



TESIS DOCTORAL

**ECOLOGÍA DEL DELFÍN MULAR DEL
INDO-PACÍFICO EN EL ÁREA MARINA
PROTEGIDA DE KISITE-MPUNGUTI,
KENIA**

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Cádiz, Noviembre 2015

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ECOLOGÍA DEL DELFÍN MULAR DEL INDO-PACÍFICO EN EL ÁREA MARINA PROTEGIDA DE KISITE-MPUNGUTI, KENIA

Memoria presentada por D. Sergi Pérez Jorge para optar
al Grado de Doctor por la Universidad de Cádiz



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CERTIFICAN:

Que la presente memoria titulada, “Ecología del delfín mular del Indo-Pacífico en el área marina protegida de Kisite-Mpunguti, Kenia”, presentada por Sergi Pérez Jorge, ha sido realizada bajo su dirección y autorizan su presentación y defensa, para optar al Grado de Doctor por la Universidad de Cádiz.

Y para que así conste y surta los efectos oportunos, firman los presentes, a 20 de Noviembre de 2015.

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Al meu pare i la meva mare

The results from this PhD have been partially presented at various national and international workshops and conferences:

- 24th Annual Meeting of the European Cetacean Society, Germany (2010).
- 7th Western Indian Ocean Marine Science Association, Kenya (2011).
- Coastal and Marine Resources Management course at Kenyatta University, Kenya (2011, 2012 and 2013).
- Workshop with tour operators and guides, Kenya (2011 and 2012).
- 1st Kenyan Marine Mammal Workshop, Kenya (2013).
- 29th Annual Meeting of the European Cetacean Society, Malta (2015).
- Devotes-Euro Marine Summer School, Spain (2015).
- 9th Western Indian Ocean Marine Science Association, South Africa (2015).

The study “Combining occurrence and abundance models to evaluate the suitability of an existing MPA for dolphins in Kenya” was elected as the best short-talk presentation at the 29th Annual Meeting of the European Cetacean Society (the award was not received due to authors’ absence at the ceremony).

Non-peer reviewed articles from the PhD studies:

- Kenya Marine Mammal Network newsletters I to IV (May 2012, January 2013, June 2013 and December 2013). <http://kenyammnetwork.wix.com/kmmnetwork>
- SWARA Magazine-The East African Wildlife Society. (2013 and 2014).
- ECOFORUM Magazine (2013).
- QUERCUS (2013).

The PhD student did not receive any financial assistance in the form of salary to carry out this work, which was funded by the student’s own economic resources, obtained through marine mammal monitoring jobs on seismic vessels. Travel expenses for a month were covered by the Population Ecology Group under the project “Demography and population models: novel applications linking conservation, evolution and exploited species”. Dr. Daniel Oro’s funds were partially provided by a grant from the Spanish Ministry of Economy – <http://www.idi.mineco.gob.es/> (CGL2013-42203-R). Dra. Maite Louzao’s funds were covered by a Juan de la Cierva Postdoctoral contract (JCI-2010-07639, Spanish Ministry of Science and Innovation – <http://www.idi.mineco.gob.es/> and a Ramon y Cajal postdoctoral contract (RYC-2012-090897).

Data sheet

Title:	Ecología del delfín mular del Indo-Pacífico (<i>Tursiops aduncus</i>) en el área marina protegida de Kisite-Mpunguti (AMPKM), Kenia. Ecology of the Indo-Pacific bottlenose dolphin (<i>Tursiops aduncus</i>) around Kisite-Mpunguti Marine Protected Area (KMMPA), Kenya.
Subtitle:	PhD Thesis
Author:	Sergi Pérez-Jorge
Affiliations:	Global Vision International (GVI) Population Ecology Group, IMEDEA (UIB-CSIC)
URL:	http://www.gvi.co.uk/ http://imedea.uib-csic.es/bc/ecopob/index.php?lang=ca
Supervisors:	Dr. Daniel Oro de Rivas. IMEDEA (UIB-CSIC) Dr. Maite Louzao Arsuaga. AZTI
Cite as:	Pérez-Jorge, S. 2016. Ecology of the Indo-Pacific bottlenose dolphin (<i>Tursiops aduncus</i>) around Kisite-Mpunguti Marine Protected Area (KMMPA), Kenya. PhD Thesis. Biology Department, University of Cadiz, Spain. Pp. 141.
Key words:	tourist exposure, environmental conditions, robust design demography, coastal dolphins, western Indian Ocean
Layout:	Sergi Pérez Jorge
Front and cover page photos:	GVI
Design cover	Inês Gomes
Number of pages:	141
Internet version:	Available in electronic format (pdf) at the Kenya Marine Mammal Network website: www.kenyammnetwork.wix.com/kmmnetwork

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Penye nia pana njia

Swahili proverb

On hi ha voluntat hi ha camí

Proverbi suahili

Agraïments, acknowledgments

Aquesta tesis és el recorregut de moltes vivències amb molta gent i a molts llocs, que va començar amb un viatge a **Kenya, en 2008**, que va fer que tot hagi acabat en molts anys treballant per aquesta tesis. Anar a treballar amb GVI a Kenya em va fer conèixer un altre realitat, una altra manera de viure i de ser feliç, un conjunt de persones que va fer que hi hagues un abans i un després a la meua vida.

Among all these people that I met in my trip to Kenya, I am really gratefull to my **GVI family** Corti, Rachel, Ekens, Nigel, Drew, Matt, Matt (Patsy), Kez, Kirsty, Sara Mayer, Sara P, Tess, Adam, Eli, Shafii, Ali, Fadhili, Shebwana, Ibrahim, Faridi, Moha, Felicity, Jamie, Kate, Monia, Nic, Zeno, Lucy, Thalia, Chloe, Edita, Karen, Val, and many more people which made living in a remote island in the western indian ocean, a great adventure. Also to all the interns and volunteers that I had the privilege to work with. Nawashukuru sana staff wote wa GVI, maaskari, **wanakijiji wa Mkwirowa na Shimoni**, na wavulana nilio cheza mpira nao. My respect to all the hard work that GVI is conducting in conservation and local community development, and thanks for allowing me to use the data collected over so many years for this PhD.

Amb totes aquestes dades em vaig presentar un dia a Esporles per preguntar-li al **Dani Oro** si em volia dirigir una tesis doctoral, i va acceptar a la primera. Li agraeixo molt tota la seva ajuda i confiança depositada en mi, per fer-me creure que era possible i per haver-me ensenyat a veure la conservació i la ciència d'una altra manera. També a tot l'equip de treball que envolta el Dani, la Xell, el Giacomo, el Manolo, l'Albert i especialment a l'Alejandro qui em va acollir com si fos un germà i em va ensenyar tota l'illa, a més vaig tenir el plaer de que vingues a Kenya a gaudir d'aquell paradís. Aquesta tesis també hagues sigut impensable sense la direcció de la **Maite Louzao**, qui es va afegir més tard però sempre amb molt força i empena. La seva experiència, suport i sobretot energia van ser una guia perfecte per tirar endavant aquest projecte, a més d'ensenyar-me la seva terra acompanyada d'en Javi. A tots dos, Dani i Maite, us agraeixo molt tot l'esforç i dedicació en aquesta tesis, la qual era algo diferent a les que estaveu habituats. Tot i això encara ens queda una cosa pendent.... i és anar tots a Kenya i espero que sigui aviat! ;)

I would also like to thank **Kenya Wildlife Service** (John Wambua, Mohamed Omar, Richard Lemakat, Jillo Katello and Mark Kinyua among others), for their interest in this marine mammal project and for allowing to conduct this research within the Kisite-Mpunguti Marine Protected Area. During this PhD, I have also worked with a very passionate and dedicated group of people from **Watamu Marine Association**, who are doing a great work in marine conservation around Watamu. Thanks to Jane, Steve, Mike, Jimmy and Kahindi Charo.

Los últimos viajes a Kenia siempre eran especiales, cuando llegaba siempre me quedaba en tu casa **Jorge**, me enseñabas Nairobi o te venias a Wasini a hacer snorkel. Los próximos viajes no seran lo mismo sin ti.

Gracias **Ruty**, por todo el apoyo logístico durante estos años, esto de hacer la tesis tan lejos de la universidad la hace más complicada. Y también por entender lo que significa hacerla a distancia y con los recursos propios.

La aventura de los delfines comenzó mucho antes con la gente de Tarifa, Sandra, Juanma, Maria, Ali y David., además de la gente que conocí en seminarios y conferencias. También als amics de IUSC, Judit, Xusen, Marta, Victor, Xavi, Andrea.

Nos últimos anos tive o prazer de conhecer um grupo de pessoas que tornaram este doutoramento mais fácil, leve e divertido; Laura, Xan, Rui, Pedro, Marta, Ana Alegre, Ana Sousa, Eva, Gabi, Rosa, Angela. Também ao Bruno, pela amizade, pelas gargalhadas e pelas suas estadias em casa e em Faro.

Aquests no serian uns agraïments de veritat, sense tots els amics de Capellades, el **Marc Llopart**, el **Ton**, el **Xavi**, el **Bisbal**, l'**Edgar**, l'**Albert**, la **Mireia**, el **Manel**, la **Sandra**, l'**Alba**, el **Jordi**, la **Núria**, la **Maria**, etc.. que fan sempre tenir ganes de tornar al poble!

Um grande obrigado à **Zé** e ao **Rui**, por me terem sempre recebido tão bem, alimentado tão bem e cuidado tanto. E também à avó Mila, avó Laura, Elsa, aos Gomes luso-macaenses e Machado da Graça luso-moçambicanos.

Una dedicació especial va per la **meva família**, que sempre em van donar suport per seguir aquest camí, per fer aquests estudis i a qui vaig poder fer segurament una de les presentacions més important de la meva vida explicant de que anava la meva tesis. Sempre estareu presents. A la **meva germana** qui sempre ha estat ajudant en tot allò que he necessitat, al **Pol** per ser un gran suport i a la **Bruna** per ser un encant, i fer-nos gaudir cada dia. També als meus tiets i iaia Casilda. I per últim, a l'**Inês** qui a vist neixer i creixer aquesta tesis, des de que ens vam coneixer a Kenya fins ara, qui m'ha donat tot el suport, ànims, hores, esforç, carinyo i motivació en aquest llarg viatge. Aquest capítol s'acaba però haviat en començem un altre amb el nostre caçula.

A molta gent que segurament m'oblido i que a sigut important al llarg de tot aquests anys "**Moltes gràcies a tots, Thank you very much to everyone, Asante sana kwa kila mtu, Muchas gracias a todos, Obrigado a todos**".

Abstract

Along the East African coast, marine top predators are facing an increasing number of anthropogenic threats which requires the implementation of urgent and effective conservation measures. However, very modest scientific research has been conducted on cetaceans in this area and little information is available on the baseline ecology of these species. Given this scenario, rigorous scientific assessments of human exposed cetacean populations are needed to investigate their conservation status, identify factors causing major pressures and mitigate any potential negative impact. In Kisite-Mpunguti Marine Protected Area (KMMPA), located in southern Kenya, the Indo-Pacific bottlenose dolphin (*Tursiops aduncus*) is considered a flagship species and the main attraction for the 60,000 yearly park visitors, thus being economically important for local communities. This IUCN data deficient population was studied through an integrative assessment of the main key habitats, population estimates, and its interactions with natural and anthropogenic factors based on data collected over the period of 2006-2013. Within this framework, a comprehensive ecological modelling approach was followed to study the environmental factors influencing the occurrence and abundance of dolphins based on the development of species distribution models (SDMs). The results showed the influence of dynamic and static predictors on the dolphins' spatial ecology: dolphins selected shallow waters (5-30 m), close to the reefs (< 500 m) and oceanic fronts (< 10 km) and adjacent to the 100m isobath (< 5 km). A significantly higher occurrence and abundance of dolphins was also predicted within the MPA through the combination of ensemble prediction maps. Although the results from these predictions identified large percentages of recurrent and occasional habitats of the species within the existing MPA, the MPA did not adequately encompass all occasional and recurrent areas, which are essential to satisfy the spatial requirements for the species. Additionally, the use of Pollock's robust design models allowed to assess the influence of oceanographic variables, fisheries and human disturbance on demographic parameters of the target species. These models indicated that exposure to tourism increased the probability of dolphins seasonally emigrating, with a return rate influenced by environmental drivers. Even though the survival rate was estimated high and constant over the study period, the abundance estimate revealed a small dolphin population of less than 100 individuals. The small population size, together with high site fidelity and coastal distribution makes them particularly vulnerable to human disturbances. Using a Markov chain analyses, we also demonstrated that tourist boat interactions affected dolphins' behavioural budgets, with a significant decrease in the overall amount of time travelling and an increase in the diving patterns. Although the cumulative tourism exposure was not significant for the dolphin population at the current levels, these impacts should be taken into serious consideration given the potential tourism growth in the area. This is particularly important if tourism reaches periods of high intensity, which have been shown to have a negative significant impact for the species. Another factor that might influence the habitat use of dolphins is the risk of predation, which depends on the spatio-temporal distribution and abundance of sharks, influencing the behavioural response of dolphins versus sharks. The predation risk was estimated through the presence of shark-inflicted wounds and scars on four populations of Indo-Pacific bottlenose dolphins along the western Indian Ocean. The predation risk for the Kenyan dolphin population was almost inexistent, with 0.7% of the individuals identified presenting any wounds or scars. Combining the information on demographic

parameters, habitat use, spatial requirements and the influence of environmental and anthropogenic factors on this local dolphin population represents crucial baseline data to understand and predict consequences on the population. Moreover, this information can help in the long-term management and monitoring programmes of the KMMPA, ensuring that the habitats and species are conserved and managed sustainably, whilst generating much needed revenue.

Resumen

A lo largo de la costa este de África, los depredadores marinos se enfrentan a un creciente número de amenazas antropogénicas que requieren de la aplicación de medidas de conservación urgentes y eficaces. Sin embargo, la investigación científica llevada a cabo sobre los cetáceos en esta área es limitada y existe muy poca información disponible sobre la ecología de estas especies. Ante este escenario, las evaluaciones científicas rigurosas de las poblaciones de cetáceos expuestas a presiones humanas son necesarias para investigar su estado de conservación, identificar los factores que causan estas presiones y mitigar cualquier impacto potencialmente negativo. En el Área Marina Protegida de Kisite-Mpunguti (AMPKM), ubicado en el sur de Kenia, el delfín mular del Indo-Pacífico (*Tursiops aduncus*) es considerada una especie emblemática y es la principal atracción para los 60.000 visitantes anuales del área protegida, siendo por tanto de importancia económica para las comunidades locales. Se estudió esta población categorizada como “Datos Insuficientes” por la UICN (Unión Internacional de la Conservación de la Naturaleza), a través de una evaluación integral de sus principales hábitats, estimas de la población, y sus interacciones con factores naturales y antropogénicos, en base a los datos recogidos durante el período de 2006-2013. Dentro de este marco, se ha seguido un enfoque de modelización ecológica integral para estudiar los factores ambientales que influyen en la presencia y abundancia de los delfines, desarrollado a través de modelos de distribución de especies (MDE). Los resultados mostraron la influencia de factores predictivos dinámicos y estáticos en la ecología espacial de los delfines: los delfines seleccionaron zonas de poca profundidad (5.30 m), cerca de la arrecifes (<500 m) y frentes oceánicos (<10 km), así como de la isóbata de los 100 metros (<5 km). También se predijo significativamente una mayor presencia y abundancia de delfines dentro del AMP a través de la combinación de mapas de predicción conjunta. Aunque un gran porcentaje de hábitats recurrentes y ocasionales de la especie se encontraba dentro del AMP existente, el AMP no abarcaba adecuadamente todas las áreas ocasionales y recurrentes, que son esenciales para satisfacer las necesidades espaciales de la especie. Además, se utilizaron modelos de diseño robusto de Pollock para evaluar la influencia de las variables oceanográficas, pesqueras y de presión humana sobre los parámetros demográficos de la especie objetivo. Los resultados obtenidos a través de los modelos indican que la exposición al turismo aumentó la probabilidad que los delfines emigraran estacionalmente, con una tasa de retorno influenciada por factores medioambientales. A pesar de que la tasa de supervivencia estimada fue alta y constante durante el período de estudio, la estimación de abundancia reveló una población pequeña de delfines compuesta por menos de 100 individuos. Debido al reducido tamaño de esta población, junto con una alta residencia y su distribución costera, esta población es particularmente vulnerable a las perturbaciones humanas. El análisis de las cadenas de Markov, también demostró que la interacción

con barcos turísticos afectaba al comportamiento de los delfines, con una disminución significativa en la cantidad total de tiempo de viaje y un aumento en los patrones de buceo. Aunque la exposición acumulada del turismo no fue significativa para la población de delfines con los niveles actuales, estos impactos se deben tomar muy en cuenta dado el potencial de crecimiento del turismo en la zona. Esto es particularmente importante si el turismo alcanza períodos de alta intensidad, que han demostrado tener un impacto significativamente negativo para la especie. Otro factor que podría influir en el uso del hábitat de los delfines es el riesgo de depredación, que depende de la distribución espacio-temporal y la abundancia de tiburones, que influyen en la respuesta de comportamiento de los delfines frente a los tiburones. Se estimó el riesgo de depredación a través de la presencia de heridas y cicatrices de tiburones infligido a cuatro poblaciones de delfines mulares del Indo-Pacífico a lo largo del Océano Índico occidental. El riesgo de depredación de la población de delfines de Kenia era casi inexistente, con el 0,7% de los individuos identificados presentando heridas o cicatrices. La combinación de la información sobre los parámetros demográficos, el uso de hábitat, los requerimientos espaciales y la influencia de los factores ambientales y antropogénicos en esta población de delfines costeros, representa datos de referencia cruciales para entender y predecir las consecuencias sobre la población. Además, esta información puede ayudar en los programas de gestión y seguimiento a largo plazo del área marina protegida de Kisite-Mpunguti, garantizando que los hábitats y las especies sean protegidos y gestionados de manera sostenible, al mismo tiempo que generan ingresos muy necesarios para la comunidad local.

CHAPTER 1

1. General introduction

1.1 General conservation background

Due to the current global loss of biodiversity, the multidisciplinary science Conservation Biology tackles the establishment of sustainable relationships between human communities and their surrounding environment (Groom et al., 2005; Primack, 1995). To achieve these objectives, this multidisciplinary discipline uses the available scientific information and resources to delineate, investigate and implement management decisions in the shortest time frame. Frequently, conservation efforts are focused at the species and/or population-level, particularly on those which are threatened or represent important ecological processes (Myers et al., 2000). Many of these threatened species or populations face an actual risk of decline, or even disappearance, highlighting the importance of investigating the causes of their limited distribution, abundance or ongoing regression. Given this scenario, proficient scientific tools are needed to investigate the conservation status of species and/or populations, identifying which factors are causing major pressures and establish the most effective conservation actions (Krebs, 2001; Norris, 2004).

Human activities have already induced negative effects on the functioning of ecosystems and population dynamics of many marine organisms (Halpern et al., 2008; Worm et al., 2005). One clear example of these impacts is the current high conservation concern of worldwide fish stocks due to overfishing (Jackson et al., 2001; Pauly et al., 2005), which is responsible for the decline of 90% of large predatory fish and the reduction of 80% of the biomass of the fish community (Lewison et al., 2004; Myers and Worm, 2003). The effect of these human-related activities has particularly influenced organisms at higher trophic levels, such as marine mammals, due to the amplification of the disturbance at these levels (Pinsky et al., 2011). Currently, various marine mammal species are threatened as a consequence of the impact of numerous anthropogenic activities, which can be separated into two major categories: direct and indirect threats. Direct threats are those which cause the immediate death of the animals, such as whaling (Gales et al., 2005), ship collisions (Panigada et al., 2006) and fisheries bycatch (Mangel et al., 2010). Indirect threats are those that are likely to cause negative effects due to repeated impact exposure and cumulative factors, which can affect the behaviour and/or physiology of individuals. Some examples include aquaculture (Watson-Capps and Mann, 2005), climate change (Elizabeth Alter et al., 2010), coastal development (Jefferson et al., 2009), chemical pollution (Reijnders et al., 2009), oil and gas exploration (Thompson et al., 2013), noise pollution (Tyack, 2008), prey exploitation (Bearzi et al., 2006) and tourism (Christiansen et al., 2013).

These activities have caused major changes on demographic parameters, affecting not only population densities but also the survival of the species (Currey et al., 2009b; Gormley et al., 2012).

1.1.1 Integrative multidisciplinary approaches

The study of population dynamics is of paramount interest in ecology, as it allows the monitoring of conservation actions and assists in quantifying the success of the management plans (Fullerton et al., 2011; Johnson et al., 2010). Thus, population dynamics investigates the causes in density variation or population structure in space and time (Krebs, 2001). Capture-recapture models are one of the key methodologies to estimate demographic parameters, as it can be applied to a wide range of species (e.g. Lukacs and Burnham, 2005; Oro et al., 2004; Sharma et al., 2010). Through these models, we can identify evolution rates of target populations, studying the demographic processes of birth, death, immigration and emigration, and determining if the population is increasing, decreasing, fluctuating, if is stable or if it will become extinct at any given time. For long-lived species, adult mortality is the demographic parameter that has a major influence on the population growth rate. Therefore, the identification of factors that adversely affect adult survival is essential to establish priority conservation actions (Thompson et al., 2000; Winship and Trites, 2006). Area-based management has been shown to be an effective corrective measure for the protection of threatened marine mammals, improving the annual survival rate of the target population before and after the implementation of the spatial protection (Gormley et al., 2012).

Marine protected areas (MPAs) have been used as an effective management tool to protect marine ecosystems (Hoyt, 2012; Pauly et al., 2002). This spatial-oriented management procedure includes limitations to commercial activities, as well as no-take areas, implemented to diminish the risk of overexploitation, particularly, in marine ecosystems where scientific knowledge is lacking (Hoyt, 2012). MPAs have been adopted worldwide to protect spawning and nursery grounds, critical habitats, conserve biodiversity, and mitigate anthropogenic threats, among others (Castilla and Fernandez, 1998; Gell and Roberts, 2002; Halpern, 2003). The number of MPAs aiming to protect and contribute to the conservation of cetacean species is increasing around the world (Gormley et al., 2012; Hinch and De Santo, 2011). In addition to this spatial management approach, time restrictions have also been applied to restrict human access to critical species or populations (Constantine et al., 2004; Notarbartolo-di-Sciara, 2009).

Before the implementation of any spatial management approach, such as marine protected areas (MPAs), it is of paramount importance to have robust estimates of the population size and critical areas of the focal population, as well as a good understanding of its biology and behaviour. To obtain this information, it is important to develop a monitoring program based on robust methodologies that allow collecting reliable and accurate data on individuals, their habitat, and main threats. Based on this information, abundance estimates, reproductive rates, behavioural budgets and habitat use preferences can be measured and passed on to management agencies to establish competent conservation measures, such as effective marine protected areas which encompass critical periods and areas for the target population.

1.1.2 Marine mammals in the western Indian Ocean

In the western Indian Ocean, there are records of 33 species of marine mammals, some of which are subjected to hunting and bycatch, by interaction with local fisheries, as well as habitat degradation due to anthropogenic activities (Fig. 1.1)(Kiszka et al., 2009). The destruction of these coastal habitats including coral reefs, mangroves and estuaries, is a major problem when these habitats are main feeding areas for marine mammals, such as the case of Indo-Pacific bottlenose and humpback dolphins (Amir et al., 2005; Karczmarski et al., 1999). Therefore, it is essential to improve our knowledge on the marine mammal populations inhabiting this region, including several aspects such as population size, distribution, social structure, behaviour and survival to allow an adequate assessment of the current status of the species (Kiszka et al., 2009).



Fig. 1.1 Map of the western Indian Ocean

To date, most studies of marine mammals held in the western Indian Ocean have been conducted in continental coastal waters. These studies described the distribution of the Indo-Pacific bottlenose (*Tursiops aduncus*) and humpback dolphins (*Sousa chinensis*), dugong (*Dugong dugon*), as well as the humpback whale (*Megaptera novaengliae*) migration (Berggren et al., 2007; Cerchio et al., 2006; Cockcroft and Ross, 1990; Findlay et al., 2011; Mendez et al., 2013; Webster et al., 2014). On some of these areas abundance estimates suggest relatively small resident populations. In the Bay of Maputo (Mozambique), the abundance of *Sousa chinensis* was estimated at 105 individuals (Guissamulo and Cockcroft, 2004), comparatively smaller than the populations off the coast of Algoa Bay (South Africa) estimated at about 470 humpback dolphins (Karczmarski et al., 1999). On the south coast of Zanzibar (Tanzania), the *Sousa chinensis* population was estimated between 58 and 65 individuals, and the

population of *Tursiops aduncus* between 136 and 179 (Stensland et al., 2006). In Mayote, the Indo-Pacific bottlenose dolphin population was calculated on 82 individuals, and was recommended to be classified as Endangered, based on the IUCN guidelines (Pusineri et al., 2014). Nowadays the knowledge of marine mammals inhabiting the western Indian Ocean region remains insufficient considering the human threats these organisms are facing.

In Kenya, there is little information on the abundance and status of marine mammal populations, and no research was being carried out except for the aerial surveys conducted along the coast in 1996 by Kenya Wildlife Service (KWS). These surveys described a total of 14 species; the sperm whale (*Physeter macrocephalus*), humpback whale (*Megaptera novaengliae*), Bryde's whale (*Balaenoptera edeni*), minke whale (*Balaenoptera acutorostrata*), killer whale (*Orcinus orca*), melon-headed whale (*Peponocephala electra*), bottlenose dolphin (*Tursiops sp.*), common dolphin (*Delphinus sp.*), humpback dolphin (*Sousa chinensis*), spinner dolphin (*Stenella longirostris*), spotted dolphin (*Stenella frontalis*), Fraser's dolphin (*Lagenodelphis hosei*), Risso's dolphin (*Grampus griseus*), striped dolphin (*Stenella coeruleoalba*) and dugong (*Dugong dugon*) (Wamukoya et al., 1996). This study indicated that potential resident populations of bottlenose and humpback dolphins inhabited coastal areas. The highlighted conclusions from this governmental report were the need to: 1) develop a monitoring and research programme for cetaceans to collect data on numbers, species, movements and mortality, to support conservation and management strategies, and 2) to encourage the development of ecotourism based on "dolphin-watching", where local communities could take tourist to areas where dolphins were common (Wamukoya et al., 1996)

1.1.3 Dolphin-watching in the Western Indian Ocean

Exposure to several anthropogenic threats are likely to occur along the East African coast, with potential overfishing and growing dolphin-watching industry being the most significant (Kenya Wildlife Service, 2011). Dolphin tourism can have a negative impact on dolphins populations whether if tourist boats are unsustainably monitored and managed (Berggren et al., 2007; Christiansen et al., 2010; Stensland and Berggren, 2007). Studies on cetaceans subjected to the continuous presence of tour vessels have shown short-term changes in animal activity including: breathing rates (Janik and Thompson, 1996), diving times (Ng and Leung, 2003), speed (Nowacek and Wells, 2001), swimming directions (Lemon et al., 2006) and specific behavioural states (Lusseau, 2003a). In addition, the cumulative exposure to tourist boats have the potential to cause significant biological effects, and may result in long-term and life-threatening consequences, both at the individual and population level (Bejder et al., 2006).

Cetacean-watching tourism is a growing industry along the Western Indian Ocean with 19500 tourists reported in 1998, amongst Madagascar, Mozambique and Tanzania (Fig. 1.1). By the end of 2008, this activity expanded to new areas such as Mauritius, Mayotte and La Réunion and accounted for nearly 79000 tourists (these numbers did not include Kenya and South Africa) (O'Connor et al., 2009). O'Connor et al (2009) reported a minimal number of dolphin-watching tourists for Kenya in 1998 and 2008, even though this activity has been in place in the southern coast since mid 90s. This coastal area

is the main nature-based tourism destination not only in Kenya but also in eastern Africa, receiving the highest number of visitors in 2006 (66400 tourists; KWS unpublished data; O'Connor et al., 2009). These activities provide important economic resources to local communities, generating more than US\$ 1.6 million excluding park entry fees (Emerton and Tessema, 2001) in 1998, and being the main attraction of the nearly 30000 tourists that entered Kisite-Mpunguti Marine Protected Area (KMMPA) during the same year.

In the nearby Zanzibar island, a study showed that Indo-Pacific bottlenose dolphins' behaviour was negatively affected by increased levels of tourism activities and by the violation of the guidelines for responsible dolphin-watching (Stensland and Berggren, 2007). Some of these reported impacts were related to changes in behavioural patterns or the increase of erratic dolphin movement in the presence of more than 2 boats around the animals. Christiansen et al. (2010) recommended decreasing the tourism pressure to avoid jeopardising the survival and reproductive success of this species in southern Zanzibar, where tourist numbers reached 6375 in 2003.. In southern Kenya, where our study takes place, tourism numbers reached 49912 visitors in 2010, with more than 27 tourist boats operating in the area.

1.2 Prevailing environmental conditions in the western Indian Ocean

The study area is predominantly influenced by the two monsoon winds, affecting temperature and rainfall and creating two distinct seasons. The monsoon winds are of major significance in the western Indian Ocean, driving water circulation and wave action and shaping the local ecology and lives of the coastal communities. The north-eastern monsoon (known as kaskazi) blows from December to March, bringing calm weather, with low wave height and temperatures comprise between 28-32°C (McClanahan, 1988). The south-eastern monsoon (known as kusi) blows from May to October, with windy, rough seas and cooler temperatures (24-26°C) (McClanahan, 1988). The transition periods are characterized by variable and weaker winds. Rainy periods occur between the monsoon seasons with the long rains occurring from March to May and the short rains from October to December, with a mean annual rainfall ranging from 1000 to 1600mm (Camberlin and Philippon, 2002; Mutai and Ward, 2000).

The flow of ocean currents can have a great impact on marine life, affecting the availability of nutrients and determining the migration of large marine animals, including cetaceans. The South Equatorial Current (SEC) brings warm waters from the eastern Indian Ocean, and from as far as northern Australia in winter months, to about 10° South of the equator (Schott and McCreary, 2001). It hits the northern tip of Madagascar and continental Africa at the Tanzanian-Mozambican border where it divides in the northern stream, becoming the East African Coastal Current (EACC), flowing the length of the Kenyan coast, and becoming stronger when driven by the South-East monsoon (Fig. 1.2).

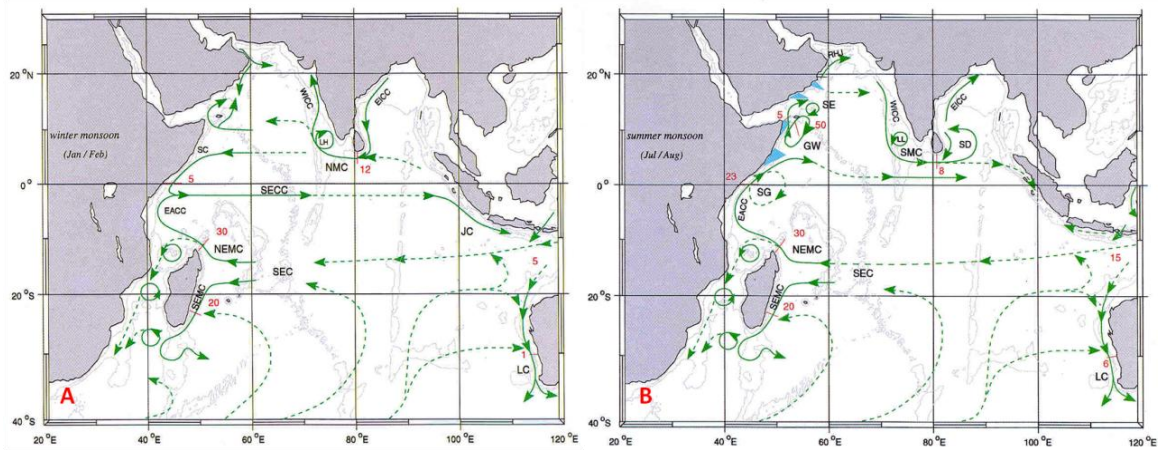


Fig. 1.2 A schematic representation of currents observed during January-February (A) and during July-August (B). The currents identified are: South Equatorial Current (SEC); South Equatorial Counter Current (SECC); Northeast and Southeast Madagascar Current (NEMC and SEMC); East Africa Coastal Current (EACC); Somali Current (SC), West India Coastal Current; Lakshadweep High (LH); East India Coastal Current (EICC); Northeast Monsoon Current (NMC); South Java Current (JC); and, Leeuwin Current (LC). Also shown are transports in Sv ($10^6 \text{ m}^3 \text{ s}^{-1}$) across sections shown as red lines. The figure is taken from Schott and McCreary (2001).

1.3 Marine Protected Areas in southern Kenya

In Kenya, there are six Marine Protected Areas (MPAs) spread along the coastline, including four fisheries closure marine parks and six restricted fishing marine reserves, covering nearly 10% of the continental shelf up to 200 m depth of the country, being one of the highest percentages along the Western Indian Ocean (McClanahan et al., 2005; Roccliffe et al., 2014; Wells et al., 2007).

1.3.1 Kisite-Mpunguti Marine Protected Area: a biodiversity hotspot

In the southern Kenyan coast, the Kisite-Mpunguti Marine Protected Area (KMMPA, $04^{\circ}04'S - 39^{\circ}02'E$) (Fig. 1.3) covers shallow waters (0-20 meters) and supports a high diversity of marine life including corals, reef fish and sea turtles. This MPA lies south from Wasini Island and incorporates the Kisite Marine Park, the largest no-take area in Kenya (28 km^2), and the adjacent Mpunguti Marine Reserve, Kenya's smallest reserve, where only artisanal fishing is allowed (11 km^2) (Fig. 1.3). This MPA was gazetted in 1978 and it is managed by the Kenya Wildlife Service (KWS) since 1988. KWS is a government parastatal institution with the aim of conserving Kenya's wildlife and it is responsible for the management of all protected areas around the country. The MPA offers excellent diving and snorkelling opportunities, and is Kenya's primary dolphin-watching location being the highest revenue-earning MPA for KWS, out-performing many of Kenya's terrestrial parks and reserves. As a result, nature-based tourism brings important revenues to this area, in a complex socio-ecological setting, where most of the population depends on fishing and tourism for living. This area has a rapidly growing human population of 1.2 million with approximately 60% of the local communities dependent on marine and coastal resources for their livelihoods (UNEP, 2013).

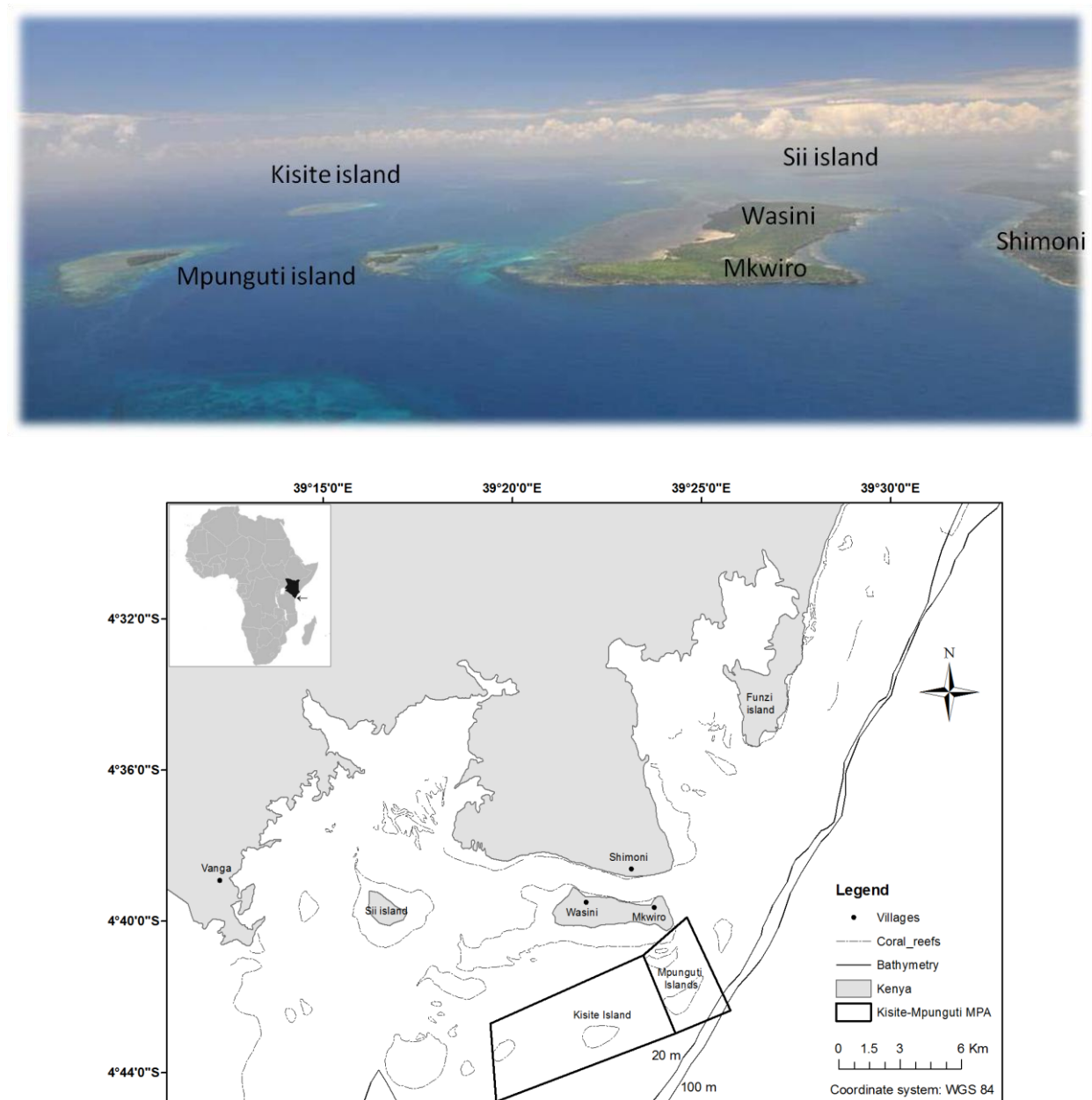


Fig. 1.3 Map of the study area including the Kisite-Mpunguti Marine Protected Area, Kenya, which contains the Kisite Marine Park (left polygon) and the adjacent Mpunguti Marine Reserve (right polygon).

Furthermore, the MPA protects islands such as Lower and Upper Mpunguti, which are home to populations of the rare coconut crab (*Birgus latro*), and Kisite, which has been considered an Important Bird Area (IBA) hosting species such as the dimorphic egret (*Egretta dimorpha*), the sooty tern (*Sterna fuscata*) and large numbers (up to 1,000 breeding pairs recorded) of roseate terns (*Sterna dougallii*) (BirdLife International 2014) (Fig. 1.4). Of equal importance for the long-term environmental management of this region are the habitats and wildlife in areas surrounding the MPA that do not fall under protection, and encompasses a wide range of habitats from mangrove forests, coral reefs, seagrass beds and offshore waters which are considered important fish nursery grounds.



Fig. 1.4 Biodiversity around Kisite-Mpunguti MPA: A) roseate tern (*Sterna dougallii*), B) dimorphic egret (*Egretta dimorpha*) and C) coconut crab (*Birgus latro*) (Photos: Zeno Wijtten).

The edge of the MPA connects to the deeper waters of the Pemba channel and hosts Spinner dolphins and Humpback whales on their seasonal migrations, while the near-shore waters of the Shimoni coast are home to resident Indo-Pacific bottlenose and humpback dolphins (Fig. 1.5). Additionally, areas of the coastline including Lower Mpunguti Island and the nearby Funzi Island are known nesting grounds for sea turtles. Importantly, and just a little further down the coast around Sii Island and Vanga, may be one of the few remaining refuges in Kenya for the endangered dugong (UNEP, 2013). The mangrove forests along the shores are also critical habitats for water birds and fish nursery grounds. It is these areas, where fishing and mangrove harvesting take place, that the impact of human activities is most acutely felt and communities need to be engaged in responsible management of their resources to ensure both their livelihoods and the wildlife.

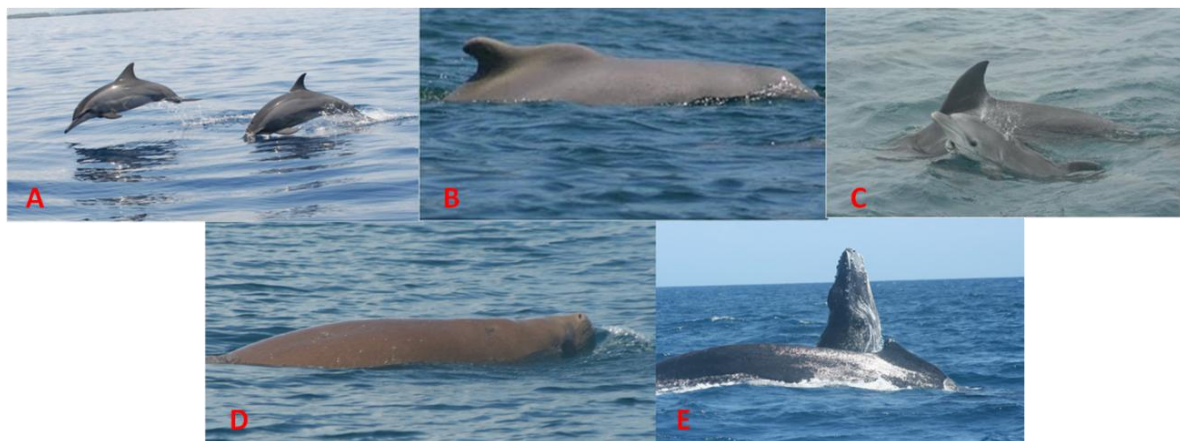


Fig. 1.5 Marine mammals around Kisite-Mpunguti MPA: A) Spinner dolphins (*Stenella longirostris*), B) Humpback dolphins (*Sousa chinensis*), C) Bottlenose dolphins (*Tursiops aduncus*), D) Dugongs (*Dugong dugon*) and E) Humpback whales (*Megaptera novaengliae*) (Photos: Global Vision International).

1.3.2 Kisite-Mpunguti Marine Conservation Area Management Plan (KMMCA-MP)

The KMMCA-MP was developed through a stakeholder's collaboration effort which included governmental and nongovernmental organizations, such as Kenya Wildlife Service (KWS), Kenya Marine Fisheries Research Institute (KMFRI), Kenya Maritime Authority (KMA), National Museums of Kenya

(NMK), Beach Management Units (BMU), World Wide Fund for Nature (WWF), Dolphin clubs, Dive operators, among others. This ten year management plan was implemented in 2011, and was developed in accordance with the KWS Protected Area Planning Framework (PAPF). The KMMCA is faced with multiple challenges in the conservation and exploitation of natural resources, which have suffered a long-term degradation over the last decades. The main aim of this management plan is to mitigate negative impacts of anthropogenic activities and promote a more sustainable use of natural resources, both in the terrestrial and marine realm. The plan also aims to contribute towards a better understanding of the conservation issues affecting the Marine Protected Area to the general public.

The main issues addressed by the KMMCA management plan are (1) increased rate of conflicts around the Marine Protected Area, (2) coordinated investments both for the MPA and users, (3) loss and degradation of marine habitats and species, (4) poor social perceptions and compliance, (5) limited involvement of indigenous communities and (6) poor biodiversity research and monitoring.

The KMMCA-MP set a list of nine conservation targets, choosing “Marine mammals” as one of the most important among them. Conservation targets represent and encapsulate unique biodiversity present within the Marine Protected Area, as well as any environmental or ecological features that may require specific management actions, such as endangered species or habitats. To achieve each conservation target a list of “Key ecological attributes (KEAs)” were described, representing ecological parameters upon which long-term survival of each conservation target depends. The table below sets the Rationale for selection of Key ecological attributes for the “Marine mammals” conservation target (Table 1.1):

Table 1.1 Marine mammal conservation target for the KMMCA describing the rationale for selection and key ecological attributes (adapted from (Kenya Wildlife Service, 2011)).

Conservation target	Rationale for selection	Key ecological attributes
Marine mammals	Biodiversity value	Water quality
	High tourism attraction	Population size and structure
	Indicator of ecosystem health food web maintenance	Genetic diversity
	Highly endangered dugong (vulnerable to extinction)	Habitat quality and utilization
	Near threatened humpback dolphin	Availability of prey species
	Endangered species	Human disturbance

Currently, few studies have provided data related to population size and human disturbance on marine mammals in this area (Wamukoya et al., 1996). The KMMCA-MP also identified a combination of stressors (threats) which can have a negative impact on conservation targets. The main “threats” identified for marine mammals due to their severity and scope were: overfishing of prey species, dolphin and whale watching and the impact from oil and gas exploration (seismic surveys)(Table 1.2; Fig. 1.6).

Table 1.2 The main threats with potential impacts on marine mammals (adapted from (Kenya Wildlife Service, 2011)).

Targets	Threats	Severity	Scope	Ranking
Marine mammals	Overfishing of prey species	High	High	High
	Entanglement in fishing gears	Medium	Low	Low
	Dolphin and whale watching	High	High	High
	Climate change	Medium	Medium	Medium
	Decreasing habitat quality (sedimentation, noise, oil spillage)	Medium	Low	low
	Impact from oil and gas exploration	Very high	High	High

**Fig. 1.6** Threats for marine mammals. A) overfishing B) dolphin-watching and C) seismic surveys (Photos: Global Vision International and Kyla Graham).

1.4 Study species

1.4.1 Species overview

Bottlenose dolphins (*Tursiops spp.*) belong to the order Cetacea, suborder Odontoceti, and Family Delphinidae (Mead and Potter 1990). The genus is composed of three species: the common bottlenose dolphin (*T.truncatus*, Montagu 1821), the Indo-Pacific bottlenose dolphin (*T.aduncus*, Ehrenber 1832) and the Burrunan dolphin (*T.australis*; Charlton-Robb et al., 2011). The taxonomic status of the genus *Tursiops* is continuously renew. Natoli et al., (2004) identified that the coastal *Tursiops aduncus* from South Africa was genetically differentiated from the coastal *aduncus* form in Asia, as well as from the *T. Truncatus* type, implying that a new species of the genus could exist. Genetic studies describe that *T.aduncus* is more closely related to *Delphinus* and *Stenella* species, than it is to *T. truncatus* (Wells and Scott, 2002). However, these studies are inconsistent with osteological and morphological analysis and further research is needed to clarify these issues (Möller and Beheregaray, 2001; Wang et al., 1999). *T.aduncus* differs from the larger species *T.truncatus* as it has a more robust body, a falcate dorsal fin, develops ventral spotting with age, usually when reach sexual maturity (Krzyszczuk and Mann, 2012; Wells and Scott, 2002), and presents a longer and better-defined rostrum (Jefferson et al., 2008) (Fig.

1.7). Adults body length of Indo-Pacific bottlenose dolphins varies geographically, ranging from 238 cm and 160 kg in Zanzibar, East Africa (Amir et al., 2007), to 270 cm and 230 kg in the eastern Indian Ocean (Jefferson et al., 2008). *T. aduncus* is monomorphic as the sex determination is not identifiable based on the size of the individual (Hale et al., 2000; Kemper, 2004). In large numbers, sex determination is undertaken by molecular analyses of biopsy samples, which have a high degree of accuracy. Other techniques to identify the sex of the individuals is through opportunistic surface observation of their genitals, or for females, by a close association with a calf over a long period of time (Mann, 2000).



Fig. 1.7 Indo-Pacific bottlenose dolphin (*Tursiops aduncus*), showing the ventral spotting (A) and the well-defined rostrum (B) (Photos: Global Vision International).

1.4.2 Distribution

T. aduncus is restricted to tropical and subtropical waters throughout the Indo-Pacific region. The species has been described in southern and eastern Africa, the Red Sea, Persian Gulf, Arabian Sea, Bay of Bengala, Japan, Solomon islands and western and eastern Australia (Reeves and Brownell Jr, 2009; Stensland et al., 2006; Wamukoya et al., 1996)(Fig. 1.8). Along the Kenyan coast, the species has been sighted in the northern region in areas such as Lamu archipelago and Watamu Marine Protected Area, and in the southern region of Kisite-Mpunguti Marine Protected Area (Kenya Wildlife Service, 2011; Wamukoya et al., 1996). Main habitats for the species are warm water temperatures of 20-30°C and shallow waters with less than 30 meters in depth (Wang and Yang, 2009).

The home range of bottlenose dolphins (i.e., the area where an individual or group spend the majority of the time, and encompasses all the resources the animal requires to survive and reproduce (Shane et al., 1986)), has been extensively studied with high differences within and between populations (Gubbins, 2002; Scott et al., 1990). In Western Australia, home range for *T. aduncus* ranged from 20 to 187 km², with larger home range areas for males compared to females (Sprogis et al., 2015). Male mating strategies, abundance of prey resources and predation risk have been suggested as the main reason for sex differences in home ranges (Gubbins, 2002; Sprogis et al., 2015). Other factors driving the home range size is the presence of calves in the groups, as maternal investment towards calf survival influences the female habitat use (Connor et al., 2000; Connor and Krützen, 2015).

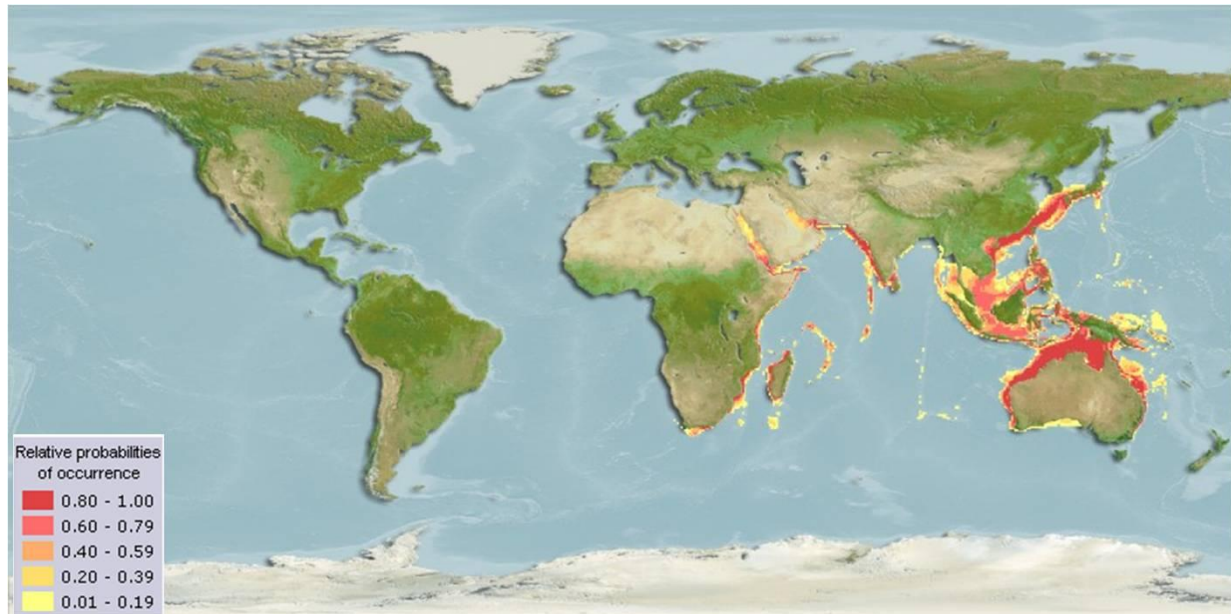


Fig. 1.8 Reviewed distribution maps for *Tursiops aduncus* (Indo-Pacific bottlenose dolphin), with modelled year 2100 native range map based on IPCC A2 emissions scenario. www.aquamaps.org, version of Aug. 2013. Web. Accessed 26 Oct. 2015

1.4.3 Population size

Population size studies conducted along the distribution range of the species differ significantly and vary both within and between populations (Table 1.3). Large aggregations have been described in Australia and Persian Gulf, with population reaching more than 1000 individuals. On the other side, regions such as Philippines and Japan contain small aggregations with population of less than 200 individuals. In the Western Indian Ocean, *T.aduncus* populations ranged from 82 individuals in Mayotte to 179 in Zanzibar.

Table 1.3 Indo-Pacific bottlenose dolphin populations distributed along the species range (adapted from Hammond et al., 2012).

Country	Area	Abundance	Reference
South Africa	KwaZulu-Natal	520-530	Cockcroft et al. 1992
Tanzania	Zanzibar	136-179	Stensland et al. 2006
Comoros archipelago	Mayotte	82	Pusineri et al., 2014
Mauritius	South-west coast	<100	Webster et al., 2015
Persian Gulf		1200	Preen 2004
Bangladesh	Swatch-of-No-Ground	400	Rubaiyat Mansur Mowgli and Brian D. Smith pers. comm.
Japan	Western Kyushu	218	Shirakihara et al. 2002
Japan	Mikura Island	169	Kogi et al. 2004
Philippines	Northern region	50	J. Y. Wang pers. comm.
Australia	Queensland	1099	Chilvers and Corkeron 2003
Australia	Shark Bay	2000-3000	Preen et al. 1997

1.4.4 Life history and mating strategies

Bottlenose dolphins are K-selected species as they are long-lived and slow growing individuals (Reynolds et al., 2000). Life-span for males and females can reach more than forty and fifty years, respectively (Connor et al., 2000). Female bottlenose dolphins reach sexual maturity between the ages of five to thirteen years (Mann, 2000). The species reproduce throughout the year, with peaks during maximum surface water temperatures. Gestation period lasts twelve-months, and give born to a single calf (Connor et al., 2000). Male bottlenose dolphins reach sexual maturity between the ages of eight to thirteen years (Wells et al., 1987). Bottlenose dolphins are polygynous, and males compete among males to maintain consortships with different females (Connor, 1996). Their distribution is widely influenced by the spatial and temporal distribution of females (Connor and Krützen, 2015).

1.4.5 Social complexity

Bottlenose dolphins live in a fission-fusion society, similar to other mammals such as chimpanzees (*Pan troglodytes*; McFarland, 1986), elephants (*Loxodonta africana*; Wittemyer et al., 2005) and spider monkeys (*Ateles paniscus*; Wrangham et al., 1993). In these complex social structures group formation are frequently changing, with specific association between individuals (Aureli et al., 2008; Lusseau et al., 2006a). These groups tend to be associated by similar age, sex and reproductive status, which leads to formation of mothers and calves, adult males and mixed-sex juvenile groups (Smolker et al., 1992; Wells et al., 1987). Females tend to form association with females of similar reproductive status (Frère et al., 2010; Smolker et al., 1992), while males form long-term alliances with other males which may or may not be related (Krützen et al., 2003; Wiszniewski et al., 2012). Based on the studies from Shark Bay, three levels of male alliances have been described for *T. aduncus*: first-, second- and third-order alliances. First-order alliances are formed by a pair or trio of individuals, second-order are constitute by two or more alliances, and finally the third-order alliances are groups of second-order alliances (Connor and Krützen, 2015).

1.4.6 Prey

Bottlenose dolphins feed on a large variety of prey, including fish and cephalopods (Cockcroft and Ross, 1990; Gannon and Waples, 2004). The distribution and availability of prey is one of the main drivers of cetacean distribution (Degrati et al., 2013, 2012). An example of this link is that dolphin tend to maintain high residency rates and small home range when preferred prey is spatially and temporally predictable (Gowans et al., 2008). In contrast, dolphins tend to larger home ranges to search for prey resources when prey distribution is patchy and ephemeral (Gowans et al., 2008; Silva et al., 2008). This is common in open coastal habitats. In Zanzibar, *T. aduncus* forage over reefs or soft bottom substrata near the shore (Amir et al., 2005). The species diet is comprised with small- and medium-sized neritic fish and cephalopods, with only five species of fish *Uroconger lepturus*, *Synaphobranchus kaupii*, *Apogon apogonides*, *Lethrinus crocineus*, *Lutjanus fulvus*, and three species of squid, *Sepioteuthis lessoniana*, *Sepia latimanus* and *Loligo duvauceli*, were the most important prey species (Fig. 1.9). In contrast

around the island of Mayotte, Indo-Pacific bottlenose dolphins are essentially epipelagic and demersal predators, foraging on prey at higher trophic levels (Kiszka et al., 2014).

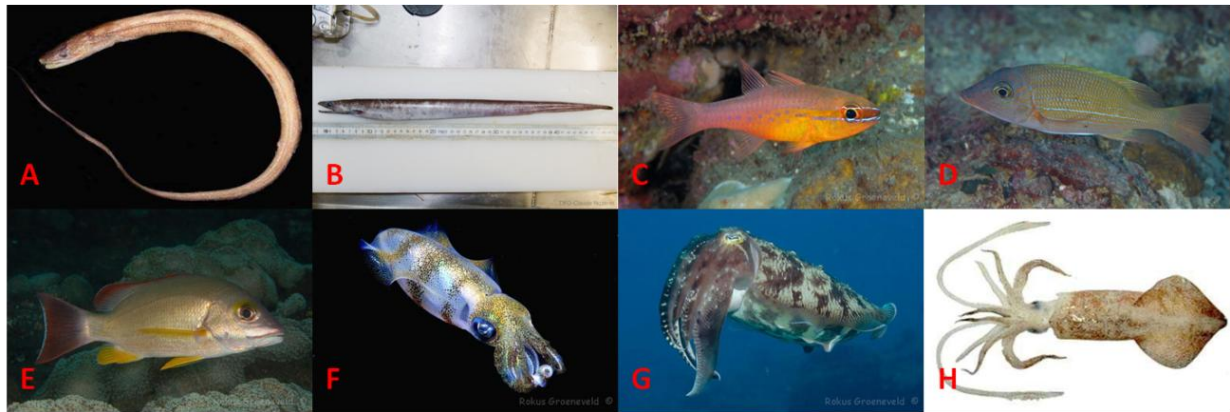


Fig. 1.9 . Most important prey species in the diet of the Indo-Pacific bottlenose dolphins in Zanzibar Island: A) Slender conger (*Uroconger lepturus*, <http://fishdb.sinica.edu.tw/>), B) Slatjaw cutthroat eel (*Synaphobranchus kaupii* <http://www.marinespecies.org/>), C) Plain Cardinalfish (*Apogon apogonides*, <http://www.diverrosa.com/>), D) Yellowtail emperor (*Lethrinus crocineus*, <http://naturalista.conabio.gob.mx/>), E) Blacktail snapper (*Lutjanus fulvus*, <http://www.diverrosa.com/>), F) Bigfin reef squid (*Sepioteuthis lessoniana*, <http://www.diverrosa.com/>), G) Broadclub Cuttlefish (*Sepia latimanus*, <http://www.diverrosa.com/>), and H) Indian squid (*Loligo duvauceli*, www.ecplaza.net).

1.4.7 Predators

The trade-off between the perceived predation risk and prey availability is one of the key elements dolphins are based to decide the most suitable habitat (Heithaus and Dill, 2002; Heithaus, 2001a; Lima and Dill, 1990). Predation risk can influence habitat selection with dolphins more likely to choose ‘safer’ habitats based on energetic return (Heithaus and Dill, 2002; Wirsing et al., 2008). Nevertheless, dolphins and sharks’ diet frequently overlap between them (Acevedo-Gutiérrez, 2002). As a consequence, dolphins adopt changes in group composition or elicit flight reactions as behavioural responses to shark presence (Heithaus, 2001a).

Sharks, such as bull (*Carcharhinus leucas*), dusky (*Carcharhinus obscurus*), tiger (*Galeocerdo cuvier*) and white sharks (*Carcharodon carcharias*; Heithaus 2001b), are the main predators of bottlenose dolphins (Fig. 1.10). The risk of predation varies among areas depending on the spatio-temporal distribution and abundance of sharks, influencing the behavioural response of dolphins versus sharks (e.g., Gibson, 2006; Mann and Barnett, 1999). The predation level in a dolphin population is calculated based on the failed predation attempts identify through shark-inflicted injuries on the dolphins’ body (Heithaus, 2001b; Melillo-Sweeting et al., 2014).

This predation risk tends to affect age-classes and sexes differently (i.e. (Lusseau, 2003b; Symons et al., 2014). For example, females with dependent calves have a higher predation risk than other dolphins due to their small body size and the dependency of the calf. Mann and Barnett (1999) described that one-third of the calves inhabiting Shark Bay, Australia, had shark bite wounds. For this reason, females with calves tend to choose those habitats that are perceived with a lower predation risk (Connor et al.,

2000; Mann and Watsoncapps, 2005). These habitats are usually near-shore and shallow waters in order to isolate calves from their main predators.



Fig. 1.10 Main predators of bottlenose dolphins: A) Bull shark (*Carcharhinus leucas*), B) Dusky shark (*Carcharhinus obscurus*), C) Tiger shark (*Galeocerdo cuvier*) and D) Great white shark (*Carcharodon carcharias*). (Photos obtained from www.arkive.org).

1.5 PhD thesis objectives

The main objective of this PhD thesis is to study the conservation of the Indo-Pacific bottlenose dolphins, *Tursiops aduncus*, in southern Kenya through an integrative assessment of the main key marine habitats, population estimates and their interactions with natural and anthropogenic factors. This research is primarily developed to provide detailed information on the impacts the species is facing, under the current and future situations. Data for this thesis was collected over an eight year period (2006-2013) in Kisite-Mpunguti MPA by Global Vision International (<http://www.gvi.co.uk/>). The PhD thesis is organized in four different chapters that are detailed below:

Chapter 2: Can static habitat protection encompass critical areas for highly mobile marine top predators? Insights from coastal East Africa

In Chapter 2, we will develop species distribution models to identify key areas for the Indo-Pacific bottlenose dolphin, *Tursiops aduncus*, in southern Kenya using a long-term database (2006-2009), and assess the performance of the existing Marine Protected Area (MPA) for the species. MPAs have been used as a main management approach to protect important habitats and ecosystems including biodiversity hotspots, but few examples have empirical evidence that they are effective for the conservation of marine mammals (IUCN, 2004). Quantifying the effects of MPAs is crucial to evaluate

their efficacy as management tools and the protection of the species (Kelleher, 1999). Within this context, it is necessary to understand the effectiveness of MPAs from a wider ecosystem-based management approach, and assess whether the existing MPAs (initially established for the protection of coral reefs), also encompass important marine areas for high trophic level species, such as marine top predators. This chapter will go a step further in the complexity of the analysis, not only including several habitat modelling techniques and combining them to get the best performance, but also providing an integrative approach to evaluate potential climate change effects on the distribution and abundance of top marine predators.

To achieve the main objective, I propose these particular objectives within this chapter:

- Identify environmental factors influencing the occurrence and abundance of dolphins based on two different modelling techniques (GLMs and GAMs)
- Identify recurrent, occasional and unfavourable habitats for the species based on the species distribution models (SDM) predictions.
- Assess the suitability of the Kisite-Mpunguti Marine Protected Area for the dolphin population by estimating the occurrence and abundance probabilities within and outside the MPA.
- Discuss the conservation implications of this integrated habitat modelling approach for identifying key marine areas for coastal dolphins and evaluate the effectiveness of existing MPA.

Chapter 3: Effects of nature-based tourism and environmental drivers on the demography of a small dolphin population

In the study from Chapter 3, we will develop Pollock's robust design models to examine the influence of oceanographic conditions, prey availability and tourism exposure on several demographic parameters (abundance, temporary emigration and survival) of the studied species. Specifically, we will analyse four years of mark-recapture data to multiple competing models to investigate a set of hypothesis about dolphin population parameters within the Information Theoretic Approach. Marine top predators are vulnerable to anthropogenic pressures such as climate variability, habitat alterations, and fisheries interactions or overfishing among others (Barbraud and Weimerskirch, 2001; Lewison et al., 2004). Particularly, demographic studies on cetacean populations are urgently needed in the western Indian Ocean, due to the increase of potential anthropogenic threats in the area (e.g., unsustainable fishing, seismic exploration, dolphin-watching)(Kenya Wildlife Service, 2011). In these circumstances, it is necessary to understand the effects of biotic and abiotic factors on demographic parameters, to improve management decisions (Weimerskirch et al., 2003). Additionally, it is of paramount importance to perceive how vulnerable this population is to human disturbance due to their high site fidelity and coastal distribution, and determine the sustainability of nature-based tourism activities in southern Kenya.

To achieve the main objective, I propose these particular objectives within this chapter:

- Assess four years of mark-recapture data to fit Pollock's robust design models to investigate a set of hypothesis about dolphin demographic parameters within the Information Theoretic Approach.
- Estimate seasonal temporary emigration movements influenced by environmental, human disturbance or fisheries covariates.
- Examine whether capture probabilities showed any time-dependent effect
- Estimate seasonal population abundances.

Chapter 4: Watch out for tourists! Current impact of nature-based activities in coastal dolphin populations in southern Kenya.

In recent years, nature-based tourism has increased in developing countries, generating high employment rates for local communities. However, this increase has serious implications for the animal populations as these activities remain poorly documented and often poorly managed. Indeed, the disturbance created by repeated human-wildlife interactions can have severe impacts on the conservation status of the targeted species (e.g. Currey et al., 2009b). The impact of human disturbance on animal populations has been extensively measured in terms of changes in behaviour in response to human presence, taking the magnitude of these changes as a means to assess the relative susceptibility of the animals to the existing disturbance (Gill et al., 2001). In Chapter 4, we will use a Markov chain approach to determine how tourists' boat interactions affect dolphins' behavioural budgets. Based on these behavioural budgets, we will assess if the cumulative exposure to tourism have significant impacts on the dolphin population, considering the current tourism levels. Taking into account the potential tourism growth in the area, it is crucial to understand the effect of human disturbance variations from previous years, which can help to predict future consequences. Furthermore, identifying the spatial and temporal extent of tourist disturbance can also guide management agencies to determine critical areas and periods where impacts could be more significant.

To achieve the main objective, I propose these particular objectives within this chapter:

- Investigate the effects of the nature-based tourism on the behaviour of the Indo-Pacific bottlenose dolphin population.
- Estimate the probability of dolphins changing between different behavioural states in the presence and absence of tourist boats.
- Investigate the cumulative behavioural budgets of the dolphin population at the current tourism intensity levels.
- Evaluate the potential disturbance caused by the nature-based tourism over the 2006-2013 period.
- Examine the proportion of the population exposed to different levels of human interactions.

Chapter 5: Spatial variation in shark-inflicted injuries to Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) of the western Indian Ocean.

Shark predation has been described to have a strong influence on dolphins habitat use, group size formation, and on their antipredatory behavioural response (Heithaus, 2001b; Heithaus and Dill, 2006; Norris and Dohl, 1980a; Wirsing et al., 2008). Although the importance of these interactions between sharks and dolphins, there are not many attacks that have been directly observed. For this reason, shark predation is assessed through alternative methods such as failed attempts, documented through the presence of shark-inflicted wounds and scars, which have been used to get indirect measure of the threat that sharks represent for dolphins (Melillo-Sweeting et al., 2014). In Chapter 5, we will use this technique to evaluate shark-inflicted rates in four populations of Indo-Pacific bottlenose dolphins along the western Indian Ocean (southern Kenya, la Réunion, Mauritius, and Mayotte).

To achieve the main objective, I propose these particular objectives within this chapter:

- Estimate rates of shark-inflicted injuries on Indo-Pacific bottlenose dolphins at four locations in the Western Indian Ocean (southern Kenya, la Réunion, Mauritius, and Mayotte).
- Identify spatial variation on the probability of an identified individual having a shark-inflicted injury.
- Determine the shark species responsible for inflicting injuries.

CHAPTER 2

2. Can static habitat protection encompass critical areas for highly mobile marine top predators? Insights from coastal East Africa

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Published in PLoS ONE 10(7) (2015). DOI: 10.1371/journal.pone.0133265

2.1 Introduction

The habitats and ecosystems of the western Indian Ocean (WIO) region hold some of the highest marine biological diversity in the world, particularly for corals and reef fish (Veron, 1995). However, the increasing overexploitation of marine resources and the degradation of the habitats are threatening the marine biodiversity (Roberts et al., 2002). To mitigate these anthropogenic pressures, Marine Protected Areas (MPAs) have been used as a main management approach to protect important habitats and ecosystems including biodiversity hotspots (IUCN, 2004). Following this concept, the Convention on Biological Diversity (CBD) aims to improve the status of biodiversity establishing a 10% of coast and marine areas worldwide, by 2020, applying effectively and equitably managed ecologically representative and well connected systems of protected areas (CBD, 2010).

MPAs have been established with a variety of conservation goals, including biodiversity conservation, maintenance of genetic diversity, conservation of rare and restricted range species, prevention of overfishing (Gell and Roberts, 2002) and enhancement of fisheries (Castilla and Fernandez, 1998), among others (Halpern, 2003). In Kenya, there are six MPAs covering nearly 10% of the continental shelf up to 200 m depth (835 km²), being one of the highest percentages along the WIO (Rocliffe et al., 2014). These MPAs were designed initially to protect the nearshore habitats and sessile or benthic organisms (Francis et al., 2002). After more than 20 years of MPAs establishment and monitoring, many studies have highlighted their positive impacts on local fish population (higher biomass and diversity) and status of coral reefs (higher hard coral cover and coral diversity)(McClanahan et al., 2001, 1999).

In contrast, relatively little is known about the role that MPAs play in the protection of marine top predators such as marine mammals, seabirds, and sea turtles. The growing number of anthropogenic

threats that these predators are facing (*e.g.* fisheries bycatch), requires the implementation of urgent conservation measures to safeguard key marine areas (Hooker and Gerber, 2004). Understanding the relationships between these highly mobile animals and their associated habitats is critical to provide the predictive power to anticipate changes in habitat use patterns and to effectively monitor and protect them. Specifically, the MPAs spatial-based conservation plans can improve population's recovery and intensify the protection of these marine predators against threats.

Comparative studies across species and functional groups are necessary to understand the effectiveness of MPAs from a wider ecosystem-based management approach. It is important to assess whether the existing MPAs (initially established for the protection of coral reefs), also encompass key marine areas of higher trophic levels such as marine top predators. For the Kisite-Mpunguti Marine Protected Area (KMMPA), on the southern coast of Kenya, dolphins are considered flagship species. As the main attraction for the 60,000 yearly park visitors, dolphin presence is of economical importance for local communities. The Indo-Pacific bottlenose dolphin is the most abundant marine mammal species in the study area (Pérez-Jorge, unpublished data), and is currently listed as data deficient by the IUCN due to the lack of information on population abundance, habitat use, genetic diversity and population structure (Hammond et al., 2012).

To identify key habitats for the population of coastal dolphins within the existing MPA, we developed species distribution models (SDM) to predict the occurrence (using presence/absence data) and abundance (combining number of sightings and group size data) of the dolphin population around the KMMPA. First, we developed a comprehensive ecological modelling approach to study the environmental factors influencing the occurrence and abundance of dolphins based on two different modelling techniques. Second, we identified recurrent, occasional and unfavourable habitats based on SDM predictions by describing those areas where dolphins are likely to occur frequently, where occurrence varies considerably inter-annually, and where no observations occur, respectively (Louzao et al., 2013). Third, we assessed the suitability of the existing MPA for the dolphin population by estimating the occurrence and abundance probabilities, as well as the percentage of recurrent, occasional and unfavourable habitats within and outside the MPA. Finally, we discuss the conservation implications of this integrated habitat modelling approach for identifying key marine areas for coastal dolphins and evaluate the effectiveness of existing MPAs.

2.2 Material and Methods

2.2.1 Ethics Statement

This study was carried out by Kenya Wildlife Service (KWS), the government authority in the area regulating research and natural resource management. Sightings data are held by Kenya Wildlife Service. Permission for all joint Global Vision International activities was granted by the Kenya Wildlife Service Director under a 5 year Memorandum of Understanding signed in 2006. The field studies did

not involve endangered or protected species, under the Kenyan Wildlife Conservation and Management Act.

2.2.2 Study area and data collection

Our study was focused on the southern coast of Kenya, in the Kisite-Mpunguti Marine Protected Area (KMMPA, 04°04'S - 39°02'E), established in 1978. This MPA lies south of Wasini Island and incorporates the Kisite Marine Park, the largest no-take area in Kenya (28 km²), and the adjacent Mpunguti Marine Reserve, Kenya's smallest reserve, artisanal fishing allowed (11 km²). KMMPA covers shallow waters (0-15 meters) and supports a high diversity of marine life including corals, reef fish and sea turtles (Fig. 2.1).

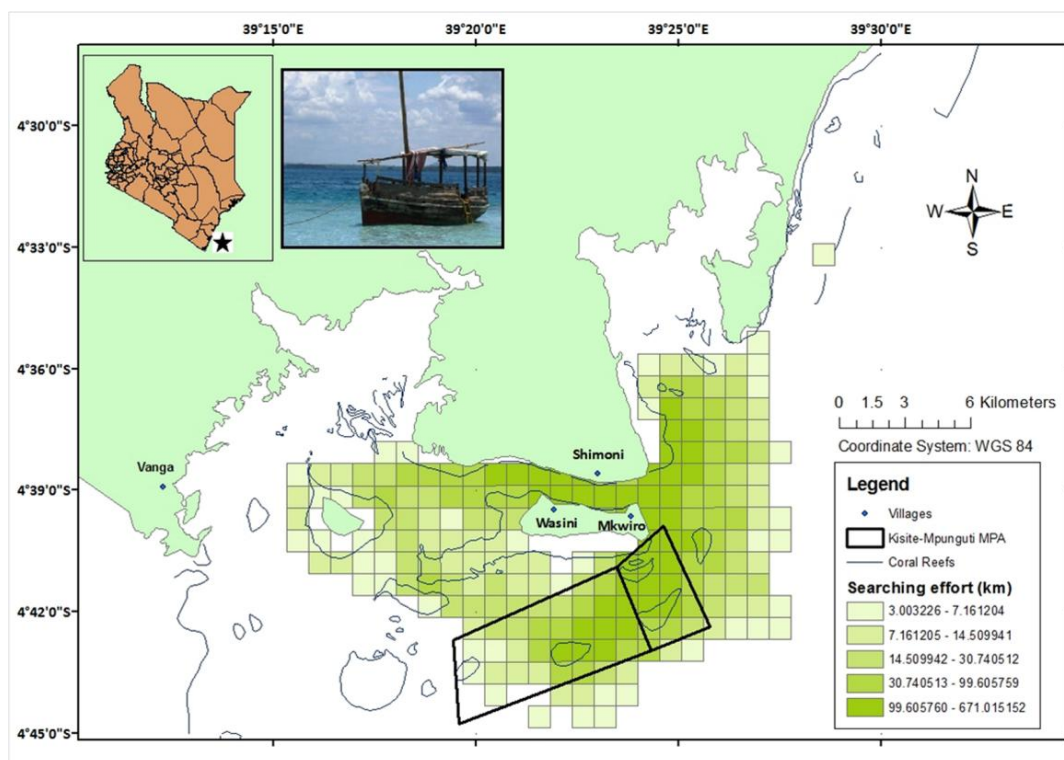


Fig. 2.1 General map of the study area showing the location of the study area and an illustration of the study vessel, showing the overall survey effort (km) between 2006 and 2009, and the location of the Kisite-Mpunguti Marine Protected Area, which contains the Kisite Marine Park and the adjacent Mpunguti Marine Reserve.

Vessel-based surveys were conducted at an average speed of 6.9 knots all year around between January 2006 and December 2009 (except the period from January and June 2008, due to national political conflicts). Four observers scanned the water surface over 180° field of vision from the two perpendiculars to the front of the boat. Each observer covered a 45° subset of the field vision. Team members shift every 15 minutes, with an eye break after an hour of observation. Non-systematic transects were carried out during the surveys, covering an average of 69% (SD ± 15%) of the whole study area every three months, depending on climate and sea state conditions (Cañadas et al., 2005). Searching effort was conducted with Beaufort sea state < 4, low swells and good visibility (≥ 1 km),

reducing the probability of missing dolphins. Once animals were sighted, the research vessel approached them at low speed to identify species and to collect information on location and time of the sighting, group size and group composition.

2.2.3 Data processing and exploratory analysis

Observations were standardized over a common spatial grid of 1 km by 1 km throughout the survey area using ArcMap 10.1 (ESRI, 2011). Survey effort was calculated on each 1 km² using a UTM37S projection. Data were divided by season: summer (January to March), autumn (April to June), winter (July to September) and spring (October to December) based on local sea weather conditions. Considering the seasonal scale in the distribution of wide-ranging marine species improves model performance compared to annual averages and, in turn, we considered this temporal scale biologically meaningful (Gallus et al., 2012). Only grids with a minimum of 1 km of survey effort per season and year were considered on the analysis in order to avoid small sample biases.

We transformed observations in three different quantitative ecological measurements. For each grid cell, we summed up the number of sightings and the number of individuals (i.e., group size) observed per each season and year. We recorded the number of sightings into a binary presence/absence variable by transforming into “presence” those grid cells with at least one sighting and “absence” otherwise.

2.2.4 Environmental variables description and selection

We selected 10 environmental variables (5 dynamic and 5 static) based on our previous knowledge on dolphin ecology, environmental conditions in the study area and the availability of oceanographic information (Table 2.1).

Regarding static variables, robust correlations between water depth and many species of marine mammals have been found in different regions and ocean basins (Baumgartner et al., 2000; Moore et al., 2002), thus making bathymetry (BAT) an appropriate variable as an environmental proxy for habitat models. To account for spatial gradients of depth, we estimated bathymetric gradients (GRAD) within every grid cell using the following formula: $[(\text{maximum depth} - \text{minimum depth}) * 100] / \text{maximum depth}$. In addition, we also estimated the closest distance to the fronts (FRONT), coast (COAST), reef (REEF) and 100 meter isobaths (ISOBATH) from the centroid of each grid cell. BAT, REEF and FRONT values were log-transformed because the minimum and maximum values differed by an order of magnitude.

Regarding dynamic variables, we included sea surface temperature (SST) and chlorophyll *a* density (CHL) since marine mammals are believed to adapt to specific temperature regimes, and to associate with highly productive areas (as indicated by high chlorophyll *a* values). Monthly composite for SST and CHL were derived from aqua-MODIS sensor and converted with the Marine Geospatial Ecology Tool (MGET, (Roberts et al., 2010)) from their original formats to raster formats compatible with ArcGIS. As the selected unit of observation (1 km) was at a finer spatial resolution than the remotely sensed

habitat variables (4 km), SST and CHL were interpolated using the ordinary kriging function in ArcMap (Geostatistical Analyst). We performed an exploratory screening to ensure that interpolated spatial patterns matched original patterns by means of semivariogram output and visual inspection. Subsequently, as SST and CHL were not normally distributed the median was used as the central tendency instead of the mean for each season within every 1 Km² grid cell. In addition, we estimated a temporal gradient for every season to account for the small scale variability of dynamic variables as follows: SSTT and CHLT = [(maximum value - minimum value)*100]/maximum value, with maximum being the highest and minimum the lowest monthly value for the six month period comprising the three months prior to the season and the actual season (Oppel et al., 2012).

Table 2.1 Description of environmental variables considered for habitat modelling, as well as their overall, absence and presence mean and range values (between brackets). The type of predictor is also described as well as their ecological interpretation.

Habitat variables	All data	Bottlenose dolphins		Predictor category	Ecological interpretation
		Absence	Presence		
Bathymetry (BAT, m)	9.90 (0.12-102.12)	10.34 (0.12-102.12)	7.44 (1.66-45.68)	Static	Coastal vs. pelagic domains
Bathymetry gradient (GRAD, %)	71.40 (3.48-100.00)	71.14 (3.48-100.00)	72.83 (12.56-99.94)	Static	Presence of topographic features (shelf-break, seamounts)
Chlorophyll a (CHL, mg m ⁻³)	0.61 (0.22-1.39)	0.63 (0.22-1.39)	0.48 (0.27-1.07)	Dynamic	Ocean productivity domains
CHL temporal change (CHLT, %)	46.59 (6.82-88.59)	46.79 (6.82-88.59)	45.43 (7.13-87.76)	Dynamic	Small-scale CHL variability
Sea surface temperature (SST, °C)	27.71 (25.43-29.95)	27.74 (25.43-29.95)	27.53 (25.46-29.49)	Dynamic	Water mass distribution
SST temporal change (SSTT, %)	10.60 (5.71-15.74)	10.59 (5.71-15.74)	10.67 (5.80-14.79)	Dynamic	Small-scale SST variability
Distance to coastline (COAST, km)	2.73 (0.03-7.22)	2.76 (0.03-7.22)	2.54 (0.09-6.25)	Static	Onshore-offshore distribution patterns
Distance to reef (REEF, km)	0.87 (0.03-4.60)	0.90 (0.03-4.60)	0.70 (0.04-3.31)	Static	Reef influence on dolphins diet
Distance to 100 m isobath (BATH100, km)	6.42 (0.19-18.44)	6.84 (0.19-18.44)	4.06 (0.63-11.61)	Static	Proximity to shelf-break (slope currents, vertical mixing and prey concentration)
Distance to oceanographic front (FRONT, km)	24.14 (0.19-106.38)	24.77 (0.19-106.38)	20.51 (0.92-102.14)	Dynamic	Mesoscale frontal systems

Finally, marine top predators are associated with oceanographic fronts as they find favourable feeding conditions and this will likely influence their distribution and abundance (Worm et al., 2005). MGET's Cayula-Cornillon Fronts tool was used to identify these fronts by detecting the edge of adjacent water masses of different SST with the Cayula-Cornillon algorithm (Cayula and Cornillon, 1992), using the SST images from AVHRR Pathfinder SST dataset (Casey and Evans, 2008).

2.2.5 Species distribution modelling

We used a habitat modelling approach to identify those environmental variables that most accurately described the key marine areas for dolphins within the information-theoretic approach (Fig. 2.2)(Louzao et al., 2009).

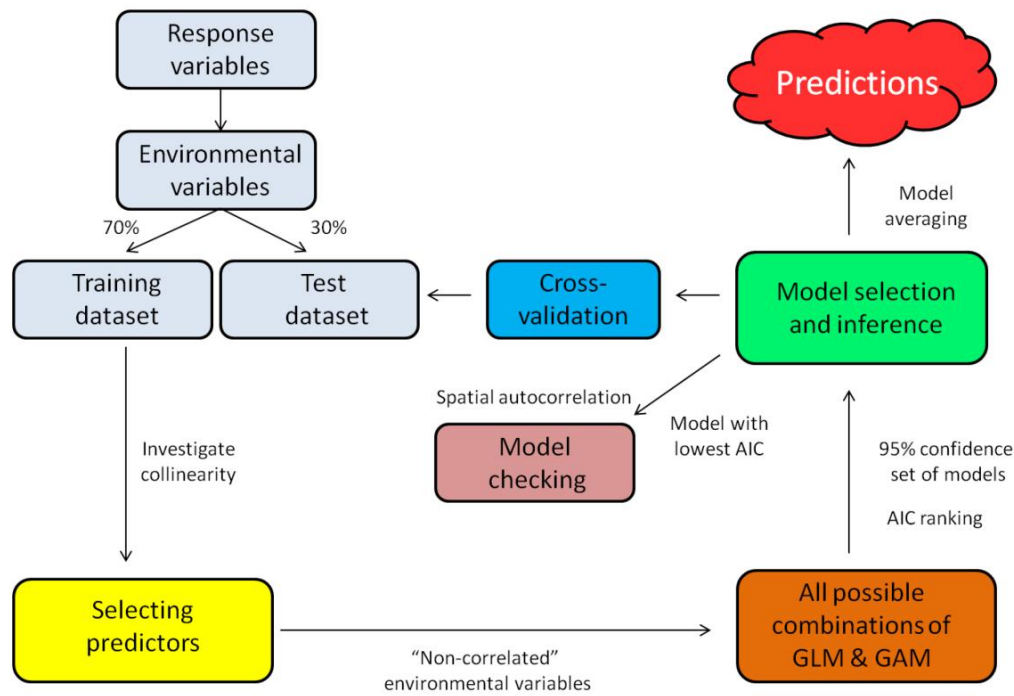


Fig. 2.2 Workflow of the habitat modelling procedure applied

2.2.5.1 Selecting environmental predictors

First, we investigated the colinearity between predictor estimating pairwise Spearman-rank correlation coefficient, which identified highly correlated variables ($|rs| \geq 0.7$), previously standardized (Mannocci et al., 2014) (Table 2.2). Second, to keep the most explanatory environmental variable we ran Generalized Linear Models (GLMs) to check which of these pairs of variables better explained the observed response variable using the Akaike Information Criteria (AIC) value, using only one predictor at a time. The model with a lower AIC value explained better the response variable. The same procedure was applied for each of the three ecological measurements (presence-absence, sightings and group size data), leading to the removal of GRADIENT and CHLA.

Table 2.2 Pairwise correlation between predictor variables by means of Spearman-rank correlation coefficient.

	Season	logBathy	Dist	logDist_reef	Dist_100	Gradient	Temp	Tempchange	Chla	Chlchange	logFront
Season		0.02	0.06	0.05	-0.03	-0.04	-0.68	-0.05	-0.30	-0.41	0.17
logBathy	0.02		0.43	0.66	-0.62	-0.44	-0.04	0.05	-0.53	-0.02	-0.10
Dist	0.06	0.43		0.44	-0.46	-0.35	-0.14	0.00	-0.46	-0.08	-0.19
logDist_reef	0.05	0.66	0.44		-0.32	-0.72	-0.08	-0.01	-0.27	0.00	-0.07
Dist_100	-0.03	-0.62	-0.46	-0.32		0.29	0.09	-0.04	0.85	0.07	0.14
Gradient	-0.04	-0.44	-0.35	-0.72	0.29		0.06	-0.01	0.25	0.01	0.06
Temp	-0.68	-0.04	-0.14	-0.08	0.09	0.06		0.64	0.26	0.14	0.28
Tempchange	-0.05	0.05	0.00	-0.01	-0.04	-0.01	0.64		-0.02	-0.13	0.45
Chla	-0.30	-0.53	-0.46	-0.27	0.85	0.25	0.26	-0.02		0.27	0.16
Chlchange	-0.41	-0.02	-0.08	0.00	0.07	0.01	0.14	-0.13	0.27		-0.21
logFront	0.17	-0.10	-0.19	-0.07	0.14	0.06	0.28	0.45	0.16	-0.21	

2.2.5.2 Model construction

We used Generalized Linear Models (GLMs) and Generalized Additive Models (GAMs) to examine the relationship between response variables and explanatory variables. In the case of occurrence data, we developed logistic regressions using a binomial distribution and logit link function. Number of sightings and group size were modelled following a negative binomial distribution. This model was selected over the Poisson distribution since the latter showed overdispersion in the null model. Additionally, the number of kilometres per grid (i.e., survey effort) was included as an offset term, therefore preventing from possible biases produced by uneven sampling. In GAM models, the smoothing splines were limited to a maximum of 3 degrees of freedom to capture non-linear associations without increasing the complexity of the functions towards unrealistic conclusions (Ferguson et al., 2006). Models were built within the R environment (version 2.15.3; R Development Core Team 2013) using 'MASS' (Venables and Ripley, 2002) and 'mgcv' packages (Wood, 2006).

2.2.5.3 Model selection and multimodel inference

We implemented the information-theoretic approach to evaluate competing models by assessing their relative support in relation to observed data, rather than using the best single model approach (Burnham and Anderson, 2002). Models were constructed for all possible combinations of explanatory variables and then ranked depending on the support of each of these models using the AIC values and the Akaike weight (Burnham and Anderson, 2002). The Akaike weight of each model is the relative likelihood of that model compared with the remaining models and was used to identify the 95% confidence set of models. To identify the 95% confidence set, we selected the model with the highest Akaike weight and added the models with the next highest weights until the cumulative Akaike weights > 0.95. When the model with lowest AIC value has an Akaike weight value lower than 0.9, a model averaging procedure might be more appropriate to account for model and parameter uncertainty (Burnham and Anderson, 2002). The model averaged predictions were expected to be more robust than those from single best model approach. Averaged coefficients were estimated using the MuMIn package (Barton, 2013).

2.2.5.4 Model checking

Species distribution data are characterised by spatial autocorrelation since distribution data in close location are more similar than would be expected in randomly distributed data (Lennon, 2000). Significant spatial autocorrelation can invalidate the common assumption that observations are independent, and identify spurious significant relationships (Type I error) (Hurlbert, 1984). Spatial autocorrelation was checked on the residuals of the model with the lowest AIC using the Moran's I index (Moran, 1950) and spatial correlograms with the 'ncf' package (Bjørnstad, 2013). The Moran's I index ranges from -1 (negative autocorrelation – perfect dispersion) to +1 (positive autocorrelation – perfect correlation), with values around zero being indicative of random spatial patterns (Moran, 1950). The spatial correlogram estimate the spatial dependence through testing significance within each

distance class by a randomization test (Bjornstad et al., 1999). We did not include any spatial autocorrelation structure in our models since we did not find significant spatial autocorrelation (Table 2.3).

Table 2.3 Model checking results (Moran's I index values).

Ecological measurement	Model	TRAIN DATA		TEST DATA	
		Moran's I index	p-value	Moran's I index	p-value
Presence/absence	GLM	0.0011	0.1373	0.0001	0.1981
	GAM	0.0008	0.1682	-0.0012	0.2274
Sightings	GLM	0.0010	0.1304	-0.0020	0.2111
	GAM	0.0003	0.1871	-0.0026	0.2684
Group size	GLM	0.0012	0.1231	-0.0044	0.1896
	GAM	-0.0003	0.2091	-0.0015	0.2058

2.2.5.5 Model evaluation

A crucial stage of the species distribution models (SDMs) is to determine the predictive ability of final models to assess their applicability in conservation and management programmes. To this end, we used a cross-validation procedure to evaluate the accuracy of final models. Models were built with the 70% of the original data (training data: 2006, 2007 and 2008) and evaluated on the remaining 30% (test data: 2009). The predictive performance of models was measured through the concordance index (*C-index*) with the R package 'Hmisc' (Harrell, 2001). The *C-index* is applicable to continuous and categorical data, as the predictive discrimination is related to a rank correlation between predicted and observed outcomes (Harrell et al., 1996). This index is identical to the most widely used measures for model discrimination, the area under the Receiver Operating Characteristic curve (AUC) (Hanley and McNeil, 1982). The *C-index* ranges from 0 to 1 and models with values from 0.7 onwards are considered with good discrimination ability (0.7-0.8: 'moderate discrimination', 0.8-0.9: 'good discrimination'; 0.9-1: 'excellent discrimination') (Swets, 1988).

2.2.5.6 Ensemble predictions

Averaged models of GLMs and GAMs were combined to produce an ensemble prediction since the accuracy of SDMs predictions could be improved by applying consensus methods (Araújo and New, 2007; Araújo et al., 2005; Crossman and Bass, 2007; Marmion et al., 2009). The weighted average (WA) consensus method was used to create the ensemble predictions from single-model predictions assigning weights to each model and using the pre-evaluated *C-index*, as follows (Marmion et al., 2009): $WA_i = \sum_j (C-index_{mji} \times mj_i) / \sum_j C-index_{mji}$, where mj_i are the probability-of-occurrence of values of the i th model in a given grid cell for the j -selected single-models for which pre-evaluation *C-index* values were the highest.

2.2.6 Identifying key marine areas for dolphins to measure the influence of the existing MPA.

To identify priority marine areas for dolphins in southern Kenya, we predicted the spatial distribution of three quantitative ecological measurements through maps of 1x1km resolution with R. We extracted seasonal predictors from 2006 to 2008, training data, and applied the 95% of confidence set of models to forecast the occurrence, sightings and group sizes distributions. From this, we obtained an average prediction of the study area and calculate the standard deviation (SD) to measure the stability of the predicted distribution, with stable and unstable habitat represented by low and high SD (Louzao et al., 2011). We combined these predictions to define three categories of distribution areas (Louzao et al., 2013) (1) recurrent areas, where dolphins are frequently observed every year, represented by grid cells with high mean (higher than the average mean across all grids cells and study years) and low SD (lower than the average SD across all grid cells and study years); (2) occasional areas, where dolphins' presence varies from year to year, represented by grid cells with high SD (higher than the average SD across all grid cells and study years); and (3) unfavourable areas, where dolphins are almost never seen, represented by grid cells with low mean (lower than the average mean across all grid cells and three years) and low SD (lower than the average SD across all grid cells and three years). Recurrent and occasional cells were used to define key areas for dolphins.

Finally, to evaluate how the existing MPA encompasses key habitat areas we compared the percentage of each category of distribution areas and mean predictions inside and outside the MPA for each of the occurrence and abundance models, and applied sequential t tests (Louzao et al., 2013).

2.2.7 Abundance estimates

The ensemble predictions obtained for sightings and group size on each grid cell were multiplied to predict abundance of dolphins (Cañadas and Hammond, 2006). As we did not apply line transect methodologies (Spyrakos et al., 2011), we calculated an approximate effective sampling width with the distance and angles data from the 2008-2009 sightings (those data were not recorded for the 2006-2007). The average effective sampling width was 92 m (SD \pm 92). Thus, we assumed that we missed only a small part of dolphins' sightings. The total number of dolphins on the study area was obtained by summing the previously predicted abundance of all the grid cells.

Table 2.4 Searching effort per year and numbers of the three ecological measurements.

Year	Seasons	Searching effort (Km)	Number of grid cells present	Sightings	Group size
2006	4	3887	73	131	981
2007	4	3757	89	137	1184
2008	2	1849	42	70	747
2009	4	4009	94	152	1601
Total	14	13502	298	490	4513

2.3 Results

We conducted a total of 551 dedicated vessel-based surveys between 2006 and 2009 (Table 2.4). Overall, dolphins were present in 77 of the total 194 surveyed grid cells, with an average of 2.53 (SD \pm 5.48) sightings and 23.26 (SD \pm 52.22) individuals per group. During the surveys, dolphins were mainly encountered on the east side of the study area, with the highest number of sightings and group sizes within and around the MPA, and the lowest in the North-East side of the survey area (Fig. 2.3).

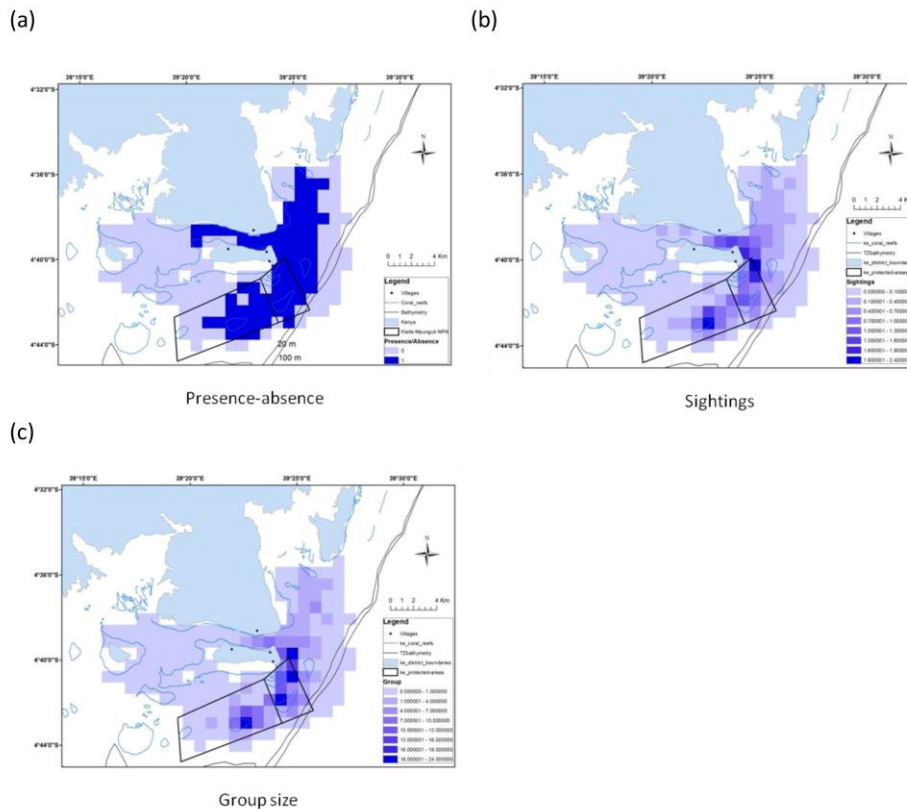


Fig. 2.3 Observed distributions of all three ecological measurements.

2.3.1 Modelling ecological measurements

2.3.1.1 Modelling occurrence data

The model with the lowest AIC (Mw/AIC) included only 3 explanatory variables with an Akaike weight (A_w) value of 0.239 in the case of GLM, indicating that a model averaging approach should be applied (Table 2.5). A total of 52 models were combined in the 95% confidence set and were used to estimate the average model and reduce model uncertainty. The deviance explained by Mw/AIC was 9.84% and 6.28% in the train and test data respectively (Table 2.5). BATH100 and FRONT were the predictors with the strongest negative effect, showing the highest presence probabilities close to the 100 meter isobath and oceanic fronts (Fig. 2.4). Regarding model evaluation, GLM had a good ability to discriminate between areas where dolphins were present and absent (note C-index values > 0.8 ; Table 2.5).

In the case of GAM modelling, the MwIAIC included 5 variables with an Akaike weight value of 0.264, and 13 models were averaged to reach the 95% confidence set (Table 2.5). REEF and FRONT were the most important variables describing dolphin occurrence; higher presence probability occurring in close proximity to the reefs and frontal systems, in shallow waters relatively close to the shelf-break (Fig. 2.4). The explained deviances were higher compared to GLM with both train and test data (approximately 18% and 19%, respectively)(Table 2.5). Model averaged showed good model performance, but poorer than the GLM in both datasets. The weighted average (WA) consensus method values indicated that ensemble predictions were the best discriminating trained data and very similar to GLM on the cross-validation (Table 2.5).

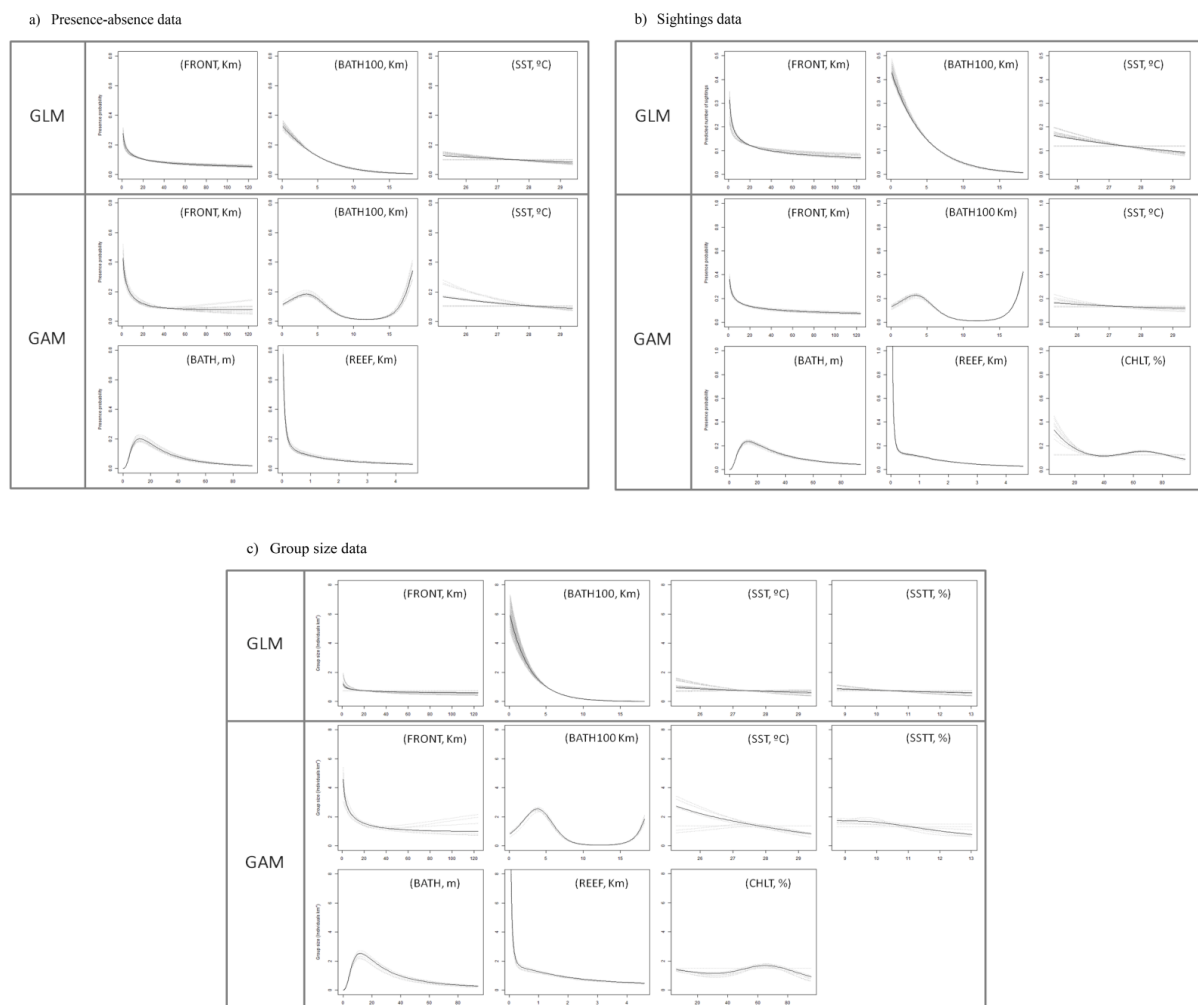


Fig. 2.4 Functional relationship between dolphins predicted probability and predictors based on GLM and GAM output

2.3.1.2 Modelling sightings data

In terms of GLM output, the MwIAIC had an Akaike weight value of 0.279, and 45 models were needed to achieve the 95% confidence set towards diminishing present uncertainty (Table 2.5). This model explained 15% of the train data of dolphin sightings, while explaining only the 10% of the test data.

BATH100 and FRONT were the most influential variables, in addition to CHLT in a minor degree, having predictive functional relationships analogous to the occurrence models (Fig. 2.4). Averaged GLM models yielded good predictions for trained and tested sightings data (Table 2.5).

For GAM models, a similar Akaike weight value to the GLM models was obtained for the best model, but explaining a much higher percentage of the variance (27.00% in train data and 31.10% in test data) (Table 2.5). Sightings probability increase adjacent to the reefs, at waters depths between 5 to 30 meters which are influenced by small variations on chlorophyll among seasons (Fig. 2.4). The 8 averaged models showed a high moderate performance for training and test datasets. By contrast, the ensemble predictions yielded the best model performance values for training data and comparable to GLM on the test data (Table 2.5).

2.3.1.3 Modelling group size data

A total of 4513 individual dolphins were counted on the 490 sightings over the four years of study period. For GLM, the MwLAIC had an Akaike weight of 0.221, and 102 models were averaged to achieve the 95% confidence set to reduce model uncertainty (Table 2.5). Explained deviances by the best models were comprised around 15% for both training and test data. BATH100 was the most important predictor showing the highest group size probability close to the shelf-break (Fig. 2.4). Averaged group size models yielded good discrimination predictions, slightly lower compared to the GLM occurrence and sightings models (Table 2.5).

Table 2.5 Summary of the habitat modelling output and model evaluation.

Ecological measurement	Model	ED from MwLAIC		# variables in MwLAIC	Number models in 95CS	TRAIN DATA		TEST DATA	
		TRAIN DATA	TEST DATA			Mean C-index	SD C-index	Mean C-index	SD C-index
Presence/absence	GLM	9.84	6.28	3	52	0.86	0.03	0.85	0.04
	GAM	17.50	19.00	5	13	0.81	0.03	0.78	0.04
	Ensemble	NA	NA	NA	NA	0.87	0.03	0.84	0.04
Sightings	GLM	15.27	10.20	3	45	0.85	0.03	0.84	0.03
	GAM	27.0	31.10	6	10	0.79	0.03	0.78	0.04
	Ensemble	NA	NA	NA	NA	0.86	0.02	0.84	0.03
Group size	GLM	15.14	15.81	4	102	0.82	0.03	0.81	0.03
	GAM	28.60	41.30	7	7	0.77	0.03	0.75	0.04
	Ensemble	NA	NA	NA	NA	0.84	0.03	0.81	0.04

ED: explained deviance. MwLAIC: Model with Lowest Akaike's Information Criteria (AIC). 95CS: 95% confidence set. C-index: concordance index

2.3.2 Dolphin abundance estimations.

The estimated total abundance for the 2006-2008 period was 91.54 ± 55.32 dolphins, with an average predicted abundance of 0.83 ± 1.74 dolphins/km². The highest abundance predictions occurred within the MPA with 54.85 ± 40.75 dolphins compared to the 36.69 ± 18.30 dolphins outside (Fig. 2.5).

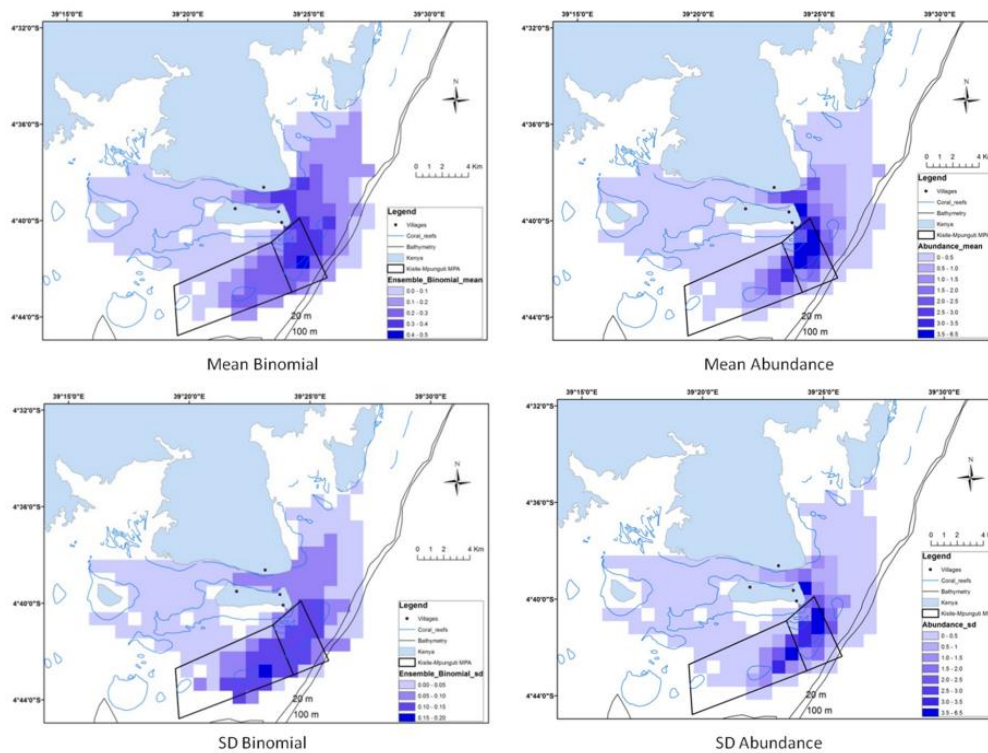


Fig. 2.5 Distribution maps of the binomial and abundance predictions (Mean and SD) over the 2006 and 2008 period (training data).

2.3.3 Key areas for dolphins

Our model predictions matched observed patterns within the range of the dolphins and identified important distribution areas on the east side of the study area (Fig. 2.5). The MPA was identified as a critical area for all three ecological measurements, with high variability (SD) in predictions probably due to seasonal variations (Fig. A1.1 in Appendix 1). The occurrence models predicted the highest dolphin probabilities within the MPA and on the east side of Wasini Island (Fig. 2.5). For abundance models, predicted maps matched the key areas identified by the occurrence models, but the maximum abundances were concentrated on a smaller area (Fig. 2.5). In this case, the highest probabilities were mostly encountered within the MPA.

The combination of the previous predictions maps resulted in the identification of recurrent, occasional and unfavourable habitats (Fig. 2.6). The ensemble predictions of the occurrence and abundance models defined a 59% and 71% of unfavourable habitats within the study area respectively, and a total of 31% and 18% combining recurrent and occasional habitats for each ensemble prediction (Fig. 2.7). However, an important percentage (47%) of these recurrent and occasional areas was identified inside the MPA using presence-absence models and a 57 % using abundance models. Moreover, presence probability and abundance predictions were significantly higher within the MPA than outside (for occurrence predictions $t=-6.622$, $P>0.05$; for abundance predictions $t=-6.618$, $P>0.05$), showing the higher preference for these areas (Fig. 2.8).

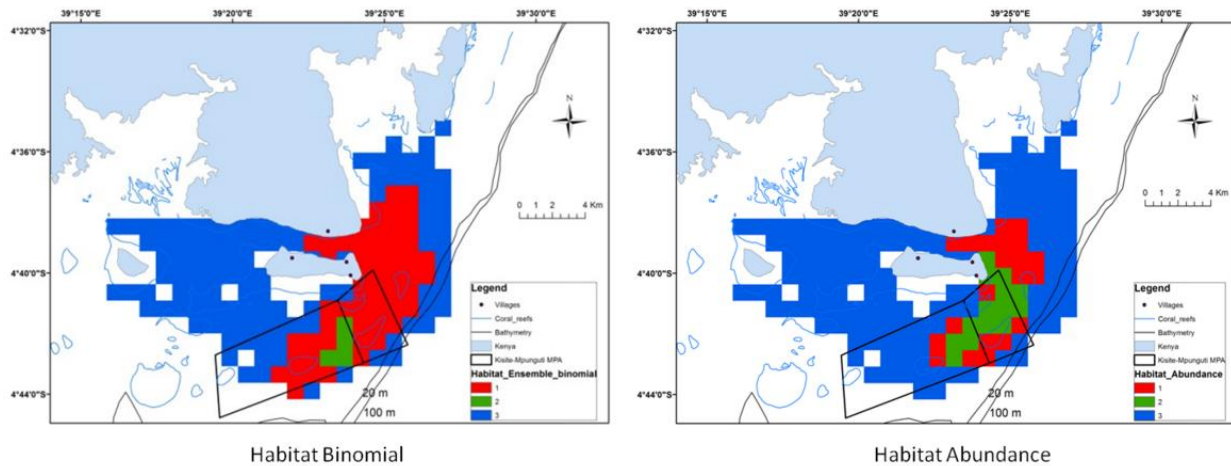


Fig. 2.6 Type of habitats for the binomial and abundance predictions over the 2006-2008 period (training data). (1) recurrent areas, (2) occasional areas; and (3) unfavourable areas.

2.4 Discussion

2.4.1 Spatial ecology of coastal dolphins

As a result of our integrative ecological modelling approach, we ascertain that both static and dynamic variables influenced the spatial ecology of the *T. aduncus*. Our modelling showed that the reefs inside the MPA and along the east side of Wasini Island are selected by coastal dolphins. This habitat preference is supported by previous studies on the foraging ecology of the species, that found *T. aduncus* to feed upon inshore reef fish and cephalopods (Amir et al., 2005). In addition to reef prey, species comprised within the *Tursiops* genera feed upon alternative prey such as bathydemersal fish and cephalopods in offshore waters along the WIO (Cockcroft and Ross, 1990). Thus, the strong influence of the isobaths of 100m on dolphin spatial ecology would likely indicate that they exploit not only inshore (shallow waters) but also offshore waters (proximity to deep waters) feeding on different prey.

In addition to static features, the spatial ecology of coastal dolphins was strongly affected by dynamic variables such as distance to frontal systems, when oceanographic fronts are closer to shore. Oceanographic fronts are important features due to their intense mesoscale activity where processes of upwelling/downwelling take place that enhance marine productivity, leading to the formation of predictable prey patches (Worm et al., 2005). Other dynamic variables that played a secondary role on driving sightings and group size patterns were SST and CHL. Several studies have linked cetacean habitat preferences to dynamic variables, showing the effect of these predictors to define the species distribution (Cañadas et al., 2005; Pirodda et al., 2011).

2.4.2 Transferring modelling outputs into a MPA context

Species distribution models (SDM) are the first essential step to understand the influence of environmental drivers on the spatial distribution of a given species. Previous studies have shown that non-parametric regression methods, such as GAMs, had better predictive performance than parametric methods, such as GLMs (Elith and Graham, 2009). In comparison, our results yield slightly higher predictive performance for GLMs than GAMs for the three ecological measurements. Despite these minor differences in predictive performance, both techniques provided very different spatial predictions, probably due to the underlying assumptions relationship between the modelling technique and the environmental predictors (Ready et al., 2010). Additionally, comparing the predictions from all models revealed that occurrence and sightings models had marginally better discrimination ability than group size models. The accuracy of the predictive models was improved by applying consensus methods and combining them into an ensemble model, reducing also the uncertainty from the most traditional approach of selecting the best model from an ensemble of forecasts (Araújo and New, 2007). Another way of minimising model uncertainty was through the multimodel inference based on the information-theoretic approach. To our knowledge this is the first time that ensemble models and model averaging are used to predict marine mammal habitats.

To develop effective conservation science, modelling outputs have to be discussed directly within the context of a MPA. For instance, this study highlights the association of coastal dolphins to static as well as dynamic oceanographic variables, revealing the need to incorporate dynamic and spatially explicit conservation actions for marine top predators (Hyrenbach et al., 2000). Recent conservation planning demands a shift to more dynamic and adaptive management of marine resources to adjust to the current challenges facing the marine environment and marine species (Game et al., 2008). While it is important to consider dynamic marine features (*e.g.*, eddies, fronts) to identify pelagic biodiversity hotspots for the establishment of dynamic MPAs (Game et al., 2009), we need to recognize that those MPAs pose a management challenge compared to static systems established as permanent closures (Silva et al., 2012).

2.4.3 Conservation implications: the role of existing MPA for coastal dolphins

An effective ecosystem-level management of a MPA depends acutely upon the quality of information available, not only for delineating boundaries but also to understand how these areas are used by animals and which components influence their distribution and abundance (Wilson et al., 1997). Our modelling output evidences the positive benefits of the existing MPA for coastal dolphins, whose occurrence and abundance were higher within this spatial-based management unit than outside. In addition, there is evidence that other taxonomic groups have benefited from the establishment of this and other MPAs along the coast of Kenya. For instance, abundance and biomass of coral reef fish have significantly increased since the establishment of the existing MPA (McClanahan et al., 2006). While the use of presence-absence data determined 31% of the total study area as recurrent and occasional

areas, the abundance data reduced to only 18% of the area. This shows the hierarchical patterns of distributions, with localised areas of high relative abundance nested within the distribution area used by the species in the study area (Fauchald and Tveraa, 2003). Nevertheless, 53% and 43% of recurrent and occasional areas occurred outside the MPA using presence-absence and abundance models respectively, suggesting that MPA does not encompass the whole ecological needs of dolphins. Finally, more than 65% of our study area was defined as unfavourable for Indo-Pacific bottlenose dolphins, probably due to multiple factors such as non-optimal environmental conditions, evolutionary strategies to reduce competition with other closely related species (*e.g.*, *Sousa chinensis* (Meyler et al., 2012)) and intensive fishing (Pérez Jorge, unpublished data).

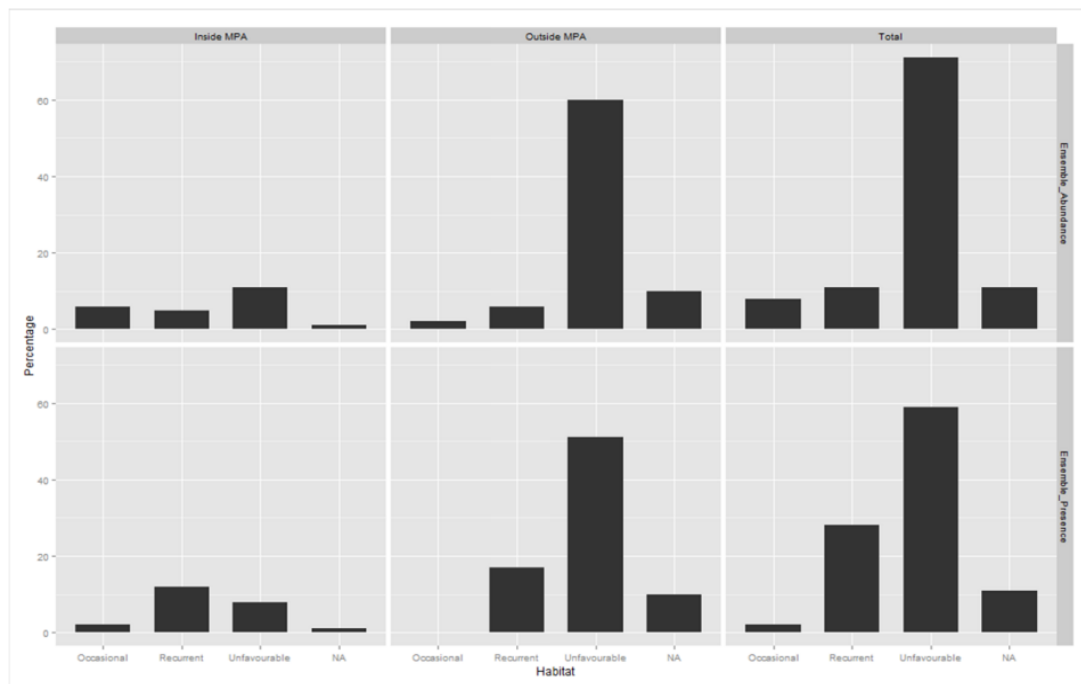


Fig. 2.7 Percentage of areas with recurrent, occasional and unfavourable habitats inside and outside the MPA for the predicted ensemble binomial and abundance. A 10.52% of grid cells have no category due to the lack of sampling during certain periods.

An optimal design of an MPA expected to protect a population would include the entire year-round distribution of that population (Reeves, 2000). Although the design for some resident or non-migratory species may be possible to achieve, the protection of highly migratory or mobile species present a major challenge for spatial management. Thus, when only a small portion of a population's range can be included within a MPA, it is crucial to protect critical habitats for the species' survival (*e.g.*, breeding and foraging areas) where they are particularly vulnerable to anthropogenic impacts (Hooker and Gerber, 2004). This study determined that the area encompassed by the MPA is certainly insufficient to satisfy the spatial requirements of the species, not covering a high percentage of the recurrent areas that constitutes critical habitat for vital activities every year. However, areas containing critical habitat outside the MPA are partially incorporated in the proposed collaborative co-management initiative introduced by the Kenyan government in 2006 (Roccliffe et al., 2014). Co-management areas are developed and enforced by local bylaws with respect to the use of and access of fisheries. Early findings

suggest that they increase fish biomass if an effective compliance takes place (Cinner and McClanahan, 2015). Nevertheless, this will require further investigation due to the recent implementation of these co-management initiatives.

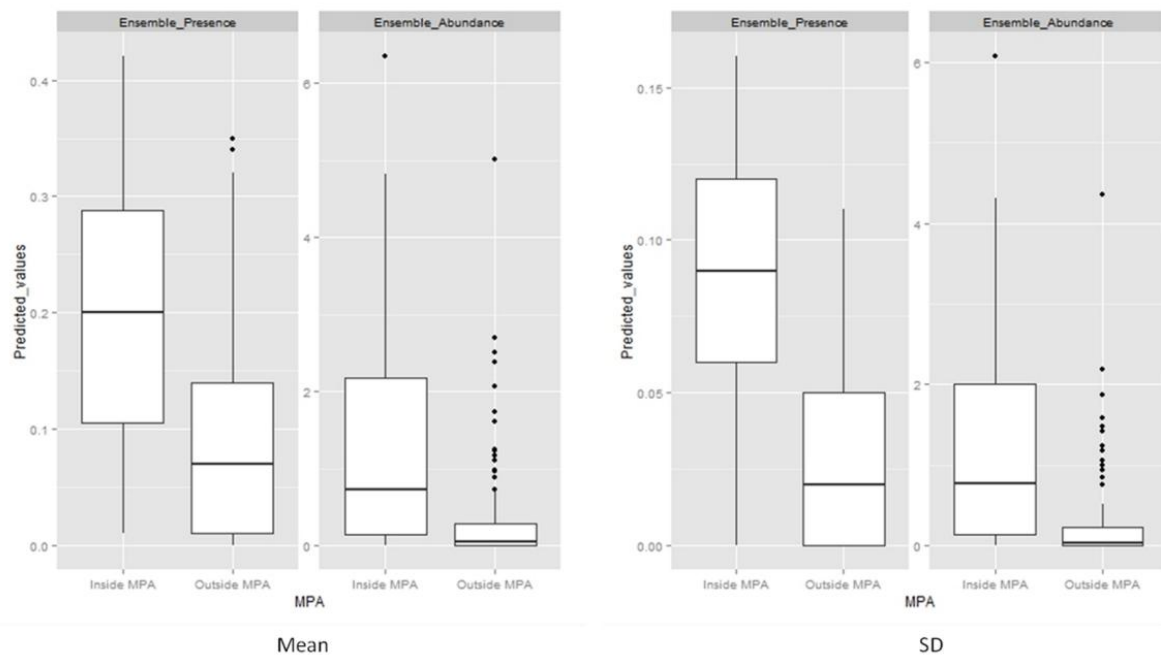


Fig. 2.8 Mean and SD of the binomial and abundance predictions (median, 25-75%, inter-quartile range, non-outlier range, and outliers) in relation to the MPA (inside-outside).

MPAs have been advocated for the conservation of marine mammals, but few examples have empirical evidence that they are effective (Gormley et al., 2012). Quantifying the effects of MPAs is crucial to evaluate their efficiency as management tools and the protection of the species (Kelleher, 1999). The results from this study suggest that Kisite-Mpunguti MPA represents an important area that seemingly encompasses key habitat features of ecological and behavioural importance to the Indo-Pacific bottlenose dolphins, and it should be considered as a critical habitat for the species which requires special management considerations. This species is important ecologically, as a potential indicator species which protection may ensure the health of other key elements of the marine ecosystem, and economically, through the growing dolphin-watching industry (Hooker and Gerber, 2004). It has been shown that dolphin tourism can have negative impacts on dolphin populations, especially when not monitored or unsustainably managed (Christiansen et al., 2010). Impacts may be long-term and life-threatening; both at the individual and population level (Bejder et al., 2006). Other anthropogenic impacts on the cetacean populations such as overfishing (Moore, 2013) and seismic exploration (Cerchio et al., 2014) have recently been identified as the main threats for marine mammals around Kisite-Mpunguti MPA (Kenya Wildlife Service, 2011). Especially taking into account the restricted inshore habitat of the species, it is important to evaluate the effectiveness of the code of conduct implemented by Kenya Wildlife Service in 2007 as well as, to assess the other identified threats.

2.5 Conclusions

We provide two key conservation and management tools: (i) an integrative habitat modelling approach to predict key marine habitats, and (ii) the first study evaluating the effectiveness for marine mammals of an existing MPA in the WIO. Our results show how the modelling technique selection may influence the identification of key marine areas, and how using ensemble models can improve the predictive performance, successfully predicting areas of importance of a given species. We recommend the use of these robust ensemble models for decision makers in designing and identifying MPAs. In the case of coastal dolphins, these ensemble predictions forecast a higher occurrence and abundance of dolphins within the MPA, covering a large percentage of recurrent and occasional areas (47% and 57% using presence-absence and abundance models respectively), but does not adequately protect all of them. We propose to extend the protection to incorporate all occasional and recurrent areas, which are critical habitats for the species. MPAs not only benefit fish and invertebrate populations, but also improve the prey base for top marine predators and reduce their threats through spatial protection (Hooker and Gerber, 2004; Reeves, 2000). We highlight the need to analyze the level of actual protection of existing MPAs as it may not provide the proper representation for upper-trophic level species. Finally, this study could also be applied to evaluate the potential effects on the distribution and abundance of top marine predators within a global change scenario, taking into account that climate change will affect the distribution and availability of prey in the short and long term (Harwood, 2001).

2.6. Acknowledgements

We are very grateful to all volunteers and staff for collecting dolphin observations and participating in the GVI conservation projects. We want to thank Graham Corti, Rachel Crouthers, Inês Gomes, Edita Magileviciute, Andrew and Kirsty Hayes for leading the marine programme. We would also like to thank the authorities and elders of Mkwiwo and Shimoni and their communities at large for their hospitality and on-going support since 2006. ML was funded by a *Juan de la Cierva* postdoctoral contract (JCI-2010-07639, Ministerio de Ciencia e Innovación) and a *Ramón y Cajal* postdoctoral contract (RYC-2012-09897). Funds were partially provided by a grant from the Spanish Ministry of Economy (CGL2013-42203-R). We are grateful for the constructive comments provided by Dr James Nifong, which helped to improve the manuscript.

CHAPTER 3

3. Effects of nature-based tourism and environmental drivers on the demography of a small dolphin population

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In Review on Biological Conservation

3.1 Introduction

As populations of marine top predators decline worldwide (Pauly et al., 1998), there is an urgent need to estimate robust demographic parameters to accurately inform and assess management decisions. Assessing population dynamics for long-lived and highly migratory marine species is complex but an essential component for managing populations. Marine top predators play a major role on the structure and functioning of marine ecosystems, and are dependent upon a broad range of trophic links within the marine food web (Heithaus et al., 2008). As a result, these species are vulnerable to anthropogenic pressures, climate variability and subsequent habitat alterations (Barbraud and Weimerskirch, 2001), fisheries interactions (Lewison et al., 2004), and overfishing among others. Thus, understanding the effects of biotic and abiotic factors on demographic parameters can provide valuable information to evaluate changes in these populations (Weimerskirch et al., 2003).

Mark-recapture modelling techniques have been widely used to estimate population dynamics and demographic parameters (Oro et al., 2004b). These methods have traditionally been developed from either closed population models, where no population losses (through emigration or death) occur along the sampling period, or open, which rely on the assumption that all emigration is permanent. Consequently, animal population studies can introduce bias into demographic parameters if temporary emigration is not correctly accounted for (Fujiwara and Caswell, 2002). Pollock's robust design, which combines close and open population models under a nested sampling framework, brings a more biologically realistic approach into the analysis by allowing animals to temporarily emigrate and return to the study area (Kendall et al., 1997; Pollock et al., 1990). The significance of estimating the probability of temporary emigration has been proved in multiple taxa: amphibians (Muths et al., 2006), bats (Frick et al., 2010), voles (Kendall et al., 1997), and marine top predators (Kendall and Bjorkland,

2001), including marine mammals (Smith et al., 2013). In fact, many studies have recognized that temporary emigration fluctuates due to temporal components that may reveal changes on environmental conditions or seasonal behavioural patterns (Dwyer et al., 2014; Smith et al., 2013). This temporal variation has also been reported in capture probability (Silva et al., 2009), which has been suggested to be partially linked to temporary emigration (Muths et al., 2006). However, to our knowledge, temporary emigration parameters modelled as a function of candidate biotic or abiotic covariates has received little quantitative attention in cetacean demographic studies.

Investigating how environmental variations shape the dynamics of animal populations is of paramount importance in an increasingly changing world (Barbraud and Weimerskirch, 2001). Recent studies have evidenced the effect of climate change and anthropogenic activities on local fish stocks, and how changes in prey availability can impact on marine top predators populations (Ford et al., 2010). In the case of cetaceans, exposure to human disturbance, through dolphin-watching, can caused short term changes on individuals activity such as: breathing rates (Janik and Thompson, 1996); diving times (Ng and Leung, 2003); swimming directions (Lemon et al., 2006) or specific behavioural states (Christiansen et al., 2010). In addition, it can cause long-term effects on cetacean vital rates, such as a decrease in female reproductive success (Lusseau et al., 2006b) or a decline in relative abundance (Bejder et al., 2006). At the population-level, consequences depend upon the proportion of the population exposed to different levels of human interactions. Moreover, repeated human disturbance is significantly more important if it occurs within the core habitat of the species, or is concentrated during critical periods, which can affect the viability of the population (Bejder et al., 2006; Williams et al., 2006). As a result, the estimation of demographic parameters is considered a crucial step for identifying negative impacts on animal populations (Gormley et al., 2012).

Particularly, demographic studies on cetacean populations are urgently needed in the Western Indian Ocean (WIO) due to the increase of potential anthropogenic threats in the area (e.g., overfishing, dolphin-watching, seismic exploration)(Kenya Wildlife Service, 2011). Based on demographic modelling, we studied the population dynamics of the IUCN data deficient Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) in southern Kenya at the Kisite-Mpunguti Marine Protected Area (KMMPA). Specifically, we assessed four years of mark-recapture data to fit multiple competing models to investigate a set of hypothesis about dolphin population parameters within the Information Theoretic Approach. We considered the effect of natural factors (oceanographic conditions and prey availability) and human disturbance. Regarding the latter, artisanal fishing and tourism are the main economic activities for local communities, and dolphins are considered flagship species and the main attraction for the 60,000 yearly park visitors (Emerton and Tessema, 2001). We estimate seasonal temporary emigration movements influenced by environmental, human disturbance or fisheries covariates. In addition, we examined whether capture probabilities showed any time-dependent effect. Finally, we estimated seasonal population abundances across the study period. This study overcomes the challenge of integrating multiple data sources to study the effect of natural and human-related pressures on the population dynamics of a highly mobile predator.

3.2 Material and Methods

3.2.1 Study area

Kisite-Mpunguti Marine Protected Area (KMMPA, 04°04'S - 39°02'E), located on the southern coast of Kenya, lies south of Wasini Island and incorporates the Kisite Marine Park, the largest no-take area in Kenya (28km²), and the adjacent Mpunguti Marine Reserve, Kenya's smallest reserve, where traditional fishing is allowed (11 km²)(Fig. 2.1). This MPA was established in 1978 and it has been under the administration of the Kenya Wildlife Service (KWS) since 1988. KMMPA covers shallow waters (<20 meters depth) and supports a high marine biodiversity from corals to marine mammals and sea turtles.

3.2.2 Sampling methods

Boat-based surveys were conducted on a monthly basis all year around between January 2006 and December 2009 off the south coast of Kenya (with the exception of the period comprised between January and June 2008 due to national political instability). Searching effort was carried out with Beaufort sea states ≤ 3 , low swells and good visibility (≥ 1 km), reducing the probability of missing dolphins. When a group was sighted, we recorded on location and time of the sighting, group size and group composition. A group was defined as the total number of individuals encountered, moving in the same direction or engaged in the same activity, within 100 metres of each other (Wells et al., 1987).

3.2.3 Data analysis

3.2.3.1 Photo-identification process

Photo-identification was performed following standard cetacean protocols (Würsig and Jefferson, 1990). Dolphins within photographic range were photographed irrespective of their level of marking in order to have an unbiased estimation of the number of animals with marks in each mark class (Wilson et al., 1999). Because several pictures contain more than one individual, the term "fin image" was used to refer to a single dorsal fin in a picture (Verborgh et al., 2009). Each fin image was given information on sighting number, frame number, date, flank, angle (every 30° starting from 0° when the dolphin was facing the camera), individual fin image quality "Q" and code of the individual in the photo-identification catalogue. The quality rating (Q) was assigned on a scale of 0 to 2 (poor to excellent) considering four characteristics: exposure, focus, size and orientation. Every individual dorsal fin image was compared to a photo-identification catalogue which included left and right dorsal fins from previously identified animals. This process was verified by two independent researchers to minimize misidentifications. Nicks and marks on the leading and trailing edges of the dorsal fin were used to identify individual Indo-Pacific bottlenose dolphins (Wilson et al., 1999). A quality marking level (M) was given to each animal in the catalogue ranging from 1 (few nicks/marks) to 3 (highly marked). Individuals showing light marks were assigned to M₁ were lightly marked and those with conspicuous marks to levels M₂ and M₃ (Verborgh et al., 2009)(Fig. 3.1).To minimise heterogeneity resulting from mark

distinctiveness, only dorsal fin images with Q1 and Q2 and well marked individuals were used on the analysis. Our analysis did not include calves, as they were not enough marked for identification and recapture. For more detail see 'Robust design assumptions' section in Supporting information

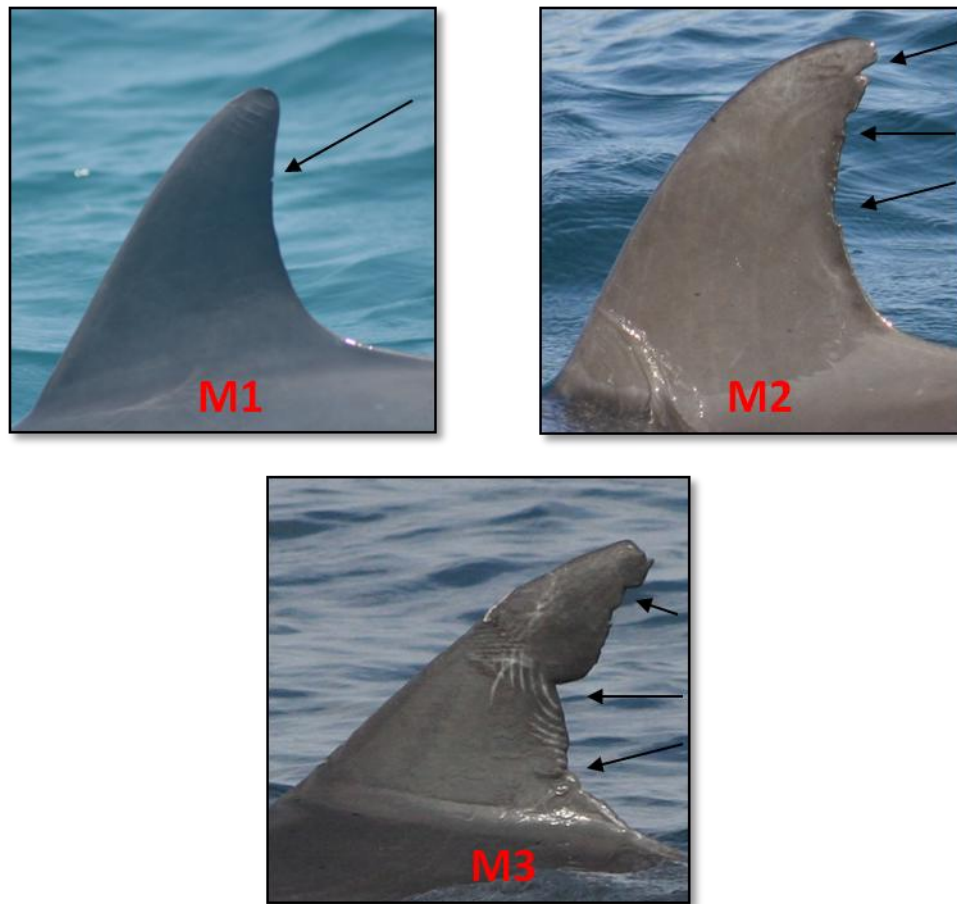


Fig. 3.1 Individual dolphins with a marking level 1 (M_1), level 2 (M_2) and level 3 (M_3)

3.2.3.2 Covariates description

Covariates were selected based on their potential influence on dolphin demography: anthropogenic factors such as tourist boats and swimmers numbers, oceanographic variables or prey availability (Table 3.1). Studies have shown that tourist boats can have negative impacts on dolphin populations, especially when dolphin-watching activities are not monitored or sustainably managed (Christiansen et al., 2010). Impacts may be long-term and life-threatening; both at the individual and population level (Bejder et al., 2006). We predicted that the number of tourist boats operating around the MPA could influence the presence of dolphins in the area. Specifically, we hypothesized that spring months (April–June) would have the largest number of dolphins, as this is the season with the lowest number of tourist boats. We also predicted that a higher number of swimmers would negatively affect the probability of dolphin encounters, as tourists snorkel during their trips around Kisite Island, which is the core habitat for the Indo-Pacific bottlenose dolphin (Pérez-Jorge et al., 2015). We obtained 4 variables to assess the possible impact of the dolphin-watching tourism: number of tourist boats (BOATS) and swimmers (SWIMMERS) having access to the MPA on a given month. We also considered both

covariates of the previous month (BOATS_1 and SWIMMERS_1) in order to account for time-lag effects. Kenya Wildlife Service collected this data through the number of tourists and boats paying park fees to enter Kisite-Mpunguti MPA (KWS, unpublished data).

Table 3.1 Description of covariates for modelling the demography of coastal dolphins considering human-related pressures, prey availability and environmental variables, as well as the overall mean and values range (between brackets). The type of predictor (human or environmental) is also described as well as the source of the data.

Habitat variables	All data	Variable category	Comments
Swimmers numbers (SWIMMERS)	3942 (640-6764)	Human disturbance	Data provided by the Kenya Wildlife Service. KWS records the number of swimmers and boats paying park fees to access Kisite-Mpunguti Marine Protected Area
Swimmers numbers (SWIMMERS_1)	3990 (282-8793)		
Boat numbers (BOATS)	190 (31-451)		
Boat numbers (BOATS_1)	178 (29-359)		
Monthly Chlorophyll a (CHL, mgm-3)	0.76 (0.33-1.17)	Environmental	Monthly composite for SST and CHL were derived from aqua-MODIS sensor. SST and CHL were averaged across the study area per month (SST and CHL) and season (three months; SST_3 and CHL_3)
Seasonal Chlorophyll a (CHL_3, mgm-3)	0.73 (0.61-1.02)		
Monthly sea surface temperature (SST, °C)	27.86 (26.02-30.07)		
Seasonal sea surface temperature (SST_3, °C)	27.89 (25.83-29.18)		
Distance to oceanographic front (FRONT, km)	47.31 (8.07-115.81)		Fronts were detected on the edge of adjacent water masses of different SST with the Cayula-Cornillon algorithm, using the SST images from AVHRR Pathfinder SST dataset. The distance to the front was averaged for the study area per month (FRONT) and season (FRONT_3).
Seasonal distance to oceanographic front (FRONT_3, km)	25.74 (7.75-102.16)		
Total pelagic species landed (PELAGICS, kg)	5244 (2151-12407)	Fisheries	Family species recorded: Euthynnus pelamis, Mulilidae, Kanaguta, Sphyrnidae, Scombridae, Chorinemustol, Istiophoridae, Arangidae, Colyphaenidae
Total demersal species landed (DEMERSALS, kg)	6859 (5097-9910)		Family species recorded: Siganidae, Lethrinidae, Lutjanidae, Scaridae, Acanthuridae, Naso brevirostris, Haemulidae, Cephalopholis argus, Gaterin sordidus, Mulidae, Aprion virescens, Serranidae, Aridae
Total cephalopods landed (CEPHALPODS, kg)	4054 (2100-10256)		Family species recorded: Vulgaris spp, Sepia oligo
Total prey landed (TOTALPREY, kg)	19777 (14328-32562)		Family species recorded (including the previous Pelagic, demersal and cephalopod species): Carcharhinidae, Clupeidae, Penulirus spp, Paenus spp, Scyllariade, Holothuroidae

We predicted that monthly differences on sea surface temperature (SST) and chlorophyll (CHL) could critically influence dolphin's seasonal movement (e.g., temporary emigration), since they can adapt to specific temperature regimes and associate with highly productive areas (e.g., high chlorophyll a values) (Redfern et al., 2006; Stevick et al., 2002). In fact, both variables have been recently shown to be crucial in determining the habitat preferences and abundances of this Indo-Pacific bottlenose dolphin population, with CHL and SST negatively related to sightings and group size data (Pérez-Jorge et al., 2015). Monthly composite for SST and CHL were derived from aqua-MODIS sensor and converted with the Marine Geospatial Ecology Tool (MGET, Roberts et al., 2010) from their original formats to raster formats compatible with ArcGIS. SST and CHL were averaged across the study area per month (SST and CHL) and season (three months; SST_3 and CHL_3). Marine top predators are associated with oceanographic fronts as they find favourable feeding conditions and this will likely influence their distribution and abundance (Worm et al., 2005). MGET's Cayula-Cornillon Fronts tool was used to identify these fronts by detecting the edge of adjacent water masses of different SST with the Cayula-

Cornillon algorithm, using the SST images from AVHRR Pathfinder SST dataset. The distance to the front was averaged for the study area per month (FRONT) and season (FRONT_3). The spatial ecology of our targeted species has been described to be strongly influenced by oceanographic fronts, showing the highest occurrence and abundance probabilities when the fronts are close to the study area (Pérez-Jorge et al., 2015).

The distribution of dolphins is strongly influenced by the abundance and distribution of its prey (Sveegaard et al., 2012). For our study region, Indo-Pacific bottlenose dolphins feed upon inshore and reef fish and cephalopods (Amir et al., 2005). In addition to reef prey, species comprised within the *Tursiops* genera feed upon alternative prey such as bathydemersal fish and cephalopods in offshore waters along the WIO (Cockcroft and Ross, 1990). We then forecast a positive relationship between prey and dolphin abundance. We acquired monthly fisheries data on total amount of prey landed (TOTAL_PREY)(i.e. as an index of prey availability), pelagic species catch (PELAGIC), demersals species (DEMERSAL) and cephalopod species (CEPHALPOD). Data was prepared by the Fisheries department of the Kenyan Ministry of Fisheries Development, from the closest harbour to our study area (Shimoni). Fishing effort was conducted by small-scale artisanal fishermen that operate near shore (Gomes et al., 2014). Finally, photo-identification effort has been shown to influence cetacean's capture probability (Verborgh et al., 2009). We used the number of survey hours (corresponding to each primary sampling occasion) and photos analysed (dorsal fin images with Q1 and Q2), to test the hypothesis of an effort-dependent capture probability.

We investigated the collinearity between predictors by calculating pairwise Spearman-rank correlation coefficient, which identified highly correlated variables ($|rs| \geq 0.7$)(Table 3.2). This led to the removal of SST, CHL_3, SWIMMERS and BOATS_1.

Table 3.2 Pairwise correlation between predictor variables by means of Spearman-rank correlation coefficient.

	Season	Year	Hours	Swimmers	Swimmers_1	Boats	Boats_1	Photos	Totalprey	Demersals	Pelagics	Cephalopods	Temp	Temp_3	Chla	Chla_3	Front	Front_3
Season		0.00	-0.18	0.43	0.25	0.27	0.18	0.06	0.06	0.00	-0.45	0.04	-0.30	-0.40	-0.16	-0.10	-0.2	0.09
Year	0.00		-0.37	-0.30	-0.42	-0.37	-0.41	0.01	0.36	0.23	0.22	0.11	0.09	0.02	-0.38	-0.30	-0.26	-0.06
Hours	-0.18	-0.37		0.30	0.45	0.39	0.46	0.70	-0.11	0.19	0.06	-0.06	0.07	-0.03	0.01	-0.05	0.3	0.41
Swimmers	0.43	-0.30	0.30		0.76	0.90	0.71	0.37	0.20	0.19	0.11	-0.18	0.50	0.06	0.25	0.12	-0.54	-0.32
Swimmers_1	0.25	-0.42	0.45	0.76		0.65	0.97	0.29	0.32	0.21	0.01	0.22	0.05	-0.45	0.27	-0.03	-0.16	0.04
Boats	0.27	-0.37	0.39	0.90	0.65		0.67	0.46	0.13	0.07	0.09	-0.17	0.54	0.20	0.11	-0.07	-0.45	-0.32
Boats_1	0.18	-0.41	0.46	0.71	0.97	0.67		0.31	0.30	0.23	-0.03	0.22	0.05	-0.40	0.16	-0.18	-0.13	-0.03
Photos	0.06	0.01	0.70	0.37	0.29	0.46	0.31		-0.06	0.24	-0.01	-0.12	0.24	0.01	-0.40	-0.24	0.14	0.27
Totalprey	0.06	0.36	-0.11	0.20	0.32	0.13	0.30	-0.06		0.33	0.48	0.54	0.13	-0.30	0.09	-0.16	-0.56	-0.08
Demersals	0.00	0.23	0.19	0.19	0.21	0.07	0.23	0.24	0.33		0.35	-0.28	0.19	-0.17	0.03	-0.20	-0.07	0.06
Pelagics	-0.45	0.22	0.06	0.11	0.01	0.09	-0.03	-0.01	0.48	0.35		-0.27	0.61	0.36	0.22	0.12	-0.46	-0.11
Cephalopods	0.04	0.11	-0.06	-0.18	0.22	-0.17	0.22	-0.12	0.54	-0.28	-0.27		-0.47	-0.60	0.01	-0.12	0.07	0.22
Temp	-0.30	0.09	0.07	0.50	0.05	0.54	0.05	0.24	0.13	0.19	0.61	-0.47		0.74	0.07	0.28	-0.36	-0.58
Temp_3	-0.40	0.02	-0.03	0.06	-0.45	0.20	-0.40	0.01	-0.30	-0.17	0.36	-0.60	0.74		0.24	0.25	-0.61	-0.54
Chla	-0.16	-0.38	0.01	0.25	0.27	0.11	0.16	-0.40	0.09	0.03	0.22	0.01	0.24	0.07		0.78	-0.12	-0.12
Chla_3	-0.10	-0.30	-0.05	0.12	-0.03	-0.07	-0.18	-0.24	-0.16	-0.20	0.12	-0.12	0.25	0.28	0.78		-0.08	-0.09
Front	-0.20	-0.26	0.30	-0.54	-0.16	-0.45	-0.13	0.14	-0.56	-0.07	-0.46	0.07	-0.61	-0.36	-0.12	-0.08		0.68
Front_3	0.09	-0.08	0.41	-0.32	0.04	-0.32	-0.03	0.27	-0.08	0.06	-0.11	0.22	-0.54	-0.58	-0.12	-0.09	0.68	

3.2.3.3 Demographic parameters

We used the full-likelihood approach of the Pollock's closed robust design, which combines open and closed capture-recapture models to estimate annual apparent survival, temporary emigration, capture and recapture probabilities, and population size (Kendall et al., 1997). This methodology incorporates open sampling events called "primary periods", within which there are a number of closed "secondary periods". Primary periods allow population gains and losses between them, and temporal closure is assumed between secondary periods. Our primary periods were based on the following seasons: summer (January-March), autumn (April-June), winter (July-September), and spring (October-December). The time interval between primary periods was two and a half months (mean: 76.3 days; SD: 0.86), except for the period of Winter 2007-Spring 2008 and Autumn 2009-Spring 2009 that was 11.5 and 5.5 months, respectively, due to lack political instability and inability to perform fieldwork. Capture probabilities were fixed to 0 for those periods separated by more than two and a half months, as robust design analyses cannot estimate temporary emigration parameters when time intervals are unequal between primary periods. Secondary sampling occasions' data was collected within 15 day periods to fulfil the assumption of temporal closure within primary periods, to minimise the probability of dolphin movements in and out of the study area. To identify these 15 day periods, we calculated the daily number of individual dolphins identified on each period within each season, and choose those same periods within each season that had the highest count across the study. In total, we had 16 primary periods (seasons) and 53 secondary periods during the four years of the study (Table 3.3). For more details see 'Robust design assumptions' section in Supporting information.

Table 3.3 Summary table for the Robust Design data set structured into primary and secondary sampling periods. Primary periods were based on the following seasons: 1= Summer; 2 = Autumn; 3 = Winter; 4 = Spring. Secondary sampling occasions data was collected within 15 day periods.

	Year																
Sampling period	2006				2007				2008				2009				Total
Primary	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4	16
Secondary	6	3	2	4	6	5	5	0	0	0	4	6	3	3	0	6	53

Two general parameters were used to describe the process of temporary emigration: γ' and γ'' (Kendall et al., 1997). γ' determines the probability that an individual dolphin not present in the study area in a given time (t_i) remains outside the study area and is unavailable for capture in the next time unit (t_{i+1}). Thus, $(1 - \gamma')$ is the probability of not being present in the study area at time i (t_i) and moving into the study area and being available for capture at time $i + 1$ - i.e., *return rate of temporary emigrants*. γ'' determines the probability that an individual dolphin present in the study area at time i (t_i) temporarily emigrates of the study area and is unavailable for capture in time $i + 1$. Thus, $(1 - \gamma'')$ is the probability of remaining in the study area between time i and $i+1$. We combined these parameters to explore different models of temporary emigration: Markovian ($\gamma'' \neq \gamma'$), where the probability of an individual is present at time $i + 1$ depends on whether or not it was present at time t , random ($\gamma'' = \gamma'$) and no movement ($\gamma'' = \gamma' = 0$). Capture and recapture probabilities (p and c) were set equal on all fitted models,

as photo-identification protocols should not affect the recapture probabilities because do not require capture and/or handling of animals (Parra et al., 2006).

We defined multiple candidate models and followed a step down-approach (Lebreton et al., 1992) to estimate each one of the demographic parameters. First, we used the no movement model to investigate the effect of constant, season, year and a combination of season and year on capture probabilities, while keeping the dimensionality of the survival probabilities high and fixed (Lebreton et al., 1992). We also allowed capture probability to vary within and between primary periods, as well as a combination of both. In addition, we integrated different factors related with survey effort (the number of survey hours and photos analysed). Second, survival was estimated as constant, varying between primary periods, per season and year, based on the best fitting capture probability models. Third, temporary emigration parameters were estimated incorporating random and Markovian models, including constant and temporal effects with the best fitting models of survival and capture probability. Moreover, these emigration parameters were also modelled as a function of the previously described covariates, and were tested with other structures in capture probabilities to be sure that they did not change our results on survival and temporary emigration. Finally, we estimated the population size of well-marked individuals (M_2 and M_3) across primary sampling periods.

Our modelling approach allowed us to estimate the population of marked animals, as it relies on individuals identified through natural marks. To obtain the total population size, we need to adjust our estimates to incorporate the proportion of unmarked and slightly marked individuals (M_1), as follows:

$$\hat{N}_{total} = \hat{N}_m / \hat{\theta}$$

Where \hat{N}_{total} is the estimated total population size, \hat{N}_m the estimated well-marked population size and $\hat{\theta}$ the estimated proportion of well-marked individuals in the population. We calculated the correction factor ($\hat{\theta}$) as the total number of well-marked individuals (M_2 and M_3) divided by the estimated group size on each secondary sampling occasion (Daura-Jorge et al., 2013). We estimated a single correction factor for each primary sampling occasion averaging all correction factors within each primary period. The total population size includes calves, juveniles, and adults of both sexes combined.

The standard errors (SE) for the estimated total population size were derived from the following formula of approximate variance of \hat{N}_{total} , using the delta methods (B. K. Williams et al., 2002):

$$SE(\hat{N}_{total}) = \sqrt{\hat{N}_{total}^2 \left(\frac{SE(\hat{N}_m)^2}{\hat{N}_m^2} + \frac{1 - \hat{\theta}}{n\hat{\theta}} \right)},$$

Log-normal 95% confidence intervals were calculated, with a lower limit of $\hat{N}_{total}^L = \hat{N}_{total}/C$ and upper limit of $\hat{N}_{total}^U = \hat{N}_{total}/C$ where (Burnham et al., 1987)

$$C = \exp \left(1.96 \sqrt{\ln \left(1 + \left(\frac{SE(\hat{N}_{total})}{\hat{N}_{total}} \right)^2 \right)} \right)$$

3.2.3.4 Model selection

Pollock's closed robust design models do not have a goodness-of-fit (GOF) test to validate the assumptions of equal probabilities of capture and survival between individuals. We used the program U-CARE to test the fit of our data, previously pooled into primary sessions, and estimate the variance inflation factor (\hat{c}) (Choquet et al., 2009). We incorporated \hat{c} into the Quasi-Akaike Information Criterion corrected for small sample size (QAICc), which accounts for overdispersion (Hurvich and Tsai, 1989). Models were compared and selected using the QAICc, and used the lowest QAICc to identify the most parsimonious model. Models were built within the R environment (version 2.15.3; R Development Core Team 2013) using 'RMark' (Laake, 2013), which uses custom scripts to call program MARK (White and Burnham, 1999).

3.3 Results

We conducted 551 dedicated vessel-based surveys between 2006 and 2009, resulting in 13850 km of survey effort (Table 2.4). A total of 367 photo-identification sessions were performed and 28601 photos were taken, resulting in 137 individuals identified. Among these, 20% were classified as slightly marked individuals (M_1) and 80% as well-marked (M_2 and M_3)(Fig. 3.1). The individual recapture rate ranged from 1 to 75 with an average of 19 (SD: 19.76) recaptures along the study period. From these data, the 15 days period with the maximum number of well-marked identifications was the fifth period of each season (first and second week of March, June, September and December), with 302 of the total 1319 identifications (23%). Using these data, the number of individual dolphins identified within primary periods was 85 well-marked individuals, ranging from 1 to 29 on each secondary sampling period. A total of 66% of the bottlenose dolphins were identified over two years and 40% of them were present over three years. The proportion of well-marked individuals using the study area was calculated to be 0.65 (SD: 0.16).

3.3.1 Model selection

The goodness-of-fit test run in U-CARE indicated a reasonable overdispersion in our data (Global Test: $\chi^2 = 72.501$, $df = 33$, $\hat{c} = 2.2$), showing the presence of transients (TEST 3. SR, $p = 0.008$) and trap-dependence (TEST 2.CT; $p = 0.01$). We acknowledge that this moderate extra-binomial variation existed, likely due to heterogeneity caused by factors such as age, sex or willingness to approach vessels. Thus, we used QAICc adjusted by that \hat{c} to account for this overdispersion.

Table 3.4 Summary of the best 12 models from model selection results. Parameters: S denotes survival, γ' and γ'' denote temporary emigration (Markovian ($\gamma'' \neq \gamma'$), random ($\gamma'' = \gamma'$)), p denotes capture probability, c denotes recapture probability, Nm denotes Number of marked individuals and session denotes time varying between primary occasions. Capture and recapture probability were set equal on all fitted models. Quasi-Akaike information criterion corrected for small sample size (QAICc).

Id	model	npar	QAICc	Δ QAICc	Weight	QDeviance
1	$S(\sim 1)\text{Gamma}''(\sim \text{BOAT})\text{Gamma}'(\sim \text{SST_3})p(\sim \text{season})=c(\sim \text{season})Nm(\sim \text{session})$	19	454.87	0.00	0.24	761.73
2	$S(\sim \text{Year})\text{Gamma}''(\sim \text{BOAT})\text{Gamma}'(\sim \text{SST_3})p(\sim \text{season})=c(\sim \text{season})Nm(\sim \text{session})$	20	455.11	0.23	0.22	759.76
3	$S(\sim 1)\text{Gamma}''(\sim \text{SWIMMERS_1})\text{Gamma}'(\sim \text{SST_3})p(\sim \text{season})=c(\sim \text{season})Nm(\sim \text{session})$	19	456.39	1.51	0.11	763.24
4	$S(\sim \text{Year})\text{Gamma}''(\sim \text{SWIMMERS_1})\text{Gamma}'(\sim \text{SST_3})p(\sim \text{season})=c(\sim \text{season})Nm(\sim \text{session})$	20	456.59	1.72	0.10	761.25
5	$S(\sim 1)\text{Gamma}''(\sim \text{season} + \text{Year})\text{Gamma}'(\sim \text{SST_3})p(\sim \text{season})=c(\sim \text{season})Nm(\sim \text{session})$	20	457.75	2.88	0.06	762.41
6	$S(\sim 1)\text{Gamma}''(\sim \text{BOAT})\text{Gamma}'(\sim \text{CEPHALOPODS})p(\sim \text{season})=c(\sim \text{season})Nm(\sim \text{session})$	19	457.82	2.94	0.06	764.67
7	$S(\sim \text{Year})\text{Gamma}''(\sim \text{SST_3})\text{Gamma}'(p(\sim \text{season})=c(\sim \text{season})Nm(\sim \text{session}))$	18	458.15	3.27	0.05	767.19
8	$S(\sim \text{Year})\text{Gamma}''(\sim \text{season} + \text{Year})\text{Gamma}'(p(\sim \text{season})=c(\sim \text{season})Nm(\sim \text{session}))$	19	458.41	3.53	0.04	765.26
9	$S(\sim 1)\text{Gamma}''(\sim \text{Year})\text{Gamma}'(\sim \text{SST_3})p(\sim \text{season})=c(\sim \text{season})Nm(\sim \text{session})$	19	459.08	4.20	0.03	765.93
10	$S(\sim 1)\text{Gamma}''(\sim \text{season})\text{Gamma}'(\sim \text{SST_3})p(\sim \text{season})=c(\sim \text{season})Nm(\sim \text{session})$	19	459.12	4.25	0.03	765.98
11	$S(\sim 1)\text{Gamma}''(\sim \text{SWIMMERS_1})\text{Gamma}'(\sim \text{CEPHALOPODS})p(\sim \text{season})=c(\sim \text{season})Nm(\sim \text{session})$	19	459.20	4.32	0.03	766.05
12	$S(\sim \text{Year})\text{Gamma}''(\sim \text{SWIMMERS_1})\text{Gamma}'(\sim \text{CEPHALOPODS})p(\sim \text{season})=c(\sim \text{season})Nm(\sim \text{session})$	20	459.28	4.40	0.03	763.93

The best fitting model incorporated a constant annual survival rate and seasonal capture probabilities (24% of QAICc weight; Model 1 in Table 3.4; Table A2.1 in Appendix 2). This model also integrated a Markovian emigration with γ'' depending on the number of boats, and γ' depending on the seasonal temperature. For comparison, the second best model had a similar percentage of support based on QAICc weights (Δ QAICc = 0.23; Model 2 in Table 1; Table A2.1 in Appendix 2) and was similar to the best fitting model except survival was year-dependent. These two models shared the same temporary emigration structure, demonstrating a significant support (46% of QAICc weight) for the influence of nature-based tourism and environmental drivers on demographic parameters. In addition, Model 3 and 4 also fitted the data adequately (Δ QAICc < 2, 11% and 10% of AIC weights, respectively; Table A2.1 in Appendix 2), and were similar to the top model except γ'' , which depended on the number of swimmers present the previous month. Markovian emigration models were supported by 91% of all models, showing a greater support for this population structure.

3.3.2 Parameters estimates

Our best fitting model estimated a constant annual apparent survival rate of 0.96 (SE: 0.002, 95% CI: 0.94-0.98). Although, an increasing apparent survival rate, ranging from 0.93 (SE: 0.007, 95% CI: 0.86-0.96) in 2006 to 0.99 (SE: 0.002, 95% CI: 0.94-1.00) in 2009, was supported by 44% of the best models (Table A2.1 in Appendix 2). Seasonal capture probabilities ranged from 0.18 to 0.21, with a mean value of 0.19 (SE: 0.007).

The two best fitting models estimated the probability that an individual available for capture on previous occasions temporarily emigrated from the study area (γ'') depend upon the number of tourist boats, and ranged from 0.12 (95% CI: 0.05-0.30) to 0.75 (95% CI: 0.54-0.89)(Fig. 3.2). This matches our predictions, indicating that as the number of tourist boats operating in the MPA increases, the probability of temporary emigration increases. For example, due to the high number of boats in March 2006, the probability of temporary emigration from the study area increased to relatively high values of

0.75 (CI: 0.54-0.89). Additionally, a positive correlation was found between the number of swimmers present on the previous month and dolphins temporarily leaving from our area (Fig. 3.3).

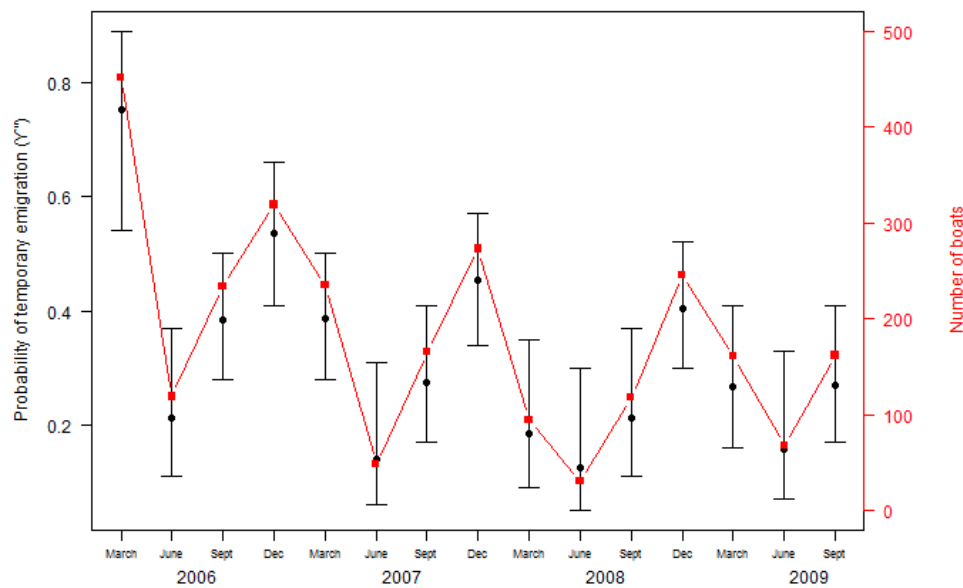


Fig. 3.2 Relationship of probability of temporary emigration (Y'') and number of boats between 2006 and 2009 around Kisite-Mpunguti Marine Protected Area (KMMPA). Vertical bars represent 95% confidence intervals.

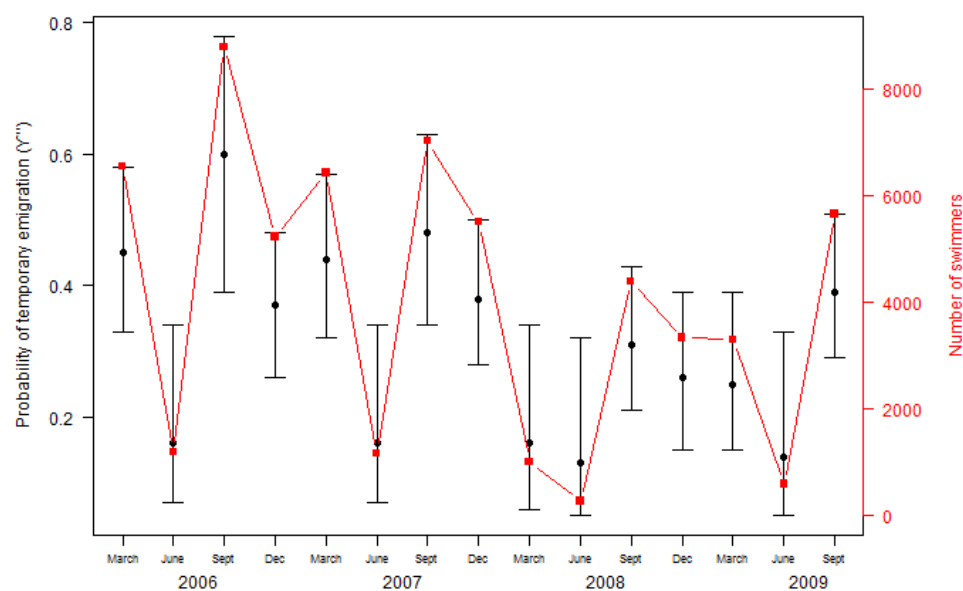


Fig. 3.3 Relationship of probability of temporary emigration (Y'') and number of swimmers of the previous month between 2006 and 2009 around Kisite-Mpunguti Marine Protected Area (KMMPA). Vertical bars represent 95% confidence intervals.

The probability that an individual that was outside the study area on a previous occasion remained outside it (Y'), relied on the seasonal temperature, ranging from 0.23 (95% CI: 0.12-0.39) to 1.00 (95%

CI: 0.73-1.00). Thus, the return rate of temporary emigrants to the study area ($1-\gamma'$) was linked to the sea surface temperature, suggesting that warmer periods had a lower probability of animals returning to the study area in the following months (Fig. 3.4). The models including the impact of tourism exposure explain an important part of our γ' variability; nevertheless we cannot discard that this variability is time-dependent, through an additive effect of season and year. Model 5 and 8 also showed the effect of season and year explaining 6% and 4% of the variance respectively (Table 3.4). None of the effects of the fisheries covariates tested on temporary emigration were retained in the best models (Table 3.4).

The number of total individuals using the study area varied along the four study years, ranging from 20 (SE: 4.50, 95% CI: 11-36) in June 2007 to 102 (SE: 10.11, 95% CI: 77-136) in December 2009 (Fig. 3.5). These abundance estimates were roughly stable from 2006 to 2009, with a mean of 62 dolphins (SE: 6.66). Heterogeneity models using two point finite mixtures (different capture probabilities among individuals)(Pledger, 2000) resulted in overparameterised models and led to non-identifiability of several parameters due to small population size and low capture probabilities.

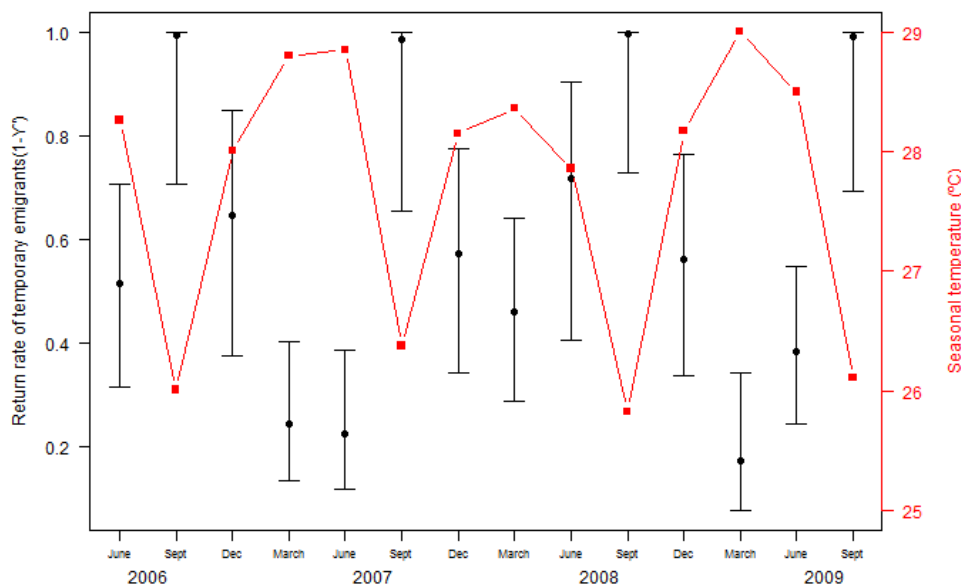


Fig. 3.4 Relationship of return rate of temporary emigrants ($1-\gamma'$) and seasonal temperature (°C) between 2006 and 2009 around Kisite-Mpunguti Marine Protected Area (KMMPA). Vertical bars represent 95% confidence intervals.

3.4 Discussion

Our results demonstrate the importance of understanding temporary emigration movements in cetacean populations, due to the effect of multiple pressures. Importantly, we found that human disturbance and seasonal temperature influence the probability of animals leaving and entering the study area. These emigration parameters have seldom been addressed, and temporary emigration

movements have often been identified as time-dependent (e.g., varying by season or year), independently of being random or Markovian (Nicholson et al., 2012; Smith et al., 2013).

3.4.1 Tourism impact on dolphins leaving the study area

Our best fitting Markovian model determines a positive correlation between the probability of animals temporarily leaving the study area and the number of boats present. Our results indicated that up to 75% of the population left the study area in March 2006, which recorded the highest number of boats entering Kisite-Mpunguti MPA since its implementation in 1978 (Ministry of Tourism, 2010), with 451 boats and 6246 tourists present. It is important to notice that no code of conduct was present and swimming with dolphin was frequent in the area. However, in 2007, a code of conduct was drawn and started to be implemented, which prohibited swim-with dolphins and limited the distance and number of boats around them, as major changes for the dolphin-watching activity. In 2008, a significant drop in tourism (40% of the 2006 tourism), along with the swimming with dolphin prohibition, resulted in few animals leaving temporally the area during the month of June (49 boats and 1555 tourists). This temporal area avoidance means that dolphins inhabiting the MPA, the most critical core habitat for the species (Pérez-Jorge et al., 2015), temporarily move away when tourism intensity increase (i.e., number of swimmers and tourist boats). Additionally, groups of females with calves are common (authors' personal observation), and these groups are known to be negatively affected by high levels of tourism (Stensland and Berggren, 2007). In New Zealand, it has been reported that an increase in swim-with dolphins' attempts led to higher levels of swimmers avoidance, suggesting that animals became more sensitive to swimmers (Constantine, 2001). The likelihood that human disturbance lead to population-level consequences rely on its potential to impact on life-history traits, as well as on the proportion of the population subjected to these perturbations, which can also modify their life-history traits (Currey et al., 2009b). Based on the above, our results may indicate that the number of temporary emigrants is likely related to the displacement of more sensitive individuals away from the perturbation area (Bejder et al., 2006; Lusseau et al., 2009). This provides strong evidence on the impact of tourism in local cetacean demography and the importance of regulating dolphin-watching tourism, specifically the presence of boats and swimming with dolphins.

In addition to the nature-based tourism influence, we should also take into account that this variability on the probability of dolphins temporarily emigrating from the study area is time-dependent, as it was identified among the best five models with higher explanatory power, through an additive effect of season and year. Previous studies have described this time-dependent effect, suggesting that some individual dolphins leave the study area for various seasons or years but subsequently return (Silva et al., 2009; Smith et al., 2013).

3.4.2 Influence of seasonal temperature on the return rate of temporary emigrants

We found a negative correlation between the probability of temporary emigrants returning to the study area and seasonal SST. The high variability of temporary emigration was likely due to seasonal

movements and behavioural aspects of the species ecology driven by environmental conditions. Dolphins had a higher return rate during winter months, not supporting the hypothesis of temporary emigrants entering the study area seeking for mating opportunities during the peak-breeding season of spring and summer as previously described in other studies (Fury et al., 2013; Smith et al., 2013). Positive relationship between lower temperatures and increased cetacean occurrence seems to be related with higher abundance of prey items (Smith and Whitehead, 1996). In this regard, Kisite-Mpunguti MPA has one of the highest fish species abundance and biomass along the Kenyan coast (McClanahan et al., 2010, 2006). However, in our study, prey availability did not show a significant effect on the temporary emigration models which can be related with a non-linear relationship among prey catch and prey abundance and availability (Pauly et al., 2013), and therefore, landing data might not be reflecting dolphin prey availability. In addition, there is a lack of studies on the local diet composition of Indo-Pacific bottlenose dolphins, which might not be fully represented on the prey landing data. For these reasons, further investigations are needed to uncover the causes behind the temporary emigration movements.

3.4.3 Survival rates and population size

Life history theory predicts high survival in marine mammals, given their low reproductive rate and long life spans (Wells, 1991). In this study, apparent survival rates were fairly high and consistent with known survival rates for *Tursiops sp.* (Nicholson et al., 2012; Silva et al., 2009). Adult survival estimates (0.970 ± 0.029 SE) have been described to be significantly higher than those for sub-adults (0.815 ± 0.083 SE) (Silva et al., 2009). Similarly, lower survival rates were estimated for adult males compared to adult females at all ages, with larger difference occurring around the age of 15 years (Stolen and Barlow, 2003). Although we cannot distinguish between ages and sexes in our study, a plausible hypothesis for our survival increase would be age or sex specific differences in apparent survival rates between years.

Our findings provide the first robust abundance estimates for the Indo-Pacific bottlenose dolphin in Kenya. This study highlights the small population size and its seasonal fluctuations, ranging from 20 to 102 individuals, similar to previous studies for this species (Fury and Harrison, 2008; Möller et al., 2002; Smith et al., 2013). It has been considered that populations with less than 100 dolphins had a higher extinction risk, regardless of conservation measures adopted (Thompson et al., 2000). Additionally, small populations might be particularly vulnerable to human disturbances due to their high site fidelity and coastal distribution. In the western Indian Ocean, a population of bottlenose dolphins has already been classified, and another one is proposed to be classified as Endangered under the IUCN Red List criteria (IUCN and MNHM, 2012; Pusineri et al., 2014). Moreover unsustainable levels of dolphins' bycatch have been reported in Zanzibar, about 100km south from our study area, where an adjacent community of Indo-Pacific bottlenose dolphin is resident (Amir et al., 2002). Despite the high survival rates estimated in this study, bycatch could represent a concern for the dolphin population inhabiting around Kisite-Mpunguti MPA, since known individuals have been already identified in other locations, like Watamu, which lies 140km north (authors, unpublished data).

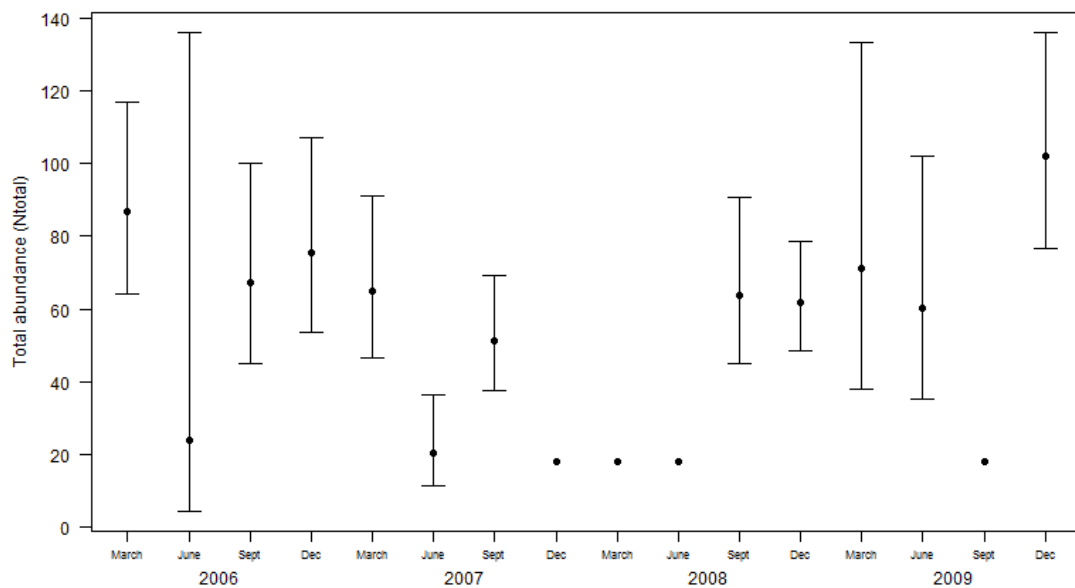


Fig. 3.5 Seasonal abundance estimates (Ntotal) of the Indo-Pacific bottlenose dolphins between 2006 and 2009 around Kisite-Mpunguti Marine Protected Area (KMMPA). Vertical bars represent 95% confidence intervals.

3.5 Conclusions

Our modelling approach highlights the importance to incorporate biotic and abiotic variables to study temporary emigration movements, which have been poorly described in cetacean species. Emigration movements are crucial in the dynamics of spatially structure populations, and have the potential to act as key aspects to determine management strategies for endangered or threatened populations. Moreover, these movements may be a resilient strategy that allows cetaceans to mitigate impacts under unfavourable situations. Our results show that seasonal SST and exposure to tourism influence temporary emigration. Understanding the effect of sea temperature variations on demographic parameters may help to predict how global change could affect local dolphin populations. Furthermore, investigating the impact of anthropogenic activities is crucial for the sustainable management of any nature-based tourism activity. The impact of tourist boats and swimmers on the dolphin's temporary emigration seems to have been reduced after the suitable implementation of a new code of conduct. Other management actions, such as area or time closures, have been successfully implemented when unregulated and unmanaged cetacean-watching tourism has been identified as a potential threat to cetacean populations (Constantine et al., 2004; Notarbartolo-di-Sciara, 2009). Finally, it is important to maintain the long-term monitoring of this dolphin population, to be able to document tourism fluctuations, their consequences and to apply adaptive management strategies (Lahoz-Monfort et al., 2014).

3.6 Acknowledgements

We are very grateful to all volunteers and staff for collecting dolphin observations and participating in the GVI conservation projects. We want to thank Zeno Wijtten, Thalia Pereira, Chloe Corne, Rachel Crouthers, Edita Magileviciute, and Andrew Hayes for leading the marine programme. We would also like to thank the authorities and elders of Mkwiro and Shimoni and their communities at large for their hospitality and their support from 2006 to 2015. Data for fisheries and tourists were provided by Fisheries Department in Shimoni. Maite Louzao was funded by a Ramón y Cajal (RYC-2012-09897) postdoctoral contract. Permission to work in the Kisite-Mpunguti Marine Protected Area was provided by Kenya Wildlife Service (KWS). We are grateful for all the support from KWS staff. Helpful comments were provided by Meritxell Genovart, Alejandro Martínez-Abraín, Daniel Ponce-Taylor, Gary White, Kenneth Pollock, Jeff Laake and two anonymous referees improved the manuscript.

CHAPTER 4

4. Watch out for tourists! Current impact of nature-based activities in coastal dolphin populations in southern Kenya

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Ready to be submitted

4.1 Introduction

Over the last decades, the impact of human disturbance on wildlife populations has increased worldwide due to the growing of nature-based tourism, which involves tours to national parks and wilderness areas where a major percentage of the world's biodiversity is concentrated (Balmford et al., 2009; Olson et al., 2001). Consequently, human-wildlife interactions are becoming more common and repeatable in time with potentially severe impacts on the conservation status of targeted species (e.g. Currey et al., 2009). In marine ecosystems, whale-watching is one of the main drivers of nature-based tourism, and the study of human disturbance on different aspects of the biology and ecology of those species have focused a growing attention in the last years (Higham et al., 2014). Indeed, the increased exposure to high levels of boat-based tourism has been shown to cause behavioural disturbance, such as changes in breathing rates, diving times (Ng and Leung, 2003), swimming directions (Lemon et al., 2006) and group formation (Bejder et al., 1999). In addition, repeated short-term behavioural impacts can have cumulative negative effects on an animal's behavioural budget, which is directly related to its energy budget (Christiansen et al., 2013). Such cumulative effects can in turn lead to long-term negative effects on individual vital rates, such as decreased female reproductive success (Lusseau, 2003b). At the population-level, negative effects of human disturbance, resulting from changes in vital rates, would depend on the proportion of the population that are subjected to the various levels of disturbance. However, as disturbances are likely to vary across space and time, it might lead to differences in impacts between individuals within a population, and also seasonally (Christiansen et al., 2015; Pirodda et al., 2014).

Whale-watching activities have grown globally at an annual rate of 12% through the 1990s, showing a much higher increasing rate than that of the overall tourism industry (Hoyt, 2001; O'Connor et al., 2009). Currently, the whale-watching industry, with 13 million whale-watchers globally, benefits coastal communities with an estimated \$US 2.1 billion per annum, and has generated more than 13,000 jobs (O'Connor et al., 2009). Indeed, Cisneros-Montemayor et al. (2010) pointed out that an extra \$413 million and 5,700 jobs could be generated within the current whale-watching industry, being half of these potential benefits created in developing countries (as defined by the UN; United Nations Development Programme, 2007). In Kenya, the whale-watching industry has grown from 8,300 tourists in 1997 to almost 42,500 in 2013, which equals an annual growth rate in tourist numbers of nearly 11% (Kenya Wildlife Service, unpublished data). However, the highest number of tourists was recorded in 2006, when more than 60,000 visitors went whale-watching. However, due to political unrest in Kenya the tourism industry suffered multiple drops along the period between 1997 and 2013, with up to a 53% decline on visitors between some years (Kenya Wildlife Service, unpublished data).

A small population of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) inhabiting Kisite-Mpunguti Marine Protected Area (KMMPA) is the main focus of the largest dolphin-watching industry in Kenya (Hoyt, 2005; Pérez-Jorge et al., 2015). This MPA attracts the largest number of visitors of all Kenya's marine parks and, in turn, this MPA provides the highest revenue along the Kenyan coast (Kenya Wildlife Service, 2013). Over 50% of these tourists were mainly interested in dolphin-oriented trips, highlighting the importance of dolphin-watching as one of the main economic activities for local communities (unpublished data; Emerton and Tessema, 2001). Dolphin tourism in KMMPA began in the early 1990s and has grown up to a total of 27 tourist boats registered in 2012, with the capacity to carry up to 48 tourists per trip (Kenya Wildlife Service, 2013). The industry has been operating year round, with peak seasons during the months of August and December-January, and a low season during the rainy period of April to June. In the early years of dolphin-watching in KMMPA, the industry was developed with limited management control, as the dolphin-watching activity was perceived to be non-harmful to the animals, and therefore did not require additional regulations (Hoyt, 2008; O'Connor et al., 2009). Due to the rapid growth of the industry between 2004 and 2006, the Kenya Wildlife Service (KWS), in collaboration with international agencies, developed a voluntary code of conduct in 2007 (Convention of Migratory Species, 2007). This code recommended boat operators to keep a minimum distance of 100m from dolphins and suggested a limit of two boats at any given time around the animals. The code of conduct also advised boats to spend no more than 20 minutes with the same dolphin group at a time, and also specified the best manoeuvres to approach the animals. Another major change for the dolphin-watching industry was the prohibition of swimming with dolphins. The code of conduct was implemented to mitigate possible impacts from the dolphin-watching activity. However, it was based on codes for other population from other parts of the world, and lacked scientific information from the targeted population.

We investigated the effects of the nature-based tourism on the behaviour of the Indo-Pacific dolphin population in southern Kenya. Specifically, we firstly used Markov chains analysis to estimate the probability of dolphins changing between different behavioural states (e.g., travelling, diving, socialising

and resting) in the presence and absence of tourist boats, from which we estimated changes in the dolphins behavioural budget (Lusseau, 2003a). Secondly, we investigated the effect of the current dolphin-watching intensity in KMPA on the cumulative behavioural budgets of the dolphin population, and quantified the tourism intensity on the area for the 2006-2013 period, to evaluate the potential disturbances caused by this activity on previous years. Finally, we analysed the spatial overlap of dolphin and tourist boat distribution based on kernel density estimations in order to determine areas where tourist boat impacts could be more significant. Our study aims to understand the impact of nature-based tourism on the behavioural ecology of the Indo-Pacific bottlenose dolphin, as this is critical to develop a sustainable dolphin-watching industry in the area.

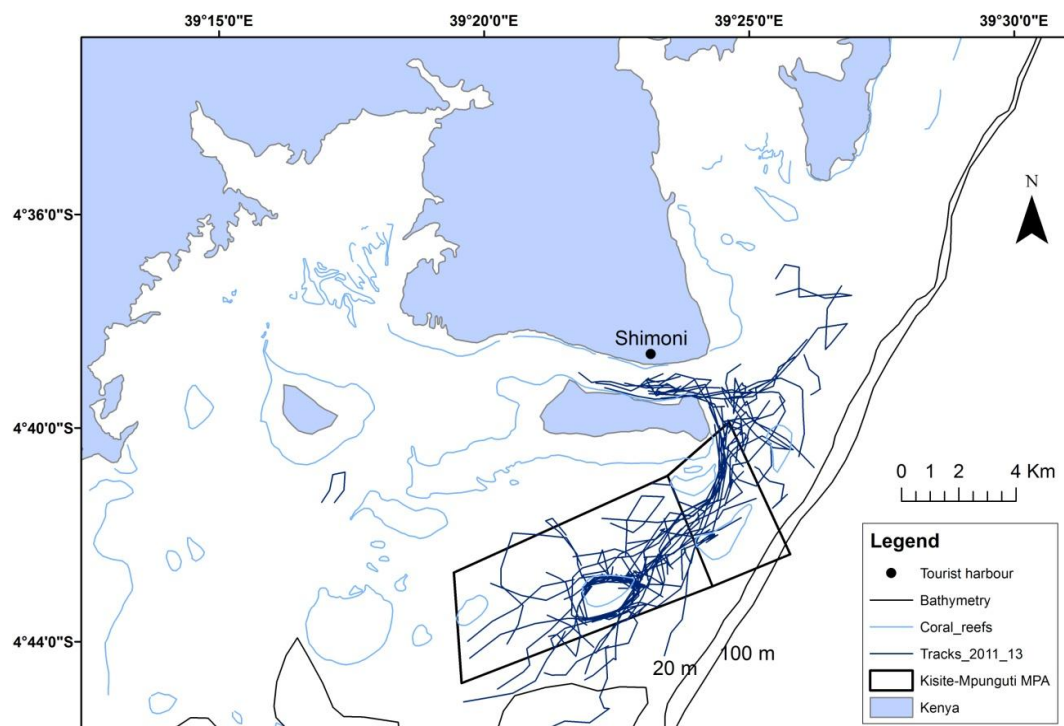


Fig. 4.1 Map of the study area including the Kisite-Mpunguti Marine Protected Area (KMPA), Kenya, which contains the Kisite Marine Park (left polygon) and the adjacent Mpunguti Marine Reserve (right polygon). The dark blue lines represent boat tracks from behavioural surveys conducted between 2011 and 2013

4.2 Material and methods

4.2.1 Study area

This study was conducted on the International Union for the Conservation of Nature (IUCN) data deficient population of Indo-Pacific bottlenose dolphins inhabiting the Kisite-Mpunguti Marine Protected Area (KMPA, 04°04'S - 39°02'E), in southern Kenya (Fig. 4.1). Recent capture-recapture modelling studies estimated a small population size for the area ranging from 20 (95% CI: 11-36) to a maximum of 102 individuals (95% CI: 77-136)(Fig. 3.5). Abundance estimations remained roughly stable from 2006 to 2009, with a mean of 65 dolphins (SE: 7.06). The presence of this species in the study area

is strongly influenced by dynamic (oceanic fronts) and static predictors (shallow areas, distance to reefs, distance to the 100m isobath), with a significantly higher occurrence and abundance of dolphins within the KMPA (Pérez-Jorge et al., 2015).

4.2.2 Data collection

Non-systematic boat-based surveys were carried out between the months of October and December 2011, 2012 and 2013. During this part of the year the sea is calm, the wind is light and rainfall is low, which makes the conditions ideal for behavioural surveys, as group-follows can be carried out for extended periods of time. Behavioural data from dolphin groups was collected from a 9.5m traditional dhow, a wooden-built sailing vessel, with one 15 HP two-stroke outboard engine. A dolphin group was defined as the total number of individuals encountered, moving in the same direction or engaged in the same activity, within 100 metres of each other (Wells et al., 1987). Once a group was sighted, the research vessel was operated in a careful way at slow speed, avoiding changes in gear and staying slightly behind or on the side of the dolphin group to minimise disturbance. Thus, focal groups were followed at a distance ranging from 20 to 100m, both in the presence or absence of tourist boats. The behaviour of dolphin focal groups was measured using focal-group scan sampling methods (Altmann, 1974). The behavioural state of each focal-group was sampled every 15 minutes and was determined by the activity of the majority (>50%) of the group. We only studied the behaviour of adults and juveniles since calves are dependent on their mothers. The four behavioural states recorded on this study were travelling, socialising, diving and resting (Table 4.1)(Lusseau, 2003a). Behavioural surveys ended when weather conditions deteriorated or the focal-group was lost.

Table 4.1 Definitions of behavioural states for dolphins in Kisite-Mpunguti MPA.

Behavioural state	Definition
Travelling	Persistent and directional movement (speed >2 knots); short and almost constant dive intervals; individuals could be meandering but still swimming in a constant direction
Resting	Low level of activity, dolphins moving slowly (speed < 2 knots); swimming with short, relatively constant, synchronous dive intervals; individuals tightly grouped
Diving	Frequent changes on direction. Majority of the group performs peduncle and tail out dives. Group spacing varies. Diving most likely represent the "foraging-feeding" category in other studies (Lusseau, 2003b)
Socialising	Various interactive behavioral events: petting, rubbing, mounting, chasing, hitting with tail and other physical contact between individuals. Dive intervals vary

Since the distance at which dolphin groups respond to tourist boats was not known, two different threshold values of distance were used to define impact situations: I) when one or more boats approached within 100 meters of the focal group and II) when one or more boats approached within 400 meters of the focal group. The analyses described in the following sections were applied to the data in two separate analyses, based on the two threshold values.

4.2.3 Behavioural transitions

Markov chains models have been widely used in wildlife ecology, particularly to assess the impact of nature-based tourism on marine mammal populations (Christiansen et al., 2013, 2010; Dans et al., 2012; Lusseau, 2003a). Markov chains measures the dependence of the current behavioural state on the preceding behavioural state. We restricted the analysis to include only the previous time step, referred to as a first-order Markov process, since impact interactions lasted on average less time than the 15 minutes scan samples (authors, personal observation; Lusseau, 2003b). To assess the effect of tourist boat interactions on the behaviour of the dolphins, we calculated the probability that a focal-group changed from a preceding to a succeeding behavioural state in the presence (impact) or absence (control) of tourist boats. We first built two-way contingency tables of preceding versus succeeding behavioural states, both for impact and control situations. If no tourist boat was present between two behavioural state samples (either during the first or the second scan sample event), we tallied this transition in a control table. If a tourist boat was present between two samples (either during the first or the second scan sample event), this transition was tallied in an impact table. Consistent with other impact studies (Christiansen et al., 2010; Lusseau, 2003a; Meissner et al., 2015; Stockin et al., 2008), we used a conservative approach and discarded any behavioural states samples immediately after an impact situation, as the potential impact of the interactions was uncertain and it was not possible to considered the transition as either control or impact. From the contingency tables, the transition probabilities of a dolphin group changing from one behavioural state to another, were calculated for both impact and control contingency tables:

$$p_{ij} = \frac{a_{ij}}{\sum_{j=1}^n a_{ij}}, \sum_{j=1}^n p_{ij} = 1,$$

where i is the preceding behavioural state, j is the succeeding behavioural state, n is the total number of behavioural states (i.e. four), a_{ij} is the number of transitions observed from state i to j , and p_{ij} is the transition probability from state i to j in the Markov chain. We tested the effect of boat interaction on the transition probability between behavioural states by comparing each control transition to its impact counterpart using a 2-tailed Z-test for proportions (Fleiss et al., 2003).

4.2.4 Behavioural bout durations

To investigate the effect of tourist boats on the duration of time, in minutes, that dolphins remain in different behavioural states, the average bout length for each behavioural state, t_{ij} , was estimated in

the presence and absence of boats from the Markov chains using the mean of the geometric distribution of p_{ii} (Guttorp, 1995; Lusseau, 2003a):

$$t_{ii} = \frac{1}{1 - p_{ii}}$$

with a standard error (SE) of:

$$SE = \sqrt{\frac{p_{ii} \times (1 - p_{ii})}{n_i}}$$

where n_i is the number of samples with i as preceding state. We compared the average bout length between control and impact situations using a Student's t-test.

4.2.5 Behavioural budgets

The proportion of time dolphin groups spent in each behavioural state under both control and impact situations was calculated by Eigen analysis of the two-way contingency tables (Christiansen et al., 2010; Lusseau, 2003a; Meissner et al., 2015). Differences between control and impact behavioural budgets were tested using a goodness-of-fit test, and differences in the relative proportion of each state was tested using 2-sample tests for equality of proportions with continuity correction. Finally, 95% confidence intervals were calculated for the estimated proportion of time spent in each behavioural state.

4.2.6 Cumulative behavioural budget

The impact behavioural budget is an instantaneous measure of the behaviour of dolphin groups during interactions with tourist boats. The proportion of time that dolphin groups spend with tourist boats per day can be added to the previous calculated behavioural budgets to estimate the cumulative (i.e. diurnal) behavioural budget of the dolphin population:

$$\text{Cumulative budget} = (a \times \text{impact budget}) + (b \times \text{control budget})$$

where a is the proportion of time (i.e. daytime hours) that dolphins spend with tourist boats (thus following a behavioural budget similar to the impact budget) and $b = 1 - a$ is the proportion of time that dolphins spend without tourist boats (thus following a behavioural budget similar to control situations) (Christiansen et al., 2010; Meissner et al., 2015). By comparing the cumulative behavioural budget of the dolphins to their control behavioural budgets, we can investigate the effect of tourist boats on the dolphins' diurnal behavioural budgets. By artificially varying the proportion of time per day that dolphins spend with boats (a) from 0 (dolphins spend 0% of their time with boats) to 1 (dolphins spend 100% of their time with boats), we can find out at what boat exposure the dolphins behavioural states are significantly affected. We used a 2-tailed Z-test for proportions for each behavioural state to test the significant differences between the cumulative behavioural budgets and control budgets, assuming that the observed effect size do not vary with daytime exposure rate (Lusseau, 2004).

4.2.7 Seasonal and yearly effects

To investigate seasonal and yearly variations in the intensity of dolphin-watching tourism in KMMPA and its effect on the dolphins' cumulative behavioural budget, we first estimated the tourist boat intensity during the study period (October to early December). We used the number of boats entering the KMMPA during these months for the period 2011-2013 to calculate a baseline number of boats corresponding to the levels of boat intensity during our study period. We did not include the month of December in the analysis, as behavioural surveys were conducted mainly in the first week of the month and the highest number of boats during this month occurs during the Christmas holiday break. We then used monthly data on the number of tourist boat between 2006 to 2013, provided by the Kenya Wildlife Service (KWS, unpublished data), to estimate the exposure of dolphins to tourism interactions during this time period. These estimates were then used to calculate dolphins' cumulative behavioural budget for each month and year to assess the seasonal and yearly effects of tourism boats on the behaviour of the dolphins. All analyses were performed using R 2.15.3 (R Development Core Team 2013), and the packages 'plyr' (Wickham, 2011), 'reshape2' (Wickham, 2007), 'ggplot2' (Wickham, 2009) and 'markovchain' (Spedicato et al., 2015).

4.2.8 Spatio-temporal overlap between dolphins and tourist boats

We used a kernel analysis approach to identify spatial overlap areas between dolphins and tourist boats distribution, based on sightings data collected from January 2009 to December 2013 (Pérez-Jorge et al., 2015). Kernel density estimators are extensively used to quantify utilization distributions, or home range, for marine and terrestrial animal populations (Kie et al., 2010; Laver and Kelly, 2008). For this, we applied a fixed kernel estimator with contours of 50% and 95% that estimated core and home-range areas respectively (Louzao et al., 2012; Soanes et al., 2013; Worton, 1989). An important decision in home-range analysis is to choose the appropriate smoothing parameter as this could bias the estimate of home-range size. In order to find this value, we sequentially reduced in 0.10 increments the reference bandwidth (href) until getting contiguous rather than disjoint 95% kernel polygons (Kie, 2013). We also took into account natural barriers such as islands and mainland, which often prevent dolphins from moving freely in all directions and tend to over-estimate the core and home ranges areas. We conducted the home-range analysis through ArcMap 10.1 (ESRI, 2011; MacLeod, 2014).

To calculate the proportion of home range overlap between dolphins and tourist boats the following formula was used (Fieberg and Kochanny, 2005; Hauser et al., 2014):

$$HR_{i,j} = A_{i,j} / A_i$$

where $HR_{i,j}$ is the proportion of population i 's (dolphin population) home-range that is overlapped by population j 's home-range (tourist boats), such that A_i is the total home-range area of the dolphin population, and $A_{i,j}$ is the area of overlap between the dolphin population and the area used by the tourist boats. We applied the same formula to estimate the proportion of core area (50% contour) overlap. We are aware that the distribution of dolphins and boats may differ temporally, e.g. between

seasons. However, we could not explore this seasonal effect due to small sample sizes mainly during autumn months (April to June), since 30 sightings is the minimum number suggested to obtain a sufficiently accurate estimate (de Azevedo and Murray, 2007; Seaman et al., 1999). To minimise the effect of sample size, we randomly selected 1,000 times an equal number of dolphin and tourist boat sightings per season to obtain a spatial overlap value for the whole 2009-2013 period. Seasons were defined as: summer (January to March), autumn (April to June), winter (July to September) and spring (October to December). Finally, we tested for differences between seasons using a Kruskal-Wallis (KW) test. Kernel density analyses were performed using the 'sp' (Bivand et al., 2013), 'fields' (Nychka et al., 2015), 'ggplot2' (Wickham, 2009) and 'adehabitatHR' packages (Calenge, 2006) in R.

4.3 Results

We spent 180 hours over 76 days following a total of 86 focal groups of Indo-Pacific bottlenose dolphins (Fig. 4.1). We recorded 567 behavioural transitions, of which 204 (36%) and 363 (64%) were considered as impact and control, respectively. During October-December 2011-2013, dolphins spent 30% (54 hours) of the time surrounded by tourist boats within a radius of 400 meters. The number of boats interacting with the same dolphin group varied from one to nine at a time (mean \pm SE: 2 ± 0.10). All parameter estimates for impact sequences at 100 and 400 meters were very close (Figs 4.2-4.5; Figs A3.1-A3.4 in Appendix 3), and we will only present the results from boats within 400 meters of the focal groups.

4.3.1 Behavioural transitions

The presence of tourist boats around dolphins had a significant effect on the behavioural state transitions ($\chi^2=54.04692$, $df= 9$, $p < 0.001$), whereas this effect was not uniform throughout all transitions (Fig. 4.2). The transition probability from travelling to travelling significantly decreased by 12% in the presence of boats ($\chi^2=4.9463$, $df= 1$, $p = 0.02$). In contrast, the transition probability from travelling to diving significantly increased by 8% when interact with boats ($\chi^2=3.9819$, $df= 1$, $p = 0.04$) (Fig. 4.2).

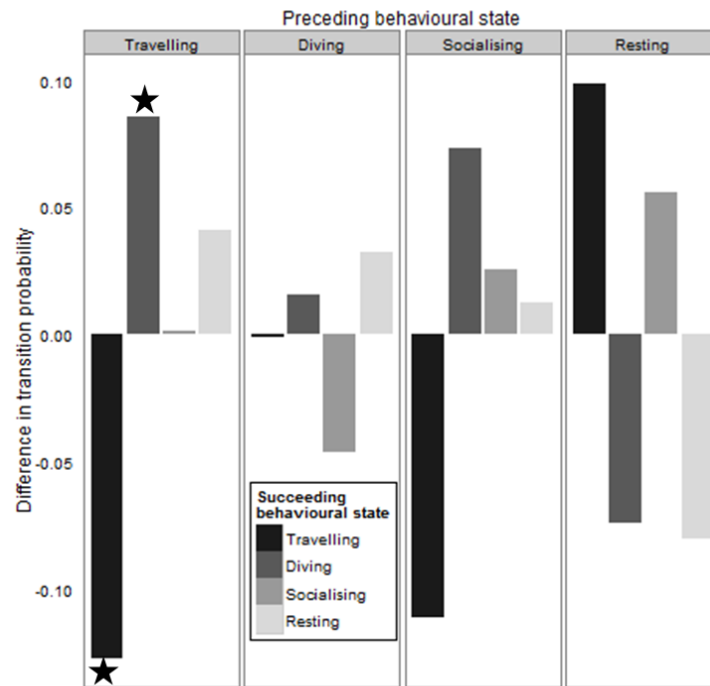


Fig. 4.2 Differences in transition probability between impact (tourist boat present within 400 meters of the dolphins) and control (tourist boat absent) situations ($p_{ij(\text{impact})} - p_{ij(\text{control})}$). The vertical boxes separate each preceding behavioural state, while the bars within each box represent the succeeding behavioural state (see colour legend). Transitions that changed significantly ($p < 0.05$) during boat interactions are marked with a star (★).

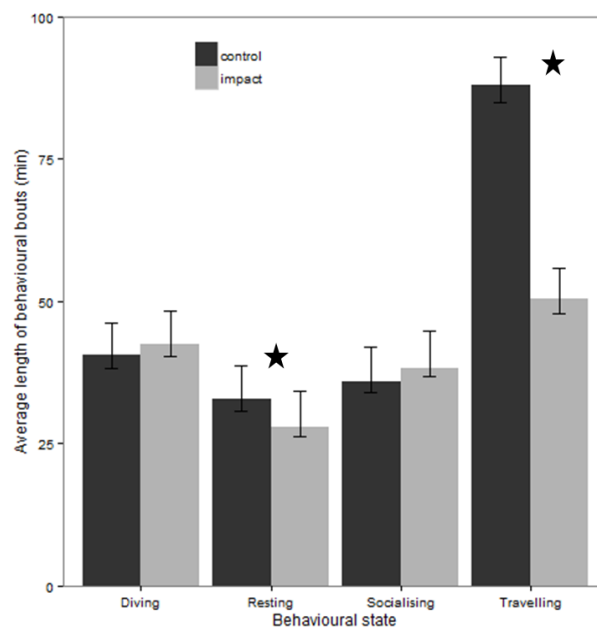


Fig. 4.3 Average bout length of dolphins represented by the duration of time (minutes) spent on each behavioural state under control (tourist boats absent) and impact (tourist boats present within 400m of the dolphins) situations. The vertical bars represent 95% confidence intervals. Behavioural states with a significant difference ($p < 0.05$) are marked with a star (★).

4.3.2 Behavioural bout durations

The average bout length for travelling and resting dolphins significantly decreased by 37.72 (95% CI: 36.17 to 39.27; $t = 47.58$, $df = 270$, $p < 0.001$) and 4.93 min (95% CI: 1.92 to 7.93; $t = 3.22$, $df = 96$, $p = 0.001$), respectively, in the presence of tourist boats (Fig. 4.3).

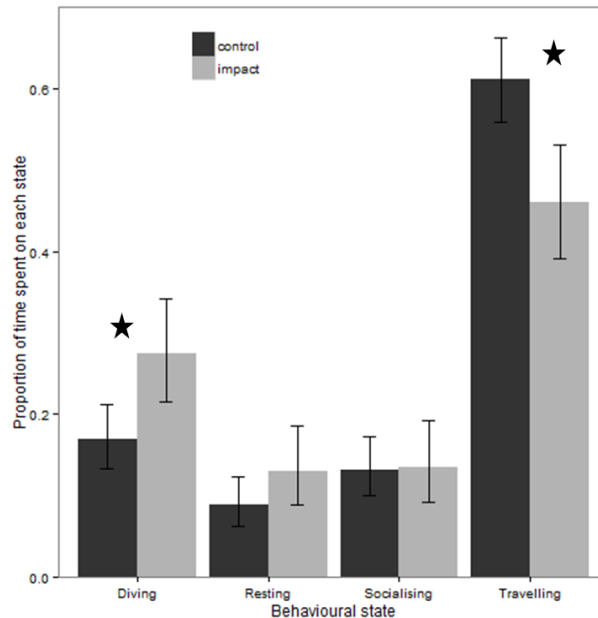


Fig. 4.4 Dolphin behavioural budgets represented by the proportion of time spent in each behavioural state under control (tourist boats absent) and impact (tourist boats present within 400m of the dolphins) situations. The vertical bars represent 95% confidence intervals. Behavioural states with a significant difference ($p < 0.05$) are marked with a star (★).

4.3.3 Behavioural budgets

The proportion of time spent in each behavioural state changed significantly during boat interactions ($\chi^2=19.91$, $df= 3$, $p < 0.001$). Travelling, being the dominant behaviour state both during control and impact situations, was significantly reduced from 61% to 46% in the presence of boats ($\chi^2=11.5216$, $df= 1$, $p < 0.001$)(Fig. 4.4). Conversely, diving increased from 17 to 27% as an effect of boat presence ($\chi^2=11.5216$, $df= 1$, $p < 0.001$).

4.3.4 Cumulative behavioural budget

The dolphins cumulative travelling and diving behaviours were significantly disrupted at boat intensities of 50 and 58%, respectively, while socialising and resting were not affected (Fig. 4.5). During October-December 2011-2013, we estimated the tourist boat intensity to be 30% of daytime hours, which falls below the threshold values for travelling and diving. The current boat intensity of 30% corresponded to a median of 160 boats (SE = 8.69) per month (Table 4.2). Based on this relationship, we identified the month of December and the years 2006 and 2007 as the highest periods of boat intensity, and consequently the periods that had the highest impact on the dolphins' cumulative behavioural budgets

(Fig. 4.6). Along these high intensity intervals, tourist boat exposure was up to 5 times higher than during the low tourist season (May-June)(Fig. 4.6).

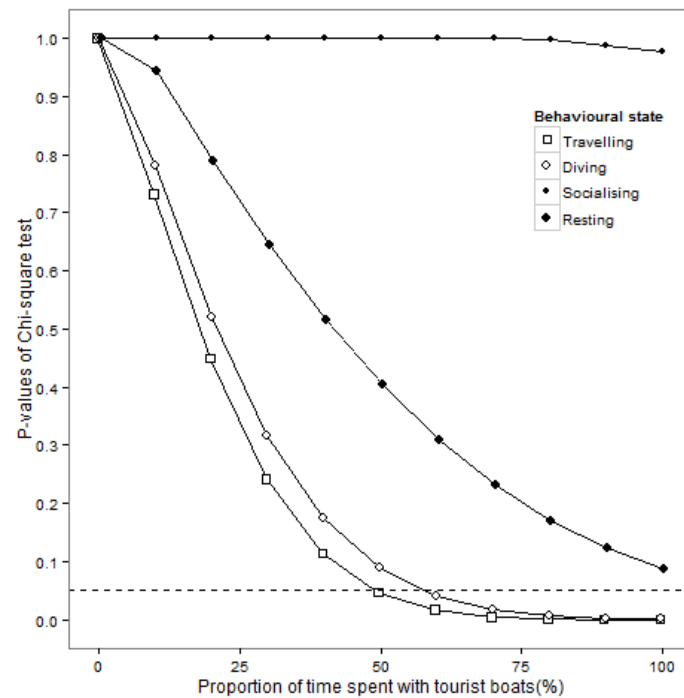


Fig. 4.5 Effect of tourist boat intensity on cumulative behavioural budget within 400m of the dolphins. P-values of the difference between the cumulative behavioural budget and the control behavioural budget for dolphin activity. The proportion of boat exposure was artificially varied from 0 to 100%. Dashed line represents the statistical level of significance ($p < 0.05$).

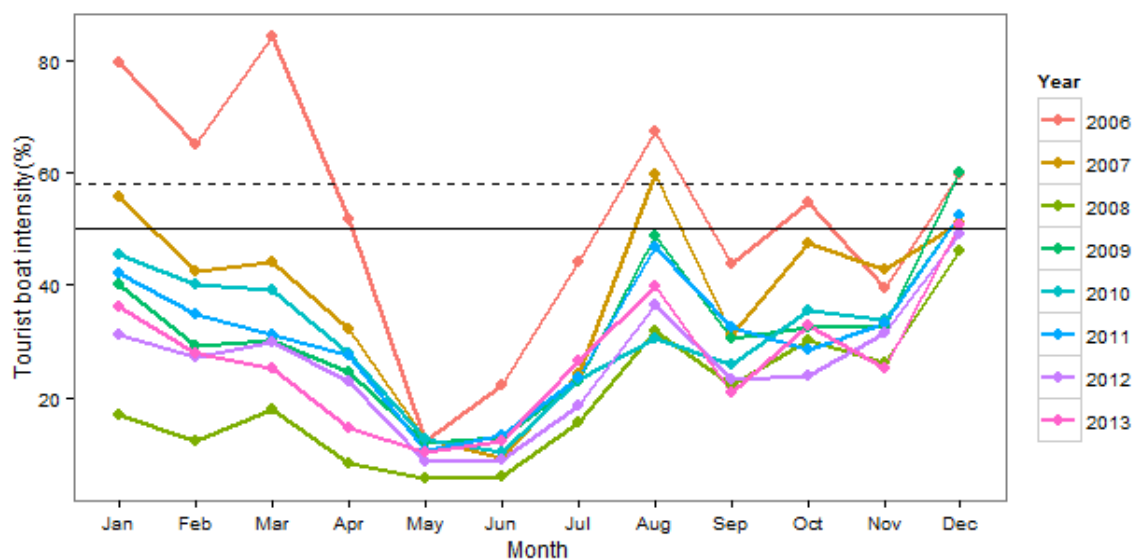


Fig. 4.6 Monthly tourist boat intensity between 2006 and 2013. The horizontal continuous and dashed lines represent 50 and 58% of tourist boat intensity respectively, which the cumulative travelling and diving behaviours are significantly affected.

Table 4.2 Number of tourist boats entering the Kisite-Mpunguti Marine Protected Area per month and year. Data provided by the Kenya Wildlife Service (KWS, unpublished data)

Season	Month	2006	2007	2008	2009	2010	2011	2012	2013
Summer	Jan	426	297	90	215	243	224	167	193
	Feb	347	227	65	156	215	185	145	148
	Mar	451	235	95	161	209	167	159	135
Autumn	Apr	277	172	43	130	149	146	122	78
	May	65	67	29	64	67	56	45	55
	Jun	119	49	31	68	54	70	48	65
Winter	Jul	236	129	82	121	124	126	98	141
	Aug	359	319	170	260	162	249	195	213
	Sep	234	166	118	162	138	174	124	111
Spring	Oct	293	254	161	173	189	152	128	176
	Nov	210	228	140	174	180	177	168	134
	Dec	319	273	246	320	280	279	263	271

4.3.5 Spatio-temporal overlap between dolphins and tourist boats

Core and home-range areas of dolphins and tourist boats were calculated based on a total of 775 and 1564 sightings, respectively (Table 4.3). The dolphins' home-range area (95% of utilization distribution) was estimated without natural barriers to be 68.99 km² for the whole period 2009-2013 (Fig. 4.7). At the 50% of utilization distribution, the core area was estimated to be 11.06 km² without natural barriers. For tourist boats, total home-range and core areas were estimated in 44.20 and 13.14 km², respectively (Fig. 4.7). This estimated tourism boat activity varied spatially across the study area, with the highest intensity concentrated within the boundaries of the MPA. The proportion of the dolphins home-range area (95%) that overlapped with the area used by the tourist boats ranged from 0.13 to 0.94, with a mean of 0.46 (SD = 0.25). The core area overlap was very similar, ranging from 0.14 to 0.94%, with a mean of 0.44 (SD = 0.18). We found significant differences in the overlapping proportion between seasons, at both 95% (KW = 3195.675, df = 3, p-value < 0.001) and 50% levels (KW = 2951.607, df = 3, p-value < 0.001). The highest overlap values for home-range were encountered during the winter season, whereas the highest overlap for core areas was found during the spring season (Fig 4.8). The lowest overlap was during autumn (April to June), at both home-range and core area levels.

Table 4.3 Number of tourist boat and dolphin sightings per season and year. Seasons were divided on the following periods: summer (January to March), autumn (April to June), winter (July to September) and spring (October to December).

	2009	2010	2011	2012	2013	TOTAL
Tourist boat sightings						
Summer	147	81	121	113	20	482
Autumn	51	24	65	64	1	205
Winter	104	184	142	98	98	626
Spring	0	131	77	23	20	251
Dolphin sightings						
Summer	42	46	34	43	34	199
Autumn	22	22	14	23	5	86
Winter	47	57	34	24	45	207
Spring	46	62	61	50	64	283

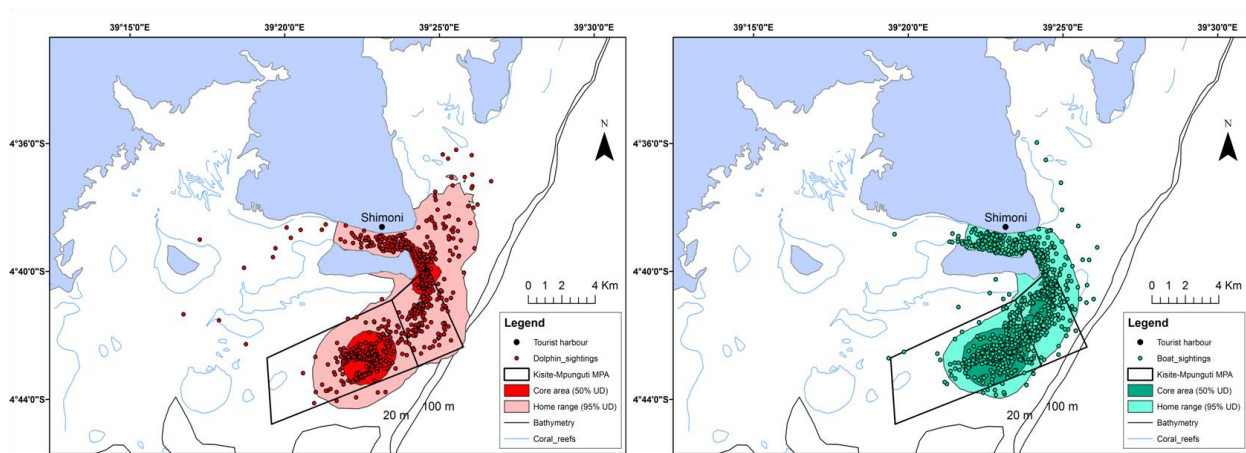


Fig. 4.7 Locations of dolphins and tourist boat sightings ($n=775$ and 1564 , respectively). Shaded polygons represent home-range and core areas (indicated by the utilization distribution contour of 95% and 50%, respectively) (based on Fieberg and Kochanny (2005)).

4.4 Discussion

This study provides an assessment of the current, past and also the potential future impact of nature-based tourism on the behaviour of Indo-Pacific bottlenose dolphins in southern Kenya. Our analyses show that tourist boat presence significantly affected the behaviour of the local dolphin population by negatively affecting travelling behaviour, while increasing diving behaviour. During spring the intensity of the dolphin tourism was sufficiently high to significantly affect the dolphins' cumulative behavioural budget.

4.4.1 Behavioural effects of tourism

The significant increase in transition probability from travelling to diving may represent a mitigation strategy by dolphins to avoid tourist boats by altering their diving patterns (Janik and Thompson, 1996; Lusseau, 2003a; Nowacek and Wells, 2001; R. Williams et al., 2002). These behavioural changes following boat interactions affected not only the transition between behavioural states, but also the entire behavioural budget of the dolphins, with a substantial decrease in the overall amount of time travelling and an increase in diving behaviour. These effects were significant both when considering a threshold of 100 and 400m to define impact situations. This suggests that dolphins responded to approaching boats already 400m away, which is much further than the recommended minimum distance suggested by the dolphin tourism guidelines in KMMPA (100m). Boat interactions also lead to a decrease in the resting bout length of dolphins, which has also been observed in other studies (Lusseau, 2003a; Stockin et al., 2008). Female dolphins are believed to mainly nurse their calves during resting periods, meaning that a reduction in resting bouts could have serious implications for nursing behaviour (Stensland and Berggren, 2007). To what extent nursing is affected by boat interactions in KMMPA is not known, but should be the focus of future impact studies.

4.4.2 Quantifying spatio-temporal interactions between dolphins and tourist boats

Dolphins are commonly distributed heterogeneously through their main habitats (Sprogis et al., 2015; Stensland et al., 2006), as they tend to aggregate in areas encompassing the resources to survive and reproduce (Gormley et al., 2012). The spatial and temporal variation in human activity can also influence dolphins' habitat use (Chilvers et al., 2003). In southern Kenya, Indo-Pacific bottlenose dolphins experience periods with variable human-disturbance levels due to high heterogeneity in tourism intensity, resulting in different levels of spatial and temporal overlap between tourist boats and dolphins' occurrence. If tourism intensity continue to increase, and as a consequence, the cumulative exposure levels to the population, the most affected individuals could potentially be those dolphins whose habitat preference is situated within and adjacent to the MPA (Christiansen et al., 2015). Although the highest occurrence and abundance of dolphins have been identified within the boundaries of the MPA, this area has shown to be insufficient for the spatial requirement of the species, as important percentage of recurrent and occasional habitats were identified outside the MPA (Pérez-Jorge et al., 2015). Thus, this spatial and temporal variability, both for tourism activity and dolphins occurrence, poses real challenges for mitigation measures aimed at reducing the potential cumulative effects of boat presence on a small dolphin population (Pirotta et al., 2014).

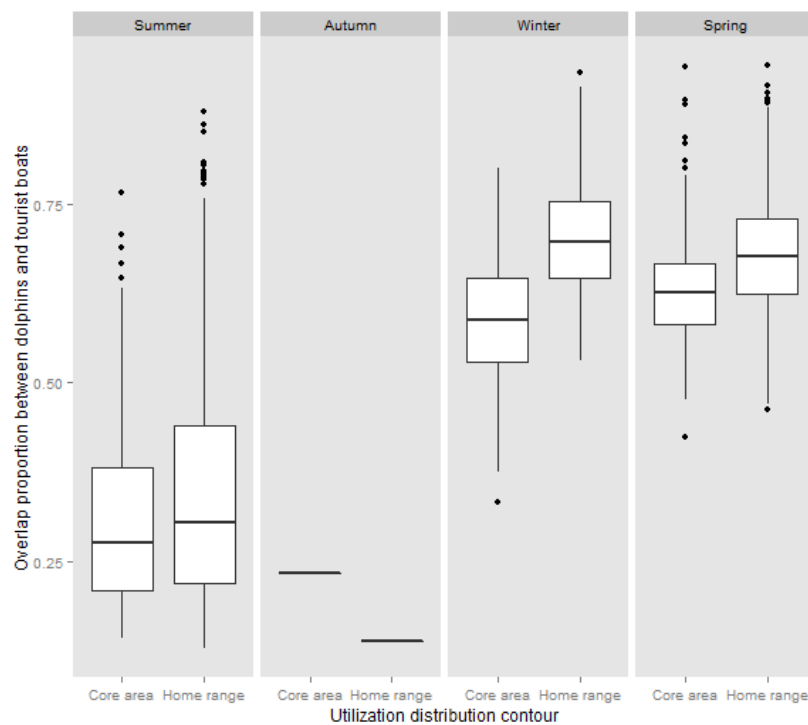


Fig. 4.8 Proportion of home-range and core areas (indicated by the utilization distribution contour of 95% and 50%, respectively) overlap between dolphins and tourist boats per season (based on Fieberg and Kochanny (2005)). Seasons were defined as: summer (January to March), autumn (April to June), winter (July to September) and spring (October to December).

During the study period, dolphins spent around 30% of their time interacting with tourist boats. At this exposure level, there was no significant effect on the cumulative behavioural budget of the dolphins. However, if we consider the tourism intensity during 2006 and 2007, when the highest number of

tourists was recorded in the KMMPA, this population could have been significantly affected. Our results showed that tourism intensity above 180 tourist boats per month can have a significant effect on the cumulative behavioural budget of these animals. The periods of highest intensity were recorded mainly during the holiday breaks of December-January, when tourism numbers were the highest. With the number of tourists in Kenya expected to increase over the coming years, it is likely that the cumulative behavioural budget of the dolphin population will again be significantly affected by tourism boat interactions. Other studies have shown that high exposure to tourism, represented by the number of tourist boats operating in an area, can lead to dolphins seasonally emigrating from an area to avoid interactions (Bejder et al., 2006). In Kisite-Mpunguti MPA, the highest temporary emigration rates of dolphins were recorded in March 2006 (Fig. 3.2), which corresponded to the period with the highest number of boats entering the MPA since its implementation in 1978 (Ministry of Tourism, 2010). This temporal area avoidance could lead to a decrease of the already small dolphin population size and consequently, to a reduction of economical benefits to the local community (Lusseau et al., 2006; see Chapter 3 for more info). Therefore, ensuring the sustainability of the dolphin-tourism activity is of paramount importance in both ecological and socio-economic terms (Higham et al., 2015).

4.4.3 The role of the MPA on the dolphin-watching tourism.

In terms of management, both government and community-based organizations should work together to implement different mitigation measures for the dolphin tourism industry in KMMPA. First, an increase in the tour prices could reduce the amount of tourists in the area, and hence the tourism boat pressure on the dolphin population, while still maintaining similar economic benefits for the local community (Curtin, 2003). This strategy has been previously proposed in Zanzibar based on the results from a socio-economic study (Berggren et al., 2007). Second, an increase in the number of tourists per boat would also help to reduce the number of boats interacting with dolphins. Third, by continuing the current tour boat operator training, already conducted in 2011 and 2012, with the aim at highlighting the code of conduct in terms of rapprochement, the behavioural impact on dolphin groups during interactions could potentially be reduced. Finally, by improving the quality of the services provided by the boat crew during a trip (e.g., improve guides talk and customers' service towards maximising tourist satisfaction, Lück, 2003), the economic benefits to the boat crew (through tipping, Buultjens et al., 2005; Wunder, 2000), which forms an important part of the employees' salary (authors, unpublished data), could increase. Thus, training tour guides can help to achieve not only the ecological sustainability but also the economic sustainability (Chen, 2011; Weiler and Ham, 2002). To successfully implement all these measures, the involvement of the local communities is fundamental.

This study shows that nature-based tourism could be a serious threat for the dolphin population in the area if this industry is not managed sustainably, especially during periods of high tourism intensity. Thus, a good understanding of how human disturbance affects animal populations is crucial for the development of sustainable management of any nature-based tourism activity (Higham et al., 2009). For these reasons, appropriate conservation measures such as setting limits of acceptable change (LAC), based on the monitoring of demographic parameters of the target population, and establishing

operators guidelines, should be implemented by management agencies (Ahn et al., 2002; Higham et al., 2009). Furthermore, incorporating the spatial and temporal extent of the tourist activity into management plans can also help to address this challenge. Future studies should evaluate the efficiency of the current code of conduct, as our results suggest that the tourist boats' zone of influence exceeds the 100 meters established in the current guidelines. Moreover, with the expected rise in coastal tourism, dolphins are also facing an increase in the number of threats along the Kenyan coast, including overfishing, increased seismic exploration operations, development of coastal infrastructures and maritime traffic (Kenya Wildlife Service, 2011). Finally, these issues should be addressed through the implementation of a science-based national conservation policy and management strategy for these species.

4.5 Acknowledgements

We are very grateful to all volunteers and staff for collecting dolphin observations and participating in the GVI conservation projects. We want to thank Graham Corti, Rachel Crouthers, Edita Magileviciute, and Andrew and Kirsty Hayes for leading the marine programme. We would also like to thank the authorities and elders of Mkwiro and Shimoni and their communities at large for their hospitality and their support from 2006 to 2015. ML was funded by a Ramón y Cajal (RYC-2012-09897) postdoctoral contract. IG was supported by a MARES grant (Erasmus Mundus Joint Doctorate programme coordinated by Ghent University (FPA 2011-0016)). Permission to work in the Kisite-Mpunguti Marine Protected Area was provided by Kenya Wildlife Service (KWS). We are grateful for all the support from KWS staff, Juan Bueno and Laura García-Peteiro.

CHAPTER 5

5. Spatial variation in shark-inflicted injuries to Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) of the western Indian Ocean

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Submitted to Marine Mammal Science

5.1 Introduction

Predation risk can be critical in shaping the behaviour and population dynamics of prey taxa (e.g. Brown and Kotler, 2004; Creel and Christianson, 2008; Lima and Dill, 1990) that, in turn, may have cascading consequences for communities (Heithaus et al., 2008). Although often considered top predators, many populations of small delphinids are at risk from predators. Killer whales (*Orcinus orca*) are a threat primarily in temperate waters while risk from large sharks dominates in tropical ecosystems (see Heithaus, 2001a; Weller, 2009 for reviews). Although often overlooked, these predators may have influence small cetacean (Delphinidae and Phocoenidae) behaviour - including daily movements (e.g. spinner dolphins *Stenella longirostris*, (Norris and Dohl, 1980b), group size (Gygax, 2002), mixed-species group formation (Kiszka et al., 2011), and habitat use at multiple spatial scales (Heithaus and Dill, 2006; Srinivasan et al., 2010) – as well as body condition (MacLeod et al., 2007).

Of key importance to identifying areas where predation risk might be important in shaping behaviours and population dynamics is understanding spatial and temporal variation in predation risk. For most populations of small cetaceans such as delphinids, however, there is no information on the relative risk of predation they face. Because predation events are uncommon enough to preclude direct estimates of mortality risk, evidence of unsuccessful predation attempts (e.g. scars and injuries) have been used to gain insights into predation risk to many taxa, including dolphins (e.g. Corkeron et al., 1987; Heithaus, 2001b). The use of scars, however, has many limitations because the probability of an individual surviving an attack to display a wound will vary with numerous factors including the relative

size of predator and prey, relative prey escape ability and predator efficiency, as well as wound healing rates (see Heithaus, 2001a for discussion). Still, in the absence of other data, injury rates are an important first step in elucidating predator-prey interactions.



Fig. 5.1 Location of study sites in the western Indian Ocean.

5.2 Material and Methods

Here, we estimated the rates of shark-inflicted injuries on Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) at four locations in the southwest Indian Ocean (southern Kenya, la Réunion, Mauritius, and Mayotte; Fig. 5.1) during photo-identification surveys (see Kiszka et al., 2012; Webster et al., 2014 for details). In Kenya, the sampling focused on the Kisite-Mpunguti Marine Protected Area (04°04'S, 39°02'E) and adjacent waters (~200 km²), and was conducted from January 2006 to December 2009 (Table 2.4). This area mostly covers shallow waters (0 – 15 m), including coral reefs, where Indo-Pacific bottlenose dolphins are common (Pérez-Jorge et al., 2015). Mayotte (12°50'S, 45°10'E) is located in the north-eastern Mozambique Channel and is part of the Comoros archipelago (Fig. 5.1). The island is almost entirely surrounded by a 197 km barrier reef, forming the largest coral lagoon in the Indian Ocean and averaging 20 m in depth (1,300 km²). Adjacent to the northern part of the lagoon, there is an immersed reef bank (Iris) that is about 215 km². Indo-Pacific bottlenose dolphins occur both in the lagoon and the Iris bank and were sampled from July 2004 to April 2009 (Kiszka et al., 2012). In la Réunion, photo-identification data were collected from January 2005 to December 2012 in the coastal waters of the west coast of the island, over an area of about 1,000 km². The island shelf is very narrow (200 m depth contour lies 3 km from the coast on average) and Indo-Pacific bottlenose dolphins occur

in waters < 80 m depth (Dulau-Drouot et al., 2008). Off Mauritius (20°17'S, 57°33'E), the study area encompassed ~30 km of coastline along the southwest coast, including sandy bays and fringing reefs where Indo-Pacific bottlenose dolphins are commonly encountered (Webster et al., 2014). Sampling in the study area has been conducted from April 2008 to June 2010.



Fig. 5.2 Representative photographs of shark-inflicted injuries on Indo-Pacific bottlenose dolphins (*T. aduncus*) from la Réunion. Photo credit: Globice Réunion.

Injuries to dolphins were assessed from photographs taken during standard photo-identification surveys. We considered an injury to be shark-inflicted if it was crescent shaped and/or contained deep and widely spaced tooth impressions that could only have been caused by a shark (Fig. 5.2). For all individuals included in the sample from all locations, photographs of each individual were available for the dorsal surface and upper flanks of the dolphin from the head to the peduncle. Therefore, the majority of shark bites on the upper body surfaces likely were recorded. Because previous studies of bottlenose dolphins (*Tursiops cf. aduncus*; Heithaus, 2001b) and Atlantic spotted dolphins (*Stenella frontalis*; Melillo-Sweeting et al., 2014) suggest that injuries are less likely to occur ventrally, it is unlikely that spatial patterns in injury rates were largely affected by this bias. Calculated injury rates, however, should be considered to be minimum estimates because of the incomplete coverage of dolphins' bodies and the likelihood that old injuries that had healed well were missed (e.g. Heithaus, 2001b).

Two experienced observers (MRH and JJK) independently assessed the species potentially responsible for a particular bite based on characteristic tooth impressions of upper and lower jaws. Most bites were scored as "unknown" and a species was only considered a likely attacker when both observers' assessments matched.

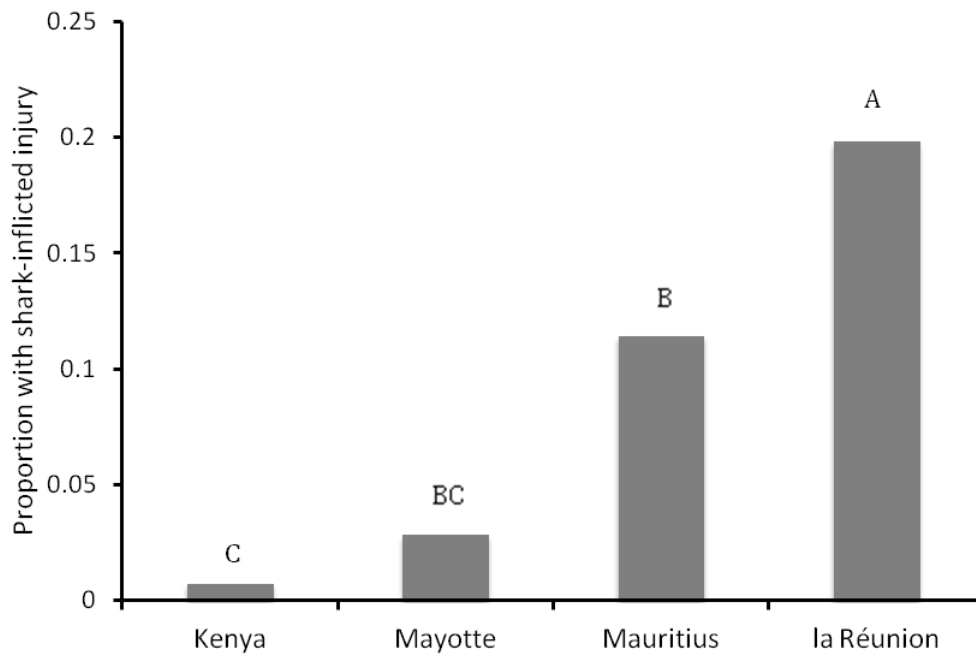


Fig. 5.3 Spatial variation in the probability of dolphins having a shark-inflicted injury. Values are the proportion of individuals where shark bites were observed in photographs of the dorsal surfaces and upper flanks. Bars with similar letters are not significantly different based on Tukeys post-hoc tests.

5.3 Results

We observed a total of 27 individuals with shark-inflicted injuries across 345 individually identifiable dolphins based on photo-identification data (Fig. 5.2). Of these 28 injuries, five were fresh and the rest had healed. Based on photographs, it was impossible to determine the species responsible for inflicting injuries in most cases. Tiger sharks (*Galeocerdo cuvier*) were identified as the likely attacker for three injuries, bull sharks (*Carcharhinus leucas*) for two, and unknown species of *Carcharhinus* for two others. Based on the estimated size of injuries on two individuals attacked by tiger sharks, the attacking sharks were likely up to 400 cm in total length. There was a significant spatial variation in the probability of an identified individual having a shark-inflicted injury (Fig. 5.3; Chi-square = 36.7, $P < 0.001$). Injuries were most common on dolphins of La Réunion (20 of 101 identified individuals) and lowest off Kenya (1 of 138 individuals) and Mayotte (2 of 71 individuals). The probability of a dolphin having a shark-inflicted injury was intermediate at Mauritius (4 of 35 individuals).

Table 5.1 Reported rates of shark-inflicted injuries on coastal dolphin populations worldwide.

Location	Species	Prop ¹	Reference
Atlantic Ocean			
Sarasota, FL	<i>Tursiops truncatus</i>	31%	Heithaus 2001b
Florida Bay	<i>Tursiops truncatus</i>	1-5%	Sarabia 2012
Aruba	<i>Tursiops truncatus</i>	1.3+%	Luksenberg 2014
Aruba	<i>Stenella frontalis</i>	0.6+%	Luksenberg 2014
Bimini, Bahamas	<i>Stenella frontalis</i>	15-31%	Melillo-Sweeting <i>et al.</i> 2014
Adriatic Sea	<i>Tursiops truncatus</i>	0%	Bearzi <i>et al.</i> 1997
Pacific Ocean			
Moreton Bay, Australia	<i>Tursiops aduncus</i>	36.6%	Corkeron <i>et al.</i> 1987
Indian Ocean			
Shark Bay, Australia	<i>Tursiops cf. aduncus</i>	74.2%	Heithaus 2001b
La Réunion	<i>Tursiops aduncus</i>	19.8%	This study
Kenya	<i>Tursiops aduncus</i>	0.7%	This study
Mayotte	<i>Tursiops aduncus</i>	2.8%	This study
Mauritius	<i>Tursiops aduncus</i>	11.4%	This study
Durban, South Africa	<i>Tursiops aduncus</i>	10-19%	Cockcroft <i>et al.</i> 1989
Durban, South Africa	<i>Sousa plumbea</i>	28%	Cockcroft 1991

¹Proportion injured: low estimates where ranges are provided represent definitive shark-inflicted injuries while high estimates represent the inclusion of injuries possibly caused by sharks.

5.4 Discussion

Variation in shark-inflicted injuries in coastal dolphin populations suggests that predation risk from sharks varies considerably worldwide (Table 5.1) and likely reflects a combination of baseline habitat differences in predation risk and overfishing of large, predatory sharks. The apparently low rates of shark attacks on bottlenose dolphins off Kenya and Mayotte are similar to those reported for shallow coastal and inshore waters of southern Florida (Sarabia, 2012), offshore of Aruba in the Caribbean (Luksenberg, 2014) and the Adriatic Sea (Bearzi *et al.*, 1997). These latter areas are typified by waters where shark populations appear to be reduced from historical numbers (e.g. Ferreti *et al.*, 2008; Heithaus *et al.*, 2007; Ward-Paige *et al.*, 2010) and, in the case of South Florida, waters that are not typically used by species that typically pose a threat to dolphins (e.g. tiger and bull sharks; Torres *et al.*, 2006). For Kenya and Mayotte, limited information is available on population trends and fisheries of

large sharks. In Kenya, however, it is likely that populations have been greatly reduced due to intense fishing effort in the coastal waters (Kiszka and van der Elst, 2015). In contrast, shark-inflicted injuries were more common on *T. aduncus* off la Réunion than in *Tursiops* spp. from South Africa (Cockcroft et al., 1989), and were similar to Indian Ocean humpback dolphins (*Sousa plumbea*) in South Africa (Cockcroft, 1991) and Atlantic spotted dolphins of the Bahamas (Melillo-Sweeting et al., 2014). *T. aduncus* off la Réunion were less likely to have scars than *T. truncatus* off Sarasota, Florida (Heithaus, 2001b) and *T. aduncus* off Queensland, Australia (Corkeron et al., 1987) and much less likely to have scars than *T. cf. aduncus* of Shark Bay, Australia (Heithaus, 2001b). It is likely that predation risk to dolphins off la Réunion, however, is underestimated relative to many of these locations where injury rates were derived from more detailed observations of individuals. Dolphins off la Réunion are threatened by both tiger and bull sharks (Blaison et al., 2015) that can grow to over 4 meters in total length. Although both of these species are present in Queensland and South Africa, sharks off la Réunion have not been subjected to the same level of fishing or shark control as dolphins in Queensland (Holmes et al., 2012) or South Africa (Dudley and Simpfendorfer, 2006). Along the Gulf of Mexico coast of Florida, adult bull sharks do not reach the same body sizes (Branstetter and Stiles, 1987). Therefore, we might expect that dolphins off la Réunion would be less likely to survive attacks and injury rates to underestimate predation risk relative to locations with smaller sharks.

Off South Africa, Cockcroft et al. (1989) were able to measure both shark-inflicted injury rates and the presence of dolphin remains in the stomachs of sharks. They estimated that ca. 2% of the dolphin population is killed by sharks each year. If comparable or greater shark-inflicted mortality rates, relative to scaring rates, are present in the southwest Indian Ocean, sharks may be an important source of mortality for dolphins off la Réunion and Mauritius but direct predation by sharks is unlikely to be important off Kenya and Mayotte. Further long-term studies of dolphin and shark populations in these locations may provide important insights into the role of shark predation in shaping coastal dolphin habitat use patterns and population dynamics. Predation, however, need not be common in order to induce anti-predator behaviour (Lima and Dill, 1990) that can lead to cascading ecological impacts in marine ecosystems (Heithaus et al., 2008). Because of their position near the top of marine food webs and potential to structure ecosystems through their ability to induce risk effects in prey and consuming large amounts of prey biomass (Bowen, 1997; Roman et al., 2014) studies of shark-dolphin interactions will provide insights into the dynamics of marine ecosystems where they are sympatric (Kiszka et al., 2015). The growing global picture of variation in predation risk to coastal dolphins provides a framework for beginning to investigate these ecological questions as well as further elucidating the role of predation risk in shaping odontocete behaviour.

5.5 Acknowledgements

The authors thank the numerous colleagues and volunteers who helped collecting data in the field across the SW Indian Ocean region. In Mayotte, data were collected during a joined program of the

University of La Rochelle, the Office National de la Chasse et de la Faune Sauvage and the Collectivité Départementale de Mayotte, and dolphin surveys funded by the later institutions, as well as the Ministère de l'Énergie, de l'Écologie, du Développement Durable et de la Mer (MEEDDM). In Kenya, we would also like to thank the authorities and elders of Mkwiro and Shimoni and their communities at large for their hospitality and their support from 2006 to 2015. Permission to work in the Kisite-Mpunguti Marine Protected Area was provided by Kenya Wildlife Service (KWS). We are grateful for all the support from KWS staff. Funding in Mauritius was provided to the Mauritius Marine Conservation Society by TOTAL Foundation, the United Nations Development Programme – Global Environment Facility. Research permits were provided by Albion Fisheries Research Centre, Ministry of Fisheries, Republic of Mauritius (F7532/27/2/2) with ethics approval from Murdoch University, Western Australia (W2249/09). This is contribution x of the Southeast Environmental Research Center. We also thank all the volunteers who participated in the collection of field data.

6. Conclusions

This PhD thesis presents an integrative study on the spatial ecology and population dynamics of the Indo-Pacific bottlenose dolphin (*Tursiops aduncus*) inhabiting southern Kenya. It focuses not only on the identification of key marine habitats for the conservation of the species, but also on key processes driving the population dynamics, considering both natural and anthropogenic factors. This represents the first consistent study of the species along the Kenyan coast, describing its biology, ecology, and main threats. These are the main conclusions from this PhD thesis:

1. The key habitats of the Indo-Pacific bottlenose dolphins in southern Kenya are influenced by both static and dynamic variables. Animals select shallow waters, close to the reef and to oceanographic fronts, and adjacent to the 100 m isobaths. These environmental drivers were important for the occurrence and abundance of dolphins. The species distribution was closely linked to the foraging ecology previously described along the western Indian Ocean.
2. The predictive performance of the species distribution models (SDMs) was improved by applying consensus methods, combining GLMs and GAMs into ensemble models. This is the first time this modelling technique is used to predict marine mammals' occurrence and abundance, and taking into account its accuracy, it should be implemented in future studies of SDMs.
3. This study highlights the importance of dynamic oceanographic variables for the habitat preference of the target species and reveals the need to integrate dynamic and spatially explicit conservation actions for marine top predators, such as the Indo-Pacific bottlenose dolphins and other marine mammals inhabiting the study area.
4. Kisite-Mpunguti MPA presents the highest occurrence and abundance of dolphins within the study area. This MPA had already reported positive impacts on coral reef fish population, adjacent fisheries catch and status of coral reefs. In this study, we highlight its importance also for marine mammals, expanding its relevance across species and functional groups.
5. The areas outside and adjacent to the MPA encompass an important 53% and 43% of recurrent and occasional areas for the species, respectively. These areas are essential for the species' spatial requirement, and should be included under some type of spatial protection. A potential measure could be the collaborative co-management areas proposed by the Kenyan government, which are developed and enforced by the local communities and have already shown to be successful.
6. The habitat modelling approach implemented on the second chapter can be used to predict key habitats, as well as to evaluate the effectiveness of marine protected areas for animal populations.

7. The species information obtained through the habitat modelling procedure can contribute to the national aims of the Convention on Biological Diversity (CBD), towards improving the biodiversity status and to apply effective and equitable managed protected areas.
8. The first robust abundance estimate for the species along the Kenyan coast was estimated to fluctuate seasonally from a minimum of 20 individuals (95% CI: 11-36) to a maximum of 102 dolphins (95% CI: 77-136). This small population may be particularly vulnerable to anthropogenic disturbance due to their high site fidelity and coastal distribution.
9. The probability of dolphins seasonally emigrating from the study area was influenced by the number of tourist boats and swimmers present around Kisite-Mpunguti MPA. An increment on the tourism exposure levels meant a higher number of dolphins temporarily leaving the area. Thus, the highest temporary emigration rate occurred during March 2006, linked to the high number of tourists visiting Kisite-Mpunguti MPA in February 2006. This was the year with the highest influx of visitors since the implementation of the protected area in 1978. The code of conduct implemented in 2007, and the significant tourism drop in 2008, resulted in few animals leaving temporally the study area.
10. The return rate of temporary emigrants was associated with the seasonal sea surface temperature, with cold periods having a higher probability of dolphins returning to Kisite-Mpunguti MPA in the following season. These results did not support the initial hypothesis of individuals entering the study area seeking for mating opportunities.
11. The annual apparent survival rate of 0.96 was estimated constant over the period 2006-2009. However, an increase on the apparent survival rate was estimated from 0.93 in 2006 to 0.99 in 2009 for a large percentage of the models.
12. Pollock's robust design models can help to understand the effects of biotic and abiotic factors on demographic parameters, providing valuable information to evaluate population dynamic changes in the target population.
13. This study demonstrates that tourist boat interactions alter dolphins' behavioural budgets, with a significant decrease in the overall amount of time travelling and an increase in diving patterns. The behavioural transition from travelling to diving may indicate a mitigation strategy by dolphins to avoid tourist boats.
14. The average bout length varied considerably between control (absence of tourist boats) and impact (presence of tourist boats) scenarios, with a significant decrease on the travelling and resting behaviours. The reduction on the resting duration could have serious implications for the calves, as these are believed to be the main periods for female to nurse their calves.

15. In Kisite-Mpunguti MPA, dolphins spent approximately 30% of their daytime surrounded by tourist boats. At these tourism levels, the cumulative tourism exposure was not significant for the dolphin population. However, critical periods for the species were detected during the month of December and along the period 2006-2007, when tourism intensity in the area is above 180 boats per month. For this reason, understanding how the human disturbance impacts the Indo-Pacific bottlenose dolphin population is crucial especially with expected rise in Kenyan tourism in coming years.
16. Spatial differences were encountered for shark-inflicted injuries along the four population of the Western Indian Ocean. The highest predation risk was identified around La Réunion, with nearly 20% of the photo-identified dolphins showing shark-inflicted injuries.
17. The predation risk for the Kenyan population of Indo-Pacific bottlenose dolphins was almost inexistent, with 0.7% of the individuals identified. This probably shows the low numbers of sharks on the area, likely linked with the local reduction of the shark population from historical numbers.
18. A national strategy should be implemented to continue to monitor this data deficient species, mainly because of their low population size, potential isolation from other populations and current anthropogenic exposure.

6.1 Conclusiones

Esta tesis doctoral presenta un estudio integral sobre la ecología espacial y la dinámica de población del delfín mular del Indo-Pacífico (*Tursiops aduncus*) que habita el sur de Kenia. Esta tesis no sólo se centra en la identificación de los hábitats marinos críticos para la conservación de la especie, sino también en los procesos que controlan la dinámica de poblaciones, teniendo en cuenta tanto los factores naturales como antropogénicos. La presente tesis doctoral representa el primer estudio de la especie a lo largo de la costa de Kenia, en la que se describe su biología, ecología y principales amenazas. Las principales conclusiones de la tesis doctoral se detallan a continuación:

1. Los principales hábitats de los delfines mulares del Indo-Pacífico en el sur de Kenia fueron influenciados por variables estáticas y dinámicas. Los animales seleccionaron zonas poco profundas, cerca del arrecife y de los frentes oceanográficos, y adyacentes a la isóbata de los 100 m. Estos parámetros ambientales fueron importantes para explicar la presencia y abundancia de los delfines. La distribución de la especie estaba estrechamente vinculada a la ecología de alimentación, la cual ha sido descrita anteriormente a lo largo del Océano Índico occidental.
2. La capacidad predictiva de los modelos de distribución de especies (MDE) mejoró mediante la aplicación de métodos de consenso, con la combinación de modelos lineales generalizados (GLMs) y modelos aditivos generalizados (GAMs) en modelos conjuntos. Es la primera vez que esta técnica

de modelado se utiliza para predecir la ocurrencia y abundancia de mamíferos marinos, y teniendo en cuenta su exactitud, se debería implementar en futuros estudios de MDE.

3. El presente estudio pone de relieve la importancia de las variables oceanográficas dinámicas para identificar los hábitats de la especie de estudio y revela la necesidad de integrar acciones de conservación dinámicas y espacialmente explícitas para grandes depredadores marinos como los delfines mulares del Indo-Pacífico y otros mamíferos marinos que habitan en el área de estudio.
4. El Área Marina Protegida (AMP) de Kisite-Mpunguti presenta la mayor presencia y abundancia de delfines del área de estudio. Los efectos positivos de esta AMP ya han sido descritos para las poblaciones de peces de arrecife de coral, capturas de pesca en zonas adyacentes y en el estado de los arrecifes de coral. Gracias a este estudio también se destaca la importancia del AMP para los mamíferos marinos, ampliando así su relevancia a través de varias especies y grupos funcionales.
5. Las zonas exteriores y adyacentes a la AMP abarcan el 53% y el 43% de las áreas recurrentes y ocasionales para la especie, respectivamente. Estas áreas son esenciales para los requerimientos espaciales de la especie, y deben ser incluidas bajo algún tipo de protección espacial. Una medida potencial podría ser la implementación de áreas de gestión conjuntas propuestas por el gobierno de Kenia, que son desarrolladas y aplicadas por las comunidades locales y ya han demostrado ser eficaces.
6. El enfoque de modelado de hábitat implementado en el segundo capítulo puede ser utilizado para predecir los hábitats principales de las especies, así como para evaluar la efectividad de las áreas marinas protegidas para poblaciones animales.
7. La información de la especie obtenida a través del procedimiento de modelado de hábitat puede contribuir a los objetivos nacionales del Convenio sobre la Diversidad Biológica (CDB), hacia la mejora de la conservación de la biodiversidad y para la aplicación de áreas protegidas gestionadas eficaz y equitativamente.
8. La primera estima de abundancia robusta para la especie a lo largo de la costa de Kenia se estimó que fluctuaba estacionalmente desde un mínimo de 20 individuos (IC 95%: 11-36) a un máximo de 102 delfines (IC del 95%: 77 a 136). Esta reducida población puede ser particularmente vulnerable a las perturbaciones antropogénicas debido a su alta residencia y distribución costera.
9. La probabilidad de emigración de los delfines a otras áreas fuera del área de estudio aumentó con el número de barcos de turistas y bañistas presentes alrededor del AMP de Kisite-Mpunguti. Un incremento en los niveles de exposición del turismo significa un mayor número de delfines que abandonan temporalmente el área de estudio. Por lo tanto, la mayor tasa de emigración temporal se produjo durante marzo de 2006, relacionado con el elevado número de turistas que visitaron Kisite-Mpunguti MPA en febrero de 2006. Este fue el año con la mayor afluencia de visitantes

desde la implementación del área protegida en 1978. El código de conducta implementado en 2007, y la caída significativa del turismo en 2008, dio lugar a un menor número de animales abandonando temporalmente el área de estudio.

10. La tasa de retorno de los emigrantes temporales se asoció con la temperatura estacional superficial del mar, con una mayor probabilidad de delfines que regresan al AMP de Kisite-Mpunguti durante la siguiente estación en los periodos de baja temperatura. Estos resultados no sostienen la hipótesis inicial de que los individuos entran en el área de estudio principalmente en busca de oportunidades de apareamiento.
11. La tasa de supervivencia aparente anual de 0.96 se estimó constante durante el período 2006-2009. Sin embargo para un importante porcentaje de los modelos, la tasa de supervivencia aparente aumentó de 0.93 en 2006 a 0.99 en 2009.
12. Los modelos de diseño robusto de Pollock pueden ayudar a entender los efectos de los factores bióticos y abióticos en los parámetros demográficos, proporcionando información valiosa para evaluar cambios en las dinámicas poblacionales de la población de estudio.
13. Este estudio demuestra que las interacciones con barcos turísticos alteran el comportamiento de los delfines, con una disminución significativa de la cantidad total de tiempo de viaje y un aumento en los patrones de buceo. La transición del comportamiento de viaje al buceo puede indicar una estrategia de evasión de los delfines para evitar los barcos turísticos.
14. La duración media de cada comportamiento varía considerablemente entre los escenarios de control (ausencia de embarcaciones turísticas) e impacto (presencia de barcos turísticos), con una disminución significativa en los comportamientos de viaje y de descanso. La reducción de la duración de reposo podría tener graves consecuencias para las crías, ya que se cree que son éstos los principales períodos en los cuales las hembras las amamantan.
15. En el AMP de Kisite-Mpunguti, los delfines estuvieron aproximadamente el 30% del día rodeados de barcos turísticos. Con estos niveles de turismo, la exposición acumulada del turismo no fue significativa para la población de delfines. Sin embargo, se detectaron períodos críticos para la especie durante el mes de diciembre a lo largo del período 2006-2007, cuando la intensidad del turismo en la zona estuvo por encima de los 180 barcos al mes. Por esta razón, es importante comprender cómo los impactos de las perturbaciones humanas afectan a la población del delfín mular del Indo-Pacífico, especialmente con el aumento del turismo previsto para los próximos años en Kenia.
16. Se encontraron diferencias espaciales en las lesiones causadas por tiburones a lo largo de las cuatro poblaciones del Océano Índico occidental. El mayor riesgo de depredación fue identificado

alrededor de La Réunion, con casi el 20% de los delfines foto-identificados mostrando lesiones causadas por tiburones.

17. El riesgo de depredación de la población keniana de delfines mulares del Indo-Pacífico era casi inexistente, con el 0,7% de los individuos identificados. Esto probablemente indica un bajo número de tiburones en la zona, relacionado con la reducción local histórica de sus poblaciones de tiburones.
18. Se debería de aplicar una estrategia nacional para seguir monitorizando esta especie categorizada como “Datos Insuficientes” según la Unión Internacional para la Conservación de la Naturaleza (UICN), principalmente debido a su reducido tamaño de población, el potencial aislamiento con respecto a poblaciones y la presión antropogénica actual.

6.2 Future perspectives

Based on the previous results and conclusions, I highlight the need to continue studying this data deficient species, as there are still many questions in order to understand the real conservation status of the Indo-Pacific bottlenose dolphins. For this, I propose the following projects and questions that should be investigated upon the conclusion of this PhD:

1. Expand the boat-based surveys conducted around Kisite-Mpunguti MPA towards identifying those areas where dolphins are moving when they temporarily emigrate from the study area. This is important considering that a transboundary area for protection has been proposed between southern Kenya and northern Tanzania as ecologically or biologically significant marine areas (EBSA)(CBD, 2010). This area covers the Pemba Channel, including Pemba Island, areas adjacent to the mainland such as Tanga Coelacanth Marine Park, and the southern shore and islands of the Kenyan coast.
2. Identify dolphin movement and population connectivity between neighbouring areas, through the comparison of photo-identification catalogues. In Watamu, northern Kenya, there is already a marine mammal research programme which has been collecting data on this species since 2010 (Gilbert Mwang'ombe et al., 2015). Also, in the nearby Zanzibar Island, two Indo-Pacific bottlenose dolphins population have been identified in the north and south of the Island (Särnblad et al., 2011). Moreover, an important dolphin population probably exist in northern Tanzania, around Tanga, near the border with Kenya.
3. A study carried out from tissue samples collected from Indo-Pacific bottlenose dolphins in Zanzibar Island, highlighted that there was a genetic differentiation showing significant separation between northern and southern populations, despite the fact that the areas are separated by approximately 80 km (Särnblad et al., 2011). It is important to find out to which extent these dolphin populations

are isolated from Kenya and to clarify whether they belong to different subpopulations within East Africa.

4. An important factor to study in any long-lived species is female reproductive success, which continues to be unexplored in the study area. It is necessary to understand how factors such as calf mortality, interbirth intervals, breeding season, group size and habitat affect female reproductive success (Mann et al., 1998).
5. Social relationships are essential to animals living in complex societies, such as Indo-Pacific bottlenose dolphins. These animals living in a fission-fusion society tend to be associated by similar age, sex and reproductive status (Frère et al., 2010; Randić et al., 2012). The extent how individuals dolphins associate between them, and its consequences on their behaviour and population level processes, remains unknown in southern Kenya. For this reason, the social structure should be investigated to find out more about the sociality of this population.
6. One of the main problem encounters during the development of this PhD thesis was the lack of information on the diet of the target species along the Kenyan coast. The study of the foraging ecology of the species is essential to identify its main prey species to elucidate, for instance, whether the species could be consider generalist or specialist, or between them. This study should be conducted from biopsy samples collected through boat-based surveys, due to the lack of stranded individuals along the coast.
7. The habitat preference of the species was determined through a habitat modelling approach using boat-based data collected during daylight periods. To improve our understanding of the three-dimensional oceanographic habitat of diving predators, it would be necessary to carry out acoustic study through Cetaceans and Porpoise Detection device or C-PODs. A CPOD is basically a hydrophone along with a data logger that records echolocation clicks made by odontocetes passing nearby (Sostres Alonso and Nuuttila, 2015). This type of information could provide more insights on the habitat use of dolphins as well as provide more information of their behaviour with the final aim at complementing the assessment of the importance of the KMPMA.
8. This PhD thesis highlights the small population size of the Indo-Pacific bottlenose dolphin around Kisite-Mpunguti MPA. For this reason, it is essential to continue the study of the demographic parameters to find out if the population size's variability identified in this thesis occurs along the coming years, and detect possible fluctuations that could lead to the decline of this population (Oro, 2003). The information obtained through demographic parameters is of paramount importance to evaluate the effectiveness of the conservation actions carried out by management agencies.
9. Studies on population dynamics including new variables such as age and sex, could help determining survival rates per males and females, which has been previously described to be

slightly higher for females, and similarly for adults versus juveniles (Silva et al., 2009; Stolen and Barlow, 2003).

10. Continuing capacity-building amongst Kenyan conservation rangers and community based organizations on marine mammal data collection, monitoring and nature-based tourism management.
11. Expand the research to other marine mammal species inhabiting or migrating through Kenyan waters, such as the Indo-Pacific humpback dolphin, spinner dolphins or humpback whales (Pérez-Jorge et al., 2011).

Appendix 1

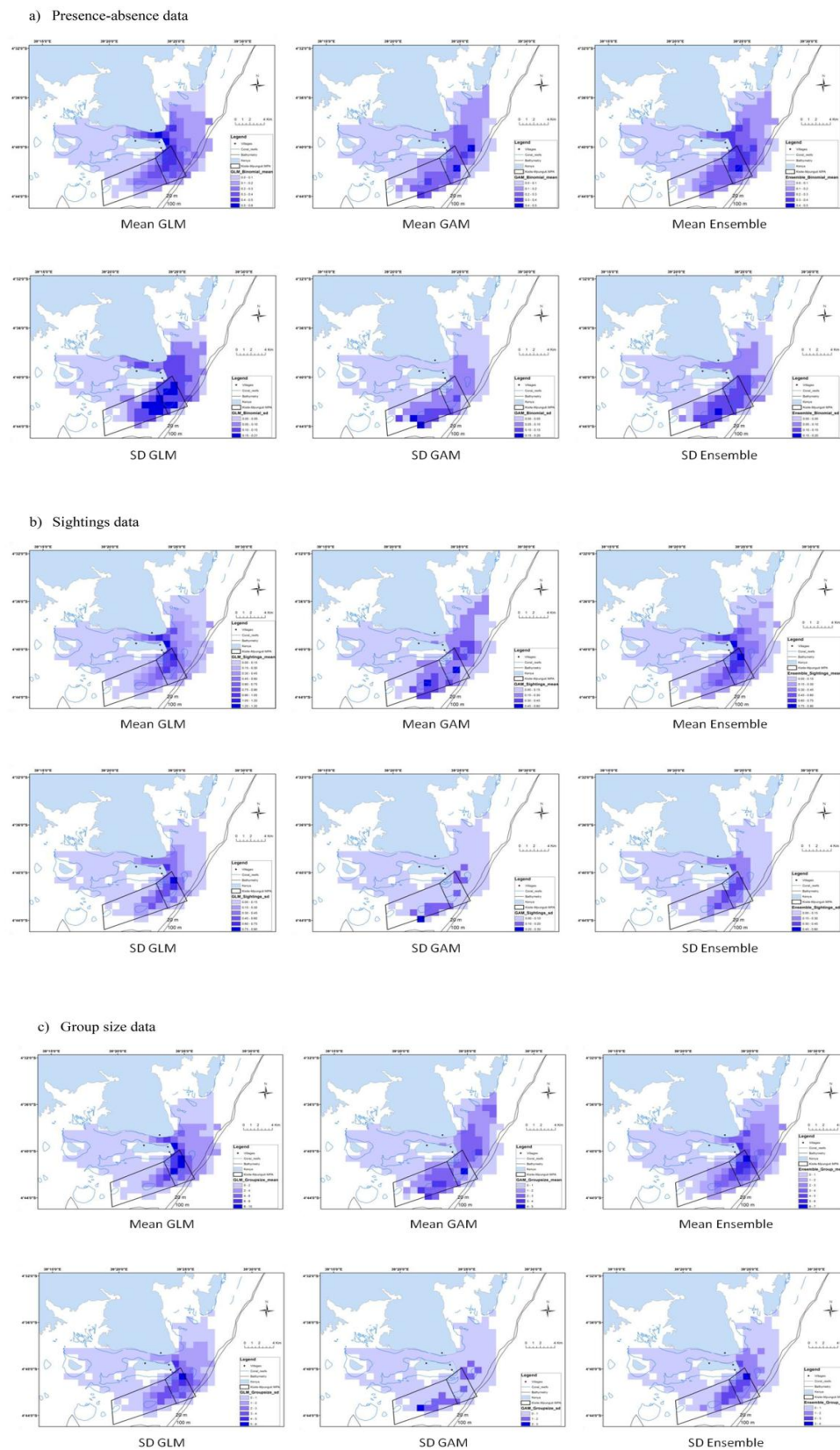


Fig. A1.1 Mean and SD predictions probability over the years 2006 and 2008

Appendix 2

Robust design assumptions

The following assumptions (highlighted) and validations were taken into account on our implementation of the Pollock's closed robust design (Pollock, 1982; Pollock et al., 1990; B. K. Williams et al., 2002):

1. All individuals have equal probability of being captured within a sampling occasion. To minimise heterogeneity resulting from mark distinctiveness, only dorsal fin images with Q1 and Q2 and well marked individuals were used on the analysis.
2. Capture and recapture probabilities are equal. Capture and recapture probabilities (p and c) were set equal on all fitted models, as photo-identification protocols should not affect the recapture probabilities because do not require capture and/or handling of animals.
3. Marks are unique, permanent and identified correctly. Every individual dorsal fin image was compared to a photo-identification catalogue which included left and right dorsal fins from previously identified animals. This process was verified by two independent researchers to minimize misidentifications. Nicks and marks on the leading and trailing edges of the dorsal fin were used to identify individual Indo-Pacific bottlenose dolphins.
4. Sampling interval for a particular secondary sample is instantaneous. Secondary periods were completed within the shortest time period possible for instantaneous sampling, as each secondary sampling occasion was represented by single sightings.
5. The population is closed over primary period. Secondary sampling occasion's data was collected within 15 day periods to fulfil the assumption of temporal closure within primary periods. This assumption was tested using the program U-CARE (see section 3.3.1 Model selection).
6. All individuals have equal probability of survival. Our analysis did not include calves, as they were not enough marked for identification and recapture. This also helps to minimise the violation of the assumption of equal survival probability among individuals, only including non-calves individuals. However, this assumption is usually difficult to satisfy, as survival can vary by age or sex in many cases. This assumption was tested using the program U-CARE (see section 3.3.1 Model selection).
7. Capture probabilities are independent between individuals. This model assumption is likely to be violated as coastal populations of Indo-Pacific bottlenose dolphins are socially driven and capturing a particular dolphin may increase the probability of capturing its closest associate.

Table A2.1 Parameter estimates from the best five models from the model selection results. Parameters: S denotes survival, γ' and γ'' denote temporary emigration (Markovian ($\gamma'' \neq \gamma'$), random ($\gamma'' = \gamma'$)), p denotes capture probability, c denotes recapture probability, Nm denotes Number of marked individuals and session denotes time varying between primary occasions. Capture and recapture probability were set equal on all fitted models.

Model 1. $S(\sim 1)\gamma''(\sim BOAT)\gamma'(\sim SST_3)p(\sim season)=c(\sim season)Nm(\sim session)$				
Parameter	Estimate	Standard Error	95% Confidence Interval	
			Lower	Upper
1:S g1 c1 c1 a0 t1	0.9907	0.0023	0.9851	0.9943
2:Gamma" g1 c1 c1 a0	0.7515	0.0918	0.5357	0.8880
3:Gamma" g1 c1 c1 a3	0.2126	0.0650	0.1120	0.3663
4:Gamma" g1 c1 c1 a6	0.3841	0.0565	0.2807	0.4991
5:Gamma" g1 c1 c1 a9	0.5365	0.0673	0.4052	0.6629
6:Gamma" g1 c1 c1 a12	0.3858	0.0565	0.2824	0.5006
7:Gamma" g1 c1 c1 a15	0.1396	0.0627	0.0551	0.3111
8:Gamma" g1 c1 c1 a18	0.2755	0.0620	0.1714	0.4114
9:Gamma" g1 c1 c1 a21	0.4530	0.0584	0.3429	0.5679
10:Gamma" g1 c1 c1 a24	0.1849	0.0652	0.0886	0.3461
11:Gamma" g1 c1 c1 a27	0.1246	0.0609	0.0455	0.2985
12:Gamma" g1 c1 c1 a30	0.2114	0.0650	0.1110	0.3655
13:Gamma" g1 c1 c1 a33	0.4049	0.0565	0.3006	0.5187
14:Gamma" g1 c1 c1 a36	0.2683	0.0624	0.1642	0.4061
15:Gamma" g1 c1 c1 a39	0.1571	0.0641	0.0673	0.3251
16:Gamma" g1 c1 c1 a42	0.2697	0.0624	0.1657	0.4072
17:Gamma' g1 c1 c1 a3 t	0.4859	0.1053	0.2926	0.6835
18:Gamma' g1 c1 c1 a6 t	0.0069	0.0142	0.0001	0.2941
19:Gamma' g1 c1 c1 a9 t	0.3537	0.1299	0.1523	0.6250
20:Gamma' g1 c1 c1 a12	0.7548	0.0689	0.5973	0.8646
21:Gamma' g1 c1 c1 a15	0.7745	0.0686	0.6140	0.8811
22:Gamma' g1 c1 c1 a18	0.0153	0.0271	0.0005	0.3453
23:Gamma' g1 c1 c1 a21	0.4264	0.1177	0.2244	0.6563
24:Gamma' g1 c1 c1 a24	0.5405	0.0937	0.3597	0.7113
25:Gamma' g1 c1 c1 a27	0.2828	0.1358	0.0959	0.5943
26:Gamma' g1 c1 c1 a30	0.0046	0.0103	0.0001	0.2710
27:Gamma' g1 c1 c1 a33	0.4371	0.1156	0.2362	0.6610
28:Gamma' g1 c1 c1 a36	0.8266	0.0671	0.6556	0.9227
29:Gamma' g1 c1 c1 a39	0.6150	0.0800	0.4517	0.7560
30:Gamma' g1 c1 c1 a42	0.0085	0.0170	0.0002	0.3075
31:p g1 s1 t1	0.1773	0.0201	0.1413	0.2201
32:p g1 s4 t1	0.1883	0.0150	0.1607	0.2194
33:p g1 s7 t1	0.1999	0.0131	0.1755	0.2268
34:p g1 s10 t1	0.2120	0.0169	0.1807	0.2471
95% Confidence Interval				
Session	N-hat	Standard Error	Lower	Upper
1	58.9239	6.4787	50.0188	76.6217
2	5.9292	2.7589	3.6144	16.9661
3	57.8536	10.7408	42.0589	85.4946
4	49.9486	6.2497	41.0935	66.5725
5	42.9790	5.2650	36.0395	57.8920
6	13.3830	2.8387	10.3740	22.9815
7	33.7138	4.3088	28.0160	45.8839
8	17.9175	6.4764	9.0156	35.6090
9	17.9336	6.4822	9.0237	35.6409
10	17.8900	6.4660	9.0022	35.5528
11	45.2421	6.0076	36.7259	61.2152
12	48.1412	4.3831	42.2970	60.4336
13	35.6015	7.5088	25.4909	56.4828
14	36.0329	6.8841	26.5728	54.8417
15	17.9438	6.4863	9.0285	35.6628
16	61.2896	5.0732	54.2735	75.0739

Model 2. S(~Year)Gamma"(~BOAT)Gamma'(~SST_3)p(~season)= c(~season)Nm(~session)				
			95% Confidence Interval	
Parameter	Estimate	Standard Error	Lower	Upper
1:S g1 c1 c1 a0 t1	0.9809	0.0067	0.9621	0.9905
2:S g1 c1 c1 a12 t13	0.9910	0.0027	0.9840	0.9949
3:S g1 c1 c1 a24 t25	0.9958	0.0026	0.9857	0.9988
4:S g1 c1 c1 a36 t37	0.9980	0.0020	0.9855	0.9997
5:Gamma" g1 c1 c1 a0	0.7419	0.0940	0.5235	0.8827
6:Gamma" g1 c1 c1 a3	0.2149	0.0653	0.1136	0.3689
7:Gamma" g1 c1 c1 a6	0.3820	0.0571	0.2778	0.4983
8:Gamma" g1 c1 c1 a9	0.5302	0.0681	0.3978	0.6585
9:Gamma" g1 c1 c1 a12	0.3837	0.0571	0.2794	0.4998
10:Gamma" g1 c1 c1 a15	0.1429	0.0636	0.0568	0.3155
11:Gamma" g1 c1 c1 a18	0.2763	0.0622	0.1718	0.4127
12:Gamma" g1 c1 c1 a21	0.4490	0.0591	0.3377	0.5655
13:Gamma" g1 c1 c1 a24	0.1876	0.0656	0.0903	0.3494
14:Gamma" g1 c1 c1 a27	0.1280	0.0619	0.0471	0.3033
15:Gamma" g1 c1 c1 a30	0.2137	0.0654	0.1125	0.3681
16:Gamma" g1 c1 c1 a33	0.4022	0.0572	0.2969	0.5175
17:Gamma" g1 c1 c1 a36	0.2693	0.0627	0.1648	0.4076
18:Gamma" g1 c1 c1 a39	0.1602	0.0648	0.0690	0.3290
19:Gamma" g1 c1 c1 a42	0.2707	0.0626	0.1662	0.4086
20:Gamma' g1 c1 c1 a3 t	0.4616	0.1112	0.2629	0.6734
21:Gamma' g1 c1 c1 a6 t	0.0066	0.0144	0.0001	0.3349
22:Gamma' g1 c1 c1 a9 t	0.3330	0.1345	0.1322	0.6207
23:Gamma' g1 c1 c1 a12	0.7339	0.0739	0.5678	0.8527
24:Gamma' g1 c1 c1 a15	0.7544	0.0738	0.5846	0.8703
25:Gamma' g1 c1 c1 a18	0.0145	0.0272	0.0004	0.3804
26:Gamma' g1 c1 c1 a21	0.4033	0.1233	0.1984	0.6486
27:Gamma' g1 c1 c1 a24	0.5156	0.0994	0.3278	0.6991
28:Gamma' g1 c1 c1 a27	0.2652	0.1391	0.0818	0.5938
29:Gamma' g1 c1 c1 a30	0.0044	0.0105	0.0000	0.3140
30:Gamma' g1 c1 c1 a33	0.4137	0.1213	0.2094	0.6529
31:Gamma' g1 c1 c1 a36	0.8095	0.0735	0.6256	0.9153
32:Gamma' g1 c1 c1 a39	0.5903	0.0851	0.4196	0.7418
33:Gamma' g1 c1 c1 a42	0.0081	0.0172	0.0001	0.3469
34:p g1 s1 t1	0.1774	0.0200	0.1414	0.2201
35:p g1 s4 t1	0.1880	0.0150	0.1604	0.2191
36:p g1 s7 t1	0.1991	0.0131	0.1746	0.2261
37:p g1 s10 t1	0.2107	0.0169	0.1794	0.2458
			95% Confidence Interval	
Session	N-hat	Standard Error	Lower	Upper
1	58.9110	6.4745	50.0119	76.5977
2	5.9390	2.7650	3.6172	16.9946
3	58.0664	10.7981	42.1854	85.8519
4	50.1616	6.3043	41.2221	66.9189
5	42.9695	5.2618	36.0347	57.8738
6	13.3996	2.8456	10.3810	23.0161
7	33.7995	4.3336	28.0640	46.0310
8	17.8999	16460.8340	0.0128	24975.0330
9	17.9162	2582.3566	0.0371	8652.7208
10	17.8602	2057.5568	0.0426	7492.2661
11	45.3723	6.0420	36.8036	61.4304
12	48.2959	4.4250	42.3863	60.6890
13	35.5905	7.5049	25.4853	56.4613
14	36.0883	6.9010	26.6035	54.9409
15	17.8898	1548.4867	0.0513	6239.2124
16	61.4861	5.1231	54.3915	75.3901

Model 3. S(~1)Gamma''(~SWIMMERS_1)Gamma'(~SST_3)p(~season)= c(~season)Nm(~session)				
			95% Confidence Interval	
Parameter	Estimate	Standard Error	Lower	Upper
1:S g1 c1 c1 a0 t1	0.9911	0.0022	0.9855	0.9946
2:Gamma" g1 c1 c1 a0	0.4522	0.0653	0.3300	0.5805
3:Gamma" g1 c1 c1 a3	0.1593	0.0625	0.0706	0.3212
4:Gamma" g1 c1 c1 a6	0.6051	0.0932	0.4164	0.7670
5:Gamma" g1 c1 c1 a9	0.3654	0.0572	0.2620	0.4829
6:Gamma" g1 c1 c1 a12	0.4445	0.0642	0.3247	0.5711
7:Gamma" g1 c1 c1 a15	0.1586	0.0625	0.0700	0.3207
8:Gamma" g1 c1 c1 a18	0.4857	0.0707	0.3516	0.6220
9:Gamma" g1 c1 c1 a21	0.3830	0.0580	0.2773	0.5010
10:Gamma" g1 c1 c1 a24	0.1527	0.0623	0.0656	0.3164
11:Gamma" g1 c1 c1 a27	0.1285	0.0605	0.0486	0.2982
12:Gamma" g1 c1 c1 a30	0.3137	0.0572	0.2135	0.4349
13:Gamma" g1 c1 c1 a33	0.2549	0.0600	0.1555	0.3886
14:Gamma" g1 c1 c1 a36	0.2531	0.0601	0.1537	0.3873
15:Gamma" g1 c1 c1 a39	0.1384	0.0614	0.0553	0.3058
16:Gamma" g1 c1 c1 a42	0.3926	0.0586	0.2853	0.5114
17:Gamma' g1 c1 c1 a3 t	0.6124	0.0845	0.4403	0.7605
18:Gamma' g1 c1 c1 a6 t	0.0192	0.0274	0.0011	0.2537
19:Gamma' g1 c1 c1 a9 t	0.4924	0.1041	0.3001	0.6870
20:Gamma' g1 c1 c1 a12	0.8193	0.0618	0.6666	0.9114
21:Gamma' g1 c1 c1 a15	0.8333	0.0604	0.6806	0.9214
22:Gamma' g1 c1 c1 a18	0.0387	0.0463	0.0035	0.3162
23:Gamma' g1 c1 c1 a21	0.5604	0.0928	0.3786	0.7274
24:Gamma' g1 c1 c1 a24	0.6576	0.0780	0.4934	0.7912
25:Gamma' g1 c1 c1 a27	0.4199	0.1149	0.2231	0.6460
26:Gamma' g1 c1 c1 a30	0.0136	0.0209	0.0006	0.2266
27:Gamma' g1 c1 c1 a33	0.5700	0.0912	0.3900	0.7333
28:Gamma' g1 c1 c1 a36	0.8701	0.0558	0.7179	0.9463
29:Gamma' g1 c1 c1 a39	0.7163	0.0712	0.5596	0.8338
30:Gamma' g1 c1 c1 a42	0.0232	0.0317	0.0015	0.2696
31:p g1 s1 t1	0.1613	0.0187	0.1279	0.2013
32:p g1 s4 t1	0.1814	0.0145	0.1547	0.2116
33:p g1 s7 t1	0.2035	0.0129	0.1794	0.2299
34:p g1 s10 t1	0.2274	0.0170	0.1959	0.2624
			95% Confidence Interval	
Session	N-hat	Standard Error	Lower	Upper
1	62.3891	7.3300	52.1311	82.1002
2	6.1271	2.8793	3.6732	17.5255
3	56.9498	10.4938	41.5251	83.9662
4	47.6513	5.6697	39.7001	62.8693
5	45.5148	5.9467	37.5092	62.0551
6	13.7193	2.9703	10.5210	23.6424
7	33.3510	4.2018	27.8143	45.2552
8	21.3950	21987.1330	0.0145	31656.7650
9	21.3935	21984.0670	0.0145	31653.3960
10	21.3937	3948.5203	0.0381	12026.2310
11	44.6895	5.8594	36.3987	60.2938
12	46.4865	3.9370	41.3429	57.7221
13	38.5203	8.3810	27.1174	61.6186
14	37.1497	7.1883	27.2246	56.7090
15	21.5206	22245.6410	0.0145	31940.5290
16	59.1881	4.5440	53.0096	71.7184

Model 4. S(~Year)Gamma'(~SWIMMERS_1)Gamma'(~SST_3)p(~season)= c(~season)Nm(~session)				
Parameter	Estimate	Standard Error	95% Confidence Interval	
			Lower	Upper
1:S gl c1 c1 a0 t1	0.9812	0.0068	0.9621	0.9907
2:S gl c1 c1 a12 t13	0.9914	0.0027	0.9843	0.9953
3:S gl c1 c1 a24 t25	0.9961	0.0026	0.9858	0.9989
4:S gl c1 c1 a36 t37	0.9982	0.0019	0.9856	0.9998
5:Gamma" gl c1 c1 a0	0.4478	0.0659	0.3247	0.5776
6:Gamma" gl c1 c1 a3	0.1621	0.0635	0.0718	0.3262
7:Gamma" gl c1 c1 a6	0.5970	0.0950	0.4059	0.7626
8:Gamma" gl c1 c1 a9	0.3635	0.0575	0.2597	0.4817
9:Gamma" gl c1 c1 a12	0.4403	0.0648	0.3197	0.5684
10:Gamma" gl c1 c1 a15	0.1615	0.0635	0.0713	0.3257
11:Gamma" gl c1 c1 a18	0.4804	0.0715	0.3452	0.6185
12:Gamma" gl c1 c1 a21	0.3806	0.0583	0.2744	0.4995
13:Gamma" gl c1 c1 a24	0.1556	0.0634	0.0668	0.3217
14:Gamma" gl c1 c1 a27	0.1316	0.0619	0.0498	0.3045
15:Gamma" gl c1 c1 a30	0.3132	0.0574	0.2127	0.4349
16:Gamma" gl c1 c1 a33	0.2559	0.0603	0.1560	0.3902
17:Gamma" gl c1 c1 a36	0.2541	0.0604	0.1542	0.3889
18:Gamma" gl c1 c1 a39	0.1414	0.0627	0.0565	0.3117
19:Gamma" gl c1 c1 a42	0.3899	0.0590	0.2821	0.5096
20:Gamma' gl c1 c1 a3 t	0.5894	0.0888	0.4115	0.7466
21:Gamma' gl c1 c1 a6 t	0.0199	0.0291	0.0011	0.2737
22:Gamma' gl c1 c1 a9 t	0.4721	0.1077	0.2772	0.6760
23:Gamma' gl c1 c1 a12	0.7995	0.0671	0.6370	0.9006
24:Gamma' gl c1 c1 a15	0.8142	0.0659	0.6511	0.9114
25:Gamma' gl c1 c1 a18	0.0393	0.0482	0.0034	0.3328
26:Gamma' gl c1 c1 a21	0.5383	0.0969	0.3518	0.7146
27:Gamma' gl c1 c1 a24	0.6343	0.0825	0.4635	0.7769
28:Gamma' gl c1 c1 a27	0.4024	0.1177	0.2051	0.6374
29:Gamma' gl c1 c1 a30	0.0143	0.0224	0.0006	0.2478
30:Gamma' gl c1 c1 a33	0.5476	0.0954	0.3627	0.7203
31:Gamma' gl c1 c1 a36	0.8534	0.0617	0.6887	0.9387
32:Gamma' gl c1 c1 a39	0.6933	0.0758	0.5293	0.8196
33:Gamma' gl c1 c1 a42	0.0240	0.0335	0.0015	0.2890
34:p gl s1 t1	0.1622	0.0187	0.1288	0.2023
35:p gl s4 t1	0.1817	0.0145	0.1550	0.2119
36:p gl s7 t1	0.2030	0.0129	0.1789	0.2295
37:p gl s10 t1	0.2262	0.0170	0.1945	0.2613
95% Confidence Interval				
Session	N-hat	Standard Error	Lower	Upper
1	62.1677	7.2679	52.0030	81.7226
2	6.1176	2.8734	3.6704	17.4982
3	57.0528	10.5226	41.5853	84.1423
4	47.8272	5.7166	39.8042	63.1611
5	45.3528	5.8982	37.4193	61.7699
6	13.7031	2.9638	10.5141	23.6093
7	33.3923	4.2143	27.8370	45.3277
8	21.1628	15377.8210	0.0172	26030.8400
9	21.1728	15385.2510	0.0172	26043.3400
10	21.1705	15381.8630	0.0172	26038.9250
11	44.7525	5.8767	36.4356	60.4001
12	46.6123	3.9730	41.4134	57.9351
13	38.3352	8.3207	27.0185	61.2746
14	37.0962	7.1725	27.1945	56.6151
15	21.1726	15385.0430	0.0172	26043.0340
16	59.3477	4.5870	53.1029	71.9826

Model 5. S(~1)Gamma''(~season+Year)Gamma'(~SST 3)p(~season)= c(~season)Nm(~session)				
			95% Confidence Interval	
Parameter	Estimate	Standard Error	Lower	Upper
1:S g1 c1 c1 a0 t1	0.9899	0.0024	0.9841	0.9936
2:Gamma' g1 c1 c1 a0	0.7353	0.0880	0.5337	0.8708
3:Gamma' g1 c1 c1 a3	0.5915	0.0777	0.4353	0.7312
4:Gamma' g1 c1 c1 a6	0.4301	0.1004	0.2527	0.6275
5:Gamma' g1 c1 c1 a9	0.2823	0.1278	0.1026	0.5752
6:Gamma' g1 c1 c1 a12	0.6098	0.0838	0.4394	0.7570
7:Gamma' g1 c1 c1 a15	0.4489	0.0621	0.3324	0.5713
8:Gamma' g1 c1 c1 a18	0.2980	0.0857	0.1599	0.4865
9:Gamma' g1 c1 c1 a21	0.1812	0.0982	0.0571	0.4473
10:Gamma' g1 c1 c1 a24	0.4679	0.0940	0.2956	0.6482
11:Gamma' g1 c1 c1 a27	0.3143	0.0752	0.1878	0.4760
12:Gamma' g1 c1 c1 a30	0.1928	0.0804	0.0799	0.3966
13:Gamma' g1 c1 c1 a33	0.1107	0.0748	0.0273	0.3556
14:Gamma' g1 c1 c1 a36	0.3309	0.1129	0.1540	0.5734
15:Gamma' g1 c1 c1 a39	0.2050	0.0862	0.0838	0.4210
16:Gamma' g1 c1 c1 a42	0.1185	0.0712	0.0341	0.3384
17:Gamma' g1 c1 c1 a3 t	0.3170	0.1612	0.0974	0.6664
18:Gamma' g1 c1 c1 a6 t	0.0011	0.0034	0.0000	0.3605
19:Gamma' g1 c1 c1 a9 t	0.1911	0.1523	0.0331	0.6196
20:Gamma' g1 c1 c1 a12	0.6664	0.1042	0.4436	0.8335
21:Gamma' g1 c1 c1 a15	0.6957	0.1010	0.4730	0.8535
22:Gamma' g1 c1 c1 a18	0.0029	0.0080	0.0000	0.4021
23:Gamma' g1 c1 c1 a21	0.2564	0.1614	0.0615	0.6445
24:Gamma' g1 c1 c1 a24	0.3782	0.1549	0.1432	0.6887
25:Gamma' g1 c1 c1 a27	0.1360	0.1340	0.0166	0.5953
26:Gamma' g1 c1 c1 a30	0.0007	0.0022	0.0000	0.3412
27:Gamma' g1 c1 c1 a33	0.2668	0.1619	0.0670	0.6483
28:Gamma' g1 c1 c1 a36	0.7743	0.0943	0.5435	0.9081
29:Gamma' g1 c1 c1 a39	0.4703	0.1388	0.2296	0.7257
30:Gamma' g1 c1 c1 a42	0.0014	0.0043	0.0000	0.3715
31:p g1 s1 t1	0.1532	0.0199	0.1181	0.1964
32:p g1 s4 t1	0.1725	0.0162	0.1431	0.2065
33:p g1 s7 t1	0.1936	0.0143	0.1671	0.2231
34:p g1 s10 t1	0.2166	0.0172	0.1847	0.2522
			95% Confidence Interval	
Session	N-hat	Standard Error	Lower	Upper
1	64.4383	8.1590	53.0793	86.4788
2	6.4073	3.0612	3.7544	18.3892
3	59.5561	11.2865	42.9796	88.6341
4	49.2317	6.0858	40.6418	65.4743
5	47.0144	6.5643	38.1984	65.3101
6	14.1982	3.1896	10.7166	24.7411
7	34.4005	4.5430	28.3720	47.1940
8	31.1735	7220.2147	0.0484	20082.7580
9	29.7804	53631.4700	0.0151	58858.6410
10	30.8926	57280.3570	0.0154	61963.7730
11	46.2858	6.3410	37.2923	63.1377
12	47.6221	4.2566	41.9857	59.6309
13	40.2274	9.0939	27.8923	65.3566
14	38.7322	7.7690	28.0130	59.8846
15	22.4005	34020.7960	0.0124	40593.9810
16	60.6303	4.9256	53.8595	74.0846

Appendix 3

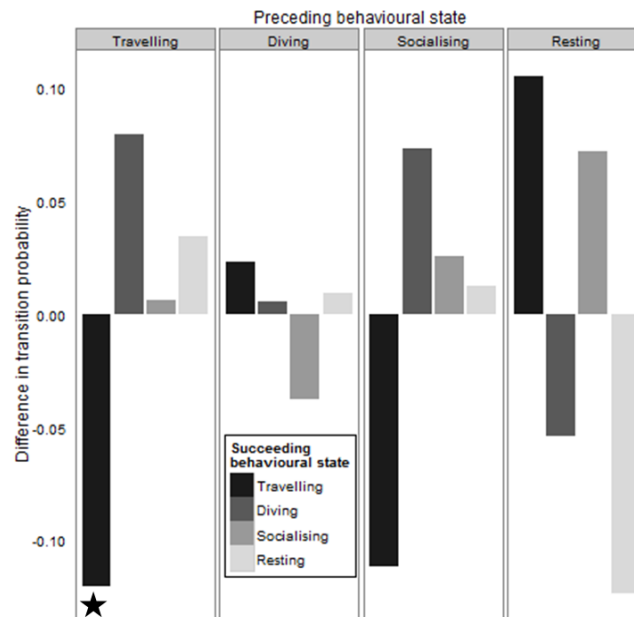


Fig. A3.1 Differences in transition probability between impact (tourist boat present within 100 meters of the dolphins) and control (tourist boat absent) situations ($p_{ij}(\text{impact}) - p_{ij}(\text{control})$). The vertical boxes separate each preceding behavioural state, while the bars within each box represent the succeeding behavioural state (see colour legend). Transitions that changed significantly ($p < 0.05$) during boat interactions are marked with a star (★)

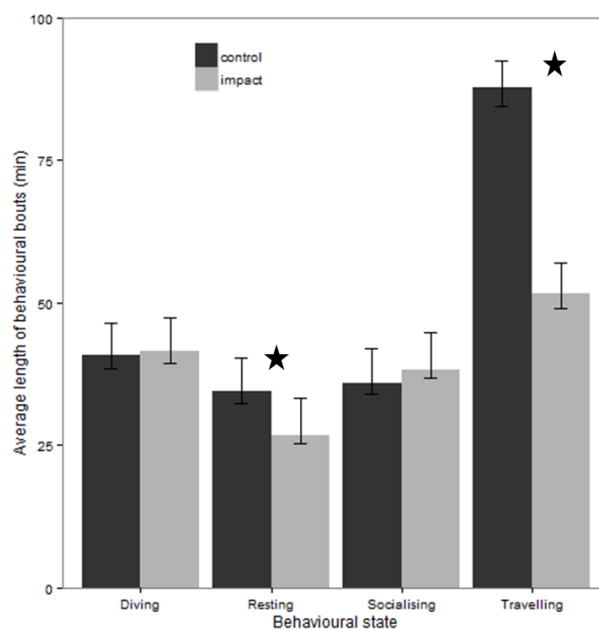


Fig. A3.2 Average bout length of dolphins represented by the duration of time (minutes) spent on each behavioural state under control (tourist boats absent) and impact (tourist boats present within 100m of the dolphins) situations. The vertical bars represent 95% confidence intervals. Behavioural states with a significant difference ($p < 0.05$) are marked with a star (★).

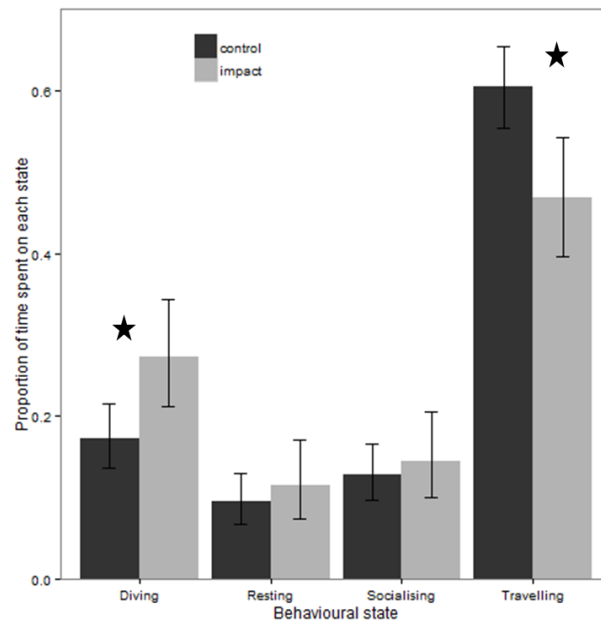


Fig. A3.3 Dolphin behavioural budgets represented by the proportion of time spent in each behavioural state under control (tourist boats absent) and impact (tourist boats present within 100m of the dolphins) situations. The vertical bars represent 95% confidence intervals. Behavioural states with a significant difference ($p < 0.05$) are marked with a star (★).

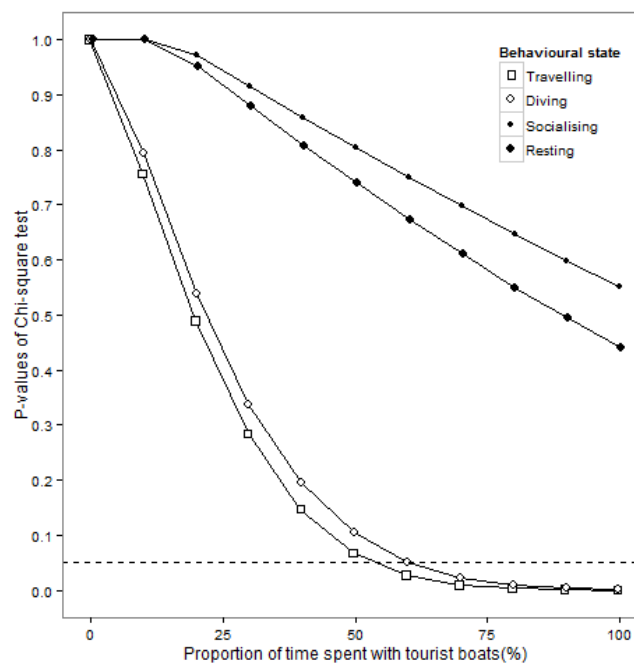


Fig. A3.4 Effect of tourist boat intensity on cumulative behavioural budget within 100m of the dolphins. P-values of the difference between the cumulative behavioural budget and the control behavioural budget for dolphin activity. The proportion of boat exposure was artificially varied from 0 to 100%. Dashed line represents the statistical level of significance ($p < 0.05$)

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