

UNIVERSIDADE FEDERAL DO RIO GRANDE

PÓS-GRADUAÇÃO EM OCEANOGRAFIA BIOLÓGICA

**ESTRUTURA SOCIAL DO BOTO, *Tursiops*
truncatus (CETACEA: DELPHINIDAE), NO
ESTUÁRIO DA LAGOA DOS PATOS E ÁGUAS
COSTEIRAS ADJACENTES, SUL DO BRASIL**

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RESUMO

Investigamos a estrutura social e padrões espaciais de uso da área por uma população de golfinhos, *Tursiops truncatus*, que habitam o estuário da Lagoa dos Patos e águas costeiras adjacentes, no sul do Brasil. Nós estimamos o índice de associação a partir de 102 indivíduos regularmente observados em 243 saídas de foto-identificação realizadas entre agosto de 2005 e outubro de 2012. As análises sociais e de rede, com a divisão proposta pela modularidade, indicou que esta população de botos é composta por três unidades sociais principais. Embora exista certa sobreposição espacial, houve distinção entre as zonas preferenciais de cada unidade. Uma das unidades esta fortemente associada com o estuário da Lagoa dos Patos, enquanto as outras duas ocuparam, respectivamente, as áreas marinhas adjacentes norte e sul. Dentro das unidades, as associações entre os indivíduos foram predominantemente de curta duração (dinâmica de fissão-fusão), embora tenham sido identificadas algumas associações de longa duração. Embora tenham ocorrido interações entre as unidades sociais, as associações foram rápidas e ocorreram apenas entre alguns indivíduos. A segregação destes indivíduos é motivada, pelo menos em parte, pelos padrões de associação entre os indivíduos e sua fidelidade a áreas específicas. Recomenda-se que as unidades sociais sejam a base para modelar a viabilidade e dinâmica intrapopulacional, bem como para investigação de padrões de fluxo gênico dentro e entre unidades sociais.

Palavras-chave: Grupo social; cetáceos; comportamento social; uso do habitat; rede social; modularidade; divisão social

ABSTRACT

We investigated the social structure and spatial patterns of area usage by a population of bottlenose dolphins, *Tursiops truncatus*, inhabiting the Patos Lagoon estuary and adjacent coastal waters, in southern Brazil. We estimated the association index from 102 individuals regularly sighted in 243 photo-identification surveys carried out between August 2005 and October 2012. Social and network analyses, with the division proposed by modularity, indicated that this bottlenose dolphin population consists of three social units. Although some spatial overlap exists, preferred areas of each unit were distinct. One of the units was strongly associated with the Patos Lagoon estuary while the other two occupied, respectively, the southern and northern adjacent marine coasts. Within unit associations among individuals were predominantly of short duration (fission-fusion dynamics), though a few long-lasting bonds were detected. Although interactions between social units occurred, the associations were brief and occurred only among a few individuals. The segregation of these individuals is motivated, at least in part, by the bonding patterns among individuals and their fidelity to specific areas. It is recommended that the social units be the framework for modeling the intrapopulation dynamic and viability as well as for investigating patterns of gene flow within and between social units.

Keywords: Social group; cetacean; social behaviour; habitat use; social network, modularity; social division

I. INTRODUÇÃO

Nos organismos com reprodução sexuada, uma população é geograficamente delimitada por um grupo de organismos capazes, em condições normais, de se reproduzirem entre si (WILSON, 1975). Dentro das populações, podem existir grupos de indivíduos que vivem em mútua associação e que possivelmente compartilham a mesma área de vida. Estes grupos são denominados unidades sociais (WHITEHEAD, 2008a). Entretanto, a segregação dos indivíduos em diferentes unidades sociais pode ocorrer dentro de uma população. Esta segregação pode estar relacionada ao sexo, idade, alimentação, comportamento, uso do habitat, ou mesmo devido a companhias preferências (KRAUSE; RUXTON, 2002). A forma como uma população está estruturada é um componente fundamental de sua biologia, influenciando na sua composição e fluxo genético (KRÜTZEN et al., 2003; FRÈRE et al., 2010), na disseminação de doenças (CORNER; PFEIFFER; MORRIS, 2003; NEWMAN, 2002), no fluxo de informações (MCCOMB et al., 2001) e na forma como os indivíduos da população irão explorar o ambiente (CONNOR et al., 1998). Portanto, as unidades sociais desempenham um papel fundamental na ecologia e sociabilidade das populações e, caso existam, devem ser identificadas e delineadas (WHITEHEAD, 2008a). As unidades sociais com áreas de vida discretas são facilmente identificadas dentro das populações. Entretanto, quando existe uma interação entre os indivíduos, mais complexa no espaço e no tempo, a distinção entre as unidades sociais não é tão clara.

Em uma população, os grupos podem se dividir em subgrupos para aumentar a eficiência na procura e captura de alimento, na reprodução ou para minimizar os

riscos da predação, e depois se reagrupar novamente (GOWANS; WÜRSIG; KARCZMARSKI, 2007). Com isso, os indivíduos podem vir a se associar com diversos outros indivíduos ao longo do tempo, embora essas associações ocorram de uma maneira fluída. Este tipo de associação corresponde à dinâmica social do tipo fissão-fusão, que representa uma ampla variação na coesão espacial e nas companhias individuais dentro de um grupo ao longo do tempo (AURELI et al., 2008), e é comumente observada em primatas (VAN SCHAIK, 1999), cetáceos (CONNOR et al., 2000), morcegos (KERTH; EBERT; SCHMIDTKE, 2006), e elefantes (WITTEMYER; DOUGLAS-HAMILTON; GETZ, 2005).

O boto, *Tursiops* sp., é um gênero com distribuição cosmopolita onde, embora exista uma ampla variação intraespecífica em muitos aspectos de sua biologia, a maioria das populações estudadas até o momento tem exibido uma dinâmica social do tipo fissão-fusão (CONNOR et al., 2000). Entretanto, apesar de essa fluidez social insinuar que a relação entre os indivíduos sejam homogêneas, as populações de boto podem conter elementos estáveis, como associações de longo período entre seus indivíduos (Lusseau et al. 2003). Além disso, diversos estudos têm encontrado unidades sociais discretamente estruturadas nas populações de boto, podendo estar relacionadas a diferenças de comportamento dos indivíduos (LUSSEAU et al., 2006), padrão de associação e de uso da área e do habitat (LASKA; SPEAKMAN; FAIR, 2008; ROSSBACH; HERZING, 1999; URIAN et al., 2009), interação com atividades humanas para fins alimentares (ANSMANN et al., 2012; CHILVERS; CORKERON, 2001; DAURA-JORGE et al., 2012), associações com ilhas (BAIRD et al., 2008), e também a conjunção de fatores ambientais e comportamentais (TOTH et al., 2012).

Contudo, mesmo nos casos onde esta estruturação não é clara (e.g. LUSSEAU; NEWMAN, 2004; LUSSEAU et al., 2006) é possível detectar divisões estatisticamente significativas nas populações, graças ao recente desenvolvimento e implementação da análise ponderada de rede aplicada a unidades sociais de animais selvagens (LUSSEAU; WHITEHEAD; GERO, 2008; NEWMAN; GIRVAN, 2004; NEWMAN, 2006).

A análise de redes sociais é uma técnica decorrente das ciências físicas, que se tornou uma poderosa ferramenta para a compreensão da estrutura social dos animais, tanto no nível de indivíduos quanto de populações (CROFT; JAMES; KRAUSE, 2008). Ela permite a descrição da rede formada pelas relações sociais entre os indivíduos, assim como os fatores que promovem, ou mesmo que governam estas relações (LUSSEAU; NEWMAN, 2004). Contudo, a análise de redes sociais falha em descrever efetivamente a forma como as associações variam ao longo do tempo (CANTOR et al., 2012), o que é um elemento fundamental para entender a estrutura social de uma população. Análises como a taxa de decaimento do índice de associação e técnicas correlatas (WHITEHEAD, 1995) podem ser utilizadas para suprir essa necessidade. Além disso, devido ao fato de as análises serem baseadas na proporção de tempo em que os animais passam associados, as estimativas também são influenciadas pela área de vida dos indivíduos, ou mesmo por preferências de habitat (LUSSEAU et al., 2006).

Recentes trabalhos sobre uma população de botos presentes no estuário da Lagoa dos Patos, sul do Brasil, mostraram a existência de uma população residente de aproximadamente 87 indivíduos (FRUET et al., 2011). Entretanto, ao explorar a área

costeira adjacente, observou-se a presença de indivíduos que nunca haviam sido encontrados na área estuarina, levantando-se a hipótese de uma possível segregação dos indivíduos em diferentes unidades sociais. Sabe-se que a desembocadura do estuário e as áreas próximas à costa são as áreas preferencialmente utilizadas pelos indivíduos da população (DI TULLIO, 2009). Além disso, com base nesta autora, nos meses frios (maio a outubro) os botos utilizam com maior frequência a área ao sul da desembocadura do estuário e, nos meses quentes (novembro a abril), a área ao norte da mesma. No entanto, são informações que correspondem a toda a população, sem levar em consideração a forma como cada indivíduo utiliza a área. Dentre os botos que nunca foram vistos no estuário, existem alguns que utilizam apenas a área ao sul, principalmente durante os meses frios. Alguns deles também já foram fotografados nas águas costeiras do Uruguai, a aproximadamente 250km ao sul do estuário da Lagoa dos Patos (LAPORTA et al., 2010). Com isso, acredita-se que os botos que habitam o estuário da Lagoa dos Patos e águas costeiras adjacentes formam diferentes unidades sociais e que o padrão de uso do habitat seja um dos fatores que determinam a formação destas diferentes unidades dentro da população.

Hipóteses de Trabalho

- 1) A população de botos que habita o estuário da Lagoa dos Patos e águas costeiras adjacentes é estruturada por unidades sociais discretas;
- 2) Aceitando-se a primeira hipótese, a área preferencial das unidades sociais é distinta;

I.1 OBJETIVOS

Objetivo geral

O objetivo deste estudo foi identificar a presença de diferentes unidades sociais dentro da população e suas áreas preferenciais.

Objetivos específicos:

- verificar a intensidade das relações entre indivíduos na área de estudo;
- verificar a existência de unidades sociais;
- estimar a área preferencial dos botos das unidades sociais;
- identificar a área de sobreposição entre as unidades sociais.

II. MATERIAL E MÉTODOS

A área de estudo compreende um total de 140km², divididos em três sub-áreas: a porção final do estuário da Lagoa dos Patos, mais abrigada, com 40km²; área costeira adjacente norte e área costeira adjacente sul, ambas com 50km² de área e mais suscetíveis às variações nas condições oceanográficas (Figura 1). As saídas de campo foram realizadas entre agosto de 2005 e outubro de 2012, somente sob condições climáticas favoráveis (e.g. boa visibilidade, estado do mar <3 na escala Beaufort). Cada saída foi destinada a cobrir ao menos uma das sub-áreas e, na medida do possível, realizou-se ao menos uma saída por mês, alternando-se o início do percurso.

Indivíduos com coesão espacial (i.e. até 100m um do outro) e que estavam envolvidos em atividades similares foram definidos como um grupo (PARRA, 2006). Os indivíduos foram fotografados aleatoriamente, a fim de identificá-los através das marcas de longa duração presentes em suas nadadeiras dorsais (WÜRSIG; JEFFERSON, 1990; WÜRSIG; WÜRSIG, 1977). Apenas grupos em que ao menos 50% dos indivíduos tivesse sido foto-identificado foram utilizados nas análises. Quanto aos indivíduos, apenas aqueles que foram avistados no mínimo em cinco ocasiões diferentes durante o período amostral foram considerados nas análises. Para verificar se as possíveis divisões sociais encontradas eram correspondentes ao uso da área, os indivíduos foram classificados de acordo com a subárea em que foram majoritariamente encontrados. A fim de verificar se essa classificação por área foi estatisticamente significativa, aplico-se um teste de Mantel de duas caudas (ver Schnell et al. 1985). Além disso, os indivíduos que foram avistados em ao menos 75% das saídas foram considerados residentes.

Escolheu-se o índice de peso-médio (HWI: CAIRNS; SCHWAGER, 1987) para mensurar a intensidade das relações entre os indivíduos (i.e. estima a proporção de tempo que um dado par de indivíduos se mantém associado, é simétrico e varia entre zero e um). Foi realizada a permutação de Monte Carlo para verificar se as associações entre os indivíduos da população ocorrem mais frequentemente do que ao acaso. Para verificar se os dados coletados eram suficientes para uma boa descrição da estrutura social desta população, foi calculado o índice de diferenciação social (S) e também a correlação entre o índice de associação verdadeiro e o índice de associação estimado (r), ambos através do método de verossimilhança

(WHITEHEAD, 2008b). Os erros padrão (ES) foram calculados através de 1000 replicações de *bootstrap*.

A detecção de unidades sociais foi feita a partir da modularidade, que é a diferença entre a proporção de todas as associações dentro dos agrupamentos e a proporção esperada, dado a soma das associações de cada indivíduo (NEWMAN, 2004). Para encontrar a melhor divisão, Newman (2006) menciona que o método baseado nos autovetores geralmente é eficiente. O coeficiente de modularidade (Q) pode mensurar a qualidade da divisão, observando se ela designou os indivíduos para agrupamentos com muitas ligações internas e apenas algumas ligações com outros agrupamentos, indicando uma boa divisão quando Q é maior ou igual a 0,3 (NEWMAN; GIRVAN, 2004). Todas as análises sociais foram feitas no software *SOCPROG*, versão 2.4 (WHITEHEAD, 2009).

Três métricas de rede foram calculadas dentro de cada unidade social: força, que é uma medida de sociabilidade e é a soma dos índices de associação de cada indivíduo; coeficientes de agrupamento, que é a medida de quão bem os parceiros de um indivíduo estão associados entre si; e afinidade, que é a média ponderada da força entre os associados de cada indivíduo (BARTHÉLEMY et al., 2005). Para verificar a significância do teste, as medidas foram comparadas com um modelo aleatório e os erros foram calculados através do *bootstrap*. A taxa de decaimento do índice de associação padronizada (SLAR) foi estimada via *SOCPROG* a fim de comparar a estabilidade temporal das associações dentro e entre as unidades sociais propostas (WHITEHEAD, 1995). Como medida de precisão da estimativa da SLAR, aplicou-se a *jackknife* temporal e testaram-se vários modelos de estrutura social, sendo que sua

seleção foi feita baseada nos Critérios de Informação Quasi-Akaike (QAIC; Whitehead 2007).

Finalmente, os pontos de avistagens de cada indivíduo foram visualizados no Arcview 9.3 (ESRI, Redlands, CA, U.S.A.). A estimativa da área principalmente utilizada por cada unidade social, e eventual sobreposição entre elas, foi feita através do estimador de densidade de kernel fixo via *Hawth's Tools* (BEYER, 2004), uma extensão do Arcview. Para tanto, calculou-se isolinhas de kernel que contivessem 25 e 50% dos pontos de avistagem. Para verificar se as análises foram influenciadas por efeitos demográficos, como mortalidade e migração, as análises de modularidade e da SLAR também foram realizadas considerando apenas os indivíduos residentes e somente as avistagens que ocorreram em suas áreas comuns (com base na análise espacial).

III.RESULTADOS

Foram realizadas 267 saídas de campo entre agosto de 2005 e outubro de 2012, que duraram em média 7h e 09min (DP = 1h e 49min) e resultaram no encontro com 1611 grupos de botos. Os tamanhos de grupo apresentaram características semelhantes entre as áreas costeiras e uma média ligeiramente menor na área estuarina (Tabela 1). Dentre os dados coletados, em 243 saídas de campo houve encontros com ao menos um grupo que tivesse sido bem amostrado, em 1472 grupos foi possível identificar ao menos 50% dos indivíduos e 102 botos apresentaram marcas de longa duração evidentes e foram avistados ao menos em cinco ocasiões amostrais. Em relação à área em que os 102 indivíduos foram majoritariamente encontrados, 64 foram

considerados como botos do estuário, 19 como da área sul e 19 como da área norte. Dentre eles, respectivamente 40, 12 e 5 corresponderam a indivíduos residentes. O teste de Mantel, a partir desta classificação dos indivíduos, corroborou com essa proposição, pois indicou que as associações entre indivíduos pertencentes à mesma área ($HWI = 0,09 \pm 0,04$) foram maiores do que entre indivíduos de áreas diferentes ($HWI = 0,01 \pm 0,01$; $t = 23,18$; *coeficiente de correlação da matriz* = 0,53; $p = 1$).

O coeficiente de variação do índice de associação verdadeiro foi relativamente alto ($S = 0,908 \pm 0,014$), indicando que esta sociedade é bem diferenciada e, conseqüentemente, apresentando variações nas relações entre os indivíduos. A correlação entre o índice de associação verdadeiro e o índice de associação estimado ($r = 0,652 \pm 0,018$) indica que as análises, através dos dados de associação entre os indivíduos, possuem um poder relativamente alto para expressar o verdadeiro sistema social desta população de botos. O índice de associação, entre todos os indivíduos, teve uma média de 0,05 ($DP = 0,01$) e o valor máximo de 0,83 (Média = 0,33 e $DP = 0,15$). Os testes de permutação indicaram que a média do índice de associação entre todos os indivíduos (real = 0,044, aleatório = 0,043; $p > 0,999$) e o coeficiente de variação (CV) do índice de associação (real = 1,39, aleatório = 1,11; $p > 0,999$) foram significativamente maiores do que o esperado, indicando a presença de algumas companhias preferenciais/evitação não aleatórias e de longo período.

A estimativa do coeficiente de modularidade foi igual a 0,304, que é praticamente o valor mínimo para uma boa divisão (0,3). A aplicação da modularidade de Newman encontrou três importantes divisões na população que utiliza o estuário da Lagoa dos Patos e águas costeiras adjacentes (Figura 2a). As divisões formaram três unidades

sociais, onde cada uma corresponde a uma das áreas: a unidade social do estuário, com 62 indivíduos subdivididos em dois grupos densamente conectados e as unidades sociais do sul e do norte, com respectivamente 21 e 19 indivíduos. A subdivisão presente na unidade estuarina parece estar relacionada com a preferência dos indivíduos de cada subunidade com os indivíduos de cada uma das unidades sociais costeiras (sul e norte). Além disso, os indivíduos da unidade estuarina apresentaram mais associações e estão conectados com um maior número de indivíduos da unidade sul do que com os indivíduos da unidade norte, onde as associações se restringiram a poucos indivíduos. Ao restringir as análises apenas aos indivíduos residentes, mas com base na mesma divisão, foi possível observar este mesmo padrão de associação (Fig. 2b), indicando que as associações entre os indivíduos foram de grande importância na divisão da população.

Exceto para o parâmetro afinidade, as diferenças no comportamento social entre as três unidades sociais e o modelo aleatório foram fortemente apoiadas pelas três medidas de rede (Tabela 2). A unidade estuarina apresentou baixos valores de força e coeficiente de agrupamento, indicando que os indivíduos desta unidade tiveram associações relativamente fracas e aleatórias. As unidades sul e norte apresentaram altos valores de força, indicando a presença de indivíduos com fortes associações.

A SLAR indicou que as associações não aleatórias persistiram durante todo o período de estudo na unidade social do norte (Figura 3b) e por praticamente todo o período de estudo nas subunidades do estuário (Figura 3a). Para a unidade social do sul, a SLAR indica que as associações entre seus indivíduos são predominantemente de curto período (Figura 3b). O menor valor do QAIC para cada unidade social indicou o

mesmo modelo, o de conhecidos casuais, onde a associação é seguida pela dissociação e uma possível reassociação, o que é característico de populações de dinâmica do tipo fissão-fusão. O mesmo padrão ocorrido dentro de cada subunidade do estuário também ocorreu quando analisado as associações entre seus indivíduos (Figura 3c). A unidade social do sul apresentou associações de curto período com a subunidade I do estuário, mas não mostrou associações preferenciais com a subunidade II (Figura 3d). Similarmente, somente cinco indivíduos residentes da unidade social do norte mostraram associações preferenciais com os indivíduos da subunidade II do estuário (Figura 3e). O baixo número de associações observadas entre os indivíduos da unidade social do norte com os indivíduos da unidade social do sul e com a subunidade I do estuário impossibilitou a estimativa da SLAR entre estas unidades.

Nas análises de uso espacial, foram utilizadas 156 saídas de campo na estimativa do kernel fixo. Devido a alta sobreposição espacial e por estarem densamente conectadas, as duas subunidades do estuário foram agrupadas para a realização da análise espacial. Os indivíduos se distribuem por toda a área amostrada, mas a área de maior concentração, dentro da área de estudo, ocorreu na desembocadura do estuário da Lagoa dos Patos e em suas adjacências (Figura 4). Quando se observa a distribuição das unidades sociais sugeridas pela modularidade, nota-se que, por mais que exista certa sobreposição espacial entre as áreas de uso, cada unidade social apresenta uma forma de uso espacial bem peculiar. A unidade social do estuário se concentra na boca do estuário (Figura 4a), a unidade social do sul preferencialmente

na área adjacente sul (Figura 4b) e a unidade social do norte ao longo da área adjacente norte (Figura 4c).

IV. CONSIDERAÇÕES FINAIS

Este estudo aplicou métodos que independem do conhecimento pretérito sobre os mecanismos que possam vir a causar a presença de subestruturas numa dada população e identificou a presença de três principais unidades sociais na população de botos que utiliza o estuário da Lagoa dos Patos e águas costeiras adjacentes. Além disso, os resultados sugerem que um possível mecanismo causador desta divisão seja o padrão de associação e de uso do habitat pelos indivíduos de cada unidade. A população vive imersa numa dinâmica social do tipo fissão-fusão que é composta predominantemente por companhias casuais que duram poucos dias, mas que também apresenta algumas companhias de longo período, que podem durar anos. A dinâmica social desta população é similar a encontrada em outras espécies altamente sociais como os primatas (VAN SCHAIK, 1999), morcegos (KERTH; EBERT; SCHMIDTKE, 2006), elefantes africanos (WITTEMYER; DOUGLAS-HAMILTON; GETZ, 2005) e, principalmente, em outras populações do gênero *Tursiops* (CONNOR et al., 2000).

Os botos que utilizam o estuário da Lagoa dos Patos e águas costeiras adjacentes estão divididos em unidades sociais que apresentam limitadas interações entre si, que estão relacionadas a um habitat característico, mas que apresentam certa sobreposição espacial. Este mesmo padrão já foi encontrado em diversas outras populações do gênero, em estudos realizados em ambientes similares (LUSSEAU et al., 2006;

URIAN et al., 2009; WISZNIEWSKI; ALLEN; MÖLLER, 2009). Em outras populações de boto a segregação dos indivíduos em grupos sociais distintos esteve claramente relacionada a estratégias específicas de forrageamento (ANSMANN et al., 2012; CHILVERS; CORKERON, 2001; DAURA-JORGE et al., 2012; KRÜTZEN et al., 2005). Entretanto, não foi identificada, até o presente momento, nenhuma estratégia de forrageamento diferenciada entre os indivíduos de cada unidade social.

No caso da população que utiliza o estuário da Lagoa dos Patos e águas costeiras adjacentes, acredita-se que o uso de áreas claramente distintas é intensificado por um comportamento territorialista por parte dos indivíduos das diferentes unidades sociais. É possível que a unidade social do estuário esteja a um bom tempo no limite de sua capacidade de carga. Nos últimos 20 anos os mesmos métodos de estimativa de abundância tem sido empregados e as estimativas indicam que o número de indivíduos que reside no estuário está estabilizado (e.g. DALLA ROSA, 1999; FRUET et al., 2011). A entrada de indivíduos da área costeira resultaria na competição tanto por espaço quanto por comida. De fato, os botos da área costeira, exceto para um ou outro indivíduo, nunca foram vistos dentro do estuário. Além disso, em duas oportunidades foi possível observar que a aproximação de indivíduos da unidade social do norte para áreas próximas ao estuário desencadeou um rápido retorno dos botos da unidade social do estuário para sua área de origem. Embora não tenha sido observado nenhum comportamento agonístico, os indivíduos da unidade do estuário claramente evitaram contato com os indivíduos da unidade do norte.

Embora existam evidências de evitação entre indivíduos de diferentes unidades sociais, ocorreram interações entre indivíduos de diferentes unidades. Isto reforça a

importância de alguns indivíduos denominados “brokers” (*sensu* LUSSEAU; NEWMAN, 2004). Estes indivíduos atuam como elo entre as unidades e podem ser peça fundamental na manutenção da coesão de toda a população, ou mesmo na transferência de informação em diversos níveis (RENDELL; WHITEHEAD, 2001), na potencial disseminação de doenças e no fluxo genético dentro da população (FRÈRE et al., 2010; NEWMAN, 2002).

Embora as associações entre os indivíduos tenham sido governadas por relações de curto período, tanto a SLAR quanto o teste de permutação indicaram a presença de algumas relações de longo período. As associações não foram aleatórias dentro das unidades, reforçando a divisão social. Além disso, a tendência de os indivíduos da subunidade estuarina II se associarem preferencialmente com os indivíduos da unidade social do sul, assim como os da unidade norte se associarem com a subunidade I, sugere que esta relação possa ser motivada por relações de parentesco. Dados genéticos preliminares indicaram a presença de dois haplótipos dominantes dentro da unidade social do estuário (LMMT, dados não publicados). Portanto, o fluxo gênico entre as subunidades estuarinas e as unidades costeiras deve ser investigado a fim de validar essa hipótese.

Alguns pontos importantes ainda não foram abordados, como os padrões de relacionamento entre os sexos, estratégias reprodutivas, relações de parentesco ou mesmo o fluxo gênico dentro da população. Embora estes pontos não tenham sido abordados ainda, foi possível encontrar fortes evidências de que a população esteja estruturada em três unidades sociais principais que utilizam habitats distintos. Recomenda-se que estes resultados sejam incorporados aos futuros modelos de

dinâmica e viabilidade populacional, considerando a estrutura social como unidade básica para estimativas de certos parâmetros demográficos, como fecundidade, sobrevivência, abundância. Além disso, sugere-se que as unidades sociais sirvam como base em futuros estudos para determinar fluxo gênico entre os grupos.

V. TABELAS

Tabela 1. Características dos grupos de botos encontrados entre agosto de 2005 e maio de 2012 nas três áreas localizadas no estuário da Lagoa dos Patos e águas costeiras adjacentes.

Área	N de grupos	Tamanho médio de grupo (DP)	N mínimo e máximo de indivíduos	Moda
Estuário	961	4,58 ± 3,57	1 - 27	3
Sul	307	6,21 ± 5,06	1 - 30	4
Norte	343	6,10 ± 4,38	1 - 23	3
Total	1611	5,22 ± 4,14	1 - 30	3

Tabela 2. Médias de força, coeficiente de agrupamento e afinidade dos indivíduos dentro de cada unidade social de botos que utilizam o estuário da Lagoa dos Patos e águas costeiras adjacentes.

O desvio padrão, calculado pelo *bootstrap*, está em parênteses.

Unidades sociais	Força	Coeficiente de agrupamento	Afinidade
Estuário I	5,24 (0,91)	0,09 (0,01)	5,18 (0,09)
Aleatório	5,32 (0,89)	0,15 (0,01)	5,04 (0,11)
	$P=1$	$P=1$	$P=1$
Estuário I	4,75 (1,31)	0,09 (0,01)	5,02 (0,16)
Aleatório	4,84 (1,32)	0,15 (0,01)	5,05 (0,12)
	$P=1$	$P=1$	$P=1$
Sul	3,59 (1,19)	0,11 (0,04)	4,14 (0,30)
Aleatório	3,15 (1,18)	0,14 (0,03)	4,05 (0,38)
	$P<0,001$	$P=1$	$P<0,001$
Norte	3,02 (0,93)	0,12 (0,04)	3,63 (0,41)
Aleatório	2,31 (0,91)	0,11 (0,02)	3,78 (0,56)
	$P<0,001$	$P=1$	$P<0,018$

VI.FIGURAS

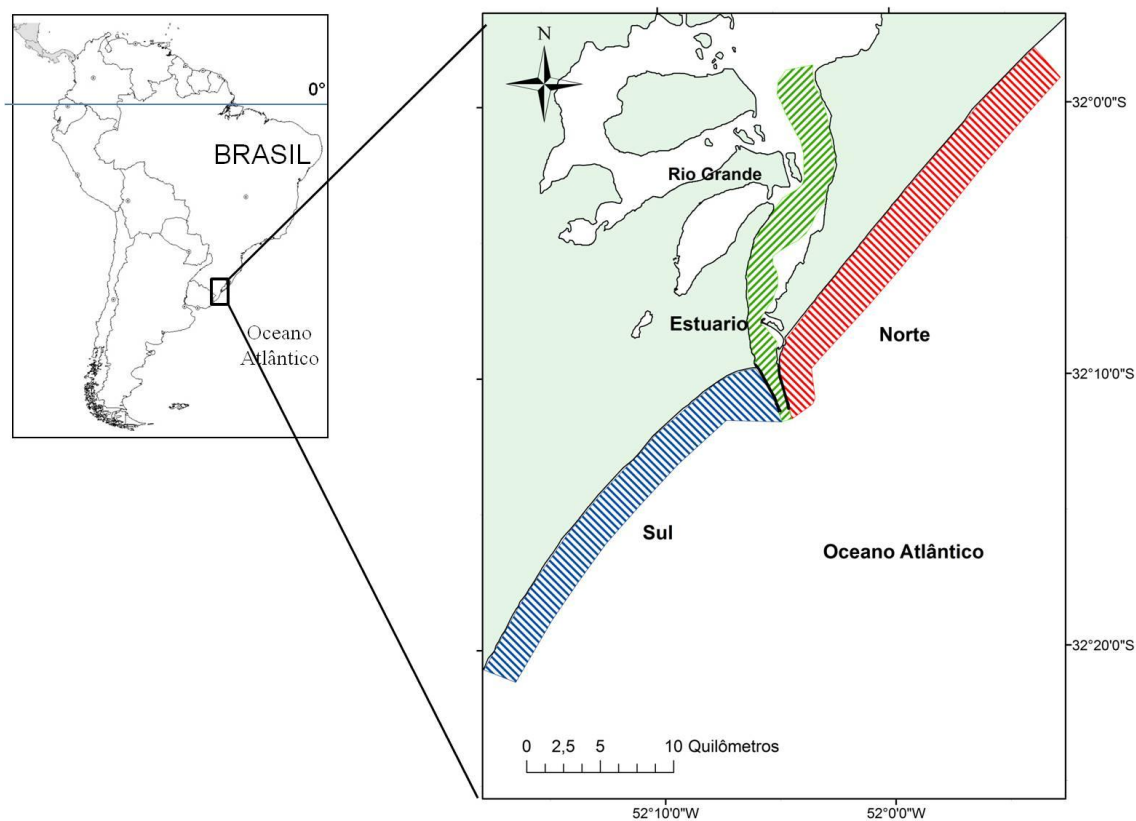


Figura 1. Área coberta durante as saídas de campo para procurar botos no estuário da Lagoa dos Patos (verde) e nas águas costeiras adjacentes (sul = azul e norte = vermelho).

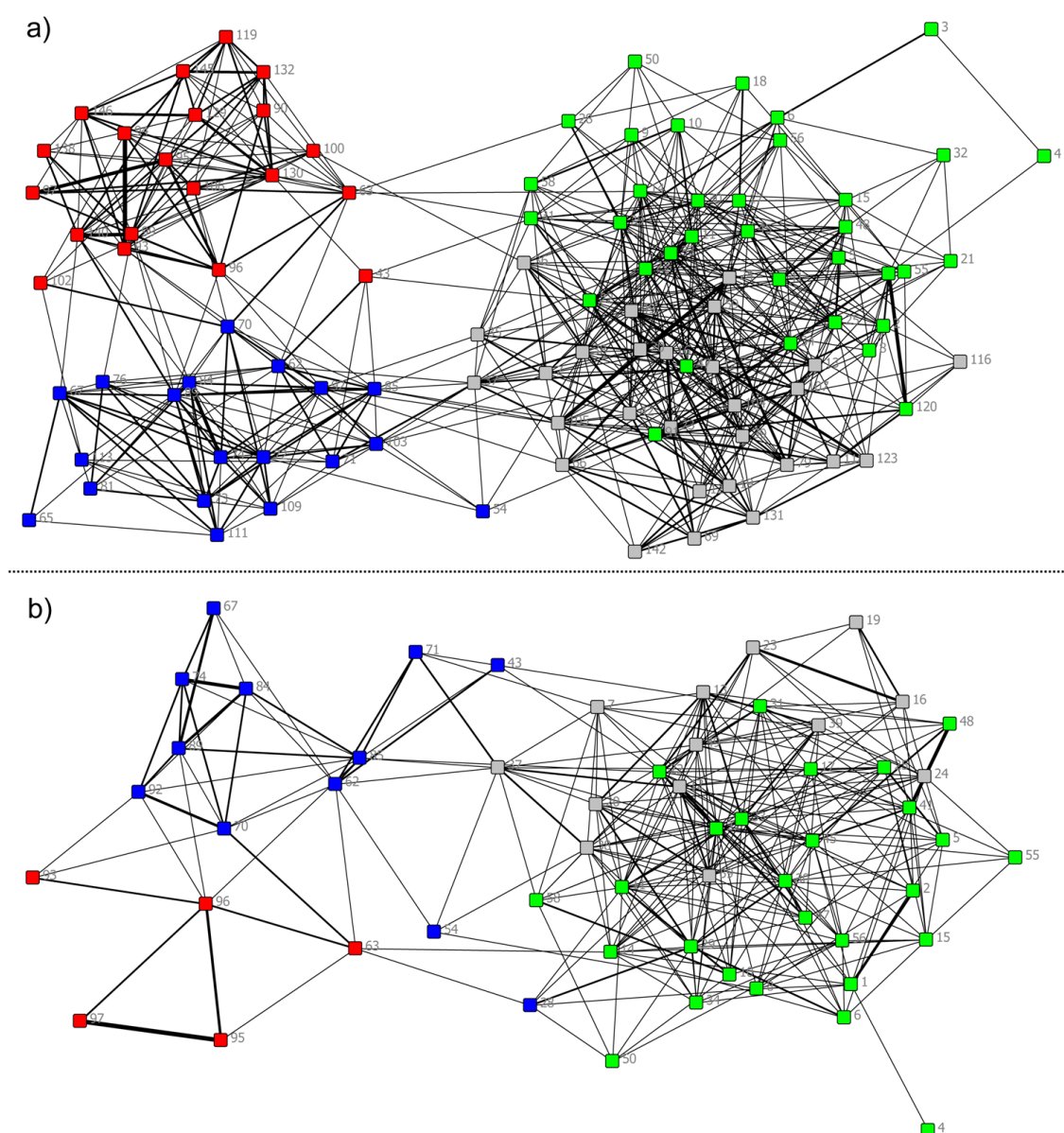


Figura 2. A rede social de todos os botos que utilizam o estuário da Lagoa dos Patos e área costeira adjacente (a) e da rede social considerando somente indivíduos residentes (b). A espessura das linhas que ligam cada par de indivíduos indica a força de suas associações (HWI) e cada ponto corresponde a um indivíduo e sua comunidade (Verde = Estuário, Azul = Sul e Vermelho = Norte).

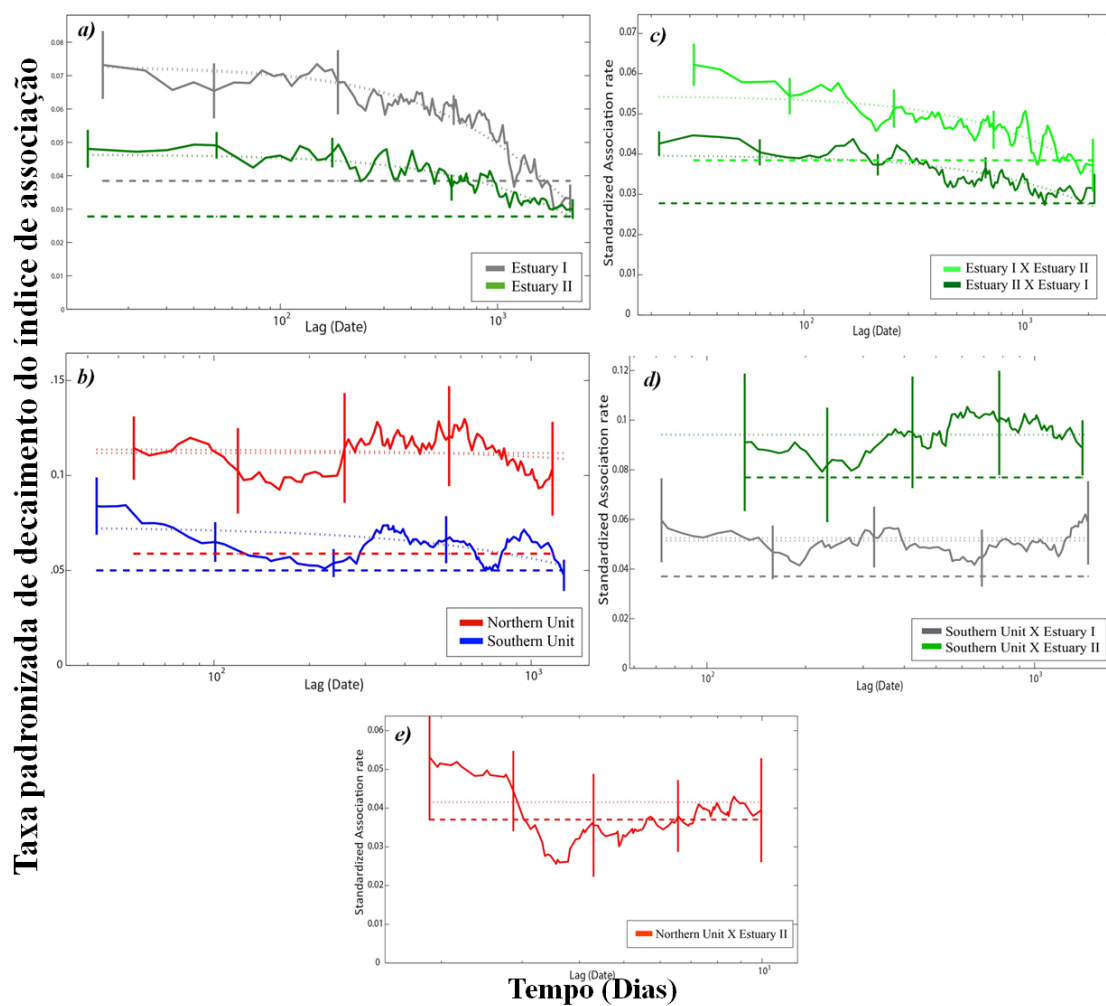


Figura 3. Taxa padronizada de decaimento do índice de associação (linha sólida), juntamente com o(s) modelo(s) que obteve o melhor ajuste (linha pontilhada) e a taxa de associação nula (linha tracejada) para cada unidade social (a e b), entre os botos das duas subunidades do estuário (c), entre os botos da unidade social do sul e os botos das duas subunidades do estuário (d) e dos botos da unidade social do norte com os botos da subunidade II do estuário (e). Os desvios-padrão (linhas verticais) foram calculados por jackknifing sobre períodos de 30 dias.

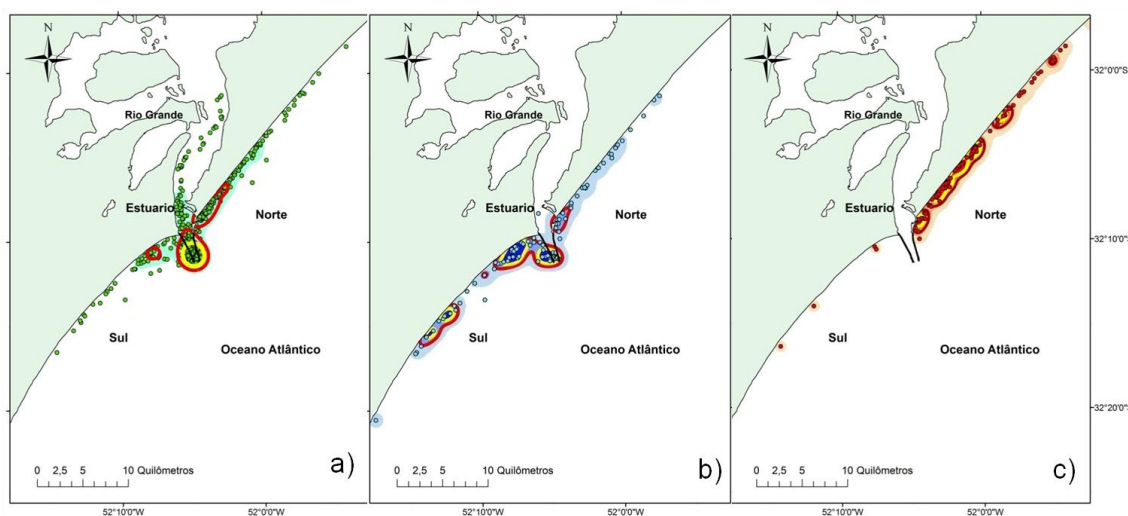


Figura 4. Pontos de avistagens de cada botos dentro da área de estudo, com as isolinhas do kernel de 25 (amarelo) e 50% (vermelho) para cada uma das comunidades: Estuarina (A), Sul (B) e Norte (C).

VII. LITERATURA CITADA

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VIII. APÊNDICE: Manuscrito formatado para o periódico *Animal Behavior*

Identifying fine scale social units of common bottlenose dolphins in subtropical western South Atlantic

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ABSTRACT

We investigated the social structure and spatial patterns of area usage by a population of bottlenose dolphins, *Tursiops truncatus*, inhabiting the Patos Lagoon estuary and adjacent coastal waters, in southern Brazil. We estimated the association index from 102 individuals regularly sighted in 243 photo-identification surveys carried out between August 2005 and October 2012. Social and network analyses, with the division proposed by modularity, indicated that this bottlenose dolphin population consists of three major social units. Although some spatial overlap exists, preferred areas of each unit were distinct. One of the units was strongly associated with the Patos Lagoon estuary and was subdivided in two subunits, while the other two occupied, respectively, the southern and northern adjacent marine coasts. Within unit associations among individuals were predominantly of short duration (fission-fusion dynamics), though a few long-lasting bonds were detected. Although interactions between social units occurred, the associations were brief and occurred only among a

few individuals. The segregation of these individuals is motivated, at least in part, by the bonding patterns among individuals and their fidelity to specific areas. It is recommended that the social units be the framework for modelling the intrapopulation dynamic and viability as well as for investigating patterns of gene flow within and between social units.

Keywords: Social group; cetacean; social behaviour; habitat use; social network, modularity; social division

INTRODUCTION

In organisms with sexual reproduction, a population is delimited geographically by a group of organisms with the capacity of reproducing, one with other, in natural conditions (Wilson 1975). Within populations groups of individuals in nearly mutual associations and possibly sharing the same home range, being termed social units, may exist (Whitehead 2008a). This segregation of individuals in different social units might be related to sex, age, feeding, behaviour, patterns of habitat use, or even due to preferential companions (Krause & Ruxton 2002). Therewith, the way that a population is structured is a key component of its biology, influencing and being influenced by the genetic composition (Krützen et al. 2003; Frère et al. 2010), the propagation of diseases (Newman, 2002; Corner, Pfeiffer, & Morris, 2003), the information flow (McComb et al. 2001) and the manner that individuals of the population will explore the environment (Connor et al. 1998). Therefore, social units play a key role in the ecology and sociability of the populations and, if present, it is usually relevant to distinguish them, as well as their individuals (Whitehead 2008a).

Social units with discrete home ranges are often easily identifiable within the population. However, when interactions among individuals are more complex in space and time, distinction between the social units is not very clear.

In a population, the groups may break into subgroups for foraging, feeding, mating and protect themselves, and then regroup again (Gowans et al. 2007). Thus, individuals can associate with several other individuals over time, though in a fluid manner. These associations correspond to the fission-fusion dynamics, which represents a wide variation in spatial cohesion and individual companions inside the group over time (Aureli et al. 2008) and is commonly found in some primates (van Schaik 1999), dolphins (Connor et al. 2000), bats (Kerth et al. 2006) and elephants (Wittemyer et al. 2005).

The bottlenose dolphin, *Tursiops* sp., is a cosmopolite genus that inhabits coastal and oceanic tropical and temperate regions (Wells & Scott 1999). Although there is a wide intra-specific variation in many aspects of their biology, most populations of the genus studied so far has displayed this social dynamic of fission-fusion (Connor et al. 2000). However, despite this social fluidity, it is suggested that populations of bottlenose dolphins may contain stable elements such as long term associations among individuals (Lusseau et al. 2003). Furthermore, several studies have found social units in bottlenose dolphin population, which can be related to differences in the association patterns of individuals (Lusseau et al. 2006), association and ranging patterns (Rossbach & Herzing 1999; Urian et al. 2009), feeding related to human activities (Chilvers & Corkeron 2001; Daura-Jorge et al. 2012; Ansmann et al. 2012), island-associate (Baird et al. 2008), the use of habitat (Laska et al. 2008) and

conjunction of environmental, physical and behavioural characteristics (Toth et al. 2012). However, even in cases where this structure is unclear (e.g. Lusseau & Newman 2004; Lusseau et al. 2006), it has been possible to detect statistically significant divisions in populations through the recent development and implementation of the network analysis in animal populations (Newman 2004, 2006; Lusseau et al. 2008).

Network analysis is an approach arising from the physical sciences that has become a powerful tool for understanding the social structure of animals at the level of either, individuals or populations (Croft et al. 2008). It enables the description of networks formed by the social relationships between the individuals, as well as the factors that promote, or govern these relationships (Lusseau & Newman 2004). The network analysis fails to effectively describe the way that the associations change over time (e.g. Cantor et al. 2012), which is a key element for understanding social structure. Approaches that directly assess the temporal scale of the associations, such as the lagged association rate and related techniques (Whitehead 1995) may be relevant in this case. In addition, because the analyses are based on the proportion of time that animals spent associated, the estimates are also influenced by the home range of the individuals, or even by habitat preferences (Lusseau et al. 2006).

Recent studies about a population of bottlenose dolphins that uses the Patos Lagoon estuary, southern Brazil, show the existence of a resident population of approximately 87 individuals (Fruet et al. 2011). However, surveys along adjacent coastal areas revealed the presence of individuals that have never been found in the estuary, raising

the hypothesis of a possible segregation of the individuals in different social units. It is known that the mouth of the estuary and the adjacent coast, near the surfing zone, are the areas preferentially used by individuals of this population (Di Tullio 2009). Furthermore, according to this author, the dolphins use more frequently the areas to the south of the estuary mouth during cold months (May to October) and to the north in warm months (November to April). Is important to emphasize that this information corresponds to the whole population, without taking into account how each individual uses the area. Among the dolphins that have never been seen in the estuary, there are some individuals that use the area just to the south, generally during the cold months. Some of them have also been photo-identified in Uruguayan waters, about 250km southward (Laporta et al. 2010). Thus, it we hypothesize that bottlenose dolphins inhabiting the Patos Lagoon estuary and adjacent coastal waters form different social units and that the patterns of residence is one of the factors that motivated the formation of different social units within this population. Our objective, therefore, was to identify fine scale social units within the population and their preferential areas.

METHODS

Study area and data collection

This study was carried out in the Patos Lagoon estuary and adjacent coastal waters, in Rio Grande do Sul state, southern Brazil. The study area of 140km² was divided in three sub-areas: the more sheltered final portion of the Patos Lagoon estuary

(32°10.92'S/052°4.65'W in the inner estuary and 32°11.18'S/052°04.63'W in the mouth of the estuary), corresponding to 40km² and the adjacent coastal marine waters to the north (estuary mouth to 31°56.55'S/051°51.42'W) and to the south (estuary mouth to 32°20.55'S/052°17.44'W) of the estuary entrance, both with 50km² and strong influence of the break zone and susceptible to sea conditions (Fig 1). The surveys were conducted between August 2005 and October 2012, onboard a powered boat with a 90Hp outboard engine. Surveys were restricted to favourable weather conditions (i.e. beaufort ≤ 3 , good visibility and swell $< 2\text{m}$). Zig-zag transects were run throughout the estuary in all sampling period. The coastal area began to be systematically surveyed in October 2006 and consisted of two different sampling designs. Initially, transects were performed perpendicularly to shoreline to investigate patterns of habitat use. During these surveys, it was verified that dolphins were only rarely found beyond the 2 nautical miles from shore, so from February 2010 onwards only zig-zag surveys were run within this area. Each survey was aimed to cover at least one of the sub-areas. As far as possible, at least one survey was conducted per month and the starting point of the route was alternated (i.e. for each sub-area, the starting point of a survey was the end point of the next).

Individuals with a spatial cohesion (i.e. within 100m from each other) and that were engaged in similar activity were defined as a group (Parra 2006). Geographic position (GPS), time and group size were recorded for each sighting. Individuals were identified using long-lasting marks in their dorsal fins through standard photo-identification protocols (Hammond et al. 1990). Individuals without distinctive marks and seen only one time during the study period were not added to the catalogue.

Furthermore, individuals sighted during at least 75% of the study period were considered residents.

Data treatment

Because of the strong mother-calf bond, calves were excluded from the analysis as their relationships with other individuals depend on the associations of the mother. Among the groups found, only those with at least 50% of photo-identified individuals were used in the analyses (Lusseau et al. 2006). Furthermore, only individuals photographed in at least five different occasions during the study period were used in the social analysis (Whitehead 2008b). Individuals sighted only during the first or last six months of the study period were not considered in the analysis, in order to exclude individuals that died at the beginning of the study and those that gained long-lasting marks recently. To verify if putative social units were determined by patterns of habitat use, the dolphins were classified according to the area (Estuary, North and South) that they were predominantly found (50% or more of its sightings in the area) to compare with the division proposed based only in the pattern of association among individuals. Two-tailed Mantel test was applied to verify if the associations between and within the area division were statistically significant (see Schnell et al. 1985).

Social analysis

Each survey that covered at least one of the sub-areas was defined as a sampling period. The associations between individuals were based in the groups. Dolphins present in the same group during the sampling period were considered associated.

The half-weight index (HWI; Cairns & Schwager 1987) was used to measure the intensity of the relationships between the individuals (i.e. it estimates the proportion of time that a given pair of individuals remains associated, is symmetric and varies between zero and one). This index enables comparisons between populations, minimizes possible bias in the sample and, therefore, has being largely used by cetologists (see Whitehead 2008a). It is defined as: $HWI = x/(x + yab + ((ya + yb)/2))$; where, x is the number of surveys in that the individuals a and b were observed in the same group; yab is the number of surveys that a and b were identified in different groups; ya is the number of surveys in which only the individual a was identified and yb is the number of surveys that only the individual b was identified.

Monte Carlo simulations, following the methodology proposed by Bejder et al. (1998) and amended by Whitehead et al. (Whitehead et al. 2005) was performed to verify if the association between the individuals of the population occur more frequently than expected by chance. The original matrix of association was randomized until the stabilization of the p value (40.000 iterations), with 1.000 flips by permutation. A significantly higher standard error (SE) or coefficient of variation (CV) of real association indices compared to that of randomly permuted data indicates the presence of long-term preferred companions in the population (Whitehead 2009). To verify if the collected data were sufficient for a good description of the social structure of this population, the social differentiation (S) and the correlation coefficient between the true association indices and their estimated values (r), were calculated using the methods described by Whitehead (2008b). The social differentiation (S) indicates the variability of the association index within the

population: if S is near 0, the relationships within the population are homogeneous; if S is close or greater than 1, the associations are very variable and much less associations are needed for detecting the preferential companions (Whitehead 2008b). The correlation coefficient (r) is a measure of precision of the representation to describe the social structure (the matrix of the association index) of a population, indicating how close it is to the reality, where values near 1 indicate an excellent representation and values close to 0 indicate a poor representation pattern (Whitehead 2008b). The standard errors (SE) were calculated through the 10000 bootstrap replications. All social analyses were done in the SOCPROG, version 2.4 (Whitehead 2009).

Detecting social units

The detection of social units was performed by modularity, which is the difference between the proportion of the total associations within clusters and the expected proportion, given the summed associations of the different individuals (Newman 2004). In order to find the best delineation, Newman (2006) suggests an eigenvector-based method as being generally efficient. This method is based on defining a parsimonious division of the individuals, which maximizes the weight and number of associations within the units and, consequently, minimizes the associations between them. The modularity coefficient (Q), from gregariousness, measures the quality of the division, observing if it designated the individuals to clusters with many internal connections and few connections with others clusters, and indicates a good division when Q is greater or equal 0.3 (Newman & Girvan 2004). The coefficient Q is the

sum of all pairs of associations belonging to the same cluster, minus the expected value if the pairs were randomly associated, given the strength of the connection between the individuals. The spring embedding layout was used to draw the social network diagram, showing only the associations with $HWI > 0.1$ in the program NetDraw (Borgatti 2002).

Network metrics

Three individual-based network statistics, calculated from the weighted network (association matrix), were averaged over and within social units: strength, which is a measure of gregariousness and is the sum of the association indices for each individual (Barthélemy et al. 2005), the clustering coefficient, which is the measure of how well the partners of an individual are themselves associated (as calculated by Holme et al. 2007), and affinity, which is higher when individuals are connect to individuals which have high strength (Whitehead 2009). To verify whether network structure was influenced by individual association preferences and whether association patterns differed significantly between social units, the calculated network metrics for each unit was compared to those of an expected network based on 20.000 permutations (Lusseau et al. 2008).

Temporal pattern of associations

The temporal variability in association patterns is essential for understanding temporal patterns of associations between social units when evidences of division, raised by other tests, are inconclusive. The HWI does not provide the proportion of

time that the pairs of individuals remain associated, even if the associations are interrupted over a certain period of time. The standardized lagged association rate (SLAR) was estimated in the SOCPROG in order to compare the temporal stability of associations within and between the proposed social units (Whitehead 1995). Briefly, SLAR is a modification of the lagged association rate used when not all individuals within the groups were identified and is an estimate of the changes in association rates over time (Whitehead 1995). The temporal jackknife method was applied (displayed as ± 1 standard error interval around the mean, over 30-day sampling) and four exponential decay models were fitted to the SLAR to provide quantitative means of describing temporal patterns of association: constant companions, where all pairs associate permanently; casual acquaintances, where all pairs disassociate over time; constant companions and casual acquaintances, where some pairs associate permanently and others disassociate over time; and two levels of casual acquaintances, where pairs disassociate over time, but at two different rates (Whitehead 2008a). The model that best described the temporal dynamics of association patterns will be indicated by the smallest quasi-Akaike information criterion (QAIC; Whitehead 2007). The results provided by SLAR estimates were compared with the expected SLAR in absence of any preferred association (standardized null association rate: SNAR).

Spatial patterns of individuals according to their social unit

The bottlenose dolphins that met the adopted restrictions, that had been sighted in at least five different occasions and had not been sighted only during the first or the last

six months of the sampling period, were classified according to the three subareas (estuary, south and north) to allow for the comparison between this classification and the division proposed by the modularity. The sighting locations of each individual were visualized in the Arcview 9.3 (ESRI, Redlands, CA, U.S.A.). The determination of the area preferentially used by each unity, and the possible overlap between them, were done through the fixed kernel density estimate in Hawth's Tools extension (Beyer 2004).

Excluding the influence of habitat use and demographic effect in the social analyze

The pattern of habitat use and mortality of individuals during the period of study, as well as the seasonal presence of some individuals (case of individuals that also use Uruguayans waters) may influence the social analyzes. To reduce the potential effect of such attributes in the social analysis, the modularity and SLAR were performed considering only the resident individuals and only sightings occurred in their common areas (based on spatial analysis). It is expected that this approach isolates associations related solely to social matters, and not those promoted by demographics and/or patterns of habitat use.

RESULTS

Between August 2005 and October 2012, 267 sampling days were conducted, which resulted in encounters with 1611 groups of dolphins. The group sizes were similar between coastal areas and slightly smaller in the estuary (Table 1). After applying the restrictions to the data, 243 sampling occasions and 1472 groups were used in the

analyses. Among all the 130 dolphins identified and inserted in the catalogue, that presented long-lasting marks and that were sighted more than once, 102 fulfilled criterion of at least five sightings during the study period. The dolphins were regularly sighted. Fifty-seven of them (55.9%) were sighted in at least six of the eight years of study and may be considered residents. If the first four years were considered as marking and the last four as recapture periods, 85.3% of individuals would be re-sightings. Regarding the area where the dolphins were mostly found, 64 were considered estuarine dolphins, 19 as southern and 19 as northern coastal dolphins. Of each area, respectively 40, 12 and 5 correspond to resident individuals. The Mantel test corroborated this division. The associations among individuals belonging to the same area ($HWI = 0.09 \pm 0.04$) were higher than among individuals from different areas ($HWI = 0.02 \pm 0.01$, $t = 20.97$; *matrix correlation coefficient* = 0.48, $p = 1$).

Social analyses

The coefficient of variation of the true association index was relatively high ($S = 0.908 \pm 0.014$), indicating that the population is well differentiated and presents variations in the relationship among individuals. The correlation between the true association index and the estimated association index ($r = 0.652 \pm 0.018$) indicated that the analysis using association data among individuals have a relatively good power to express the true social system of this bottlenose dolphin population. The index of association among all individuals averaged of 0.05 ($SD = 0.01$) and reached a maximum value of 0.83 (mean = 0.33, $SD = 0.15$). The permutation tests indicated that the mean association rate among all individuals (real = 0.044, random = 0.043, p

>0.999) and the coefficient of variation (CV) of the association index (real = 1.39, random = 1.11, $p > 0.999$) were significantly higher than expected, indicating the presence of some non-random preferred/avoided companies of long period. The same pattern was observed (mean association rate of real = 0.059 and random = 0.058; and CV of real = 1.05 and random = 0.82, both with $p > 0.999$) when only resident individuals were considered.

Defining social units

The estimated modularity coefficient ($Q = 0.304$) was equal to the minimum value of 0.3 suggested for a good division. The application of the modularity of Newman indicated three major divisions in the population that uses the Patos Lagoon estuary and adjacent coastal waters (Fig. 2a). These major divisions represented three clear social units, each one corresponding to an area: the estuarine social unit, with 62 individuals and subdivided in two clusters densely connected (estuarine subunit I and estuarine subunit II); and the southern and the northern social units, with 21 and 19 individuals, respectively. Regarding individuals that were responsible for principal connections ($HWI > 0.1$) between the three major social units, ten individuals from the estuary were linked to six from the south, other six individuals were bonded with four from the north and ten individuals from the south were connected with six individuals from the north. It is worthwhile noting that although subunits of the estuarine unit are densely connected, each coastal social unit (south and north) are preferably connected with a different estuarine subunit. Furthermore, individuals from the estuarine unit presented more associations and were connected to a larger number of individuals

from the southern unit than from the northern unit, for which the associations were restricted to a few individuals. Restricting analyses for resident individuals only, but with the same characterisation, the same pattern was observed (Fig. 2b), indicating that the associations among individuals was of great importance in this division of the population.

Network metrics

The differences in social behaviour between the four social units (considering the estuarine subunits separately), comparing each one with a null model generated by a random matrix, were strongly supported by the three network metrics (Table 2). The estuary social units I and II showed lower values for strength and clustering coefficient and an affinity higher than random, suggesting that individuals belonging to this unit had relatively weak and random associations. The southern and northern social units presented higher values for strength than expected by chance, indicating the presence of individuals with strong associations. In general, the clustering coefficient was low for all four social units, indicating that individuals were only associated with their neighbours and these, in turn, do not necessarily associate with each other, which is a characteristic of societies with fission-fusion dynamics. Furthermore, the clustering coefficient demonstrates that dolphins from the northern coast presented a denser network structure compared with the other social units.

Temporal pattern of associations

The SLAR indicated that the non-random associations persisted throughout the study period within the northern coast social unit (Fig. 3b) and along practically the entire study period in the two subunits of the estuary (Fig. 3a). For the southern social unit, the SLAR remained above the SNAR, but from the hundredth day, when SLAR almost overlaps SNAR, there is a high probability of dissociation, indicating short-term relationships (Fig. 3b). However, the lower value of QAIC was obtained for the same model in all social units, which indicate casual acquaintances, where the association is followed by a possible dissociation and reassociation, a characteristic of populations with fission-fusion dynamics. There was also some support for another model in the northern coast social unit, based on the small difference QAIC values ($\Delta\text{QAIC} = 0.6$), which indicates the presence of permanent associations. The same pattern within each subunit of the estuary occurred between them too (Fig. 3c). The southern social unit presents short-term associations with the subunit I of the estuary, but does not show preferential associations with the subunit II (Fig. 3d). Similarly, the only five resident individuals of the northern social unit showed preferential associations with individuals of subunit II of the estuary (Fig. 3e). In both cases, the constant companions were the model with best fit, followed by the model of casual acquaintances. The small number of observed associations among dolphins identified in the northern social unit prevented comparisons with the southern social unit and with subunit I of the estuary.

Spatial patterns of individuals according to their social unit

The northern marine coast was the area with fewer surveys ($n = 52$). Therefore, 52 were randomly selected from those carried out in the estuarine and 52 in the southern coastal areas, totalling 156 surveys for determining the preferred area through fixed kernel estimation of density. Due to the high spatial overlap and by being densely connected, the two estuarine subunits were clumped for spatial analysis. Therewith, individuals were distributed throughout the sampled area, though the higher concentration occurred at the mouth of the Patos Lagoon estuary and its surroundings (Fig. 4). When analyzing the distribution of the social units suggested by modularity, it can be noticed that, despite some spatial overlap, each social unit has a peculiar pattern of spatial usage. The estuarine social unit has a wide distribution, which is primarily aggregated near the mouth of the estuary and its adjacencies (Fig. 4a). The southern coast social unit is distributed throughout the coastal area including the end portion of the estuary with some pockets of preferential area to the south and besides the jetties to the north (Fig. 4b). Individuals from the northern coast social unit were never seen in the estuary and appeared only sporadically in the southern coast (Fig. 4c). Their preferential area was restricted to the north of the estuary mouth. Resident individuals accounted for most of the sightings, showing the same pattern found when considering all individuals. Therefore, their preferred area was not estimated.

DISCUSSION

This study applied methods that did not depend on previous knowledge of the mechanisms that may cause the presence of substructures in a given population and identified three major social units in the population of dolphins that uses the Patos

Lagoon estuary and adjacent coastal waters. Furthermore, the results suggested that the possible mechanisms shaping this social division are the pattern of associations and environment usage by individuals of each unit. The estuarine social unit is somewhat structured into two subunits, which are possibly related to selective association of their individuals with each of the coastal units. This population presented a fission-fusion social dynamics, which is composed predominantly of casual acquaintances that maintain individuals associated for a few days, but it also presented some long-lasting associations of several years. The fission-fusion dynamics of this population was similar to that found in other highly social species such as primates (Van Schaik 1999), bats (Kerth et al. 2006), African elephants (Wittemyer et al. 2005) and especially in other populations of the genus *Tursiops* (Connor et al. 2000).

Among the 64 individuals of the estuarine units, 40 were sighted in almost every year over the study period. This is a very high rate of re-sighting if we consider that some individuals have died and others gained long-lasting marks after the beginning of the study. This unit contemplates all marked individuals of the estuarine area and corresponds exactly to the group of individuals that are considered residents and has been studied sporadically since 1977 (e.g. Castello & Pinedo 1977; Dalla Rosa 1999; Mattos et al. 2007), but systematically monitored from 2005 onwards (Fruet et al. 2011). Individuals of this social unit are associated in a different way with individuals of the coastal area. Some individuals (subunit I) seem to have signed relationships with individuals using preferably the area to the south of the estuary, while others are more connected with individuals occupying the area to the north. The relationships

among individuals from the estuarine subunits with the northern unit, however, are not as intense as their relations with individuals from the southern unit. At least two individuals considered residents of the estuarine area were seen in Uruguay, suggesting a relatively strong bond among individuals from the Patos Lagoon estuary and the southern area. This sort of relationship was not observed among individuals from the estuary and the northern social units.

At least six individuals of the southern unit have already been sighted in Uruguay, 250 km to the south of the Patos Lagoon estuary (Laporta et al. 2010). These individuals typically appear in the southern area during cold months (May to October), thus reducing to zero the chances of encounter with these animals during some months of the year. Individuals from the northern unit also rove beyond the study area but, differently from the southern area, the individuals from the estuary have not been seen at far distances to the north and the northern individuals do not enter in the estuary and are hardly seen in the southern area. Several groups had been found at approximately 50 km northward the estuary, but none of them had estuarine individuals. Because of this great displacement of the coastal dolphins, it is still unknown whether the current number of identified individuals in the coastal area corresponds to a significant portion of individuals of their units. However, at least 17 individuals (twelve from the southern and five from the northern unit) can be considered resident to the adjacent coastal waters. These individuals have been frequently sighted in the sampled area along the study period. The investigation of these individuals allowed for the exclusion of demographic effect on the analyses and demonstrated that social relationships influenced the social division, regardless of the

presence of temporary individuals. Therefore, from a social standpoint, the presence of temporary individuals only increases the number of individuals of the coastal units during some time, with no effect on the detected social division.

The bottlenose dolphins that use the Patos Lagoon estuary and adjacent coastal waters are divided into units that have limited social interactions with each other. Although some spatial overlap exists between these units, the social structuring is related to social relationships and patterns of habitat use. This same pattern has been observed in several other populations of the genus inhabiting similar environments (Lusseau et al. 2006; Urian et al. 2009; Wiszniewski et al. 2009). In other populations of bottlenose dolphins, however, clumping of individuals into distinct social groups are clearly related to specific foraging strategies (e.g. Chilvers & Corkeron 2001; Krützen et al. 2005; Daura-Jorge et al. 2012; Ansmann et al. 2012). No differences in feeding strategy of individuals from the estuary and coastal areas have been detected thus far in this population.

In the case of the population using the Patos Lagoon estuary and adjacent coastal waters, it seems that the use of clearly distinct areas is intensified by a territorial behaviour of individuals from different social units. The estuarine social unit has possibly been at its carrying capacity for some time. For decades, the abundance of dolphins in the estuary remains below 100 individuals (e.g. Castello & Pinedo 1977; Dalla Rosa 1999; Fruet et al. 2011). Since the late 1990s to the present, the same estimation methods have been employed and abundance estimates show stability in the number of individuals residing in the estuary (e.g. Dalla Rosa 1999; Fruet et al.

2011). The entry of individuals from the coastal units would represent competition for both space and food resources. In fact, dolphins from the coastal units were never seen within the estuary, except for a few individuals during a very short period of time. Likewise, on two occasions we observed that the approach of individuals from the northern unit to areas nearby the estuary triggered a rapid return of dolphins from the estuary unit to its area of origin. Although no agonistic behaviour was observed, individuals from the estuary clearly avoided contact with individuals from the northern unit. This reinforces the theory that the relationship of estuarine with northern individuals is not strong and occurs among a few key individuals only.

These key individuals, known as brokers (*sensu* Lusseau & Newman 2004), are responsible for the main relationships between individuals of different social units and can play a crucial role in maintaining the cohesion of the entire population, the transfer of information at different levels (Rendell & Whitehead 2001), and potentially the spread of disease and gene flow within the population (Newman 2002; Frère et al. 2010). Among individuals in the coastal area that are responsible for the main connections between social units, eleven are considered residents of the coastal area. These dolphins were present in the study area throughout the seasons and appear to be the basis for the connection between coastal and estuarine units. They are the individuals that, somehow, allowed the linkage between temporary individuals and those that preferably used the inner estuary.

Although associations among individuals are governed by short-term relationships, both the SLAR and the permutation tests indicated the presence of long-term

associations within social units. The associations did not occur at random within each social unit, reinforcing the existence of three major units. The subunits of the estuary had strong associations among their individuals. Nevertheless, dolphins belonging the estuarine subunit I were more associated with the dolphins from the southern unit while individuals from the estuarine subunit II were more connected with individuals from the northern unit. This connection with individuals from the coastal areas seems to shaping the social organization within the estuarine unit. The southern social unit was the only unit that did not demonstrate long-term associations among its individuals. This is due to the presence of temporary individuals that typically interact with resident dolphins in the coastal area during cold months. These temporary dolphins, on the other hand, are not observed during the warm months, which correspond to the breeding season of this population. The stronger relationship among individuals of the southern and the estuarine subunit II is possibly due to kinship associations. Preliminary genetic data have indicated the presence of two dominant haplotypes in the estuarine unit (MRTL, unpl. Data). Gene flow among individuals from the estuarine and coastal units should be investigated at the subunit level to validate this hypothesis. The weak interaction among individuals of the northern unit and estuarine unit was also reflected in the SLAR. The northern unit was the only one that showed stable and long lasting associations among its individuals, demonstrating that this unit is more socially segregated from the other units. The few significant relationships with members of the estuarine subunit II occurred mainly through the brokers.

Even in areas where the species can rove freely, genetically differentiated populations can be found. In the coastal waters of the western North Atlantic, even without geographic barriers to delineate the distribution of the bottlenose dolphins, at least five genetically different populations have been found, some inhabiting coastal marine areas while others occurring in estuaries (Rosel et al. 2009). In Australia, it is suggested that fidelity to the local area and resource and behavioural specializations of a bay resident and an open coast social units of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) resulted in small scale genetic structuring (Möller et al. 2007). A similar pattern appears to occur in the bottlenose dolphins population from the Patos Lagoon estuary and adjacent coastal waters. Nevertheless, whether the social division within the population is sufficient to differentiate them genetically has yet to be determined.

The spatial patterns of habitat use by the three major social units were similar to those observed by Di Tullio (2009) for the entire population. The individuals preferentially utilized the mouth of the estuary and its surroundings (next to the jetties), as well as coastal areas just behind the surf zone. The region has a high productivity (Seeliger et al. 1998), especially at the mouth of the estuary and its vicinity, exactly where dolphins concentrate (Di Tullio 2009) and feeding behaviour is more frequently observed (Mattos et al. 2007). A previous study had demonstrated that the dolphins tend to use the northern area more intensely during the warm months and the southern area during the cold months (Di Tullio 2009). This occupation during warm months might be related to higher concentrations of spawning fish in the estuary and surroundings (Sinque & Muelbert 1998). Individuals from Uruguay use the southern

area only during part of the cold months. This northward movement of individuals from Uruguay (Laporta et al. 2010) is possibly due to water mass-related displacement of their prey (Haimovici & Umpierre 1996), which much probably influences the pattern of area usage by the southern unit. A similar pattern of northward movement is observed for the South American fur seal (*Arctocephalus australis*) and southern sea lion (*Otaria flavescens*) that rove from Uruguay to southern Brazil during cold months, possibly following prey (Pinedo 1998b).

In theory, when resources are spatially and temporally unpredictable, bottlenose dolphins tend to rove in search of feeding resources (Gowans et al. 2007). The mullet (*Mugil* spp.), one of the main prey of the dolphins, form large schools inside the estuary between April and May and then begin to migrate to its spawning grounds, in coastal areas (Vieira & Scalabrin 1991). Similarly, the croaker (*Micropogonias furnieri*) approaches the estuary from spring to summer to reproduce and facilitate the entry of its larvae (Vieira et al. 1998). Although a specific foraging strategy among individuals of the different social units was not detected, this social segregation can also be related to individual preference for different types of prey. This can be investigated by examining the stomach contents of catalogued individuals that died and were found stranded on the beach or through stable isotopes analyses of biopsies collected from both estuarine and coastal individuals.

Some important points have not yet been considered in these social structure analyses, such as the patterns of relationships between the sexes, reproductive stages and kinship. Although these points have not been investigated so far, it was possible

to find strong evidence that the population is divided into three major social units that are associated to different environments. Before genetic evidence of structuring is obtained, we recommend that the social units should be the framework for modelling the dynamic and viability of this population as well as for investigating patterns of gene flow within and between social units.

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Table 1. Characteristics of the groups of bottlenose dolphins found between August 2005 and October 2012 in the three subareas located in the Patos Lagoon estuary and adjacent coastal waters.

Area	N of groups	Mean group size (SD)	Minimum and maximum number of individuals	Mode
Estuary	961	4.58 ± 3.57	1 – 27	3
South	307	6.21 ± 5.06	1 – 30	4
North	343	6.10 ± 4.38	1 – 23	3
Total	1611	5.22 ± 4.14	1 – 30	3

Table 2. Mean strength, clustering coefficient and affinity of individuals within each social unit of the bottlenose dolphin population that uses the Patos Lagoon estuary and adjacent coastal waters. The standard deviation, estimated by bootstrap, is in brackets.

Social Unit	Strength	Clustering coefficient	Affinity
Estuary I	5.24 (0.91)	0.09 (0.01)	5.18 (0.09)
Random	5.32 (0.89)	0.15 (0.01)	5.04 (0.11)
	$P=1$	$P=1$	$P=0.01$
Estuary II	4.75(1.31)	0.09(0.01)	5.05(0.16)
Random	4.84(1.32)	0.15(0.01)	5.05(0.12)
	$P=1$	$P=1$	$P=1$
South	3.59 (1.19)	0.11 (0.04)	4.14 (0.30)
Random	3.15 (1.18)	0.14 (0.03)	4.05 (0.38)
	$P<0.001$	$P=1$	$P<0.001$
North	3.02 (0.93)	0.12 (0.04)	3.63 (0.41)
Random	2.31 (0.91)	0.11 (0.02)	3.78 (0.56)
	$P<0.001$	$P=1$	$P<0.001$

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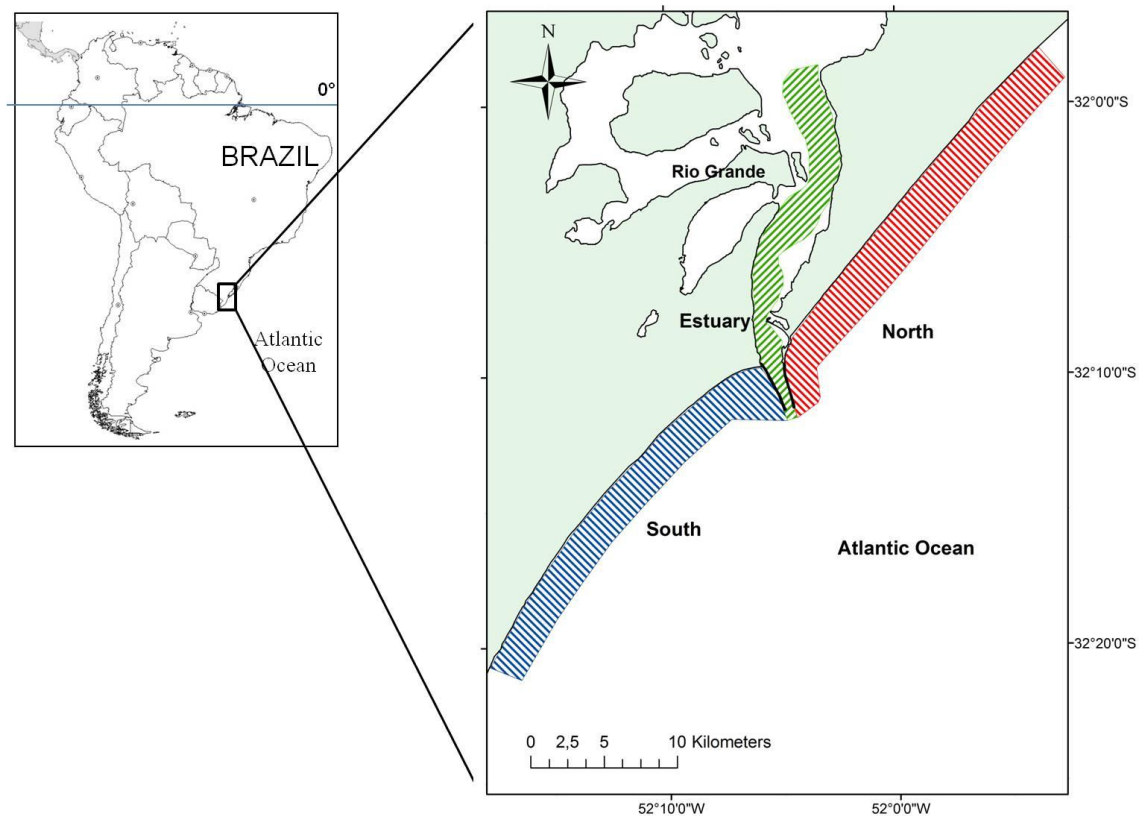


Figure 1. Area covered during the surveys to search for bottlenose dolphins in the Patos Lagoon estuary (green) and the adjacent coastal waters (south = blue and north = red).

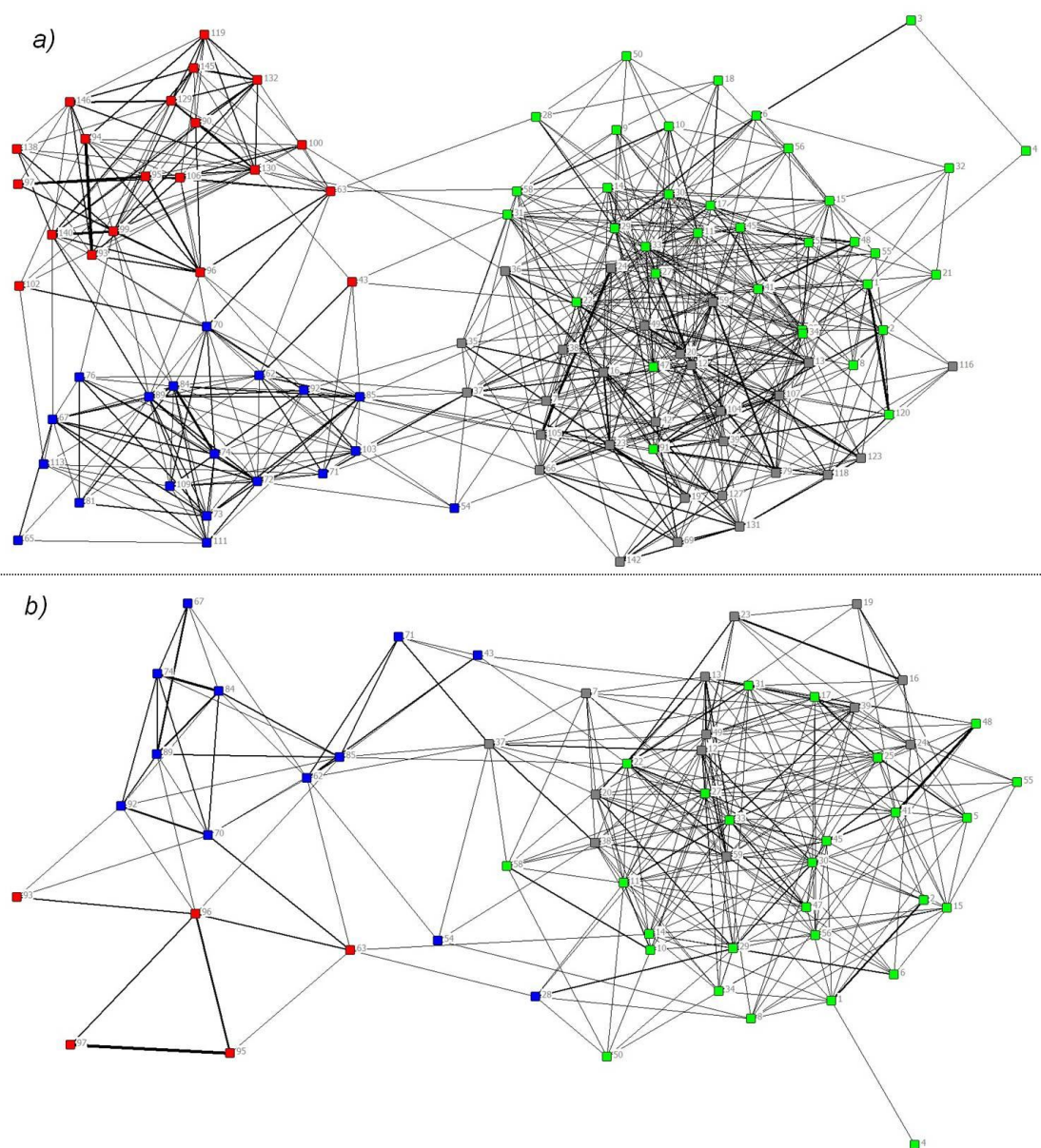


Figure 2. The social network of all dolphins using the Patos Lagoon estuary and adjacent coastal waters (a) and the social network considering only resident individuals (b). The thickness of the lines connecting each pair of individuals indicates the strength of their associations (HWI) and each node corresponds to an individual and their social unit (green and gray = estuary, blue = southern marine coast and red = northern marine coast).

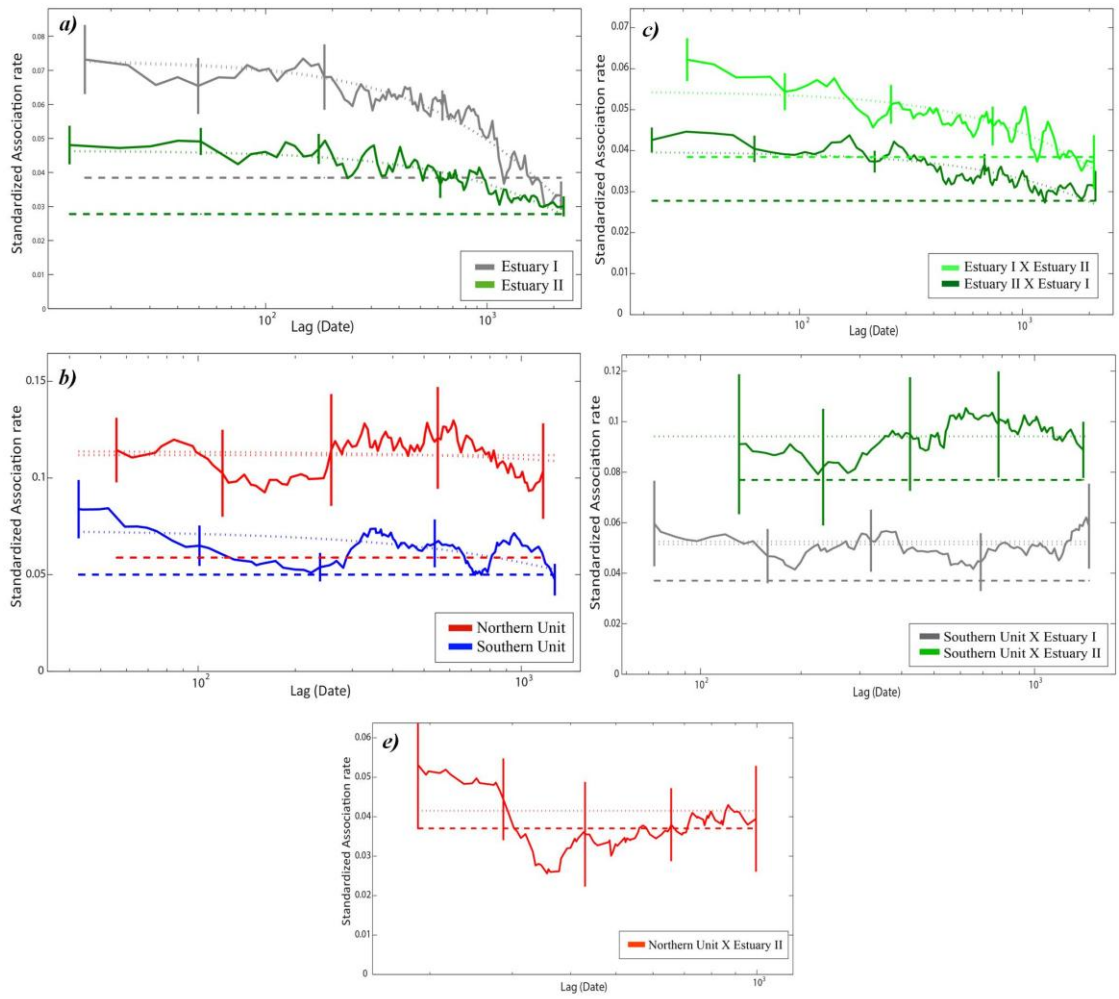


Figure 3. Standardized lagged association rate (solid line) together with the model(s) that best fit the data (dotted line) and the null association rate (dashed line) for each social unit (*a* and *b*), among dolphins from the two subunits of the estuary (*c*), among dolphins from the southern social unit and dolphins of the two subunits of the estuary (*d*) and from the northern social unit and the subunit II of the estuary (*e*). The standard deviations (vertical lines) were calculated by jackknifing periods of about 30 days.

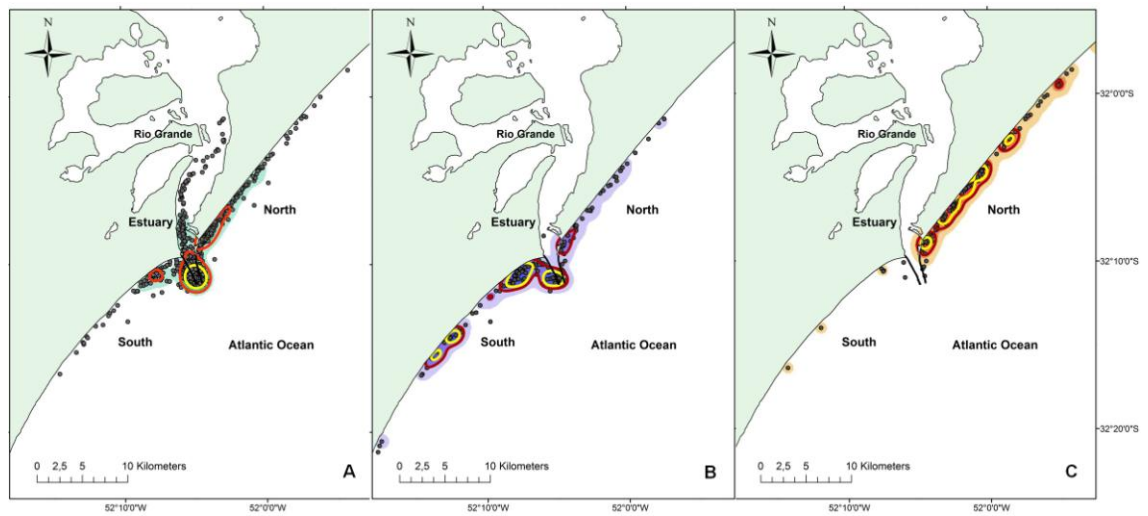


Figure 4. Locations where bottlenose dolphin groups were photographed within the study area, with the kernel isopleths of 25 (yellow) and 50% (red) for each social unit: estuary (A) southern coast (B) and northern coast (C).