UNIVERSIDADE DE LISBOA
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Behavioural ecology and habitat use of bottlenose dolphin (*Tursiops truncatus*) in São Tomé and Príncipe

ANDREIA FILIPA DA SILVA PEREIRA

DISSERTAÇÃO

MESTRADO EM BIOLOGIA DA CONSERVAÇÃO

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To my dogs, Lady and Simba, who taught me to love, respect and care for animals and nature…

To my mother who taught me to be a fighter...

“The sea, once it casts its spell, holds one in its net of wonder forever.”

Jacques-Yves Cousteau

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ABSTRACT

Ecological factors related to habitat type that influence food resources are major determinants in the way animals occur, select habitats, behave and interact with each other. The bottlenose dolphin is a cosmopolitan species, and because of its coastal habits in some areas populations have been declining. Additionally, in open environments there is a gap regarding information and assessment of this species. Although the ocean around São Tomé and Príncipe is relatively undisturbed, human activities such as artisanal fisheries, may affect directly cetaceans. Whale watching and oil exploration are factors that are beginning to emerge in the region and are also relevant for cetaceans. The aim of this thesis was to study the behavioural ecology of bottlenose dolphin through distribution, abundance, social structure, behaviour and group characteristics, residency patterns and site fidelity. Sighting effort from boat-based surveys was conducted between 2002-2006 and in 2012 around São Tomé Island and subsequently photo-identification techniques were used A total of 140 individuals were photo-identified and data suggested the existence of an open population of about 214 individuals. Group size had a mean of 44.7 individuals and it seemed to be influenced by habitat characteristics and composition. Key areas for bottlenose dolphin in São Tomé Island were determined using maximum entropy modelling. The most important environmental variables influencing distribution were distance to the coast and to river mouths, depth and seabed aspect. The eastern coast of São Tomé and Rolas islet presented the most suitable areas but they overlapped with intense fishing areas. Consequently, negative interactions between humans and cetaceans may occur through by-catch, direct hunting and competition. The assessment of key areas for bottlenose dolphins and the study of behaviour and abundance will contribute towards to the implementation of adequate conservation efforts for São Tomé and Príncipe from which all marine biodiversity would benefit.

Keywords: bottlenose dolphin, São Tomé and Príncipe, habitat use, maximum entropy modelling, cetacean conservation

RESUMO

Os factores ecológicos relacionados com o tipo de habitat que fazem variar os recursos alimentares são determinantes na forma como os animais ocorrem, seleccionam habitats, comportam-se e interagem entre si. O golfinho-roaz é uma das espécies de cetáceos com uma distribuição mais cosmopolita mas que, em algumas áreas costeiras, tem populações a diminuir. Adicionalmente, em ambientes abertos existe uma lacuna de conhecimento e de avaliação desta espécie. São Tomé e Príncipe é um país em desenvolvimento, que apresenta um rápido crescimento populacional e diminuto desenvolvimento industrial. A crescente necessidade por alimento e materiais de construção conduziu a uma depleção de recursos nalgumas áreas. No entanto, existe baixa prioridade por considerações ambientais. Em São Tomé e Príncipe actividades humanas como a pesca artesanal, através da captura acidental e intencional, podem afectar directamente os cetáceos. O *whale watching* e a exploração petrolífera são factores que também começam a ganhar expressão e que também são relevantes para os cetáceos. Apesar disto, São Tomé e Príncipe parece consistir numa importante área para pequenos cetáceos devido à existência de baías pouco profundas e protegidas e à abundância de presas. Existe uma necessidade crescente de investigar o estado das populações de golfinhos e os factores que as ameaçam na zona Oeste Africana. Investigação sobre a distribuição de cetáceos assume um papel importante na identificação de limites adequados para áreas marinhas protegidas e também no desenvolvimento de programas de gestão e de monitorização. O golfinho-roaz como um animal com longa esperança de vida, grande mobilidade e sensível a factores antropogénicos é considerado uma boa espécie indicadora que serve como um importante barómetro do estado do ecossistema. O objectivo desta tese consistiu em estudar a ecologia comportamental do golfinho-roaz através da distribuição, abundância relativa, estrutura social, comportamento e características de grupo, padrões de residência e fidelidade local. Entre 2002-2006 e em 2012, foram realizadas saídas de mar na ilha de São Tomé, nas quais, aquando um avistamento de cetáceos, se registavam diversos parâmetros, como a posição geográfica, hora, espécie, comportamento, tipo e tamanho de grupo, assim como o registo fotográfico dos indivíduos. As fotografias foram utilizadas para foto-identificação dos indivíduos. A influência do tipo de grupo e composição de grupo no comportamento assim como o tipo de grupo na dimensão do grupo foram estatisticamente testadas. O programa de análise SOCPROG foi utilizado para determinar o tipo de população e estimar a sua dimensão, avaliar o nível e o tipo de associações entre os indivíduos re-avistados assim como o seu grau de residência. A identificação de áreas úteis para o golfinho roaz na ilha de São Tomé e uma avaliação preliminar das mesmas para a ilha de Príncipe foram realizadas simultaneamente através de modelação de máxima entropia. No total, foram realizadas 226 saídas de mar, das quais resultaram 51 avistamentos de golfinho-roaz. A média do tamanho de grupo consistiu em 44,7 indivíduos e grupos compostos por adultos, crias e juvenis foram os mais avistados. O comportamento mais registado consistiu na deslocação, seguido de alimentação. De acordo com os testes estatísticos realizados, o tamanho de grupo e o tipo de grupo não influenciaram o comportamento observado. No entanto, os testes estatísticos revelaram uma influência da composição de grupo na dimensão do grupo. Deste modo, a maior dimensão do grupo parece estar associada à presença de crias. Através de técnicas de foto-identificação, cerca 140 indivíduos foram adequadamente foto-identificados. Destes, apenas 48 indivíduos foram re-avistados e utilizados para a análise das associações. O padrão observado das associações entre indivíduos ajustou-se a um modelo teórico composto por “conhecidos casuais”, com um valor médio de 0,18. As associações demonstraram ser de longo prazo e preferidas, estendendo-se até uma média de 627,8 dias. Através do histórico de re-avistamentos de todos os indivíduos, foram identificados 37 “residentes nucleares”, 11 “residentes” e 92 “não-residentes”. Os resultados dos padrões de residência para os indivíduos re-avistados efectuado através do SOCPROG estimou um grupo de cerca de 34 indivíduos residentes, que permanecem na área de estudo cerca de 2,8 anos, e cujos movimentos se assemelham a um modelo teórico de “emigração + remigração”. Para a estimativa da dimensão da população todos os indivíduos foto-identificados (“marcados”) foram utilizados. Os dados sugeriram a existência de uma população aberta de cerca de 214 indivíduos, com uma taxa de migração de 12,6%. O modelo de máxima entropia para o golfinho-roaz obteve um bom desempenho, com um valor médio de AUC de 0,992. As variáveis ambientais mais importantes que influenciaram a distribuição do golfinho-roaz consistiram na distância à costa, distância à foz dos rios, profundidade e aspecto do fundo oceânico. A costa este de São Tomé e o Ilhéu das Rolas apresentaram-se como as áreas mais adequadas para esta espécie. Contudo, estas áreas são também zonas de intensa actividade pesqueira e, consequentemente, interacções negativas entre cetáceos e humanos podem ocorrer através de capturas acidentais, caça e competição. As características observadas a nível do comportamento e das associações foram as esperadas para o golfinho-roaz e estão ultimamente relacionadas com o tipo de habitat, disponibilidade de recursos alimentares, estratégias de forrageio e protecção e sociabilidade.

Este trabalho é uma contribuição na aquisição de uma linha de base sobre o golfinho-roaz uma das espécies mais comuns em São Tomé e Príncipe e no Golfo da Guiné. A avaliação de áreas-chave para o golfinho-roaz e o estudo do comportamento e abundância no futuro poderá contribuir para a avaliação de tendências a longo prazo e na implementação de esforços de conservação adequados para São Tomé e Príncipe dos quais toda a biodiversidade marinha poderia beneficiar.

Palavras-chave: golfinho-roaz, São Tomé e Príncipe, uso do habitat, modelação de máxima entropia, conservação de cetáceos

CONTENTS

CHAPTER I: INTRODUCTION

THE COMMON BOTTLENOSE DOLPHIN

The common bottlenose dolphin (*Tursiops truncatus*, Montagu 1821), hereby bottlenose dolphin, is probably the most distinct of all dolphin species. It has a long history of association with humans in coastal waters since the Greeks (Lockyer, 1990) and it is easily recognisable as it is the most common cetacean on display in aquaria (Defran & Pryor, 1980). Its cosmopolitan distribution and frequent presence in coastal areas allows it to be one of the better studied cetaceans in the world (Shane *et al.*, 1986). It occurs in a variety of habitats from inshore, coastal, shelf to pelagic oceanic waters, exhibiting a mixture of degrees of residence that range from transient to year-round residency (e.g. Leatherwood & Reeves, 1990). The best well studied bottlenose dolphin communities are those that are coastal and have a high resident status, such as in Sarasota Bay, Florida, USA (e.g. Irvine *et al.*, 1981) and Moray Firth, Scotland (Wilson *et al.*, 1997). However the environmental plasticity of the bottlenose dolphin leads to a range of intra-specific variations in site fidelity, individual and group movements, group composition, and behaviour patterns that make worldwide generalizations difficult. Information about populations centred on islands is relatively scarce, although some research has been done in volcanic islands such as Azores, Hawai'i and other pacific islands (Scott & Chivers, 1990; Baird *et al.*, 2001; Silva, 2007) as well as in coral reefs islands in Belize and in the Bahamas (Campbell *et al.*, 2002; Parsons *et al.*, 2003). Ecological features related to habitat type that influence food resources, such as sea surface temperature, depth, slope, seabed aspect and productivity are believed to be factors influencing distribution of bottlenose dolphins around the world.

The social structure of bottlenose dolphins is composed by dynamic units, continually changing in size and membership, with some individuals maintaining long-term associations with each other and others more fluid within the group, in a fusion-fission style (Irvine & Wells, 1972; Würsig, 1978). Group size of these units commonly ranges between 2 and 15 individuals in coastal areas but groups of hundreds or thousands have been reported in offshore waters (Scott & Chivers, 1990). Environmental factors related to food resources and social factors, including mating and strengthening bonds influence group size of bottlenose dolphins (Norris & Dohl, 1980; Würsig, 1986). Behavioural patterns of common bottlenose dolphins, such as travelling, foraging/feeding, socializing and resting are influenced by a complex array of temporal, environmental and social factors, such as time of day, season, tides, depth, group size and group composition (e.g. Shane, 1990; Ballance, 1992).

The development and over-exploitation of coastal regions has resulted in significant environmental degradation of marine habitats of cetaceans (Reeves & Leatherwood, 1994). Due to its coastal habits, close to human activity, bottlenose dolphins are vulnerable to various threats such as by-catch, direct hunting, habitat degradation, acoustic and chemical pollution, marine debris, physical habitat destruction and tourism (Hooker & Gerber, 2004). Several populations around the world are threatened and have been declining over the years. Such cases arise in Europe, in the Mediterranean Sea, where bottlenose dolphins are genetically differentiated from those inhabiting the contiguous North Atlantic Ocean (Bearzi *et al.*, 2009) and in the Black Sea where a subspecies occur (Buckland *et al.*, 1992). Other tropical countries such as Sri Lanka, Peru, Ecuador and Thailand bottlenose dolphin populations face the same tendency (Hammond *et al.*, 2008). Population trends of bottlenose dolphins in open oceanic environments are less well known although incidental catch, hunting, habitat degradation, and tourism may be threats to the occurrence of this species.

CETACEANS IN THE GULF OF GUINEA

The Gulf of Guinea has a diverse cetacean fauna, which includes at least 28 cetacean species (Jefferson *et al.*, 1997; Van Waerebeek *et al.*, 2009; Weir, 2010). Despite this richness, these areas are poorly studied (Hooker *et al.*, 1999). Historical information about cetaceans in the region comes from whaling activity that dates back to the 19th century when humpback whales and other baleen whales were hunted (Figueiredo, 1958). Recent scientific research has been undertaken almost exclusively on humpback whale (e.g. Rosenbaum *et al.*, 2009; Carvalho *et al.*, 2011) and information about small cetacean species is still very sparse (e.g. Picanço *et al.*, 2001; Weir 2011).

São Tomé and Príncipe archipelago seems to be an important marine area for small cetaceans probably due to prey abundance and the existence of shallow and protected bays (Picanço *et al.*, 2009). In São Tomé Island, the most sighted species is the humpback whale that uses the area as a calving and nursing or resting ground, between August and November (Carvalho *et al.*, 2011). Other small cetaceans, such as the bottlenose dolphin and pantropical spotted dolphin seem to have year round occurrence, since they were present throughout all sampling periods (Picanço *et al.*, 2009). However, the status of cetaceans in this area has not been assessed due, in part, to lack of sufficient information (Reynolds *et al.*, 2009).

The main priorities in developing countries are economic development and the feeding of growing human populations. This is also true for São Tomé and Príncipe which has fast population growth, and little industrial and infrastructural development. Growing demands for fish, wood and building materials have resulted in depletion of some types of resources in many areas (Ngoile & Linden, 1997; Coughanowr *et al*., 1995) and environmental considerations often have low priority (Stensland *et al*., 1998). There is a critical need to investigate the status of dolphin populations and the factors that threaten them in the West African region (IWC, 2010). Information on cetacean distribution plays an important role in the identification of suitable boundaries for marine protected areas, but is also crucial for developing management and monitoring programmes.

THESIS AIMS

This thesis is a contribution to the knowledge of bottlenose dolphins and to the conservation of cetaceans in the Gulf of Guinea. In this region there are no studies that allow the determination of their status and information that can be used as baselines for evaluating tendencies of the populations. Bottlenose dolphins are long-lived, highly mobile animals, sensitive to anthropogenic stressors. They are considered as a good indicator-species, serving as an important barometer of the health of the ecosystem. In addition, knowledge of the behavioural ecology of this species in the area may help in the future to plan efficient management measures and further research designs.

The primary objectives are to:

1. Estimate population size around São Tomé Island, using mark-recapture methods;
2. Investigate the site fidelity and residency patterns of this species in São Tomé;
3. Analyze the behaviour patterns, group characteristics and describe the social structure of re-sighted individuals around São Tomé;
4. Identify key habitat preferences for bottlenose dolphin in relation to physiographic and oceanographic characteristics around São Tomé and predicting suitable habitat areas in Príncipe Island.

The thesis is organized as follows: one introductory chapter, presenting an overall description of the bottlenose dolphin ecology, behaviour and conservation as well as the current knowledge in São Tomé and Príncipe. Next there are two research chapters: The first chapter addresses the initial three objectives and the second chapter the last one. A final discussion chapter gives an overview of results with conservation implications and future research.

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CHAPTER II: COMMON BOTTLENOSE DOLPHIN (*TURSIOPS TRUNCATUS*) IN SÃO TOMÉ (SÃO TOMÉ AND PRÍNCIPE) – ABUNDANCE, SITE FIDELITY, HABITAT USE AND SOCIAL STRUCTURE

COMMON BOTTLENOSE DOLPHIN (*TURSIOPS TRUNCATUS*) IN SÃO TOMÉ (SÃO TOMÉ AND PRÍNCIPE) – ABUNDANCE, SITE FIDELITY, HABITAT USE AND SOCIAL STRUCTURE

ABSTRACT

The bottlenose dolphin is one of the most common small cetacean species occurring in São Tomé Island. Studies in oceanic islands regarding bottlenose dolphins are limited and prior to the present study, no research has focused on this species. This study represented the first attempt to assess the status of bottlenose dolphins in São Tomé (São Tomé and Príncipe), between 2002-2006 and 2012, studying relative abundance, behaviour site fidelity and social structure. A total of 140 individuals were photo-identified: 92 classified as non-residents, 37 presented year-round site fidelity and the remaining 11 were re-sighted within years. Data suggested the existence of an open population of estimated 214 (95% CI = 104.2 – 429.0) individuals with an immigration/emigration rate of 12.6%. Group size had a mean of 44.7 individuals and it seemed to be influenced by habitat characteristics and group composition. Most observed behavioural activities were travelling and feeding which may be related to foraging strategies.

Keywords: bottlenose dolphin, São Tomé, mark-recapture, group composition, habitat use

INTRODUCTION

The common bottlenose dolphin is widespread throughout the world's temperate and tropical waters. In the Gulf of Guinea, especially in São Tomé and Príncipe, it is one the most common cetacean species. However, there is a gap on focused research about bottlenose dolphins in the area adding to the lack of information regarding oceanic islands. The assessment of the number of individuals and trends and how groups utilize and vary with the environment is essential for appropriate management and conservation efforts, as it can provide important insights into the spatial and temporal distribution of resources, as well as into foraging strategies and energetic requirements of individuals (Brown & Orians, 1970). However the environmental plasticity of the bottlenose dolphin leads to a range of intra-specific variations in site fidelity, individual and group movements, group composition, and behaviour patterns that make worldwide generalizations difficult. Occurrence and distribution data through sighting effort and photo-identification techniques are the most used and adequate to obtain this type of information, because of their relatively accessible and non intrusive nature. They allow for observations of natural behaviour with minimal disturbance, the assessment of ranging patterns and habitat use (Irvine & Wells, 1972) as well as research into social associations (Wells *et al.*, 1980) and when in long-term they can provide insights of life history and population dynamics (Hohn *et al.*, 1989). The collection of data on the geographical and temporal distribution of cetacean species is also sufficient to identify particular 'hotspots' of occurrence that could be used to focus conservation measures (Evans & Hammond, 2004). Although considerable research has been undertaken in some parts of the world, studies about bottlenose dolphins in oceanic islands are limited mainly due to logistical and financial constraints. Work by Acevedo-Gutierrez (1999) at Cocos Island, suggests that some oceanic island bottlenose dolphin populations are both large and transitory. In the archipelago of Azores a large portion of sighted bottlenose dolphins seem to be either temporary migrants or transients, but a group of individuals shows strong site fidelity (Silva, 2008). Bottlenose dolphins in Hawaii were found to be island-associated, and not part of a pelagic population that occasionally passes the islands (Baird *et al.*, 2002). These results show the importance of long-term research and comparative studies to understand the behaviour and social structure of these long-lived animals (Wells, 1991). In the Gulf of Guinea, information about common bottlenose dolphin comes from general studies of occurrence (e.g. Picanço *et al.*, 2009; Weir, 2011). In São Tomé impacts of human activity such as by-catch, direct hunting and habitat degradation may pose a threat to bottlenose dolphins and the lack of legal protection hinders its protection. Therefore, it becomes imperative to have dedicated research to one of the most common species in the area so that conservation and management recommendations can take place. The aim of this study was to have a first assessment of the population of common bottlenose dolphins in São Tomé (São Tomé and Príncipe) through estimates of relative abundance, analysis of social structure, behaviour and group characteristics, residency patterns and site fidelity.

METHODS

Study area

The Democratic Republic of São Tomé and Príncipe, is situated in the west coast of Africa, in the equatorial region (between 1º44 N and 0º01 S) and is composed by two main islands and several islets (Fig. 1). South of São Tomé is Rolas Island that lies on the equator. The archipelago has an area of 1 000 km^2 and a continental shelf of 1 455 km^2 and São Tomé is the largest island, with an area of 860 km^2 and a continental shelf of 435 km^2.

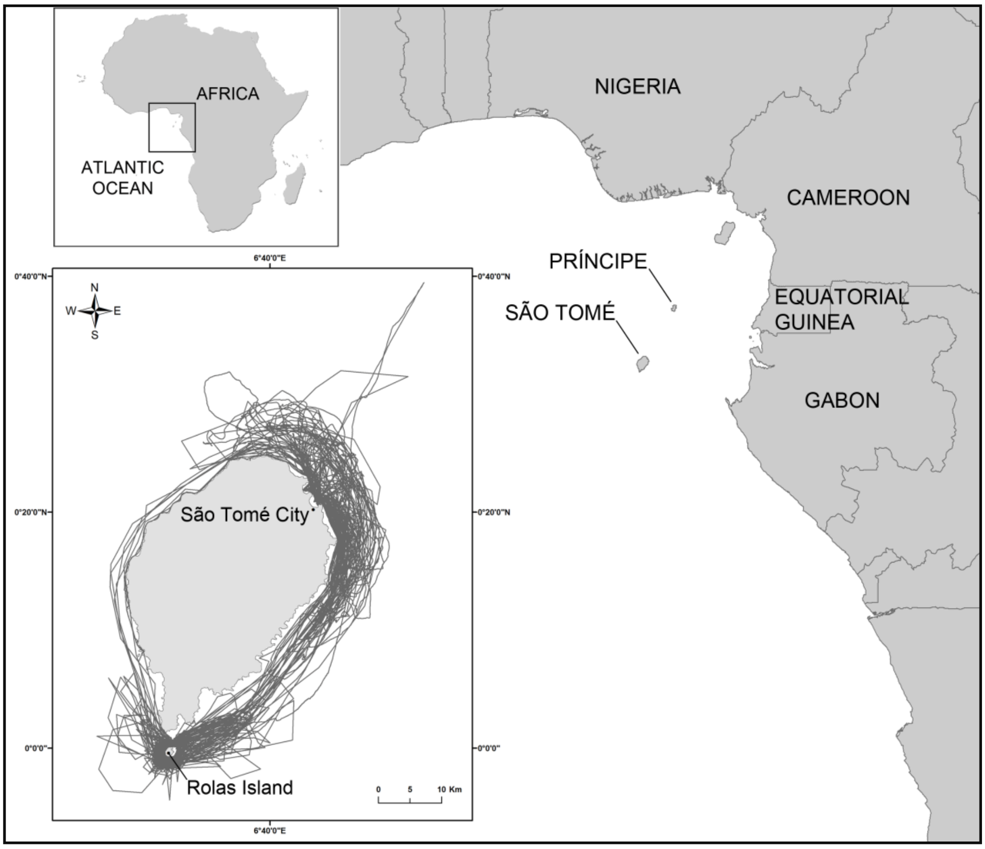

Figure 1. Geographical location of São Tomé and Príncipe, showing the survey effort around São Tomé Island during 2002-2006 and 2012 (left).

Data collection

Dedicated surveys were conducted between 2002 and 2006, and were part of a project focused on population structure of humpback whales (Fig. 1). Additional surveys were undertaken in 2012. Surveys routes were carried out using various fibreglass boats, ranging in length from 6 to 8 m (powered by engines from 25 hp to 200 hp) and were not pre-determined, but normally ran parallel to the coastline, with some variation, depending on prevailing weather conditions. When bottlenose dolphins groups were sighted, GPS position and time were collected as well as data about animals, such as group size, composition and behaviour (travelling, feeding, socializing, resting and mixed behaviours) (see Appendix I). A group was defined as any number of animals observed in apparent association, moving in the same direction, and engaging in the same activity (Shane, 1990). Group size was estimated based on a minimum count of animals observed at surface at one time. Group composition was determined by counting the minimum number of adults and documenting the presence of juveniles and calves. Photographs were taken at the maximum of individuals possible and its dorsal fins for individual recognition and confirmation of group size and group composition, with 35 mm cameras using ISO 100 or 400 colour slide film (2002–2004), or digital cameras equipped with 75–300 mm zoom lenses (2005, 2006 and 2012).

Data analysis

Photo-id analysis

During analyses, all non-digital images were scanned at high resolution (2 000 dpi) and converted to an electronic format (JPEG). Individual animals were identified based on the number, size and location of nicks and scars on their dorsal fins and on the back directly behind the dorsal fin (Würsig & Würsig, 1977; Würsig & Jefferson, 1990). The best photograph of each new dolphin recognized was used to construct a photo-id catalogue. Calves and individuals with few distinct marks were not included in the dataset for analysis. In order to have a value of occurrence of bottlenose dolphin relative to the sampling effort (hours) a number of sightings per unit of effort (SPUE), expressed as the number of sightings per hour of search effort at sea was calculated. For spatial analysis, a grid was created using ESRI® ArcMap 9.2 (ESRI 2006) and overlaid onto the survey area with a cell size of 2 x 2 nautical miles (13.72 km^2) to have the best representation of sampling effort (total kilometres travelled in each cell). Chi-square tests (χ^2, p = 0.05) were performed to determine if behavioural patterns differed with social factors, such as group size and group type and if group size was influenced by group composition. Group sizes were defined as small (< 30), medium (31-60) and large (> 60) and composition was defined as: Adults only; Adults and juveniles; Adults and calves; Adults, juveniles and calves. The null hypothesis was that behavioural patterns are independent of social factors considered and group size is independent of group composition.

Social structure analysis

Data on social structure was analysed using the SOCPROG 2.4 program (Whitehead, 2009). Only data of individuals with re-sighting frequency above the mean or median were used, depending on the distribution of the data. Coefficient of association among dyads (CoA) was calculated using the half-weight index (HWI, Eq. 1). HWI is the index most commonly used in the analysis of social structure in cetaceans because it is a less biased index that takes into consideration occasions when not all associates are identified (Cairns & Schwager, 1987) and since it is the most used it allows for comparisons between other studies. Association levels ranged from 0 (two individuals never seen together) to 1 (individuals always seen together) and were classified as low (0.01-0.20), medium-low (0.21-0.40), medium (0.41-0.60), medium-high (0.61-0.80) and high (0.81-1) (Quintana-Rizzo & Wells, 2001).

Equation 1

$$HWI = \frac{X}{X + \frac{1}{2}(Y_A + Y_B)}$$

X = number of sampling periods both individual A and B were seen together.

Ya = number of sampling periods in which A was present and B was not.

Yb = number of sampling periods in which B was present and A was not

To determine the existence of preferred or avoided associations and differences in sociality of individuals, CoA values were compared to a random distribution by permuting the observed dataset 10000 times using the Manly/Bedjer procedure (Manly, 1995; Bejder *et al.*, 1998; Whitehead, 1999). Social organisation based in the CoAs was graphically represented in a dendogram, using the average linkage method of the hierarchical cluster analysis. Cophenetic correlation coefficient was determined in order to indicate how well the dendogram represented the population (values above 0.8 indicate a good match) and to assess the level of population clustering, modularity was calculated (value greater than 0.3 is considered a good indicator) (Newman, 2006). To determine temporal variations in association values with time a standardized lagged association rate (SLAR) analysis was performed. The SLAR was compared with the null association rate, i.e. the SLAR expected if all individuals are associating at random. Several standardized theoretical models representing different social structures were fit to the SLAR's in order to determine which model had the best fit (see Apendix II). To determine the best-fit model the quasi Akaike's Information Criterion (QAIC) was calculated for each model (Ottensmeyer & Whitehead, 2003). The model with the lowest QAIC value was considered the best fit.

Population size estimates

A discovery curve (cumulative rate of identification of new individuals during sampling period) was plotted to assess a general tendency of the population and investigate if whether the population was closed or open. Population size and trends were statistically analysed using the SOCPROG 2.4 program with mark-recapture techniques, using all recognizable "marked" individuals. SOCPROG was chosen over other programs as CAPTURE and MARK because it provided the most useful population analysis for cetacean data (Whitehead, 2008) and other authors have demonstrated good results as a first assessment (e.g. Gowans *et al.*, 2000; Baird *et al.*, 2001; Merriman, 2007; Mahaffy, 2012). The designation "population" was used here to describe bottlenose dolphins occupying the study area during the sampling period and did not refer to a condition of reproductive isolation (Hansen, 1990; Krebs, 1994). Theoretical population models were compared with the real data (see Apendix III) and the one with the lowest Akaike's Information Criterion (AIC) value was chosen as the best-fit model. Estimate of the population size of the best fitted model was then adjusted using the mean mark rate for the population (Baird, 2001; Merriman, 2007). Mark rate, or the percentage of individuals uniquely marked, was estimated counting the number of photographs with marked versus unmarked individuals (Markowitz *et al.*, 2004).

Site fidelity and Residency

Site fidelity can be described as the tendency of an individual to return to an area previously occupied or remain in an area over an extended period (White & Garrot, 1990). Potential site fidelity to the study area was examined using all individual sighting histories. Individuals with year-round occurrence were classified as "core residents", while individuals sighted more than one time within sampling years were termed "residents". Individuals only sighted in only one occasion were termed "non-residents''. The lagged identification rate (LIR) gives information about movements within a study area and it estimates the probability that an individual sighted in the study area at a given time will still be present (t) time lags in the future (Whitehead, 2008), which is determined as a residency value. LIR was calculated using the movement analysis in SOCPROG 2.4. Residency is generally defined based on the amount of time spent in a predefined area (Wells & Scott, 1990). LIR was then fitted with theoretical models (see Appendix III) and the one with the lowest quasi-Akaike Information Criterion (QAIC) values was determined the best-fit model.

RESULTS

A total of 226 surveys were conducted, with 626.9 hours spent of search effort (Table 1). Survey effort differed between years due to changes in location of the team base. In 2002 and 2003 most of the survey effort was concentrated in the waters south of São Tomé and since 2004 most of the survey effort occurred on the north and east coast of São Tomé (Fig. 2).

A total of 51 bottlenose dolphin sightings occurred with a mean SPUE of 0.076 sightings per hour.

Table 1. Summary of research effort in São Tomé for the years 2002-2006 and 2012.

	Sampling effort			Sightings		
Year	Months surveyed	Number of surveys	Search effort (h)	Number of sightings	Mean group size±SD	SPUE (sightings h^{-1})
2002	Jul-Dec	87	172.88	22	44.1±44.1	0.127
2003	Jan, Aug-Oct	61	137.25	12	45.3±36.3	0.087
2004	Oct-Nov	22	106.30	3	58.3±28.9	0.028
2005	Aug-Oct	33	129.62	6	66.7±25.8	0.046
2006	Sep	7	28.57	1	25.0	0.035
2012	Feb-Jun	16	52.28	7	23.9±10.9	0.134
Total		**226**	**626.90**	**51**	**44.7±36.9**	**0.076**

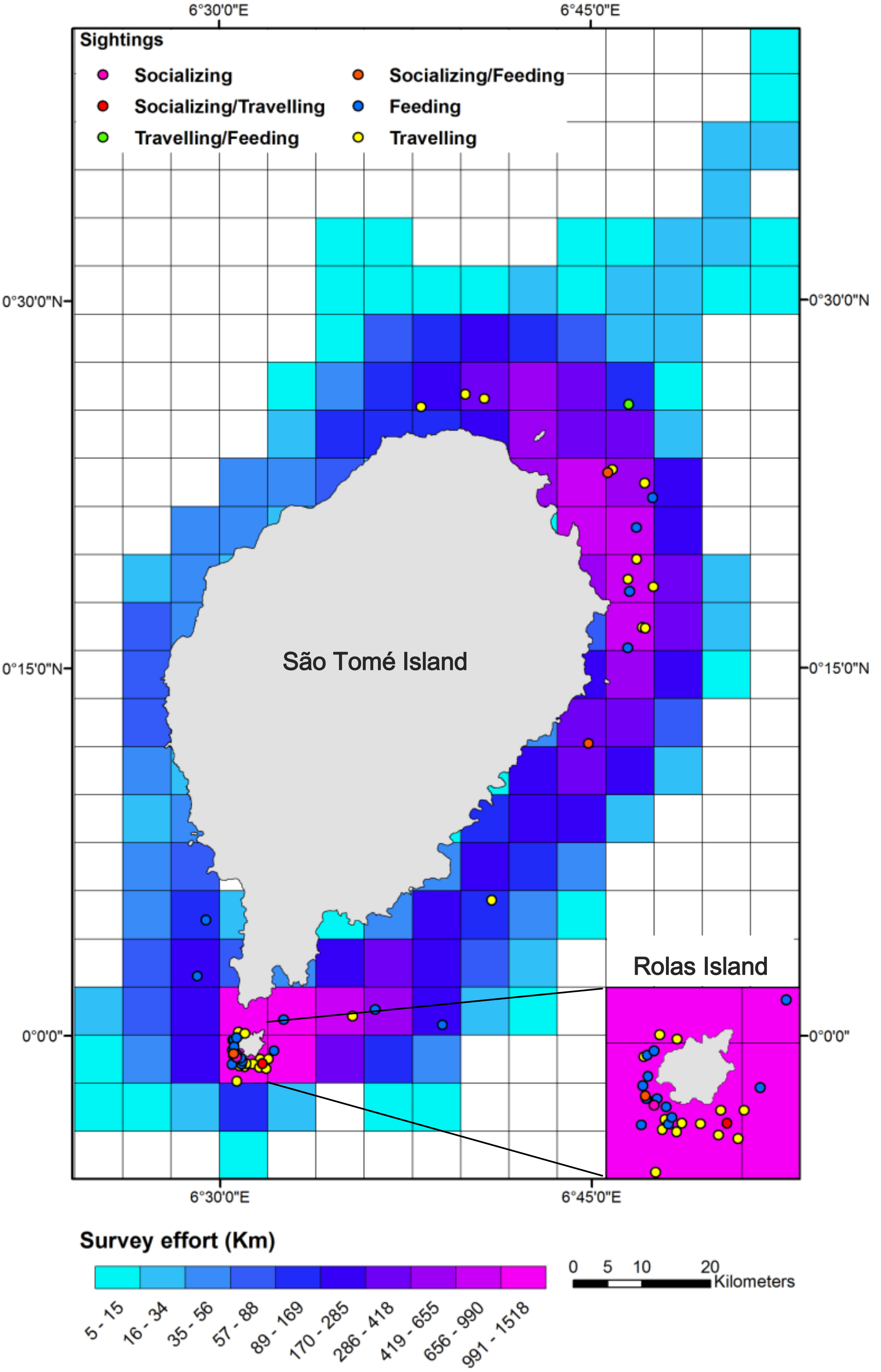

Figure 2. Bottlenose dolphin occurrence in São Tomé between 2002 and 2012, showing behavioural patterns and survey effort (km).

Group size of bottlenose dolphin ranged from 3 to 200, with a mean of 44.7 individuals (median = 35, SD = 36.9). Six behavioural categories were observed throughout the study area (Fig. 2). Travelling was the behaviour most observed (49%), followed by feeding (39%), and socializing (2%) (Fig. 3). Resting was never observed. Data suggested that there was no association between observed behavioural categories and group type (χ^2 = 9.53, df = 15, p = 0.8482) (Fig. 3) and group size (χ^2 = 8.63, df = 10, p = 0.5675)(Fig. 4). All types of group sizes were observed and in terms of group structure, groups composed by adults, juveniles and calves were the most observed (Fig. 5). Groups of only adults were the smallest and groups with calves present seem to be the largest. Data suggested that there was an association between group composition and group size (χ^2 =17.44, df = 6, p = 0.0078).

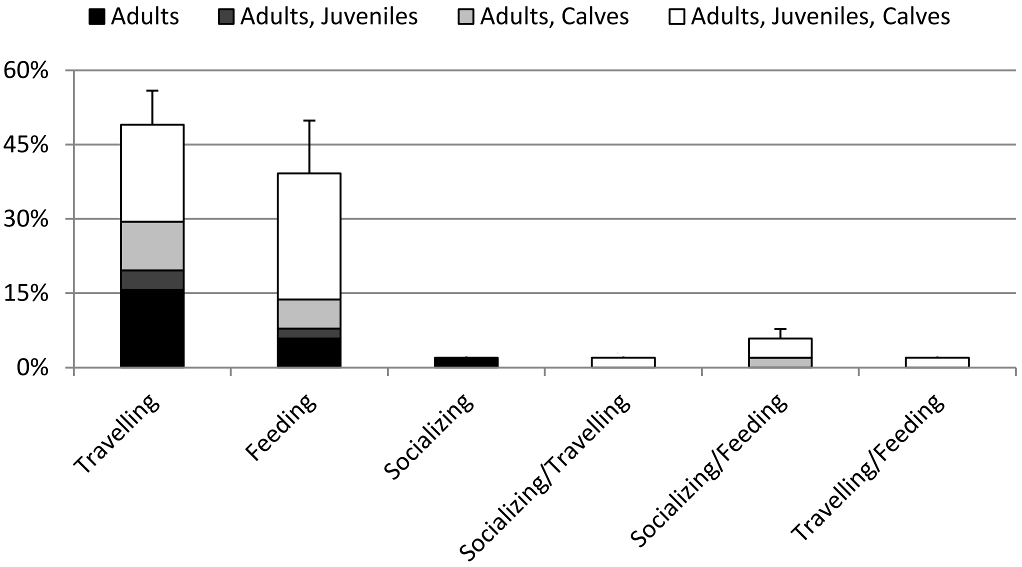

Figure 3. Frequency of behaviour per group type of bottlenose dolphin in São Tomé (n = 51). Error bars represent SD.

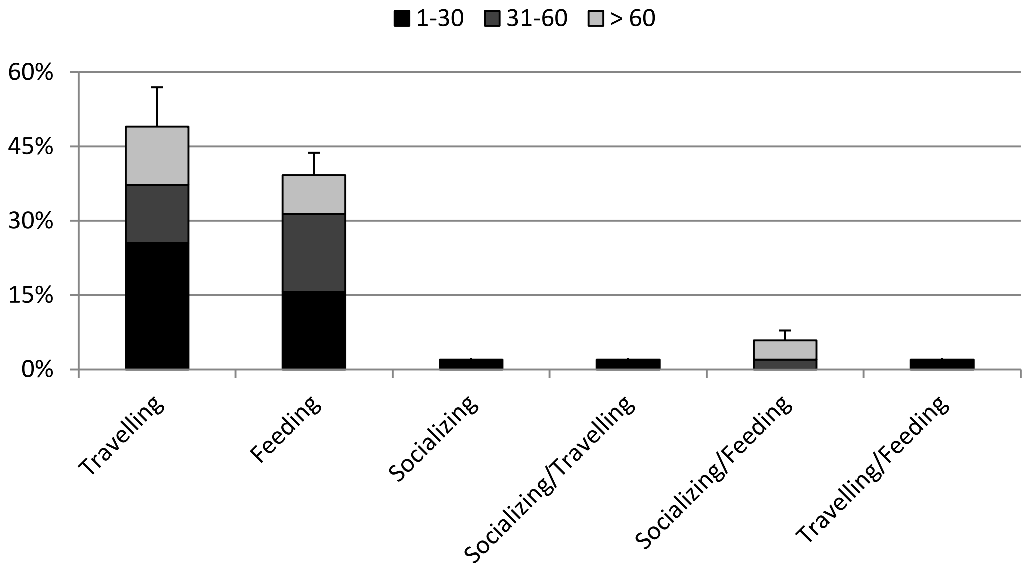

Figure 4. Frequency of behaviour per group size of bottlenose dolphin in São Tomé (n = 51). Error bars represent SD.

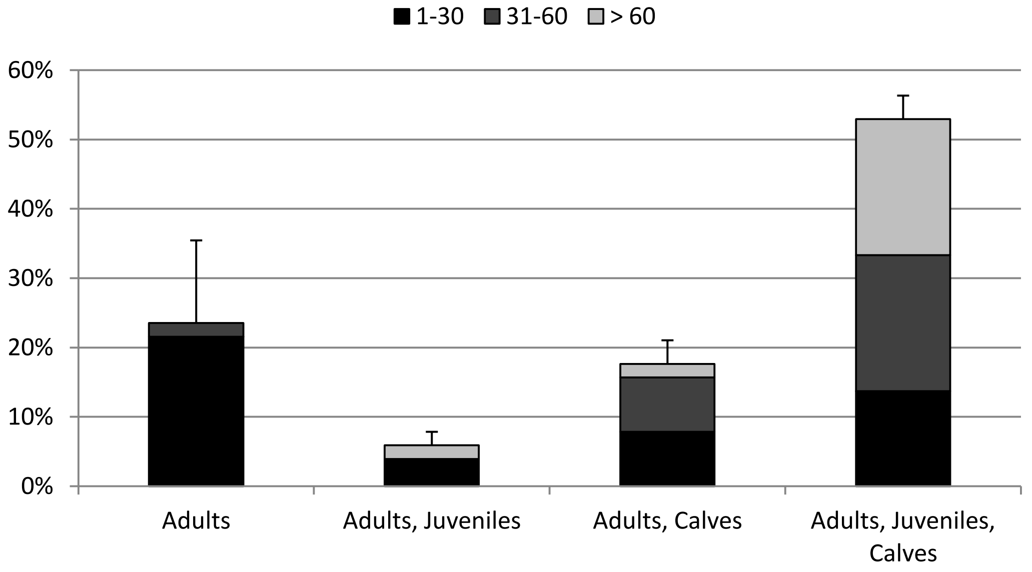

Figure 5. Frequency of group type per group size of bottlenose dolphin in São Tomé (n = 51). Error bars represent SD.

A total of 2011 photographs were taken, of which 1058 were considered for photo-identification analysis but due to quality only 727 were suitable for individual identification. Overall, 197 adult individuals and 8 calves were identified between 2002 and 2012, but due to the quality of photographs, markings and age class, only 140 were used in the analysis. Of the 140 individuals, most were only sighted once (65.71%), but others were observed between 2 and 6 times, with an average re-sighting frequency of 2.92 (SD = 1.33) and a median of 2 times (Fig. 6). Mean mark rate showed that 62.56% (SD = 13.69) of individuals were marked.

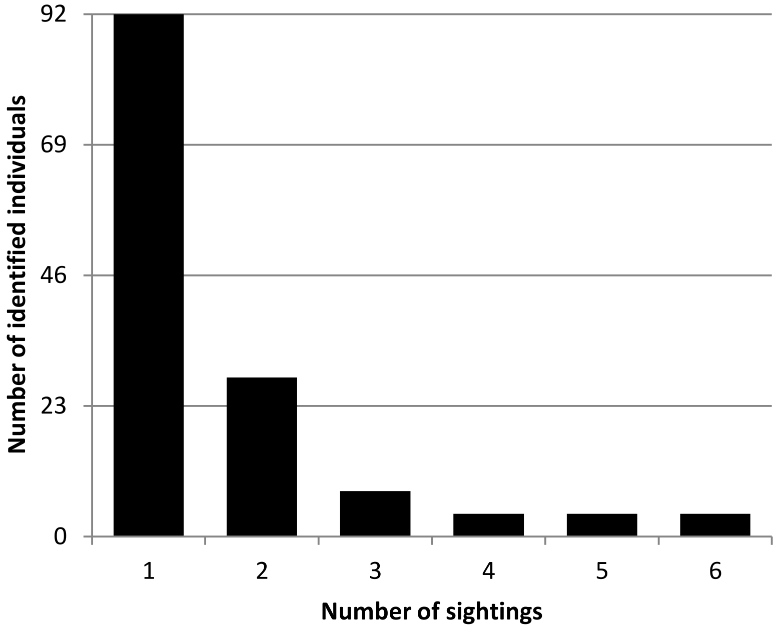

Figure 6. Sighting frequencies of bottlenose dolphins identified from 2002 to 2012 in São Tomé (n = 140).

Social structure

Since the distribution of re-sightings was skewed to the right, the cut-off level used for choosing individuals for social analysis was the median. Thus, individuals with a re-sighting frequency equal or above 2 were used, totalling all 48 re-sighted individuals. Association matrix of individuals resulting from HWI ranged from 0 to 1 with an average of 0.18 (SD = 0.10, Fig. 7). Only 6 high association levels between adult individuals were registered and other 40 associations were moderate to high.

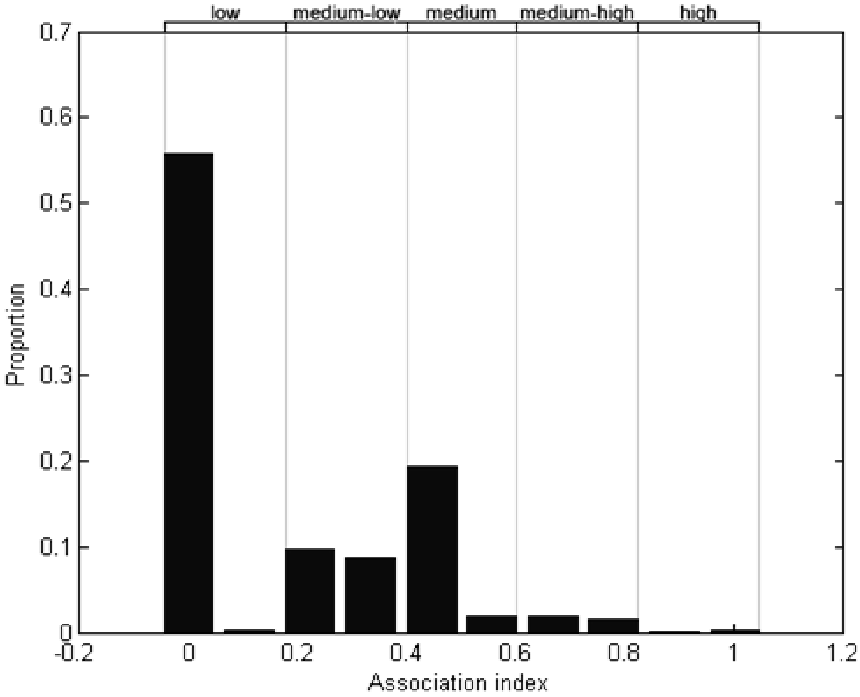

Figure 7. Distribution of coefficient of association (CoA) of bottlenose dolphins seen ≥ 2 times in São Tomé.

Results of preferred/avoided associations test showed a higher value of the real standard deviation and coefficient of variation than the permuted data suggesting that companionships are preferred and long-term (Table 2). There were differences in sociality of individuals given the high value of standard deviation of typical group size for the real dataset.

Table 2. SOCPROG results for preferred/avoided associations test. Permuted data were calculated using 10.000 random permutations.

	Real	Random	p-value
Mean association index	0.18123	0.00002	0.0001
Standard deviation	0.22831	0.00002	0.0001
Coefficient of variation	1.25977	0.00013	0.0000
Standard deviation of typical group size	5.24821	0.00052	0.0001

Cluster analysis of the associations is displayed in Fig. 8. However, a cophenetic correlation coefficient of 0.770 showed that this representation was not accurate and division was not possible given the modularity of 0.183.

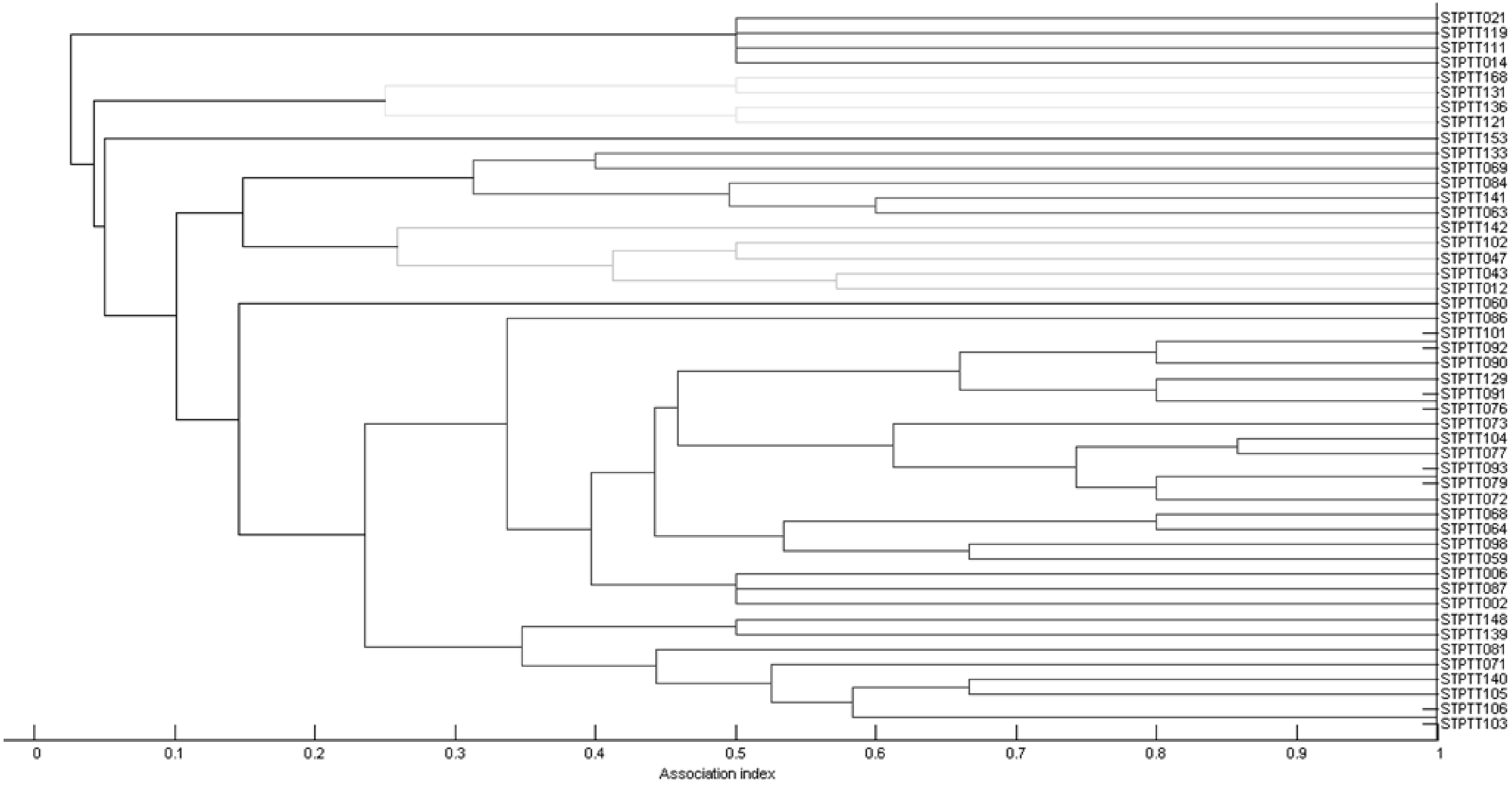

Figure 8. Dendogram showing the average-linkage cluster analysis of associations between bottlenose dolphins seen ≥ 2 times in São Tomé.

Rate of associations between individuals over time is represented by the SLAR in Fig. 9. The curve showed a downward tendency, staying above the null rate until at least 627.8 days which represents the duration of long-term associations of bottlenose dolphins. The social system model that best fitted the SLAR was composed by casual acquaintances (see Appendix IV).

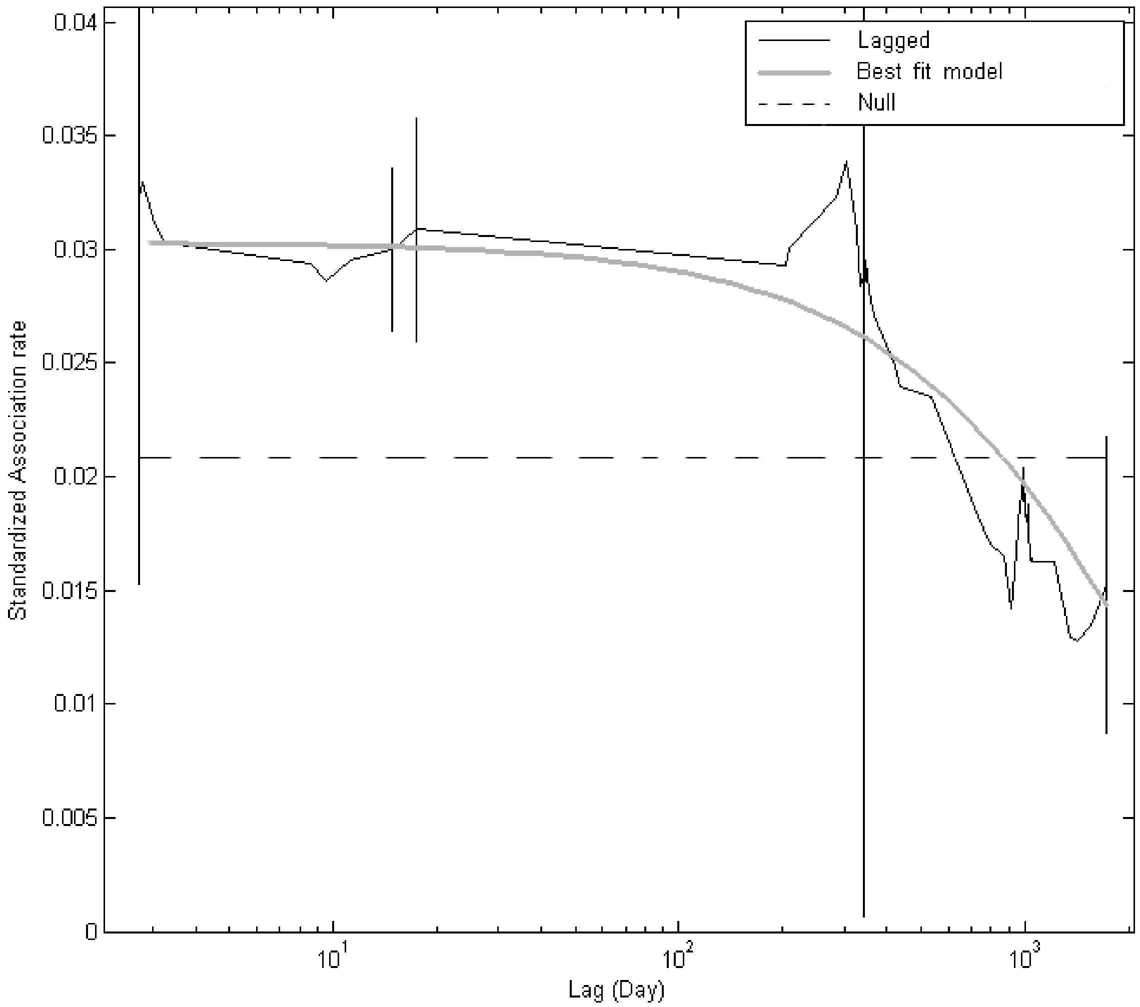

Figure 9. SLAR of bottlenose dolphins seen ≥ 2 times in São Tomé with a moving average of 1400 associations. Error bars were calculated using the jackknife technique. The maximum-likelihood best fit model represents casual acquaintances. The null association rate represents the theoretical SLAR if individuals associated randomly.

Population size estimates

The discovery curve showed a steady increase since 2002 (Fig. 10), with most individuals being first identified in the last years (2005 and 2012). Re-sighting curve was always above the discovery curve confirming the previous tendency. Only the last sighting in 2005 was composed mostly of re-sighted individuals.

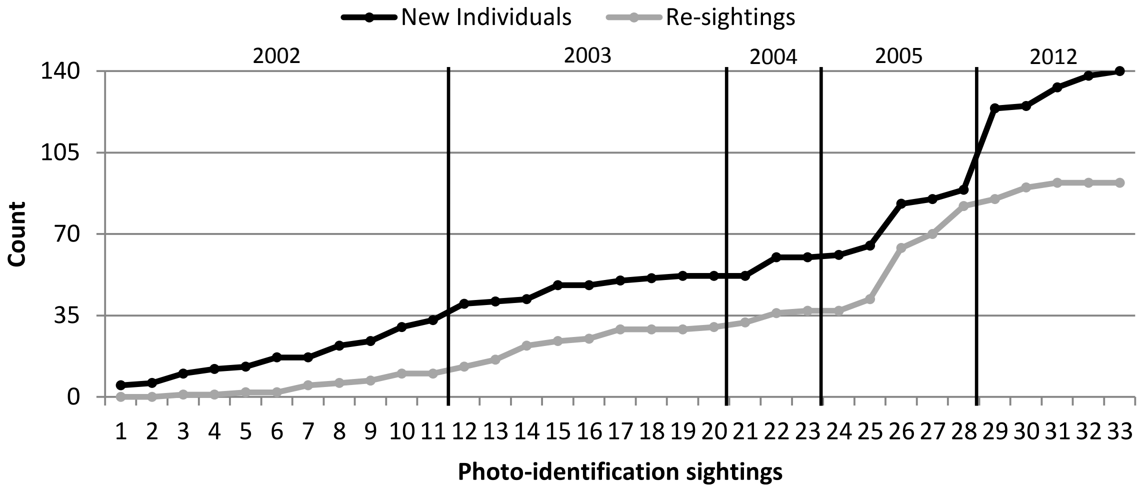

Figure 10. Cumulative rate of identification of new individuals and re-sighting frequency over time ('rate of discovery') between 2002-2006 and 2012 for São Tomé.

According to AIC values, "Mortality + Trend" was the most appropriate population model (Table 3), with an estimate of 133.835 (SE = 53.2) individuals and an annual migration rate of 12.6% (SE = 0.1). This model assumes a population growing or declining at a constant rate where mortality (which may include permanent emigration) is balanced by birth (which may include immigration). Adjusting the estimate of population size to the mean mark rate of 62.56%, annually the population is composed by 214 individuals (95% CI = 104.2 – 429.0).

Table 3. SOCPROG fit of theoretical population model results for bottlenose dolphins in São Tomé in 2002-2005 and 2012. Bootstrapped (n = 100), 140 individuals, 5 sampling periods (2002, 2003, 2004, 2005, 2012).

Model	Est. Pop. size	±SE	95%CI	Est. mort. rate	±SE	95%CI	Log likelihood	AIC
Schnabel	214.867	26.5	184.6 - 284.6	-	-	-	-124.1657	250.3313
Mortality	80.497	13.7	63.4 - 113.5	0.235	0.053	0.159 - 0.344	-105.7497	215.4995
Mort. + Trend	**133.835**	**53.2**	**65.2 - 268.4**	**0.126**	**0.1**	**0.000 – 0.336**	**-104.6887**	**215.3773**

Site Fidelity and Residency

Based on the established criteria a total of 37 “core residents”, 11 “residents” and 92 “non-residents” were identified (see Appendix V). “Core resident” individuals were sighted, in average, 2.32 years (median = 2, SD = 0.71). One core resident individual was seen during all sampling period and two others were seen between four years. “Residents” were sighted within the years of 2002 (n = 1), 2003 (n = 3), 2005 (n = 5) and 2012 (n = 2). Of the “non-resident” individuals 49 were sighted in 2012, 22 were seen in 2005, 13 observed in 2002, 5 observed in 2003 and 3 individuals were seen in 2004. LIR, calculated using a sampling period of a day, is represented in Fig. 11. The model with the best fit that described the movements of the population was “Emigration + Remigration” (see Appendix VI). The model indicated that on average 34 (SE = 4.2842) individuals were at the study area at any one time and that an individual remained in the study area an average of 1046.456 (SE = 720.8574) days (~2,8 years). Individuals were estimated to spend an average of 1337.801 (SE = 246720051108072.3) days outside the study area. The standard error of the estimate of the residency period outside of São Tomé was large in comparison to the actual estimate, which could indicate that individuals spend variable time periods outside and/or that sampling effort was not sufficient to account for all large number of exits from and re-entries to the area.

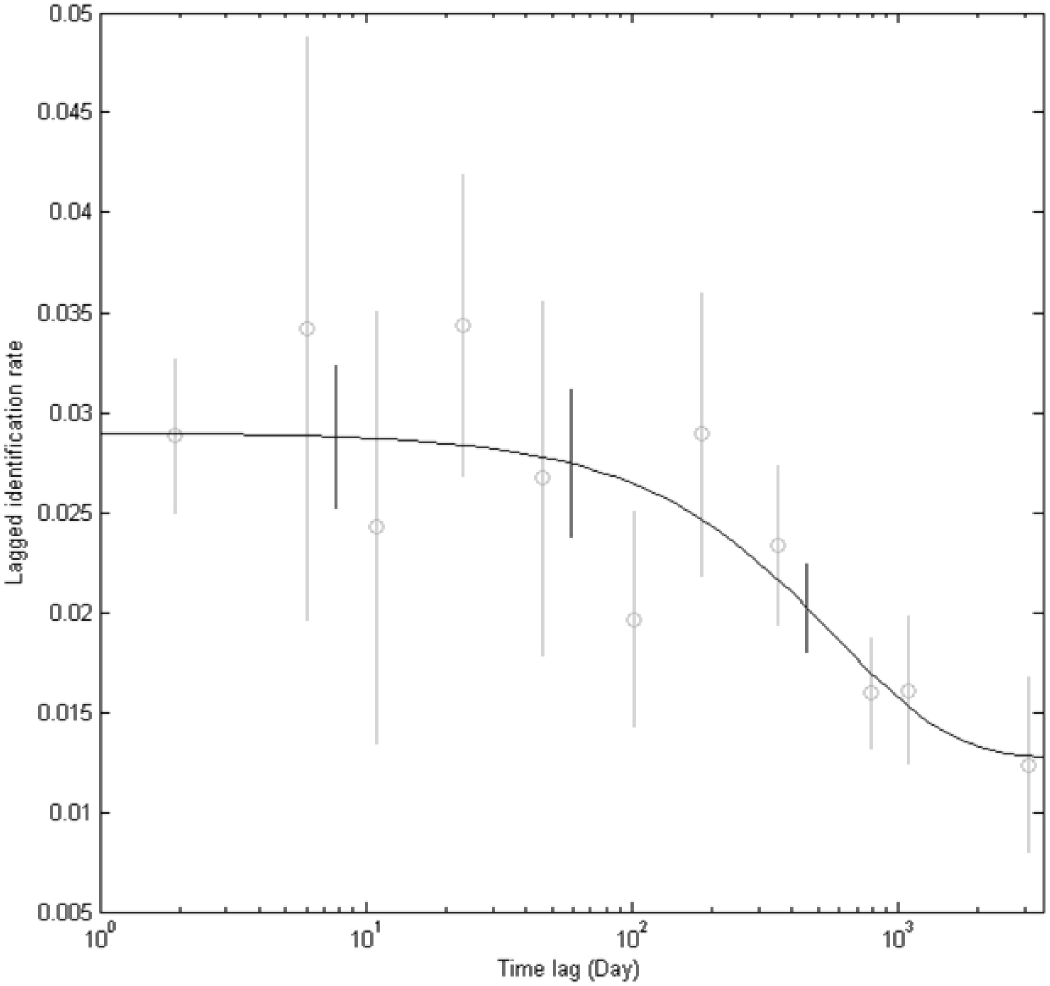

Figure 11. LIR for bottlenose dolphins seen ≥ 2 times in São Tomé. Data points are represented as circles and the best-fit model (Emigration + remigration) is displayed as the line. Error bars were calculated using 100 bootstrap replications.

DISCUSSION

This study contributes to the gap of knowledge in this region assessing for the first time the status of bottlenose dolphins in São Tomé by studying behaviour, relative abundance and social structure. Mean group size of bottlenose dolphins of 44.7 in São Tomé was the second highest value observed for this species in oceanic islands, only below the results for Eastern Pacific Ocean (Scott & Chivers, 1990). This result is in agreement with the findings that larger groups of bottlenose dolphins tend to occur in more open and pelagic waters (Shane *et al.*, 1986). However, it should be noted that there is a range of definitions used to define a group unit (e.g. group, pod, herd, school, subgroup, and sighting) and different criteria to determine membership, which in turn may influence the comparison among other works. Data suggested that there was an association between group size and group type. It is reported that group size, additionally to habitat characteristics, may be influenced by an array of factors which include the following: food resources, predation and sociality. Wells *et al.* (1980) suggested that larger group sizes may benefit from cooperative feeding on patchy, rich food resources found in open and deeper habitats, where schooling fish become the main food resource. In São Tomé group size may be a response to a patchy distribution of prey where the large number of individuals increases the probability of locating and herding prey. Sharks (Herzing & Johnson, 1997) and killer whales (*Orcinus orca*) are known to be potential predators of bottlenose dolphins which may increase group size for avoidance (e.g. Norris & Dohl, 1980). Anecdotal information and fisherman common reports that sharks are frequent in São Tomé waters but there was no relation with scars in identified individuals to sharks. Killer whale occurrence in São Tomé seems to be seasonal (Weir *et al.*, 2010) but both species occur in the same time and in the same area (in the South part, near to Rolas Island). Group size was influenced by the presence of juveniles and calves, with groups tending to be larger when individuals of these age classes were present. The influence of calves in group size had been reported for several areas, as Marlborough Sounds, New Zealand (Merriman, 2007), Adriatic

Sea (Bearzi *et al.*, 1997) and Sarasota Bay, Florida (Wells *et al.*, 1987). In larger groups the enhanced assistance of the young by other members allows reducing maternal investment (Bearzi *et al.*, 1997) and allows for constantly changes in group composition. Therefore, group size of bottlenose dolphins in São Tomé seems to be influenced by group composition. Behavioural patterns of bottlenose dolphins in São Tomé showed that the most observed activities were travelling and feeding. The high values of travelling could be explained by foraging strategies which cannot be directly observed (Bearzi *et al.*, 1999). Certain habitats may have a lower density and a patchy distribution of food resources (Balance, 1992; Defran *et al.*, 1999) which could increase the necessity of travelling for bottlenose dolphins in search of prey, as could be the case of open environments, such as oceanic islands. It should be noted that most feeding activities were concentrated in the south region of São Tomé, around Rolas Island, which could be an area of concentration of food resources.

Social Structure

The group of bottlenose dolphins in São Tomé demonstrated low to moderate association values, with an average of 0.18. Low association coefficients values are characteristic of the fission-fusion society of bottlenose dolphins, with highly fluid groups varying membership within a very small time frame (Connor *et al.*, 2000). Also the large group sizes in São Tomé allows for a wide range of potential associates between individuals largely influencing coefficients of association. Preferred and long-term companionships were present in São Tomé and there were differences in gregariousness in which certain individuals are seen in large groups and others small groups. Association patterns are commonly influenced by factors such as the age and sex of the individuals. The previous association between group size and group composition may be reflected in this association patterns as well, as females with calves may prefer larger groups for the benefits mentioned. It is reported that males may also form small groups, subadults by response to aggression of adult male individuals when attempting to copulate with females (e.g. Norris, 1967; Caldwell & Caldwell, 1972) and adults for cooperation to maintain female consorts (Connor *et al.*, 1992). Thus, it may be possible that group size is influencing social structure of bottlenose dolphins in São Tomé. Standardized lagged association rate showed that long-term associations of bottlenose dolphins in São Tomé lasted 627.8 days and the pattern found was best fitted in a model composed by casual acquaintances. Although this model is characteristic of a fission-fusion society, associations show a longer duration than it is expected (Augusto, 2011). As long-lived animals, bottlenose dolphins benefit of these associations passing on knowledge and developing social skills that may be vital to a successful function in their environment (Lusseau, 2003; Rendell & Whitehead, 2001).

Population size estimates

Discovery curve for bottlenose dolphins in São Tomé showed an increase of individuals since 2002, which indicated an open population with continuing influx of new individuals that may represent births, immigration into the population, mark change or captures in subsequent years of individuals which had been previously un-photographed. Mark-recapture adjusted estimates showed that around 214 individuals occur in São Tomé annually, with an immigration/emigration rate of 12.6%. Only few abundance estimates are available for other oceanic islands. Baird *et al.* (2001) estimated a closed population of 134 bottlenose dolphins around the islands of Hawaii between 1999 and 2001 using photo-identification methods, but aerial surveys conducted around the main Hawaiian Islands produced a much larger abundance estimate (740 individuals)(Mobley *et al.*, 2002). Silva *et al.* (2009) estimated that approximately 600 bottlenose dolphins (312 adults, CI = 254-384; 300 subadults, CI = 232-387 occur around the islands of Faial and Pico (Azores) in a single year. The existing tendency demonstrated by the discovery curve and mark-recapture models added to the fact that most individuals were only sighted one time, suggested the existence of a large transient population in São Tomé. Although results found had less data compared with the work done by Silva *et al.* (2009), tendencies appear to be similar to those found in Azores and seemed to be in accordance to the suggestion of Acevedo-Gutierrez (1999).

Site Fidelity and Residence

Although the population of bottlenose dolphins in São Tomé appeared to be large and transient, a small group of individuals seem to use the area regularly. Overall, 48 bottlenose dolphins showed site fidelity, of which 37 were classified as “core residents” and 11 individuals were classified as “residents”. This fidelity pattern, a mixture of residents, transients and temporary migrants, is also found for the Azores islands and it seems to be a common trait among populations of bottlenose dolphins (e.g. Würsig & Würsig, 1977; Bearzi *et al.*, 1997; Silva, 2007). Lagged identification rate indicated that on average 34 individuals were at the study area at any one time and were estimated to remain in the study area around 2.87 years. The results found in SOCPROG are in agreement with the ones found by sighting histories of individuals. The best fit model “Emigration + Remigration” was also in agreement with the findings of site fidelity criteria, as it states that populations with a fall of LIR and a consecutive stabilization may be a mixed population of residents and transients.

Final considerations

Understanding the behaviour and ecology of bottlenose dolphin in the area is essential to develop management strategies and protected areas. This study represents the first assessment of bottlenose dolphin in São Tomé, demonstrating the regular presence of these animals in São Tome waters, very close to shore, and highlights the importance of the area for feeding activities in general. Individuals with a residency status seem to use all sampled extension of the island and most bottlenose dolphin sightings occurred in some of the most intense fisheries areas in São Tomé and other areas associated to boat traffic. Incidental entanglement and/or deliberate catch, disturbance, boat-strikes and alteration or loss of critical areas could lead to a downward tendency in bottlenose dolphin abundance, especially in the resident group. Identification and subsequent protection of habitats and critical areas are ways of ensuring a sufficient amount of space, shelter and food for those animals. Further research and monitoring population tendencies are needed so that in the future, these results may be considered for the implementation of conservation efforts for cetacean species.

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CHAPTER III: PREDICTING KEY AREAS FOR COMMON BOTTLENOSE DOLPHIN (*TURSIOPS TRUNCATUS*) IN SÃO TOMÉ AND PRÍNCIPE USING SPECIES DISTRIBUTION MODELLING

PREDICTING KEY AREAS FOR COMMON BOTTLENOSE DOLPHIN (*TURSIOPS TRUNCATUS*) IN SÃO TOMÉ AND PRÍNCIPE USING SPECIES DISTRIBUTION MODELLING

ABSTRACT

Determining suitable areas and assessing what environmental attributes attract a species are becoming increasingly important to design Marine Protected Areas and management strategies. This study aimed to predict key areas in São Tomé and Príncipe for bottlenose dolphin in relation to physiographical and oceanographical variables using Maxent models as a first approach to recommend suitable areas for future MPAS. A total of 51 sightings of bottlenose dolphin were recorded between 2002 and 2012. Maxent models performed well with AUC values of 0.992 and the most important environmental variables were distance to coast and to rivers, depth and seabed aspect. The eastern coast of São Tomé and Rolas Island presented the most suitable conditions for the occurrence of bottlenose dolphin. Identified key areas overlapped with intense fishing areas where negative interactions may occur as a result of by-catch, direct hunting and competition. In the future these areas may be incorporated in management plans for these species in this archipelago.

Keywords: maximum entropy modelling, bottlenose dolphin, São Tomé and Príncipe, Gulf of Guinea, distribution

INTRODUCTION

Describing and understanding the processes that determine the distribution of organisms is a fundamental problem in ecology, and is a necessary step in planning management and conservation measures (Redfern *et al.*, 2006; Cañadas & Hammond, 2006). The complexity and heterogeneity of habitats influence how animals distribute in a certain area by variations in abundance, distribution and availability of food resources (Balance, 1992). Therefore it is likely that certain areas that present the best conditions will be more used than others and therefore have a greater importance to the occurrence of a species. Management efforts to conserve marine biodiversity are increasingly focusing on spatial-based measures, as the protection of key areas and habitats (Agardy, 1994). Marine Protected Areas (MPA) have been used for protection of cetacean species (Hoyt, 2005), but its effectiveness is questioned since the large ranges and life-history traits of many species poses particular difficulties. Despite these challenges MPAs can be effective for many species as they are not equally vulnerable over their entire range. Critical areas, such as breeding or foraging areas or migration routes can be included when designing a MPA (Game *et al.*, 2009). Additionally, encompassing areas where cetacean occurrence overlap with threatening human activities may minimize impacts.

In open and dynamic pelagic environments, MPAs are more difficult to use because of the nature of the high seas that inhibit MPA design and enforcement (Hyrenback *et al.*, 2000). Nonetheless, in oceanic islands as the Hawaii and the Azores, MPAs have been designated for cetacean protection (Reeves, 2000; Silva *et al.*, 2011). Many studies have shown that habitat preference of dolphin populations can be closely linked to several physiographic (e.g. depth, slope, seabed), oceanographic (e.g. sea surface temperature) and biological variables (e.g. chlorophyll *a* surface concentration) (e.g. Davis *et al.*, 2002; Yen *et al.*, 2004, Cañadas *et al.*, 2005). Bottlenose dolphin is one of the most widespread cetacean species, occurring in both pelagic and coastal habitats (Connor *et al.*, 2000). In open waters, it is commonly encountered over the continental shelf and along the shelf break, over seamounts and around islands (Cañadas *et al.*, 2002; Davis *et al.*, 2002).

To design a MPA and management strategies it is necessary to assess what environmental attributes attract a species and that make a key area to their range. Habitat preference modelling has been used as a tool to identify key areas for cetacean species (e.g.

Gregr & Trites, 2001; Johnston *et al.*, 2007; Gill *et al.*, 2011) and predict potential habitats for unsurveyed areas (e.g. Reilly, 1990; Moses & Finn, 1997). A wide range of approaches have been used to study species distribution, but presence-only modelling methods, such as Maximum entropy method (Maxent), have been increasingly used. This is mainly due to excellent performance compared with other modelling methods (Hernández *et al.*, 2006), since these models require few data points (Wisz *et al.*, 2008) and they can handle the problems of missing absence data and spatial sampling bias (Philips *et al.*, 2009).

In São Tomé and Príncipe systematic research about small cetaceans and determining its key areas has never been undertaken and sighting surveys occurred only in São Tomé Island. This study aimed to predict key areas for bottlenose dolphin around São Tomé Island in relation to physiographical and oceanographical variables and to conduct a preliminary assessment around Príncipe Island of the same type of areas using Maxent models, as a first approach to recommend suitable areas for future MPAS.

METHODS

Study area

The Democratic Republic of São Tomé and Príncipe is located in the equatorial region of the Gulf of Guinea (between 1º44 N and 0º01 S) and is composed by two main islands and several small islets (see Fig. 1, Chapter II). The volcanic origin gives it a high relief and great sea bottom depths near the shore, especially in the west side of the island were bathymetries of around 200 meters can be found almost near the shore (Picanço *et al.*, 2009). The coast line is profiled by shallow bays and rocky recesses, with several rivers, cascades and other water streams some of which give rise to mangroves. Oceanographic conditions in the Gulf of Guinea are influenced mainly by the Guinea Current and Benguela Current (Hardman-Mountford & McGlade, 2003). The warm-water Guinea Current, the main one, is an eastward and shallow flow fed by the North Equatorial Counter Current that flows southwards along the African coastline. The north-flowing cold Benguela Current is formed in the eastern part of the South Atlantic and is driven by the prevailing South Easterly Trade winds. The cold waters coming from Antarctica are rich in nutrients and its upwelling fuel high rates of phytoplankton growth in coastal waters. Sea surface temperature (SST) in the Gulf of Guinea has fairly stable values, between 27°C and 29°C outside of the upwelling seasons (Allersma & Tilmans, 1993), but it can drop to below 22°C at the coast during the major upwelling (Longhurst, 1962).

Data collection and Environmental data

Research surveys were conducted in São Tomé between 2002 and 2006 and in 2012. The survey route was non-systematic and was selected depending on the weather and sea state constraints on each day. Once a cetacean was sighted, time, location, group size and composition and behaviour were recorded as well as photographic data.

Based on literature review six environmental variables potential explanatory of the distribution of bottlenose dolphin were used: water depth (stp_depth), seabed slope (stp_slope), seabed aspect (stp_seabed), distance to coast (sst_discoast), distance to river mouths (stp_disrivers) and sea surface temperature (SST, stp_sst). Water depth (meters) was extracted from a worldwide relief model with a 1 arc-minute resolution from NOAA (National Oceanic and Atmospheric Administration http://www.ngdc.noaa.gov/mgg/global/global.html), that integrates land topography and ocean bathymetry from numerous global and regional data sets (Amante & Eakins, 2009). Slope and seabed aspect were derived from the bathymetric model using the Spatial Analyst Tool from ESRI® ArcMap 9.2 (ESRI, 2006). Slope was calculated as the gradient of maximum change in depth for each grid cell, ranging from 0º to 90º. Seabed aspect consisted in the geographical orientation of the bottom slopes, measured in degrees, and values for this variable were classified in 10 categories: 1=Flat (-1), 2=North (0-22.5), 3=Northeast (22.5-67.5), 4=East (67.5-112.5), 5=Southeast (112.5-157.5), 6=South (157.5-202.5), 7=Southwest (202.5-247.5), 8=West (247.5-292.5), 9=Northwest (292.5-337.5), 10=North (337,5-360). Distance to coast and to river mouths were also derived using the Spatial Analyst Tool, as the Euclidian distance, in degrees, between the midpoint of each grid cell and the closest point to the source (land and river mouths). Only rivers with a Strahler stream order equal or above 4 were considered. SST (ºC) was extracted from a global dataset of monthly average values with a resolution of 5 arc-minute, distributed by Bio-ORACLE (Ocean Rasters for Analysis of Climate and Environment http://www.oracle.ugent.be/index.html), a set of Geographic Information System raster that provides marine environmental information for global-scale applications (Tyberghein *et al.*, 2012). All environmental grids were re-sampled to a cell size of 1 nautical mile (1852 m).

Statistical Tests

All environmental variables were tested for multicollinearity by examining cross-correlations (Pearson correlation coefficient, r) using STATISTICA 7.0 (StatSoft, 2004).

Maximum entropy modelling

The maximum entropy algorithm available in MAXENT 3.3.3 (Phillips *et al.*, 2008) was used to model bottlenose dolphin distribution for São Tomé and Príncipe. Maxent is a machine-learning method that estimates a species' distribution by estimating the probability distribution of occurrence that is closest to maximum entropy (closest to uniform) subject to a set of constraints that represent incomplete information about the target distribution (Phillips *et al.*, 2006). The model uses an algorithm to extract a relationship between presence-only species occurrence (sample points) and environmental variables (features), as the pixels of the study area make up the space on which the Maxent probability distribution is defined (Philips *et al.*, 2006). Using a logistic output, it then evaluates the suitability of each grid square, assigning a value ranging from 0 (unsuitable habitat) to 1 (optimal habitat) (Phillips & Düdik, 2008). Occurrence data usually exhibits strong spatial bias because survey effort is essentially connected to accessibility (Phillips *et al.*, 2009). Therefore sample spatial bias affects habitat modelling and is a matter that should be considered prior to building the distribution model. Maxent can be set to use background data (or "pseudo-absence" data) to only evaluate the model output (e.g. ROC, AUC). To ensure the pseudo-absence data reflected the same bias as the presence data, 100 random points were generated in a convex hull limited by sighting points (see Phillips *et al.*, 2008). Models were run in replicate using the cross-validation method with default settings except the number of replicates, which was set to 10. This method splits occurrence data randomly into a specified number (in this case, 10) of equal-sized groups ("folds"), and runs the model leaving out each fold in turn. The withheld fold is used for evaluation of the model (Phillips *et al.*, 2006). Each final model results from the average of the 10 replicates.

Model Evaluation and Analysis

Models were evaluated using the Area Under the Receiver Operating Characteristic Curve (AUC) (Pearson, 2007) which is defined by plotting “sensitivity” (the proportion of observed occurrences that are correctly predicted by the model) against “1-specificity” (the proportion of observed absences that are correctly absences (or pseudo-absences) that are correctly predicted by the model) has been a widely used tool for model evaluation (e.g. Thuiller *et al.*, 2004; Elith *et al.*, 2006; Phillips *et al.*, 2006). The AUC ranges from 0 (under 0.5 for models have no predictive ability) to 1 (models with perfect predictive ability) (Phillips *et al.*, 2009). When pseudo-absences are used, the AUC tests if the model can classify presence better than a random prediction (Pearson, 2007).

RESULTS

Between 2002-2006 and 2012, 226 surveys were conducted from which 51 bottlenose dolphins sightings around São Tomé Island were recorded. Correlations between environmental variables were considered not significant (r < 0.7, see Appendix VII).

Performance model

Maxent model for bottlenose dolphin performed very well with mean AUC value of 0.992 (SD = 0.005) (Fig. 1).

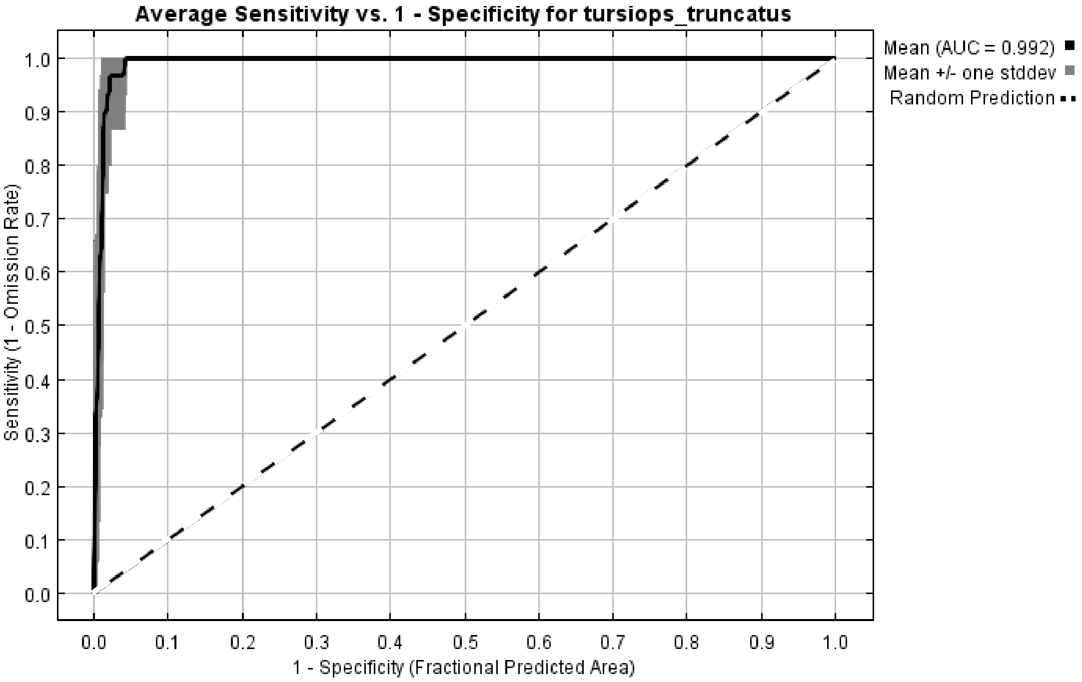


Figure 1. Maxent receiver operating characteristic (ROC) curve for bottlenose dolphin.

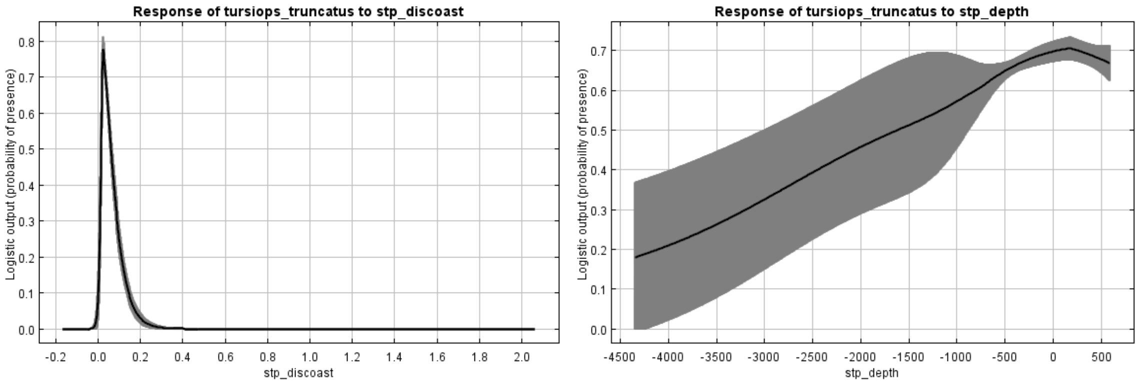
Environmental variable contributions

The environmental variables of greatest importance were distance to coast and to rivers and depth (Table 1). Jackknife test of variable importance also demonstrated an important contribution of seabed aspect, which no other variable contained.

Table 1 - Estimates of relative contributions of the environmental variables to the Maxent models of bottlenose dolphin around São Tomé and Príncipe.

Variable	**Percent contribution**	**Permutation importance**
stp_depth	**13.5**	**4.8**
sst_discoast	**71.5**	**57.5**
stp_disrivers	**6.6**	**34.3**
stp_seabed	4.9	2.3
stp_slope	3.1	0.6
stp_sst	0.4	0.4

Fig. 2 represents the most important response curves which show the probability of species occurrence, given x values of predictor variable. Suitable habitat for bottlenose dolphin was predicted to occur at low values of depth, close to 0 meters. However, it should be noted that ETOPO2 dataset has accuracy issues for shallow areas that may be reflected in observed depth values. Suitable distance to coast and to river mouths values were no greater than ~0.02 degrees (1.89 km) and most suitable seabed aspect values were classified as northeast and east (50-100).



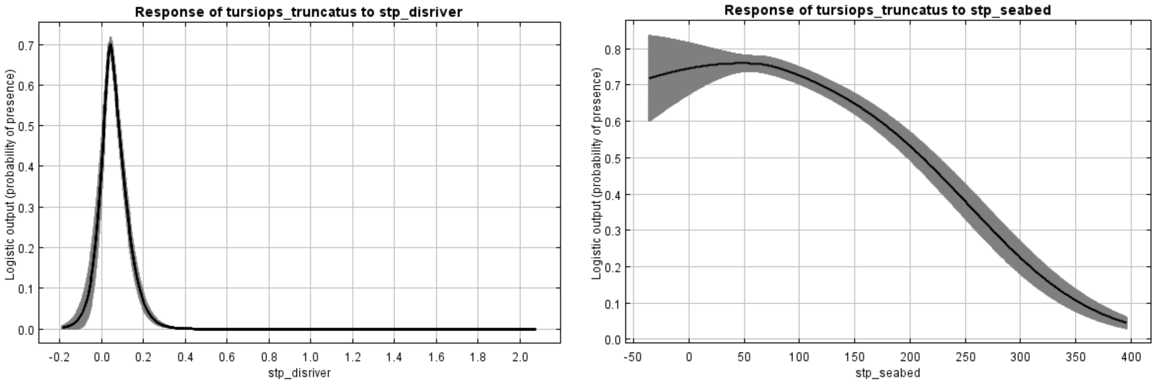


Figure 2. Response curves of Maxent prediction relating to environmental variables for bottlenose dolphin.

Distribution map of the model

Most suitable habitat predicted by Maxent for bottlenose dolphin in São Tomé and Príncipe is represented in Fig. 4. The map showed that the eastern coast of São Tomé and Rolas Island presented the most suitable conditions for the occurrence of bottlenose dolphin. Príncipe Island appeared to have fewer suitable areas, but there were also appropriate spots.

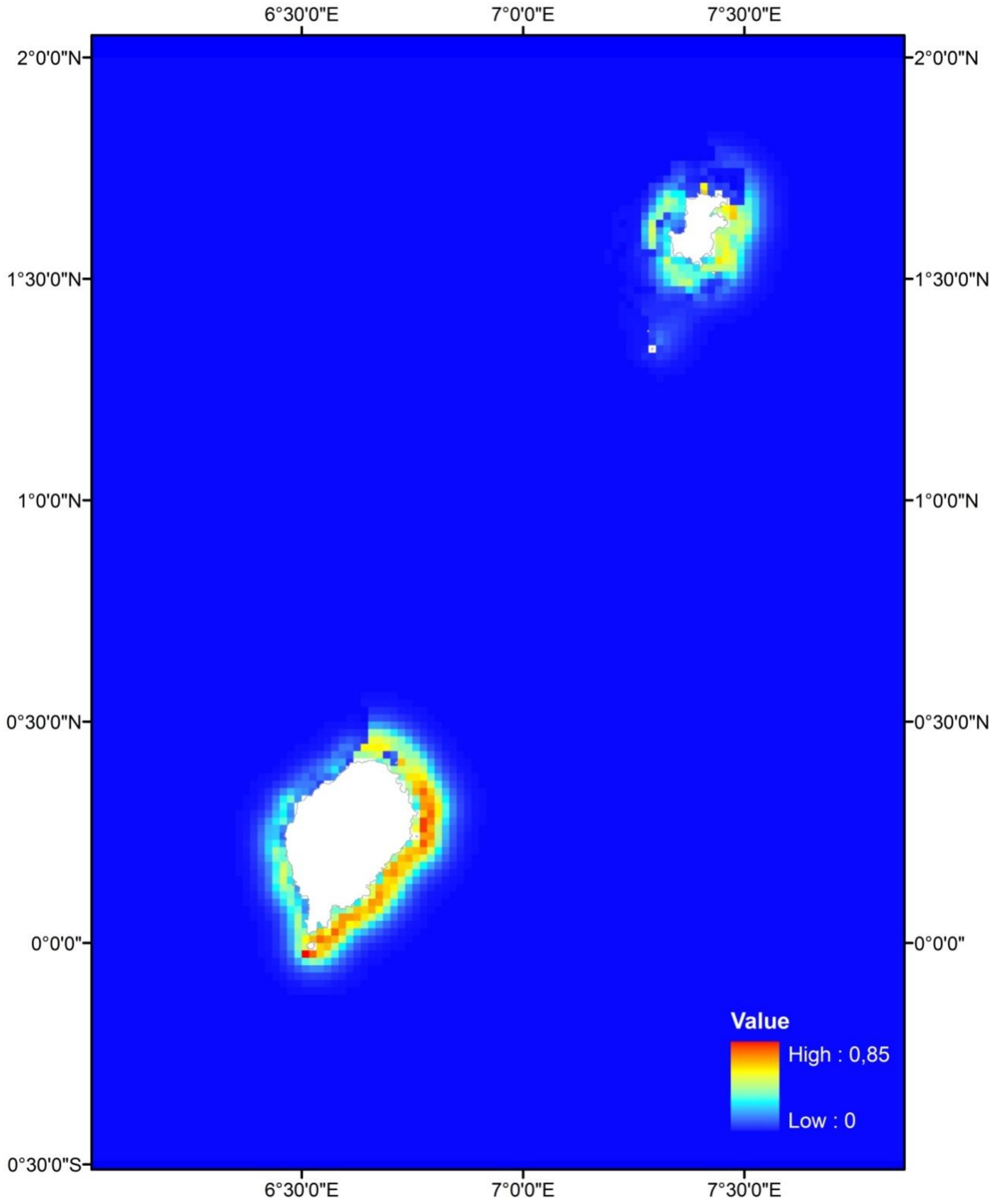


Figure 4. Maxent average model for bottlenose dolphin in São Tomé and Príncipe. Most suitable habitats are indicated by warm colours (red) and lighter shades of blue have low predicted probability of suitable conditions.

DISCUSSION

Habitat modelling techniques constitute a useful tool to understand and describe the processes that determine the distribution of organisms (Redfern *et al.*, 2006). This study represents the first attempt to identify key areas through distribution modelling of bottlenose dolphin around São Tomé and Príncipe based on essentially habitat physiography. Maxent models showed that probability of occurrence of bottlenose dolphin was most influenced by distance to coast, distance to rivers, depth and seabed. However, depth values used for sightings closer to the coast may not be completely accurate. The bathymetric dataset used in this study, ETOPO2, has accuracy issues in shallow areas and is insufficient to resolve small-scale changes (Sindhu *et al.*, 2007). Habitat use is mainly influenced by food resources (Balance, 1992), so it is likely that species distribution may reflect foraging strategies adjusted to physiographic characteristics, as certain areas may provide high concentrations of prey (Wilson *et al.*, 1997; Hastie *et al.*, 2004). The eastern coast of São Tomé and Rolas Island presented the most suitable habitat for bottlenose dolphin which preferred waters close to shore and river mouths and a northeast-eastern seabed orientation. The strong affinity to short distances to the coast was also found for another open ocean environment as in the Azores (Seabra *et al.*, 2005) and for bottlenose dolphin in general (Shane *et al.*, 1986). Bottlenose dolphin preferred a northeast-eastern orientation that may be related to protection from distant wind waves. In São Tomé Island the swell comes from northwest and looses strength when arriving to the coast. River mouths are typically rich nutrient zones and fish nursery areas and in São Tomé many of them are classified as Mangroves. Rivers may constitute a feeding area for schooling fishes. Bottlenose dolphin was sighted in atlantic flyingfish range (*Cheilopogon melanurus*), one of the main targets of artisanal fisheries in São Tomé with a high percentage of capture (Graciano, 2008). Occasional observations of predation of bottlenose dolphin on this species were also registered (I. Carvalho pers. comm., 13 August 2012). Most sightings of bottlenose dolphin consisted in feeding activities or travelling which at times may be related to foraging (see Chapter 1). Therefore, it seems that the identified areas are important to feeding.

Occurrence for Príncipe Island was predicted by information gathered in São Tomé and had less optimum results. This could be explained by the differences between the two islands: the existence of fewer rivers, an extended continental shelf which causes lower depth values and a more complex bottom which may influence species occurrence. Further research in Principe is needed for a better understanding of how occurrence of these of bottlenose dolphin varies with the environmental variables considered. São Tomé and Príncipe is a country highly dependent of artisanal fishery activities (Graciano, 2008). Água-Grande and Caué districts (see Appendix VIII), comprise one of the most intense fishing areas (Graciano, 2008) where bottlenose dolphin occurs. Rolas Island, other important area for bottlenose dolphin, is known for its tourism which may be associated to boat traffic. Most sightings occurred close to human activity and in intense fishing areas where negative interactions may occur as a result of by-catch, direct hunting and competition. These areas seem to be important for feeding activities of bottlenose dolphin the large group sizes observed in São Tomé only increases the probability of these impacts. Although Príncipe Island was not surveyed, the same risk factors mentioned above are present and may pose a threat. In addition, oil exploration is going to take place in the waters around Príncipe and may also influence the distribution of bottlenose dolphin. The west coast of São Tomé is also an intense fishing area where survey effort was reduced and further research is needed for a better understanding of habitat preferences and human impacts on bottlenose dolphin. This study provided a valuable insight in determining environmental attributes that attract bottlenose dolphin in São Tomé and Príncipe. In addition, with habitat preference modelling it was possible to identify potential key areas of habitat that overlap with human activities, that in the future may be incorporated in management plans in this archipelago.

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CHAPTER IV: GENERAL DISCUSSION

BOTTLENOSE DOLPHIN IN SÃO TOMÉ AND PRÍNCIPE

In São Tomé and Príncipe impacts of human activity such as by-catch, direct hunting and habitat degradation may pose a threat to cetaceans. Whale watching and oil exploration are factors that are beginning to emerge in the region and are also relevant for cetaceans (Brito *et al.*, 2010). This work is a contribution in the acquisition of a baseline about bottlenose dolphin which in the future might help in the assessment of long-term tendencies and in the construction of management and monitoring plans (Wells, 1991). This thesis aimed to analyse bottlenose dolphin ecology by determining occurrence, relative abundance, behavioural patterns, social structure and site fidelity. Bottlenose dolphins occurring around São Tomé Island consisted of a mixture of residents, non-residents, and temporary migrants. In general, individuals were most seen travelling and feeding. In addition, resident individuals were also observed in social activities. Mean groups that were observed were large and seemed to be influenced by habitat characteristics and group composition which in turn probably influenced the low association values between individuals. Less productive and dynamic habitats, such as oceanic islands, highly influence behaviour, movements and site fidelity to the area. Bottlenose dolphins may need to travel more between favourable zones, demonstrating transitory fidelity (Defran & Weller, 1999).

Sampling effort was highly seasonal, occurring mostly between June and October, which may not have allowed a total understanding of all ranging and behavioural patterns, especially at a fine scale. Also, bottlenose dolphins are highly mobile and range over extensive distances (Defran *et al.*, 1999). Príncipe Island appears to be a favourable area for bottlenose dolphins since it has a large continental shelf and low depths. Thus, since Príncipe was not surveyed, patterns that were observed in this sampling period may not be well representative for the identified individuals. Occurrence of bottlenose dolphin was most influenced by distance to coast, distance to river mouths, depth and seabed aspect. However, the strong influence of river mouths was unexpected. Several river mouths are classified as mangroves and they may be a high density area of food resources. Other potential explanatory variables, such as chlorophyll and upwelling might help to assess the importance of river mouths in future habitat modelling. Therefore, it seems that the study of bottlenose dolphin ecology in this environment is far from over, and presents interesting topics for future research. Moreover, the obtained results raises initial conservation issues to this species and other small cetaceans in São Tomé and Príncipe that need to be addressed.

CONSERVATION IMPLICATIONS

São Tomé and Príncipe seems to be an important area for bottlenose dolphins, where resident animals use the waters of São Tomé on a regular basis for the main activities and transient individuals use it as a feeding area. Habitat use and key areas are concentrated in shallow waters close to the coast and to river mouths, where most anthropogenic threats exist. Overfishing and the use of inadequate fishing gears, such as grenades, can cause direct mortality and by-catch of cetaceans (Brito *et al.*, 2010). Preliminary interviews in fishery communities showed that at least 52% of the interviewed caught dolphins, 40% of them used dolphins as a food resource and 60% said that dolphins interfere with their fishing activities (unpublished data, 2012). There has been a drastic decrease in fisheries catches in São Tomé, especially in the more coastal zones where artisanal canoes and gears constitute the main food resource for a large part of the local population (B. Loloum pers. commun.). As the fishery activities need to be more intense to compensate for this loss, the conflicts between humans and cetaceans may also increase. The implementation of MPAs encompassing important areas for humans and cetaceans would be a valuable investment for the future. MPAs can contribute for the increase of fish in abundance and size by allowing bigger fish to move around areas and to have a larger contribution in eggs and ultimately larvae to adjacent fishing areas (Hilborn *et* *al.*, 2004). However, results are not guaranteed and depend on careful planning and evaluation that needs to account for specific species characteristics, the impacted area and human communities. But, in this way a MPA would be a beneficial tool for fisheries management and conservation of biodiversity, attenuating human impacts on cetacean occurrence and enriching important areas not just for animals but for humans also.

Whale-watching and related tourism activities (scuba diving and snorkelling) are developing in São Tomé and may pose a risk to cetaceans. These activities are conducted with no type of guidelines and regulation and without any information by several tourist operators. Despite the seasonality of this study, it seems that throughout the year various species occur in São Tomé, some on a regular basis (e.g. bottlenose dolphins and pantropical spotted dolphin) and others with seasonal movements (e.g. humpback whale, killer whale). Specific legislation regarding conduct of these activities around cetaceans is required, taking into account cetacean behaviour in order to avoid disturbance of the animals involved. Also groups with calves need to have special attention as young and inexperienced calves are likely to be particularly susceptible to various disturbance factors (Karczmarski, 2000). Whale-watching has been expanding and it is an important part of the tourism industry worldwide. If sustainably managed and with proper legislation, whale watching in São Tomé and Príncipe would hold a great potential for the development of the country as a diverse touristic area and could stimulate further interest in coastal conservation.

This study gave a contribution towards understanding spatial and temporal distribution of one of the most common species in the area, the bottlenose dolphin. As a ‘charismatic megafauna’ it could be used as a ‘flagship species’ for the coastal marine environment and conservation of its biodiversity in São Tomé and Príncipe. The assessment of key areas for bottlenose dolphins and the study of behaviour and abundance will contribute towards to the implementation of adequate conservation efforts for São Tomé and Príncipe from which all marine biodiversity would benefit.

FUTURE RESEARCH

Further photo-identification effort is required to assess the overall status of the bottlenose dolphin population and to determine residency status of the majority of recognized individuals. Additionally, a more detailed study of habitat use and ranging patterns in the archipelago and a photo-identification effort in Príncipe Island could provide further insight into the full extent of the movements and home range for this population. A multi-scale and long-term approach is also needed to further assess temporal and spatial patterns of key areas and behaviour, including a more extended sampling period within the years and other areas adjacent to the archipelago of São Tomé and Príncipe. Also other environmental variables that are known to influence distribution of cetaceans need to be incorporated in modelling design to improve prediction models. Future studies on molecular and sex specific data may provide additional insight into the population structure and the relatedness of these animals to other adjacent groups. Finally, future studies focused on assessing the relation between cetaceans and human activities, such as the effect of depredation on fishery activities, whale-watching feasibility, boat disturbance and carrying capacity for whale-watching activities would benefit the co-existence of both cetacean and human in this area.

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APPENDICES

Appendix I. Definitions of age classes and behavioural patterns used during this study.

Age classes (based on Bearzi *et al.*, 1997)	
Adult	Large marked or un-marked individuals that are 3 meters in length.
Juvenile	Two-thirds the size of an adult usually swimming in association with an adult, but sometimes independently; coloration generally slightly lighter than the adult.
Calf	One-half the size of an adult dolphin, light gray coloration, with lighter vertical striping left by fetal creases. Often observed in close association with an adult, swimming along side.
Behavioural patterns (based on Shane *et al.*, 1990 and Bearzi *et al.*, 1999).	
Travelling	Moving steadily in constant direction.
Feeding	Conspicuous feeding behaviours, such as repeated dives in varying directions in one location, fish kicking and fish tossing. Concentration of marine birds over the dolphins.
Socializing	Some or all group members in almost constant physical contact with another, oriented toward one another, and often displaying surface behaviours; no forward movement.
Resting	Moving very slowly or drifting in constant direction.
Socializing/feeding	Two activities performed by different group members.
Socializing/travelling	Moving steadily in one direction while socializing intermittently.

Apendix II. Theoretical models fitted to the standardised lagged association rates of bottlenose dolphins of São Tomé in SOCPROG.

Name	Equation	Description
Constant Companions (CC)	$g' = a$	All associations persist during the study
Casual acquaintances (CA)	$g' = a \, . \, e^{-bt}$	Animals associate for a period of time, then disassociate and may re-associate later
CC + CA	$g' = a + c \, . \, e^{-bt}$	Animals associate for a period of time, then disassociate and stabilize associations to a lower level
Two levels of CA	$g' = a \, . \, e^{-bt} + c \, . \, e^{-dt}$	Animals have two levels of association and disassociation which decay because of shifts in preferred companionship, mortality, emigration, or a combination of these.

Appendix III. Theoretical models fitted to the population estimates of bottlenose dolphins of São Tomé in SOCPROG.

Model	Type	Description
Schnabel	Closed	Population has no mortality, birth, immigration or emigration
Mortality	Open	Population has a constant size with mortality balanced by birth (mortality includes permanent emigration or mark change that prevents recapture and birth includes permanent immigration or mark change that causes a previously identified animal to be identified as a new animal)
Mortality + Trend	Open	Population grows or declines at a constant rate

Appendix IV. SOCPROG fit of theoretical social models to the standardized lagged association rate for bottlenose dolphins in São Tomé in 2002-2005 and 2012.

Model	Best fit	QAIC	ΔQAIC
Constant companions (CC)	$g(t) = 0.024902$	1294.7458	6.399
Casual acquaintances (AC)	$g(t) = 0.0303e^{(-0.00043265*td)}$	1288.3466	0
CC + AC	$g(t) = 0.021506+0.021118e^{(-0.25947*td)}$	1293.3660	5.019
Two levels of CA	$g(t) = 0.016911e^{(-1.0945*td)}+0.029684e^{(-0.00041303*td)}$	1292.2873	3.941

Appendix V. Re-sighted bottlenose dolphins in São Tomé during 2002-2005 and 2012.

	2002											2003									2004			2005					2012		
	08-08-2002	22-08-2002	12-09-2002	14-09-2002	27-09-2002	28-09-2002	05-10-2002	06-10-2002	08-10-2002	17-10-2002	18-11-2002	11-01-2003	17-01-2003	19-01-2003	21-01-2003	24-01-2003	08-09-2003	15-09-2003	17-09-2003	16-10-2003	20-10-2004	25-10-2004	05-11-2004	03-09-2005	04-09-2005	03-10-2005	05-10-2005	06-10-2005	07-02-2012	08-02-2012	14-02-2012
STPTT002																										■					■
STPTT006																										■				■	
STPTT012			■											■																	
STPTT014									■																				■		
STPTT021																													■		■
STPTT043	■		■				■							■															■		
STPTT047			■																											■	
STPTT059																									■	■	■	■			
STPTT060					■		■			■															■			■			
STPTT063	■													■			■								■	■				■	
STPTT064															■										■	■					
STPTT068																									■	■					
STPTT069																	■								■						
STPTT071		■						■				■		■												■		■			
STPTT072																						■				■		■			
STPTT073												■										■	■			■		■			
STPTT076															■											■		■			
STPTT077																						■				■	■				
STPTT079																						■				■					

(continues)

Appendix V (continuation). Re-sighted bottlenose dolphins in São Tomé during 2002-2005 and 2012.

	2002											2003									2004			2005					2012		
	08-08-2002	22-08-2002	12-09-2002	14-09-2002	27-09-2002	28-09-2002	05-10-2002	06-10-2002	08-10-2002	17-10-2002	18-11-2002	11-01-2003	17-01-2003	19-01-2003	21-01-2003	24-01-2003	08-09-2003	15-09-2003	17-09-2003	16-10-2003	20-10-2004	25-10-2004	05-11-2004	03-09-2005	04-09-2005	03-10-2005	05-10-2005	06-10-2005	07-02-2012	08-02-2012	14-02-2012
STPTT081								■		■																■					
STPTT084	■																■			■						■	■				
STPTT086				■			■		■						■							■				■					
STPTT087																		■								■					
STPTT090	■																									■		■			
STPTT091															■											■		■			
STPTT092																										■		■			
STPTT093																						■				■					
STPTT098																										■	■				
STPTT101																										■		■			
STPTT102			■											■							■					■	■			■	
STPTT103												■														■					
STPTT104																						■				■	■	■			
STPTT105								■				■													■	■					
STPTT106												■														■					
STPTT111										■																			■		
STPTT119																													■	■	
STPTT121			■										■																		
STPTT129															■													■			

(continues)

Appendix V (continuation). Re-sighted bottlenose dolphins in São Tomé during 2002-2005 and 2012.

	2002											2003									2004			2005					2012		
	08-08-2002	22-08-2002	12-09-2002	14-09-2002	27-09-2002	28-09-2002	05-10-2002	06-10-2002	08-10-2002	17-10-2002	18-11-2002	11-01-2003	17-01-2003	19-01-2003	21-01-2003	24-01-2003	08-09-2003	15-09-2003	17-09-2003	16-10-2003	20-10-2004	25-10-2004	05-11-2004	03-09-2005	04-09-2005	03-10-2005	05-10-2005	06-10-2005	07-02-2012	08-02-2012	14-02-2012
STPTT131						■							■																		
STPTT133																	■				■	■									
STPTT136													■									■									
STPTT139												■	■																		
STPTT140								■				■																			
STPTT141	■				■									■			■														
STPTT142														■		■															
STPTT148												■					■														
STPTT153											■				■																
STPTT168						■				■																					

Appendix VI. SOCPROG fit of theoretical population model results of lagged identification rates for bottlenose dolphins in São Tomé in 2002-2005 and 2012.

Model	Best fit	Explanation	Parameters	QAIC	ΔQAIC
A	R = 0.01936	Closed population (1/a1=N)	-	1737.2498	10.9898
B	R = 1/51.6818	Closed population (a1=N)	N = 51.65	1737.2497	10.9897
C	$R = 0.024481e^{(-0.00027883t)}$	Emigration/mortality (*a1*=emigration rate, ER; 1/*a2*=*N*)	ER = 0.00027883 N = 40.85	1728.9980	2.738
D	$R = (1/40.8012)e^{(-t/3576.8837)}$	Emigration/mortality (*a1*=*N*; *a2*=Mean residence time, MRT)	N = 40.8012 MRT = 3576.8837	1728.9979	2.7379
E	$R = 0.01902+0.049213e^{(-1.2405t)}$	Closed: emigration + remigration (*a1*=emigration rate, ER; *a2*/(*a2*+*a3*)=proportion of population in study area at any time, PP)	ER = 1.241 PP = 0.279	1740.2777	14.0177
F	$R = (1/34.481)*((1/1337.8011)+(1/1046.4506)e^{(-(1/1337.8011+1/1046.4506)*t))/(1/1337.8011+1/1046.4506)}$	Emigration + remigration (*a1*=*N*; *a2*=Mean time in study area, MTI; *a3*=Mean time out of study area, MTO)	N = 34.481 MTI = 1046.4506 MTO = 1337.8011	**1726.2600**	0
G	$R = -3.0131e^{(-3.0605t)}+0.025053e^{(-0.00029289*t)}$	Emigration + remigration + mortality		1816.3831	90.1231

(continues)

Appendix VI (continuation). SOCPROG fit of theoretical population model results of lagged identification rates for bottlenose dolphins in São Tomé in 2002-2005 and 2012.

Model	Best fit	Explanation	Parameters	QAIC	ΔQAIC
H	$R = (e^{(-0.0005294*td)/35.2891).*((1/9156.1569)+(1/810.2305)*}e^{(-(1/9156.1569+1/810.2305)*td))/(1/9156.1569+1/810.2305)}$	Emigration + remigration + mortality (*a1*=*N*; *a2*=Mean time in study area, MTO; *a3*=Mean time out of study area, MTO; *a4*=Mortality rate, MR)	N = 35.2891 MTI = 810.2305 MTO = 9156.1569 MR = -0.0005294	1727.2784	1.0184

Appendix VII. Correlation matrix for all environmental variables for bottlenose dolphin. Bold correlations are significant at $p < 0.05$; r, first row, p, second row; N=51.

	Depth	Distance to coast	Distance to river mouths	SST	Seabed aspect	Slope
Depth	1.0000	**-0.4913**	**-0.5004**	--	-0.0613	-0.2741
	p= ---	**p=0.000**	**p=0.000**	p= ---	p=0.669	p=0.052
Distance to coast	**-0.4913**	1.0000	0.0121	--	**-0.5815**	**-0.3000**
	p=0.000	p= ---	p=0.933	p= ---	**p=0.000**	**p=0.032**
Distance to river mouths	**-0.5004**	0.0121	1.0000	--	**0.3580**	**0.6997**
	p=0.000	p=0.933	p= ---	p= ---	**p=0.010**	**p=0.000**
SST	--	--	--	1.0000	--	--
	p= ---	p= ---	p= ---	p= ---	p= ---	p= ---
Seabed	-0.0613	**-0.5815**	**0.3580**	--	1.0000	**0.3701**
	p=0.669	**p=0.000**	**p=0.010**	p= ---	p= ---	**p=0.008**
Slope	-0.2741	**-0.3000**	**0.6997**	--	**0.3701**	1.0000
	p=0.052	**p=0.032**	**p=0.000**	p= ---	**p=0.008**	p= ---

Appendix VIII. Districts of São Tomé Island.