivo e entalhado sistemas complexos e auto-organizados como as estruturas sociais de Delphinidae.