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POPULATION ECOLOGY OF COASTAL BOTTLENOSE DOLPHINS (*TURSIOPS TRUNCATUS*) IN NORTHERN PATAGONIA ARGENTINA

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You are not a drop in the Ocean,
you are the entire Ocean in a drop
(Rumi)

Yagui, calf of Grace (RN-BSA-56/07), born February 2011. ©E. Vermeulen

Dedicated to these wonderful creatures I love dearly,
the bottlenose dolphins of Northern Patagonia

Para estos animals que tanto amo,
las toninas de la Patagonia Norte

Acknowledgements

Over the past 33 years, I have been able to identify a total of '*a lot of*' individuals of my own species based on their unique physical and mental traits. The technique used for identification and subsequent re-identifications, was primarily based on social memory. Of these individuals, '*many*' have contributed significantly to where I am today. Therefore I wish to write these sincere acknowledgements.

My earliest memories go back to my parents, **Fons** and **Aleyde.** Their parental investment has been enormous! Ever since I was born, they have provided me with love, care, shelter and resources, and have been the most important part in my learning and growing processes throughout life. Furthermore, they have created my core habitat, my *home*, to which I have showed a long-term site-fidelity over the years. It has truly been a safe harbour to which I could always sail! However, most importantly, they have given me the tools and support to pursue my dreams, to expand my home range and roam along many desolated coastlines. It is a gratitude I will never be able to express in words! Mama, Papa, vanuit het diepste van mijn hart 'dank je wel!'.

I would also like to thank my siblings, **An** and **Tom**, for their life-long love and support. They have been the core unit of the group of juveniles I grew up in, giving me the ability to take part in many important aspects of social learning. Also into adulthood they have continued to show their friendship and support together with their partners **Liesbeth** and **Stijn**, and their children **Juul, Janne, Nel, Stan, Eline** and **my godchild in development**! Ook voor jullie uit het diepste van mijn hart 'dank je wel!'.

While the years passed by, my home range continued to expand, and so did my social network. My association patterns fluctuated, indicating the clear fission-fusion tendencies of our species. However some strong bonds were formed over the years and have continued to exist on a long-term basis. And especially these **friends** I wish to thank today, for their years of friendship, support, love and kindness. For the many talks, laughs, beers and tears, and for showing that physical distance is irrelevant when there is a true connection!

There are two of these friends I wish to mention specifically, as they have contributed significantly to where I am today. First of all, a person who has not only proven to be a close friend but also a life-long mentor, the person behind the biologist I am today, **Ludo Holsbeek**. When I first wrote Ludo explaining him about my dream to work with marine mammals he answered (and I quote) 'We passen er wel een mouw aan' ('we'll make it happen'). I think today it is safe to say we did, wel een hele kleerkast! He is the starting point of my career as a marine biologist, my life and work in Argentina and of the realisation of my dreams. There are no words that can express the support Ludo has given me over the years, being there as a mentor when in doubt and a true friend in times of need! And although he is not always 'in view', he has been there for me, always! And as if I was not lucky enough with Ludo's support, I have also met **Stefan Bräger**. Thanks to Stefan's many hours of

correcting, teaching and advising, and vast amounts of patience, he has been the best guide in this life as a marine biologist, making me grow exponentially as a scientist, expanding my thought processes and skills. Thanks to his help this PhD has come to a safe end, opening doors for future possibilities! However, most importantly, thanks to the many hours of talking (on Skype or over a glass of wine) about biology and other life-related things, he has grown to be a true friend, for which I wish to thank him the most.

Ludo and Stefan, thank you for your guidance, friendship and for believing in me as a person and a scientist. May the long-term association we form continue for many more years!

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As my dream to work with marine mammals started to develop, my home range expanded from Belgium to Argentina. During the years I have lived in Argentina, '**mi familia Argentina**' has continuously given me love, friendship and support. The life I have lived and work I have done in this South American country would not have been possible without them. Para mis hermanos, no hay palabras para expresar mis agradecimientos. Mil gracias por siempre estar, por su apoyo y su amistad, por inlcuirme en su casa y familia, y por siempre apoyarme en el trabajo y en la vida. La conexión que siento con ustedes es de por vida, son mi familia y siempre los tendré en mi corazón!

Over the years, my home range continued to grow, crossing many oceans and continents, and so did my social network. From people in Belgium and Argentina to those in e.g., Scotland, the Netherlands, Germany, Brazil, South Africa and Australia, all of which have given me friendship and support on my life's path. Many thanks to all of you, for your friendship and care, for giving me the gift of learning other cultures, languages and habits, for blessing me with an open mind. Thanks to all of you, my heart will never be in one place anymore, but continuously be able to travel the vast distances of this planet!

And vast distances it travelled to finally meet the most important person, the person with whom I now form my own core family unit, the most amazing person I have ever met, my best friend and husband to be **Kevin Ovenstone**. The love and support Kevin has given me ever since the day I met him is unconditional and indescribable. Thank you sweetie, for always supporting me in my dreams and ambitions, for laughing and playing, for helping and being my safe heaven, for walking with me through life, simply loving me for who I am and being my true companion. I could not imagine a life without you and am very excited for our future ahead!

Els

Abstract

The population ecology of bottlenose dolphins (*Tursiops truncatus*) was assessed between 2006 and 2011 in Northern Patagonia, Argentina. Over these years, 356 systematic photo-identification surveys were conducted in Bahía San Antonio, of which 227 were land-based and 129 were conducted from a small outboard-powered rigid-hull inflatable boat. In total, 1472 h was spend searching for dolphins, and resulted in 215 h of observation of 415 dolphin groups.

Photo-identification data resulted in the identification of 67 individual dolphins. Based on mark-recapture analysis, total abundance had a maximum corrected estimate of 83 (95%CI = 46 - 152) individuals. Adult survival rates varied between 0.97 (SE = 0.04) and 0.99 (SE = 0.01). Average calving interval of the 14 reproducing females equalled 3.5 ± 1.0 years. This results in 3.5 births/year in the entire population and a minimum annual birth rate of 4.2%. However, data suggest that calves may have been born and lost before being documented, underestimating birth rate, calf mortality and possibly the number of reproductive females. Either way, the recruitment rate of calves appears to be insufficient to compensate the overall mortality in the population. Additional data further indicated the genetic isolation and extremely low genetic diversity within this community, thus indicating this community of bottlenose dolphins is highly vulnerable and at risk.

Association patterns within the studied community were relatively strong (HWI 0.30 ± 0.08), re-indicating the small size of the population. Nonetheless, the fluctuation in prey density and availability appeared to be the most important factor determining their fission-fusion dynamics. It appears that a combination of aspects inherent to the species and this habitat, such as low cost of locomotion, low predation pressure and food predictability, has helped reduce the costs of fission in response to intraspecific competition.

Behavioural data indicated that Bahía San Antonio is mainly used to rest and forage, with a marked diurnal and seasonal pattern in their activity. Furthermore, dolphins appeared to show a preference for the shallower waters inside their core area; they moved in and out with the tide to remain in the intertidal zone as much as possible. The observed variation in foraging activity and spatial distribution is suggested to be driven by a seasonal and locally predictable variation in prey density and availability.

Most of the identified dolphins showed a yearlong residency and long term site-fidelity to Bahía San Antonio, suggesting it is the core area within the larger home range of this community. Furthermore, based on the frequent presence of calves and high residency of reproductive females, this protected coastal environment appears to provide shelter for nursing calves.

Many individuals of this community ranged along the entire northern coastline of the San Matías Gulf, up to the Río Negro Estuary (approx. 200 km). Further to the north, in the southern part of the Province of Buenos Aires, a neighbouring community of bottlenose dolphins was shown to exist. Both communities are largely isolated from each other, and the environmental discontinuities between two adjacent oceanic regimes in which these communities live are hypothesised to promote their coexistence. Additionally, four individuals from another community, originating from the more southern Province of Chubut, are known to reside in Bahía San Antonio. These individuals are genetically differentiated from all other individuals in the area, clearly shown in their distinct morphology.

The apparent fine-scale population structure of bottlenose dolphins over the relative small geographical distances in Argentina has conservation implications and indicates the need for further detailed research. Currently, the populations of bottlenose dolphins in the Provinces of Buenos Aires and Chubut are reported to have nearly vanished. However, this disappearance has been largely ignored in the past 40 years resulting in the studied communities to be one of the last ones remaining in the country. It seems that the coastal lifestyle and site-fidelity of coastal bottlenose dolphins, and the belief of the species to be common, may have obfuscated the need for more extensive research and conservation efforts in Argentina in former years.

Local declines of common species are easily overlooked when establishing priorities for conservation, and Argentina is not a unique case. An ever-increasing number of coastal bottlenose dolphin populations are reported to be vulnerable or declining worldwide. This study provides insight into how the failure to recognise local population declines can threaten the regional status of a common species like the bottlenose dolphin. Continued research and urgent conservation measures are therefore strongly recommended to prevent the disappearance of the bottlenose dolphin from the coasts of this South American country.

Resumen

La ecología poblacional del delfín nariz de botella (*Tursiops truncatus*) fue estudiada entre los años 2006 y 2011 en el norte de la Patagonia, Argentina. Durante estos años, se realizaron 356 salidas de campo en la Bahía de San Antonio, de las cuales 227 fueron realizadas desde la costa y 129 desde una pequeña embarcación. El esfuerzo total de 1472 horas dio como resultado 215 horas de observación de 415 grupos de delfines.

A lo largo de los años, 67 delfines fueron identificados individualmente. Utilizando la técnica de marca y recaptura, y teniendo en cuenta la proporción de individuos no identificables (juveniles y crías), los cálculos indicaron una abundancia máxima de 83 individuos (95%CI = 46 - 152). La sobrevivencia de adultos fue estimada entre 0.97 (SE = 0.04) y 0.99 (SE = 0.01). El intervalo reproductivo de las 14 hembras reproductivas fue de 3.5 ± 1.0 años, lo que resulta en un promedio de 3.5 nacimientos por año en la población o una tasa de natalidad anual de 4.2%. Sin embargo, los datos sugieren que muchas crías podrían haber muerto antes de ser registradas, lo que resultaría en una subestimación de la tasa de nacimientos, la mortalidad de crías y posiblemente la cantidad de hembras reproductivas. En todo caso, el reclutamiento de crías parece ser insuficiente para compensar la mortalidad en la población. Considerando además el aislamiento genético y la baja diversidad genética registrada, se puede concluir que esta comunidad de delfines está en riesgo y es altamente vulnerable.

Los datos indican que todos los delfines de la población se relacionan muy frecuentemente entre ellos (HWI 0.30 ± 0.08). Esto es, probablemente, otra indicación de que la población es pequeña. Sin embargo, las variaciones en la densidad y cantidad de especies presa podría ser el factor más importante para determinar las dinámicas de fisión y fusión en la población. Parecería que aspectos inherentes a la especie y su habitat, como el bajo costo de locomoción, la baja cantidad de predadores en la zona y la predictibilidad del comportamiento de la presa, han ayudado a reducir el costo de fisión para disminuir la competencia intraespecífica.

Los datos de comportamiento indican que los delfines utilizan la Bahía de San Antonio principalmente para descansar y alimentarse, con una notable variación según la hora del día y la época del año. Además, los delfines mostraron preferencia por las aguas pocas profundas dentro de la Bahía y siguieron el ritmo diario de las mareas para quedarse principalmente en la zona intermareal.

La mayoría de los delfines identificados mostraron, a largo plazo, un alto grado de residencia y fidelidad para la Bahía de San Antonio, por lo que se sugiere que es el área clave dentro del área de acción de los delfines. Además, considerando la alta presencia de crías y el alto grado de residencia de las hembras reproductivas, la Bahía de San Antonio parece ser un lugar ideal para criar a los cachorros.

Pero la Bahía de San Antonio no es el único lugar donde viven. Muchos individuos utilizan toda la zona costera del norte del Golfo San Matías, y nadan hasta la desembocadura del Río Negro (aprox. 200 km). Más al norte, y ya en el sur de la Provincia de Buenos Aires, existe otra comunidad de delfines. Ambas comunidades parecen estar aisladas entre sí, y probablemente separadas a causa de los distintos regímenes oceánicos que habitan. Además, cuatro individuos de otra comunidad de delfines nariz de botella, originarios de la Provincia de Chubut, también residen en la Bahía de San Antonio. Estos individuos son genéticamente distintos, lo que se demuestra claramente por sus diferencias morfológicas.

La marcada estructura poblacional de los delfines nariz de botella, a lo largo de la costa de la Argentina, tiene implicaciones para su conservación e indica la necesidad de estudios más detallados. En la actualidad, las poblaciones de delfines nariz de botella que habitaban las costas de las Provincias de Buenos Aires y Chubut casi han desaparecido. Sin embargo, la notable disminución de las poblaciones no ha recibido atención en los últimos 40 años. Como resultado, las poblaciones estudiadas en este trabajo podrían ser las últimas poblaciones residentes que quedan en el país. Parecería que la presencia de estos delfines en la costa, y su grado de residencia en ciertos lugares, junto a la creencia que se trata de una especie común, ha generado un olvido en cuanto al estudio y conservación del delfín nariz de botella.

Cuando se generan prioridades de investigación y conservación, muy frecuentemente se ignoran las disminuciones de las poblaciones locales de especies comunes, y esto no solo ocurrió en la Argentina. Cada vez más poblaciones de delfines nariz de botella en el mundo se describen como vulnerables o en disminución. Este estudio demuestra claramente como la falta de reconocimiento en la disminución de las poblaciones locales puede amenazar el estado nacional (y eventualmente internacional) de una especie 'común' como el delfín nariz de botella.
Es por esto que recomiendo continuar con las investigaciones científicas y la implementación de medidas de conservación para el delfín nariz de botella, ya que solo de esta manera podremos prevenir la desaparición total de esta especie de las costas de la Argentina.

Résumé

L'écologie d'une population de grand dauphin (*Tursiops truncatus*) a été étudiée entre 2006 et 2011 en Patagonie du nord, Argentine. Au cours de ces années, 356 prospections de photo-identification ont été conduites dans la Baie de San Antonio, dont 227 à partir de la côte et 129 en mer, à bord d'un semi-rigide à moteur. Au total, 1472 h d'effort de recherche ont permis d'aboutir à 215 h d'observation de 415 groupes de dauphins.

La technique de photo-identification a permis d'identifier 67 individus. En utilisant les analyses de marquage-recapture et en tenant compte de la proportion d'individus non-indentifiables (les juvéniles et les nouveau-nés), les estimations indiquent une abondance maximale corrigée de 83 individus (95%CI = 46 – 152). Le taux de survie des adultes varie entre 0.97 (SE = 0.04) et 0.99 (SE = 0.01). L'intervalle moyen entre deux naissances, estimé pour les 14 femelles reproductrices, est de 3.5 ± 1.0 ans. Ceci équivaut à 3.5 naissances par an dans la population et à un taux de naissance minimal de 4.2%. Cependant, les données suggèrent que des nouveau-nés pourraient naître et mourir avant d'avoir été observés, entrainant une sous-estimation du taux de naissance, de la mortalité des nouveau-nés et du nombre de femelles reproductrices. Quoi qu'il en soit, le taux de recrutement des petits paraît insuffisant pour compenser le taux de mortalité global de la population. De plus, d'autres données montrent un isolement génétique et une très faible diversité génétique de cette communauté de grands dauphins, indiquant qu'elle est hautement vulnérable et menacée.

Les données sur les associations entre individus montrent qu'elles sont relativement fortes (HWI 0.30 ± 0.08), soulignant à nouveau la petite taille de la population. Néanmoins, les variations de la densité et de la quantité des proies seraient le facteur le plus important déterminant la dynamique de fission-fusion de la population. Il apparaît qu'une combinaison des traits inhérents à l'espèce et à cet habitat, tels qu'un faible coût de la locomotion, une faible pression de prédation et la prédictibilité des ressources alimentaires, a contribué à réduire les coûts de la fission en réponse à la compétition intraspécifique.

Les données comportementales indiquent que les dauphins utilisent la Baie de San Antonio principalement pour se reposer et se nourrir, avec des variations journalières et saisonnières marquées. De plus, les dauphins montrent une préférence pour les eaux peu profondes et suivent le rythme journalier des marées afin de rester le plus possible dans la zone intertidale. Il est suggéré ici que les variations observées dans le comportement d'alimentation et dans la distribution spatiale des individus sont corrélées aux variations saisonnières et locales de la densité et de la disponibilité en proies.

La plupart des dauphins identifiés montrent une fidélité à long terme et une résidence tout au long de l'année dans la Baie de San Antonio, suggérant qu'elle constitue le cœur de leur espace vital, plus étendu. De plus, en considérant la grande fréquence de la présence de nouveau-nés et le haut taux de résidence chez les femelles reproductrices, cet environnement côtier protégé paraît fournir un abri idéal pour élever les petits.

Cependant, de nombreux individus circulent dans toute la zone côtière nord du Golfe de San Matias jusqu'à l'embouchure du Rio Negro (approx. 200 km). Plus au nord, dans le sud de la province de Buenos Aires, il existe une communauté voisine de grands dauphins. Les deux communautés sont isolées l'une de l'autre et leur coexistence est probablement rendue possible grâce aux discontinuités environnementales entre leurs régimes océaniques. En outre, quatre individus d'une autre communauté, provenant de la province de Chubut plus au sud, résident également dans la Baie de San Antonio. Ces individus sont très différents de tous les autres d'un point de vue génétique, et leur morphologie permet également de les distinguer.

La structure des populations de grands dauphins est apparemment de petite échelle sur toute la côte argentine, ce qui indique le besoin de recherches plus détaillées. Actuellement, les populations de grands dauphins dans les provinces de Buenos Aires et de Chubut ont presque disparu. Cependant, cette diminution des populations a été relativement ignorée ces 40 dernières années, faisant peut-être des communautés étudiées dans ce travail les dernières populations résidentes du pays. Il semble que le mode de vie côtier et la fidélité à certains sites des grands dauphins, ainsi que la croyance qu'ils sont tout à fait courant, pourraient avoir obscurci les besoins de recherche et d'effort de conservation en Argentine au cours des années passées.

Le déclin local d'espèces communes est facilement négligé lors de la mise en place de priorités de conservation, et l'Argentine n'est pas un cas unique. Un nombre sans cesse croissant de populations côtières de grands dauphins sont décrites comme vulnérables ou en déclin. Cette étude démontre clairement comment la non-reconnaissance du déclin de populations locales peut menacer le statut d'une espèce commune, telle que le grand dauphin, à l'échelle nationale (et éventuellement internationale). Plus de recherches et des mesures urgentes de conservation sont dès lors fortement recommandées pour prévenir la disparition imminente les grands dauphins des côtes de ce pays sud-américain.

LIST OF RELATED PUBLICATIONS

1. SCIENTIFIC PUBLICATIONS

Vermeulen, E. and Cammareri, A. 2009a. Residency, Abundance and Social Composition of bottlenose dolphins (*Tursiops truncatus*) in Bahía San Antonio, Patagonia, Argentina. Aquatic Mammals 35: 379-386.

Vermeulen, E. and Cammareri, A. 2009b. Variation in external morphology of resident bottlenose dolphins (*Tursiops truncatus*) in Bahía San Antonio, Patagonia, Argentina. Journal of Marine Animals and Their Ecology Vol2 N°2.

Fruet, P., Secchi, E.R., Daura-Jorge, F., **Vermeulen, E.**, Flores, P.A.C., Simões-Lopes, P.C., Genoves, R.C., Laporta, P., Di Tullio, J.C., Freitas, T.R., Dalla Rosa, L., Valiati, V.H., Behereharay, L.B., Möller, L.M. 2014. Remarkably low genetic diversity and strong population structure in common bottlenose dolphins (*Tursiops truncatus*) from coastal waters of the Southwestern Atlantic Ocean. Conservation Genetics DOI: 10.1007/s10592-014-0586-z.

Failla, M., Seijas, V.A., **Vermeulen, E**. in press. Occurrence of bottlenose dolphins (*Tursiops truncatus*) of the Río Negro Estuary, Patagonia, Argentina and their mid-distance movements along the Northeast Patagonian coast. Latin American Journal of Aquatic Mammals.

Laporta, P., Di Tullio, J.C., **Vermeulen, E**., Domit, C., Albuquerque, C., Lodi, L. in press. Report of the working group on habitat use of *Tursiops truncatu*s in the Southwestern Atlantic Ocean. Latin American Journal of Aquatic Mammals.

Vermeulen, E. submitted a. Effect of prey availability on fission-fusion dynamics of bottlenose dolphins (*Tursiops truncatus*) in Northern Patagonia. Behavioral Ecology and Sociobiology.

Vermeulen, E. submitted b. A shared habitat for humans and dolphins: conservation implications of the intertidal habitat selection of bottlenose dolphins. Aquatic Conservation: Marine and Freshwater Ecosystems.

Vermeulen, E and Bräger, S. submitted. Demographics of the disappearing bottlenose dolphin in Argentina: a common species on its way out? PLoS-One.

Vermeulen, E., Balbiano, A., Belenguer, F., Colombil, D., Failla, M., Intrieri, E., Bräger, S. submitted a. Limited ranging patterns of a highly mobile marine species: conservation implications for bottlenose dolphins (*Tursiops truncatus*) in Argentina. Biodiversity and Conservation.

Vermeulen, E., Holsbeek, L., Das, K. submitted b. Diurnal and seasonal activity budget of bottlenose dolphins (*Tursiops truncatus*) in Bahía San Antonio, Patagonia, Argentina. Mammalian Biology.

2. BOOKS

Vermeulen, **E.**, Suarez, H., Balbiano, A. 2013. Toninas de la Bahía, descubriendo a los delfines de Patagonia Norte. Los Biologos Ediciones, Buenos Aires, Argentina, 18 pp.

Vermeulen, **E.**, Suarez, H., Balbiano, A. 2014. Dolphins of the Bay, discovering the bottlenose dolphin of North Patagonia. Los Biologos Ediciones, Buenos Aires, Argentina, 18 pp.

3. CONFERENCES AND REPORTS

Holsbeek, L., Cammareri, A., Failla, M., **Vermeulen, E**. 2008. Sighting frequency and photo identification of bottlenose dolphins (*Tursiops truncatus*) along the coast of Bahía San Antonio, Patagonia, Argentina. 22th annual congress European Cetacean Society, 10 – 12 March 2008, Egmond aan Zee, the Netherlands, pp. 279.

Vermeulen, E., Cammareri, A., and Failla, M. 2008. A photo-identification catalogue of bottlenose dolphins (*Tursiops truncatus*) in North Patagonia, Argentina: A tool for the conservation of the species. SC/60/SM1 IWC 60th conference, Chile.

Vermeulen, E., Cammareri, A., Failla, M., Holsbeek, L. 2008. An identification study on bottlenose dolphins (*Tursiops truncatus*) in Northeast Patagonia, Argentina. XII Reunion de Trabajo de Especialistas en Mamíferos Aquaticos de America del Sur, 7° Congreso SOLAMAC, 13 – 17 October 2008, Montevideo, Uruguay, pp. 209.

Vermeulen, E. and Cammareri, A. 2010. Variation in external morphology of resident bottlenose dolphins (*Tursiops truncatus*) in Bahía San Antonio, Patagonia, Argentina. 24th annual congress European Cetacean Society, 22 – 24 March 2010, Stralsund, Germany, pp. 179.

Cransveld, A., Das, K., Denoël, M., **Vermeulen, E**. 2012. Habitat use and implications for the conservation of a population of bottlenose dolphins, *Tursiops truncatus*, in the San Antonio Bay, Rio Negro Province, Argentina *In:* Mees, J. et al. (Ed.), Book of abstracts - VLIZ Young Scientists' Day. Brugge, Belgium, 24 February 2012. VLIZ Special Publication 55, pp. 18.

Vermeulen, E., Cammareri, A., Holsbeek, L., Das, K. 2012. Seasonal variation in abundance and time-budget of bottlenose dolphins (*Tursiops truncatus*) in Bahía San Antonio, Patagonia, Argentina. 26th annual congress European Cetacean Society, 26 - 28 March 2012, Galway, Ireland.

Fruet, P.F., Secchi, E.R., Daura-Jorge, F., **Vermeulen, E.**, Ott, P.H., Flores, P.A.C., Oliveira, L., Simões-Lopes, P.C., Genoves, R.C., Domit, C., Laporta, P., Di Tullio, J.C., Freitas, T.R.O., Dalla Rosa, L., Valiati, V.H., Beheregaray, L., Möller, L.M. 2012. A survey on the population structure of coastal common bottlenose dolphins (*Tursiops truncatus*) in the Southwestern Atlantic Ocean. 15th Reunion de Trabajo de Especialistas de Mamíferos Acuaticos, 16 - 20 September 2012, Puerto Madryn, Argentina.

Vermeulen, E. and Bräger, S. 2013. Adult survival and reproduction in an Argentine bottlenose dolphin population: The science needed for its conservation. Poster presented at the 20th Biannual conference of the Society of Marine Mammalogy, 9 - 13 December 2013, Dunedin, New Zealand.

Vermeulen, E., Das, K., Bräger, S. 2014. Population ecology of a resident population of common bottlenose dolphins (*Tursiops truncatus*) in North Patagonia, Argentina: the most popular dolphin species on its way out? 28th annual congress European Cetacean Society, 7 - 9 April 2014, Liège, Belgium.

Colpaert, S., Vanreusel, A., **Vermeulen, E.** 2014. Bottlenose dolphins (*Tursiops truncatus*) in Bahía San Antonio, Patagonia, Argentina: behaviour, social composition and abundance. Poster presented at the 28th annual congress European Cetacean Society, 7 - 9 April 2014, Liège, Belgium.

Cransveld, A., Denoël, M., Das, K., **Vermeulen, E.** 2014. Habitat use of a population of bottlenose dolphins, *Tursiops truncatus gephyreus*, analysed by means of Kernel Density Estimation (KDE) method. Poster presented at the 28th annual congress European Cetacean Society, 7 - 9 April 2014, Liège, Belgium.

Fruet, P., Secchi, E.R., Daura-Jorge, F., **Vermeulen, E.**, Flores, P.A.C., Simões-Lopes, P.C., Genoves, R.C., Laporta, P., Di Tullio, J.C., Freitas, T.R., Dalla Rosa, L., Valiati, V.H., Behereharay, L.B., Möller, L.M. 2014. Remarkably low genetic diversity and strong population structure in common bottlenose dolphins (*Tursiops truncatus*) from coastal waters of the Southwestern Atlantic Ocean. Poster presented at the 28th annual congress European Cetacean Society, 7 - 9 April 2014, Liège, Belgium.

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ABBREVIATIONS

AICc	Akaike's Information Criterion
BBE	Bahía Blanca Estuary
BSA	Bahía San Antonio
BSB	Bahía San Blas
CITES	Convention on International Trade in Endangered Species of Wild Flora and Fauna
CSW	Coastal shelf water
DG	Dolphin group
ER	Encounter rate
ESU	Evolutionary Significant Unit
GOF	Goodness-of-fit
HWI	Half-weight index
IUCN	International Union for Conservation of Nature
LRT	Likelihood ratio test
MDMT	Mean depth at mid-tide
MPA	Marine protected area
PAH	Polycyclic aromatic hydrocarbons
RI	Residency Index
RN	Río Negro
RNE	Río Negro Estuary
SAREM	Argentine Association for the Study of Mammals
SF	Sighting frequency
SMG	San Matías Gulf
SPUE	Sightings per unit effort
SST	Sea surface temperature
SWA	Southwestern Atlantic Ocean
TBT	Tributyltin
TGS	Typical group size
UTM	Universal Transverse Mercator

1

GENERAL INTRODUCTION

1. THE COMMON BOTTLENOSE DOLPHIN (MONTAGU, 1821)

1.1. GENERAL INFORMATION

Kingdom: Animalia
Phylum: Chordata
Subphylum: Vertebrata
Class: Mammalia
Order: Cetacea
Suborder: Odontoceti
Family: Delphinidae
Genus: Tursiops
Species: Tursiops truncatus

The common bottlenose dolphin (*Tursiops truncatus*) is the most widely distributed species within the genus *Tursiops* (Gervais, 1855). It is a cosmopolitan species that occupies a wide range of inshore and offshore habitats in tropical and temperate regions worldwide (Wells and Scott, 1990; Reynolds et al., 2000) (Figure 1). Due to its global distribution, adaptable nature, its frequent coastal presence and ability to survive in captivity, it is believed to be one of the best-studied cetacean species in the world (Leatherwood and Reeves, 1990; Reynolds et al., 2000). However, despite decades of research, global threat assessments have been hampered by the wide geographic range of the species (Reeves and Leatherwood, 1994; Reeves et al., 2003).

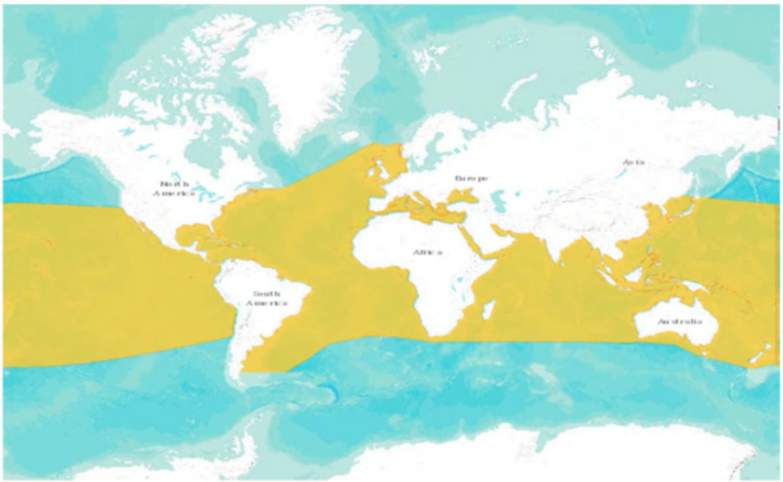

Figure 1 – Common bottlenose dolphin (*Tursiops truncatus*) distribution map (http://maps.iucnredlist.org/map.html?id=22563)

Bottlenose dolphins are grey in colour, range in length from 2.5 to 3.5 m and in weight from 200 to 400 kg. Newborn calves vary in length between 85 and 140 cm and in weight between 10 and 30 kg. However, the genus *Tursiops* exhibits striking regional variations in size, with larger body size typically associated with colder sea surface temperatures (Ross and Cockcroft, 1990).

Bottlenose dolphins are long-lived animals. Females can live for about 50 years although males rarely live more than 40 years (Wells and Scott, 1999). They have, like all cetacean species, a low reproductive rate. Females become sexually mature at age 5 - 13, the males a bit later, at age 9 - 14. Females have a single calf every 3 to 6 years. Reproductive senescence is not believed to occur in the species, as even the oldest females continue to give birth and raise young (Wells and Scott, 1994). Maternal investment is high; the gestation period is about 12 months and typically a calf is nursed for

12 to 18 months, although they also start to eat solid food at the age of 4 months. However, some calves may nurse for up to five to six years (Mann and Smuts, 1999; Mann et al., 2000). Variations can be explained by different body sizes and nutritional requirements for lactating females (Connor et al., 1996). Female offspring live closely with their mother for up to 6 years or even during their entire life. Male offspring however tend to leave their mother after they are weaned. In general, males are not involved in the raising of their offspring.

Bottlenose dolphins are known to be generalist feeders (Barros and Odell, 1990) but they seem to be selective when given the opportunity (Corkeron et al., 1990). They are known to feed on a wide variety of species including fish, cephalopods and crustaceans. According to the species available, these dolphins can exhibit a wide variation in foraging techniques and strategies among populations.

Bottlenose dolphins are highly social mammals. Studies have shown that this species of dolphin has a fluid and dynamic social structure (Würsig and Würsig, 1979; Ballance, 1990; Smolker et al., 1992; Williams et al., 1993; Wilson, 1995) often referred to as a fission-fusion society (Würsig and Würsig, 1977; Wells et al., 1987; Smolker et al., 1992; Connor et al., 2000). However, the intensity of the association patterns varies among the populations, and several studies have revealed long-term associations among identified bottlenose dolphins within fluid groups (Connor et al., 2000). It has been stated that sex, age and kinship may influence the association patterns of this species (Connor et al., 1992; Wells and Scott, 1994; Connor and Whitehead, 2005; Whitehead and Connor, 2005) although it is believed that ecological constraints are the most important factors shaping their social interactions (Lusseau et al., 2003).

Basic social units consist of females and young and mixed groups of juveniles, stable over the long term. Several of these units can join together to form larger groups, up to 100 individuals. Adult males live mostly alone or in groups of 2 - 3 and join the units for short periods of time. Despite this social fluidity, individuals in some populations form communities, defined by their shared patterns of associations and residency (Wells, 1986). These dolphin communities are not necessarily closed demographic units, as gene flow can occur across communities and individuals can be part of different communities over time (Wells, 1986; Connor et al., 2000).

Because of their high adaptability to diverse habitats, bottlenose dolphin ecology and behaviour can vary significantly. Therefore, studies on different populations in different microhabitats provide a better understanding on the species' ecology and response to varying environmental constraints. Examples of long-term studies on the species include the ones conducted in Sarasota Bay (USA; Wells, 1986), Texas (USA; Maze and Würsig, 1999), Shark Bay (Australia; Connor et al., 1992) and in the Moray Firth (Scotland; Lusseau, 2006).

The taxonomy of bottlenose dolphins has been a debate for a long time. *Tursiops* is known to be a polytypic genus, which in the past has been divided into as many as 20 different species (Hershkovitz, 1966), although often based on very limited data. Currently, based on phylogenetic variation, body size, tooth count and colouration, two species are recognised within the genus, being *T. truncatus* (common bottlenose dolphin) and *T. aduncus* (Indo-Pacific bottlenose dolphin) (Ross, 1977; Curry, 1997; LeDuc et al., 1999). Both species predominantly occupy different geographical ranges, although sympatric populations have been identified (Wang et al., 2000). Recently, the existence of a third species within the genus is being argued: *T. australis*, endemic to South Australia (Möller et al., 2008; Charlton-Robb et al., 2011). In South America, the species *Tursiops gephyreus* (Lahille, 1908) was originally used for bottlenose dolphins from the Southwestern. Its use gradually decreased when the morphological plasticity of the genus was recognised, but nowadays its use is again sought for Atlantic (Bastida and Rodríguez, 2003; Barreto, 2004).

Additionally, based on morphology, haematology, parasite load and genetic distinctions, two forms are often suggested to occur within the same area referred to as 'inshore' and 'offshore' (Hersh and Duffield, 1990; Van Waerebeek et al., 1990; Hoelzel et al., 1998).

As can be seen, the taxonomy of the genus *Tursiops* remains confusing and it is very likely that additional species will be recognised in the future (Hammond et al., 2012). This would unambiguously bring along major conservation implications for this once thought 'cosmopolitan species'.

1.2. BOTTLENOSE DOLPHINS IN ARGENTINA

In Argentina, the bottlenose dolphin (*Tursiops truncatus*) can be seen from Bahía Samborombón (Province of Buenos Aires) until the Province of Chubut, although some records have been made further south in the Provinces of Santa Cruz and Tierra del Fuego (Figure 2; Bastida and Rodríguez, 2003). Research has been made on wild coastal bottlenose dolphins in the early 1970s in the San José Gulf (Province of Chubut; Würsig, 1978; Würsig and Würsig, 1979) and in the Province of Buenos Aires (Bastida and Rodríguez, 2003). These studies suggested the existence of two coastal populations based on their morphology (Bastida and Rodríguez, 2003). A northern population was described to range along the coasts of Southern Brazil, Uruguay and the Province of Buenos Aires (Argentina). The latter included a resident community of about 100 individuals, known to reside in the region of Mar del Plata with a range extending to Bahía Samborombón (Figure 3; Bastida and Rodríguez, 2003). A southern population was reported to range along the coast of the Province of Chubut and included a resident community of at least 53 individuals in the San José Gulf in Península Valdés (Figure 3; Würsig and Würsig, 1977).

However, research on wild bottlenose dolphins in Argentina was discontinued in the 1980s due to the noted population decreases and the subsequent lack of sightings (Bastida and Rodríguez, 2003; Coscarella et al., 2012). Nowadays only infrequent and isolated observations are reported in areas where they were once common (Bahía Samborombón, Bastida and Rodríguez, 2003; Península Valdés, Coscarella et al., 2012; Bahía Engaño, Coscarella and Crespo, 2009) (Figure 3). Although the clear disappearance of the species in Argentina is believed to be caused partially by increasing human pressures such as overfishing, contamination and habitat destruction (Bastida and Rodríguez, 2003; Coscarella et al., 2012), no historical baseline data are available to help identify exact causes. Furthermore, no information is available on the presence of the offshore ecotype of the species in Argentina.

All other past studies on bottlenose dolphins in Argentina were made in captivity (Bastida and Rodríguez, 2003) which did not help to improve the understanding of the wild populations of bottlenose dolphins in the country.

1.3. CONSERVATION STATUS

Internationally, bottlenose dolphins are listed as of 'Least Concern' by the IUCN. Notwithstanding the general belief that the species is common and widespread, the global population trend is listed as 'unknown' (Hammond et al., 2012). The species is further listed in the Appendix II of CITES. The international trade in bottlenose dolphins is tightly controlled, as they are still caught to be held in captivity. The future of bottlenose dolphins is generally believed to be stable because of their abundance and high adaptability. Nonetheless, over the past decades an increasing number of coastal populations have been reported to be declining and/or are seriously threatened by human activities (see Table 7). Due to their ecological flexibility, they inhabit a wide variety of coastal habitats (enclosed bays, estuaries, lagoons, fjords, harbours and open coasts), which often overlap with human activities (Wells and Scott, 1990; Reeves et al., 2003). This can be regarded as the main reason why so many populations are increasingly affected by the increasing amount of anthropogenic coastal activities and developments.

In Argentina, the bottlenose dolphin is considered as 'conservation dependent' in the 'red book' of the SAREM (Bastida and Rodríguez, 2003).

2. STUDY AREA

2.1. SAN MATÍAS GULF

With a surface area of 19,700 km², the San Matías Gulf (SMG; Figure 3) is located in North Patagonia and is the second largest gulf in Argentina. It is a macro-tidal region (tidal range between 4 - 9 m). Approximately 45% of the area is less than 100 m deep and its maximum depth is little less than 200 m (Piola and Scasso, 1988). A particular characteristic of the gulf are two large, 160 m deep depressions situated symmetrically in respect to the parallel 41° 40´ S. The wide mouth that connects it to the outer continental shelf is a shallow sill with no more than 50 m water depth (Villarino et al., 2002). As a result, the waters in the gulf are more isolated from adjacent waters and form a separate oceanic regime as reflected by its characteristics of salinity and SST. The waters in this gulf show a relatively high salinity year-round (> 35 ppm). This is the result of a combined effect of net evaporation and an increased residence time, caused by a decreased advection imposed by the geomorphology of the area (Scasso and Piola, 1988; Rivas and Beier, 1990; Lucas et al., 2005).

Studies conducted on the spatial distribution of SST within the SMG correspond well to the different seasons. In summer and spring a zonal front is situated near 41° 50´ S, which separates warmer and saltier waters of the northern sector from the colder and less salty ones that ingress from the South with a difference of temperature between both regions reaching 3°C, becoming negligible in the winter (Carreto et al., 1974; Piola and Scasso, 1988; Gagliardini and Rivas, 2004). However, when compared to adjacent waters, the waters in the gulf are typically warmer; due to its isolation it is more directly affected by the surface flux of heat (Krepper and Bianchi, 1982).

The observed gradient of salinity and SST creates a density field, which separates the denser waters from the SMG from adjacent less dense waters from both the El Rincón region (South Province of Buenos Aires) and Coastal Shelf Waters (CSW; Lucas et al., 2005). There is, however, a low influx from CSW, which occurs at the southeast part of the mouth of the gulf. There, CSW enter the gulf where it is subject to two inner gyres (caused by the bathymetry of the gulf). Subsequently CSW are leaked from the gyre to the northeastern part of the mouth, intersecting the coast of the Province of Buenos Aires east of Bahía Blanca (Figure 3). In the SMG, tidal currents are known to be larger than the residual currents. Consequently, there is an increasing tendency towards stratification of the water column (Moreira et al., 2011). However, the currents increase in strength towards the northeast and southeastern parts of the mouth of the gulf, where the tide appears to have enough kinetic energy to overcome stratification and produce a tidal front (Moreira et al., 2011). Such a tidal front it is known to be related to high primary production (Sabatini, 2004; Pisoni and Rivas, 2006; Romero et al., 2006), and is often used by marine top predators (Mendes et al., 2002), such as bottlenose dolphins and sharks, for foraging.

Based on its isolation, the gulf can be defined as a semi-enclosed ecosystem. Consequently, multiple studies have shown that most fish stocks within the gulf are independent demographic units (e.g., Di Giacomo et al., 1993; Sardella and Timi, 2004; González et al., 2007; Romero et al., 2010; Machado-Schiaffino et al., 2011).

2.2. BAHÍA SAN ANTONIO

The main study area Bahía San Antonio (BSA, 40° 45´ S 64° 54´ W; Figure 3) is a shallow bay with an average depth of approx. 6 m. With a surface area of around 655 km^2, it is located to the northwest of the SMG. It has a length of 20 km in the East-West direction, a width of 10 km North-South and a maximum depth not exceeding 30 m. The bay is known for its relative high salinity compared to the waters south of the gulf and its large seasonal fluctuations in SST. Measured average SST: winter: 9.4°C (SD = 1.3°C); spring: 17.4°C (SD = 2.8°C); summer: 18.4°C (SD = 1.4°C); autumn: 12.8°C (SD = 2.0°C) (for monthly measurements see Figure 15). The tidal regime is semidiurnal and the tidal amplitude varies between 6.5 m at neap and 9.3 m at spring tide, leaving up to 86% of its total surface exposed during low tide (Figure 4; Naval Hydrographical Service, Argentina). The area can count on many sandy beaches, although large parts of the shoreline may additionally contain large rocky flats (up to 800 m wide; González et al., 1996) and shells.

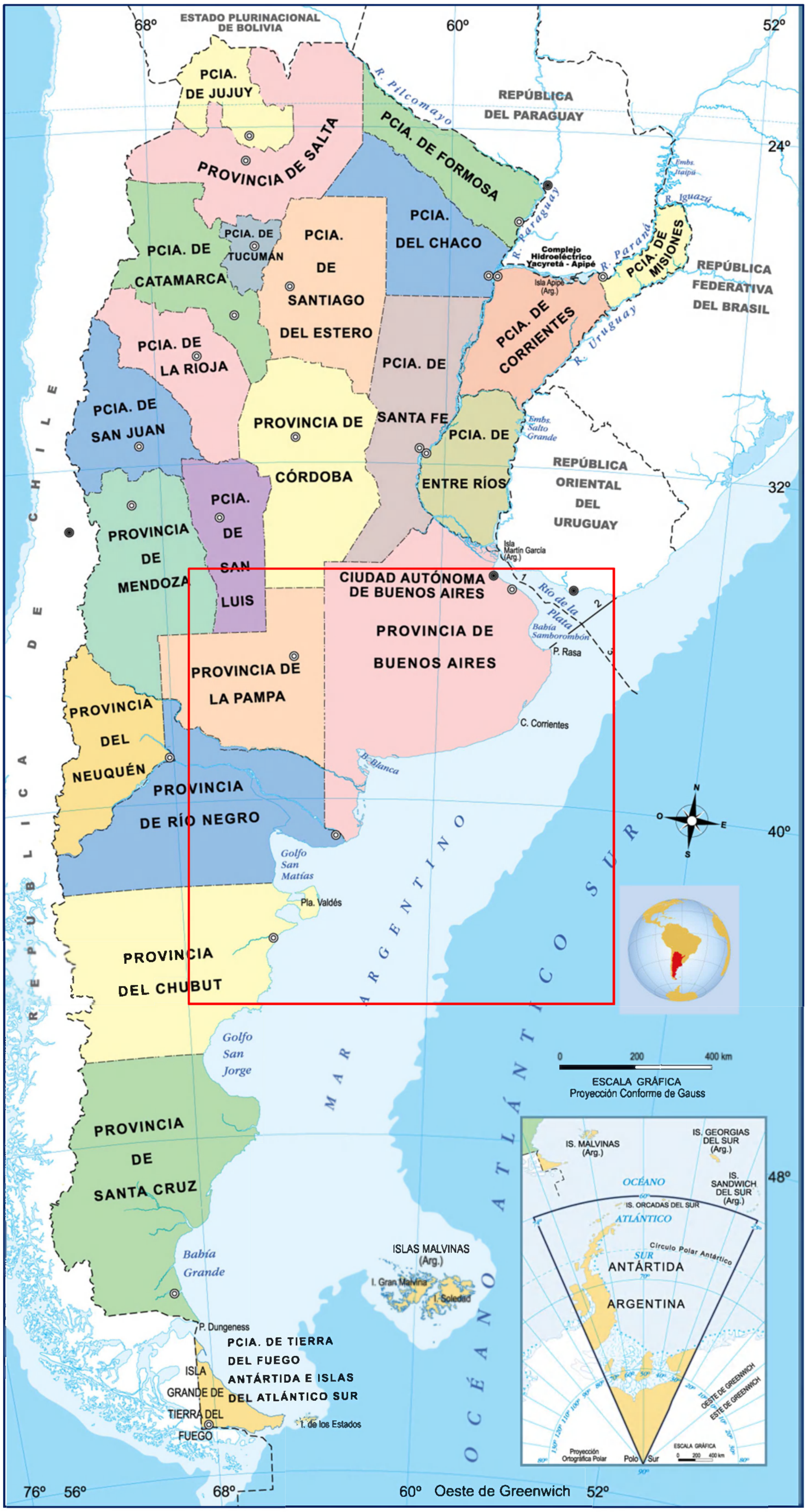

Figure 2 – Political map of Argentina (http://mapoteca.educ.ar/mapa/republica-argentina/)

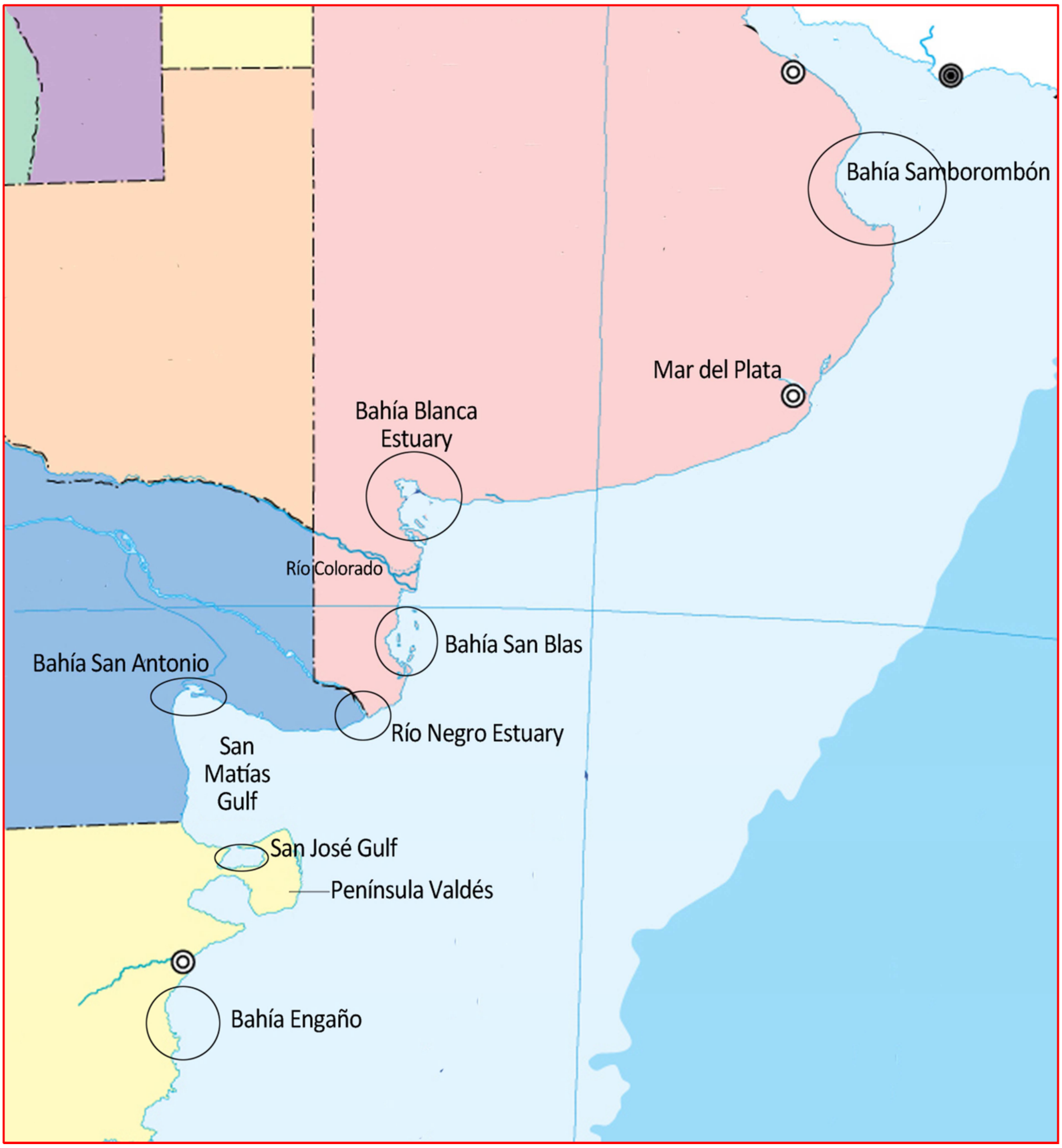

Figure 3 – Map of Argentina, indicating the main study area Bahía San Antonio and other areas of interest. Patagonia is the region located south of Río Colorado (http://mapoteca.educ.ar/mapa/republica-argentina/)

BSA is an important spawning and nursing area for many fish species such as the South American silver porgy (*Diplodus argenteus*), Patagonian blenny (*Eleginops maclovinus*), Brazilian flounder (*Paralichthys brasiliensis*), silverside (*Odonthestes sp.*), Argentine hake (*Mercluccius hubbsi*) and silver warehou (*Sironella porosa*) (Di Giacomo et al., 1993; Perier and Di Giacomo, 2002). These fish species show a strong seasonality in their occurrence and behaviour (Perier, 1994). During the Austral winter and early spring, they form dense shoals inside the bay to spawn near the coast. Consequently an increased amount of fishing activities can be found near the study area, peaking in September (Ocampo-Reinaldo, 2010; Ocampo-Reinaldo et al., 2013). In summer and autumn some fish species seek shelter from predators near rocks and caves although most show a seasonal movement out of the bay. BSA is of great ecological value due to its high biodiversity, and it is one of the most important resting and feeding sites of the Southwestern Atlantic Ocean for several migratory bird species. This is reflected in the declaration of BSA as a 'BirdLife International Important Bird Area' (Di Giacomo, 2005) and a 'Western Hemisphere Shorebird Reserve Network Site' (González et al., 1996). Additionally, BSA was declared a 'Natural Reserve' in Argentina by provincial law 2670 of June 1993.

BSA is the most important touristic coastal region of Northeast Patagonia, relying on three expanding towns under the municipality of San Antonio (Figure 4):

1. San Antonio Oeste: A relative antique city (approx. 25,000 inhabitants), which originated from a small fishing port.
2. San Antonio Este: A small village of approx. 100 inhabitants, which operates one of the largest harbours of Argentina for the export of e.g., Patagonian fruits.
3. Las Grutas: A small town (approx. 5,000 inhabitants) declared to be one the most important touristic towns on the coast of Patagonia. The region is not only famous for its shallow shores and lack of strong currents, it is also well known for having the warmest waters of the entire Argentine coastline, with maximum temperatures around 24°C in summer. Therefore it is an excellent place for many tourists (over 350,000 per year) to dive, surf, sail or just to enjoy the sandy and rocky beaches.

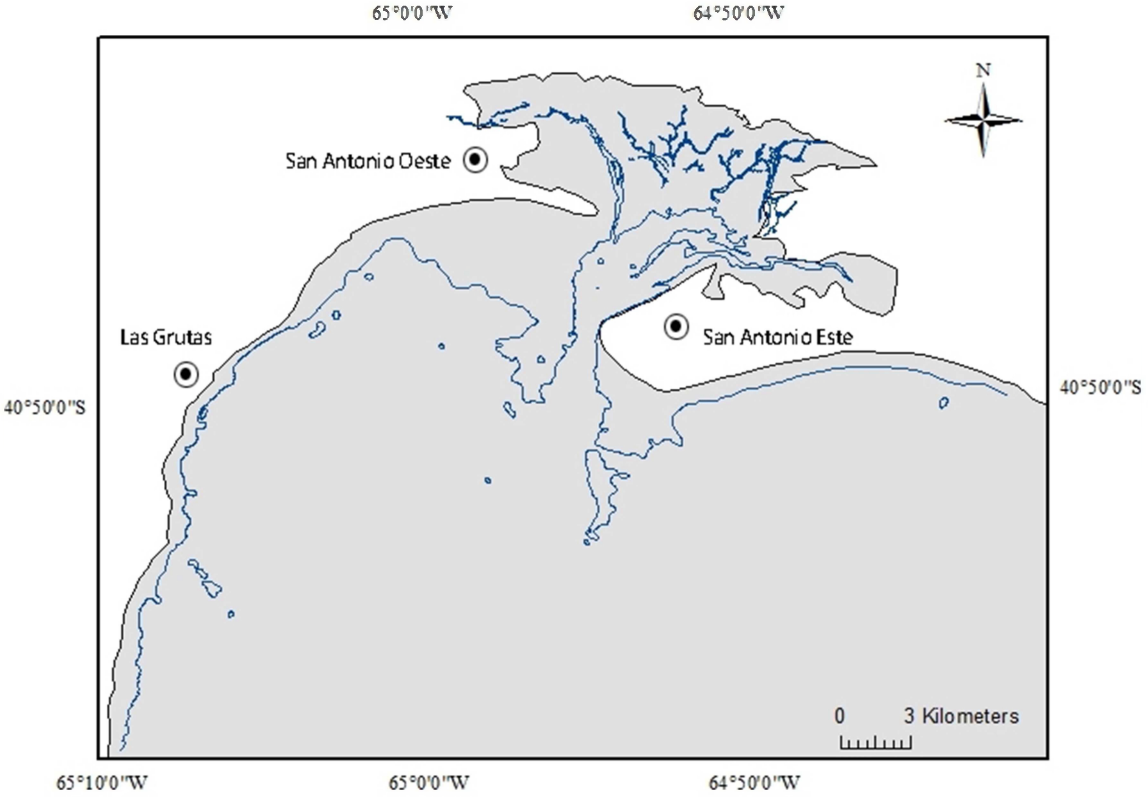

Figure 4 – Detailed map of BSA marking the three urbanised areas. Contour line of the bay indicates the shoreline at high tide, the isobath indicates the shoreline at low tide

2.3. LOCAL CONSERVATION NEEDS

The enormous increase of human activities along the coasts of the Provinces of Buenos Aires and Chubut has most likely led to a notable decrease of bottlenose dolphin sightings in these areas (Bastida and Rodriguez, 2003; Coscarella et al., 2012). In the Province of Río Negro, however, the species can still be observed frequently. Nonetheless, also in this Province anthropogenic pressures are increasing drastically, especially in BSA. Some examples are given.

2.3.1 Commercial fishing

Commercial fishing activities in the SMG began only in the 1970s (Fernanda et al., 2002; Romero et al., 2010). First target species were bivalves (mussels *Mytilus edulis platensis* and scallops *Aequipecten tehuelchus*), and later included several fish species such as the Argentine hake (*Merluccius hubssi*), mackerel (*Scomber japonicus*), sharks (*Callorhynchus callorhynchus*), flatfish (*Paralichtys sp.*, *Xystreuris sp.*) and other demersal fish species (e.g., *Seriolella porosa*, *Macruronus magellanicus*, *Acanthistius brasiliensis*, *Genypterus blacodes*) (Lasta, 1988).

The fleet inside the SMG included at least 61 ships (Di Giacomo and Perier, 1992; González, 2000), composed of three different types of vessels targeting mainly Argentine hake. The larger vessels were approximately 30 m long and equipped with bottom trawl nets. The medium-sized vessels were on average 25 m long and equipped with longline, and the artisanal fleet was composed of small boats that were between 8 to 15 m long and also equipped with longline.

However, the decline of Argentine hake as a result of overexploitation resulted in the implementation of several regulations between 1997 and 2000, which included a change in fishing gear to be used and a seasonal closure within a nursing area. These regulations were expected primarily to reduce juvenile catches and therefore to reduce the amount of discard (Ehrlich, 1998; Perier and Di Giacomo, 2002; Romero et al., 2010). Additionally, recommendations to diversify the fisheries targets suggested the Patagonian Grenadier (*Macruronus magellanicus*) as a major alternative (Wöhler et al., 1999). Furthermore, the Province of Río Negro endorsed law 3384 in 2000, which mandated fishing activity control by means of an electronic monitoring system: the Fishery and Oceanographic Monitoring System (FOMS). The aim of such a monitoring system was to improve the management and sustainable use of aquatic resources. This system should moreover improve the quality of data available for scientific research and other relevant data for fisheries management (Gonzales et al*.,* 2004).

Nevertheless, a decade later these management measures were shown to have been ineffective so far (Romero et al., 2010). Today, both industrial bottom trawl and artisanal midwater longline fleets are still active in the SMG (Gandini and Frere, 2006; Romero et al., 2013), and annual catch rates for *M. hubbsi* in this area still reach 15,000 metric tons leading to an annual gross rent exceeding US$ 10 million (Gonzales et al*.,* 2007; Millán, 2011). Most of the catch is exported and not used for domestic consumption (Fernanda et al., 2011).

Most of the species present in SMG occur in the adjacent waters of the platform. However, multiple studies have shown that most fish stocks within the gulf are independent demographic units (e.g., Di Giacomo et al., 1993; Sardella and Timi, 2004; González et al., 2007; Romero et al., 2010; Machado-Schiaffino et al., 2011). This provides a justification for assuming that the SMG behaves as a largely enclosed ecosystem, with a minimal exchange of biomass with the shelf (Villarino et al., 2002), exacerbating the overexploitation.

2.3.2 Dolphin-watching

As from 2013, a commercial dolphin-based tourism is being carried out in BSA. Currently the activity is being executed by 3 different tour operators (total of 5 vessels) conducting one or two trips daily depending on weather conditions. Currently, no regulations are in place to manage the activity.

Previous studies all over the world have shown bottlenose dolphin behaviour can be affected seriously by dolphin-watching activities. Several investigations showed a significant decrease in the amount of surfacing behaviour performed by dolphins after a boat had encountered them and an increase in the 'milling', 'change in direction' and 'prolonged diving' when boats where present (Janik and Thompson, 1996), interpreted as avoidance behaviour (Constantine, 1995; Lütkebohle, 1995; Janik and Thompson, 1996; Constantine et al., 2003). Moreover, Constantine et al. (2003) concluded that dolphin-watching boats have a greater effect on the dolphin behaviour than any other type of boat (recreational or commercial boat) and that the presence of only one tourist boat is sufficient to cause these observed changes in behaviour.

The effect of tourism on the dolphins could result in an increase in stress, which in turn may result in an increase of mortality or simply in the disappearance of the dolphins in the area. It is therefore very important to consider how people manage 'marine mammal based tourism'.

If managed appropriately, it might not only be educational, but also create an increase in the public awareness leading to a possible increase of conservation efforts of the local community like inhabitants, operators, fishermen and off course the tourists themselves. Even more, it will create an increase in jobs and financial resources during the whole year for a town that, up to now, concentrates all its tourism and financial profits only in the summer months. It's to be hoped that management policies guided by research might create an educational, sustainable and economically viable industry with the least possible impact on the dolphins themselves.

2.3.3 Contamination

The accumulation and potential effects of human anthropogenic chemical agents in the aquatic environment is of increasing concern (Fair et al., 2009). Marine mammals are often considered as one of the best sentinels for coastal and ocean health. This is because they are long-lived, feed at a high trophic level and have large blubber stores that can accumulate high levels of anthropogenic chemicals and toxins (Reddy et al., 2001). Especially coastal bottlenose dolphins are often highly susceptible and thus excellent sentinels (Aguilar et al., 2002). This is not only due of their often long-term site-fidelity in coastal areas near urban and industrial areas, but also because they are top level predators that forage on a wide variety of fish and invertebrates, and thus integrate broadly in the ecosystem in terms of exposure to contaminants (Wells et al., 2004).

Within BSA, high levels of polycyclic aromatic hydrocarbons (PAHs) were found in the soil and sediment (Fundación Patagonia Natural, 1999). The levels found in this region were higher than any coastal area of Argentine Patagonia and was related to the local harbour and ship activities (Fundación Patagonia Natural, 1999). PAHs can enter the food chain through organisms such as plankton or fish and are known for their carcinogenic, mutagenic and teratogenic properties. Further data exist on tributiltyn contamination in BSA (Vidal, 2004; Delucchi et al., 2011). Tributyltin is a trialkyl organotin compound (TBT; Bu_3SnH), the main active ingredient in biocides used to control a broad spectrum of species mainly used in wood preservation and the antifouling of boats (Minchin et al., 1995; Tolosa et al., 1996; Chau et al., 1997; Willers et al*.,* 2004). The TBT contamination was therefore also directly related to the extensive boat traffic in the harbour of BSA (Vidal, 2004; Willers et al*.,* 2004). Additionally, water from drainpipes in urbanised areas in BSA shows evidence of eutrophication, which was related to the lack of cloacae systems (Estevens et al., 1996; Vidal, 2004). However, it appears that especially metal pollution has reached levels of considerable concern along the entire Argentine coastline (Gil et al., 1999). High concentrations of metallic elements, such as Cd, Pb, Zn, Cu, Cr, Hg and Ni, have been found in several marine mammal species along the Argentine coast, such as the Franciscana dolphin (*Pontoporia blainvillei*) (Gerpe et al., 2002; Panebianco et al., 2011), dusky dolphins (*Lagenorhynchus obscurus*), Commerson's dolphins (*Cephalorhynchus commersonii*), South American sea lion (*Otaria flavescens*) (Marcovecchio et al., 1994; Gil et al., 2006) and southern fur seal (*Arctocephalus australis*) (Gerpe et al., 1990). Although specific information on bottlenose dolphin toxicology in Argentina is scarce, some records indicated high concentrations of metallic elements (including Hg, Zn, Cu, Cd and Cu) in specimens recovered from the coast of Buenos Aires (Marcovecchio et al., 1990; 1994).

In BSA, severe elevated levels of heavy metals (Pb, Cu, Zn, Hg and Cd) were found in the soil, crabs (*Chasmagnathus granulata)*, molluscs (*Brachydontes rodriguezi*) and sea lions (*Otario flavescens*) (Gil et al., 1999). The high levels of these heavy metals were directly related to an old mining activity three decades ago, as levels in its vicinity where notably higher. Most of these levels are much higher (up to 3 orders of magnitude) than the levels reported for other coastal regions of Argentine Patagonia and are up to 6 times higher than the upper limits of human consumption (Commendatore et al*.,* 1996; Gil et al., 1999; 2006; Bonuccelli et al*.,* 2004; Vázquez et al., 2007). Vázquez et al. (2007) raised concerns about the consequences of the reported high levels of heavy metals in molluscs at a higher trophic level in BSA, suggesting that '*although future studies should be pursued, enough is already known to require immediate action*'. Claps (2005) adds that '*the high levels of accumulation in mussels of lead, zinc, copper and cadmium in the bay of San Antonio might pose a contamination risk throughout the food chain, proving a great threat to larger predators.*'

As apex predators, bottlenose dolphins are known to accumulate heavy metals, and negative health effects have been shown or are presumed also in other parts of the world, including the South Atlantic (e.g., Parsons and Chan, 2001; Roditi-Elasar et al., 2003; Carballo et al., 2004; Stavros et al., 2007; Vázquez-Medina et al., 2007; Lemos et al., 2013).The Argentine coastal area, especially the region of Patagonia, is in a stage of rapid development and new chemical and mining activities are continuously being incorporated (Gil et al., 1999). Consequently, increasing levels of pollution can be expected as a consequence. It is therefore considered of high importance to accurately assess the present and possible future effects upon the marine environment, as well as the public health.

3. REFERENCES

Aguilar, A., Borrell, A., Reijnders, P.J.H. 2002. Geographical and temporal variation in levels of organochlorine contaminants in marine mammals. Marine Environmental Research 53: 425-452.

Ballance, L.T. 1990. Residence patterns, group organization, and surfacing associations of bottlenose dolphins in Kino Bay, Gulf of California, Mexico. *In*: Leatherwood, S. and Reeves, R.R. (Eds.), The bottlenose dolphin. Academic Press, San Diego, CA, pp. 267–283.

Barreto, A.S. 2004. *Tursiops* in Atlantic South America: Is *Tursiops gephyreus* a valid species? Abstract at the Symposium on Cetacean Systematics, La Jolla, California.

Barros, N.B., Odell, D.K. 1990. Food habits of bottlenose dolphins in the south-eastern United States. *In*: Leatherwood, S. and Reeves, R.R. (Eds.), The bottlenose dolphin. Academic Press, San Diego, CA, pp. 309–328.

Bastida, R. and Rodríguez, D. 2003. Mamíferos Marinos Patagonia Antartida. Vázquez Mazzini Editors, Buenos Aires, Argentina, 206 pp.

Bezzi, S. 1996. Sobre la unidad poblacional de la merluza (*Merluccius hubbsi*) del Golfo San Matías. Informe Técnico Interno INIDEP N°110/96: 2.

Bonuccelli, R., Malan, J., Luna, L.I., Torres, L. 2004. Contaminación por metales pesados derivados de la lixiviación de escorias de fundición San Antonio Oeste-Río Negro. IBPM – Serie Publicaciones 3: 63-66.

Bonuccelli, R. and Malan, J. 2005. Vulnerabilidad del medio hídrico ante el vertido de efluentes industriales en el Bajo del Riñón (San Antonio Oeste, Río Negro). *In*: Masera, R.F., Lew, J., Serra Peirano, G. (Eds.), Las mesetas Patagónicas que caen al mar: La costa rionegrina. Viedma: Gobierno de Río Negro. ISBN 987-22604-0-0.

Calvo, J. 1985. Caracterización de los períodos de crecimiento de la merluza (*Merluccius hubbsi*) en el Golfo de San Matías, y variación de parámetros tisulares. Dissertation, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, Argentina.

Carballo, M., De la Peña, E., Fernández, A., Aguayo, S., Esperón, F., De la Torre, A., Muñoz, M.J. 2004. Accumulation of persistent organic chemicals and metals in stranded bottlenose dolphins (*Tursiops truncatus*) in Canary Islands (Spain). Toxicology and Applied Pharmacology 197: 235.

Carreto, J.I., Verona, C.A., Casal, A.B., Laborde, M.A. 1974. Fitoplancton, pigmentos y condiciones ecológicas del golfo San Matías III. Comisión de Investigaciones Cientificas de la Provincia de Buenos Aires. Instituto de Biologia Marina de Mar del Plata 10: 49–76.

Cauhépé, M.E. 1999. Management of the Argentine hake. Final project UNU Fisheries Training Program, Reykjavic, Iceland.

Charlton-Robb, K., Gershwin, L.A., Thompson, R., Austin, J., Owen, K., McKechnie, S. 2011. A new dolphin species, the burrunan dolphin *Tursiops australis sp. nov.,* endemic to southern Australian coastal waters. PLoS-One 6: e24047.

Chau, Y.K., Maguire, R.J., Brown, M., Yang, F., Batchelor, S.P. 1997. Occurrence of organotin compounds in the Canadian aquatic environment five years after the regulation of antifouling uses of Tributyltin. Water Quality Research Journal of Canada 32: 453-521.

Christiansen, H.E. 1980. Aplicación de la histometría en el estudio de las variaciones en las microcelulas de la musculatura blanca de la merluza (*Merluccidae, Merluccius hubbsi*), en la plataforma argentina; su importancia. Dissertation, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, Argentina.

Claps, E.L. 2005. A Heavy Legacy: lead contamination in San Antonio Oeste, Argentina. Mines and Communities, http://www.minesandcommunities.org/article.php?a = 5363. Downloaded on 11 June 2013.

Commendatore, M., Gil, M., Harvey, M., Colombo, J.C., Esteves, J.L. 1996. Evaluación de la contaminación por hidrocarburos y metales en la zona costera patagónica. Informe Técnico del Plan de Manejo Integrado de la Zona Costera Patagónica Fundación Patagonia Natural, Chubut, Argentina 21.

Connor, R.C., Smolker, R.A., Richards, A.F. 1992. Two levels of alliance formation among male bottlenose dolphins (*Tursiops sp.*). Proceedings of the National Academy of Sciences 89: 987-990.

Connor, R.C., Richards, A.F., Smolker, R.A., Mann, J. 1996. Patterns of female attractiveness in Indian Ocean bottlenose dolphins. Behaviour 133: 37–69.

Connor, R.C, Wells, R.S., Mann, J., Read, A.J. 2000. The bottlenose dolphin: Social relationships in a fission-fusion society. *In*: Mann, J., Connor, R.C., Tyack, P.L., Whitehead, H. (Eds.), Cetacean societies: Field studies of dolphins and whales. University of Chicago Press, Chicago, IL, pp. 91–126.

Connor, R.C. and Whitehead, H. 2005. Alliances II. Rates of encounter during resource utilization: a general model of intrasexual alliance formation in fission–fusion societies. Animal Behaviour 69: 127–132.

Constantine, R. 1995. Monitoring the commercial swim-with-dolphin operations with the bottlenose (*Tursiops truncatus*) and common dolphin (*Delphinus delphis*) in the Bay of Island, New Zealand. Dissertation, University of Auckland, Auckland.

Constantine, R., Brunton, D.H., Dennis, T. 2003. Dolphin-watching tour boats change bottlenose dolphin (*Tursiops truncatus*) behaviour. Biological conservation 117: 299-307.

Corkeron, P.J., Bryden, M.M., Hedstrom, K.E. 1990. Feeding by bottlenose dolphins in association with trawling operations in Moreton Bay, Australia. *In*: Leatherwood, S. and Reeves, R.R. (Eds.), The Bottlenose Dolphin. Academic Press, San Diego, CA, pp. 329-336.

Coscarella, M.A. and Crespo, E.A. 2009. Feeding aggregation and aggressive interaction between bottlenose (*Tursiops truncatus*) and Commerson's dolphins (*Cephalorhynchus commersonii*) in Patagonia, Argentina. Journal of Ethology 28: 183–187.

Coscarella, M., Dans, S.L., Degrati, M., Garaffo, G.V., Crespo, E.A. 2012. Bottlenose dolphins at the southern extreme of the Southwestern Atlantic: local population decline? Journal of the Marine Biological Association of the United Kingdom 92: 1843-1849.

Curry, B.E. 1997. Phylogenetic relationships among bottlenose dolphins (genus *Tursiops*) in a worldwide context. Dissertation, Texas A&M University, USA.

Delucchi, F., Narvarte, M.A., Amin, O., Tombesi, N.B., Freije, H., Marcovecchio, J. 2011. Organotin compounds in sediments of three coastal environments from the Patagonian shore, Argentina. International Journal of Environment and Waste Management 8: 3-17.

Di Giacomo, A.S. 2005. Áreas importantes para la conservación de las aves en la Provincia de Río Negro. *In*: Di Giacomo, A.S. (Ed.), Áreas Importantes para la conservación de las Aves en la Argentina. Aves Argentinas and Asociación Ornitológica del Plata: Buenos Aires, Argentina, pp. 334–349.

Di Giacomo, E.E. and Perier, M.R. 1992. Retracción de las pesquería demersal del Golfo San Matías: ¿Escaséz de recursos o disminución de la eficiencia? Frente Marítimo 11: 7-13.

Di Giacomo E.E., Calvo, J., Perier, M.R., Morriconi, E.R. 1993. Spawning aggregations of *Merluccius hubbsi*, in Patagonian waters: Evidence for a single stock? Fisheries Research 16:9-16.

Ehrlich, M.D. 1998. The early life history of the hake *Merluccius hubbsi* Marini, 1933 in the Argentine Sea for understanding its recruitment and population structure. Dissertation, Universidad de Buenos Aires, Argentina.

Esteves, J.L., Solís, M., Sastre, V., Santinelli, N., Gil, M., Commendatore, M., González Raies, C. 1996. Evaluación de la contaminación urbana de la Bahía de San Antonio. Informes Técnicos del Plan de Manejo de la Zona Costera Patagónica, Fundación Patagonia Natural (Puerto Madryn, Argentina) ISS N° 0328-462X. 20:1-26.

Fair, P.A, Lee, H., Adams, J., Darling, C., Pacepavicius, G., Alaee, M., Bossart, G.D., Henry, N., Muir, D. 2009. Occurrence of triclosan in plasma of wild Atlantic bottlenose dolphins (*Tursiops truncatus*) and in their environment. Environmental Pollution 157: 2248-2254.

Fernanda, V.M., Lasta, M.L., Pájaro, M. 2002. Exploring alternative management policies: a preliminary ecological approach for the San Matias Gulf fishery, Argentina. Fisheries Centre Research Reports 10: 109.

Fruet, P.F., Secchi, E.R., Daura-Jorge, F., Vermeulen, E., Flores, P.A.C., Simões-Lopes, P.C., Genoves, R.C., Laporta, P., Di Tullio, J.C., Freitas, T.R.O., Dalla Rosa, L., Valiati, V.H., Beheregaray, L., Möller, L.M. 2014. Remarkably low genetic diversity and strong population structure in common bottlenose dolphins (*Tursiops truncatus*) from coastal waters of the Southwestern Atlantic Ocean. Conservation Genetics 10.1007/s10592-014-0586-z.

Fundación Patagonia Natural. 1999. Prevención de la Contaminación Costera y Gestión de la Diversidad Biológica Marina. Analisis técnico de los problemas de contaminación en la zona costera Patagonica, Argentina.

Gagliardini, D.A. and Rivas, A.L. 2004. Environmental characteristics of San Matías Gulf obtained from landsat – TM and ETM+ data. Gayana Concepción 68: 186-193.

Gandini, P. and Frere, E. 2006. Spatial and temporal patterns in the bycatch of seabirds in the Argentinian longline fishery. Fishery Bulletin 104: 482-485.

Gerpe, M., Moreno, V., Pépez, A., Bastida, R., Rodríguez, D., Marcovecchio, J. 1990. Trace metals in the South American fur seal, *Arctocephalus australis* (Zimmerman, 1783). *In*: Barceló, J. (Ed.), Environmental contamination. CEP Consultants, Ltd. Edinburgh, UK, pp. 591-594.

Gerpe, M., Rodríguez, D., Moreno, V.J., Bastida, R.O., Moreno, J.D. 2002. Accumulation of heavy metals in the Franciscana (*Pontoporia blainvillei*) from Buenos Aires Province, Argentina. Latin American Journal of Aquatic Mammals 1: 95-106.

Gil, M.N., Harvey, M.A., Esteves, J.L. 1999. Heavy metals in intertidal sediments from Patagonian coast, Argentina. Bulletin of Environmental Contamination and Toxicology 63: 52 – 58.

Gil, M.N., Torres, A., Harvey, M., Esteves, J.L. 2006. Metales pesados en organismos marinos de la zona costera de la Patagonia argentina continental. Revista de Biología Marina y Oceanografía 41: 167–176.

Giussi, A.R., Hernandez, D., Abachian, V.E. 1999. Differences in growth of long tailed hake (*Macruronus magellanicus*) from two areas of South Western Atlantic Ocean. Seminario Final Proyecto INIDEP – JICA, pp. 135-138.

González, P.M., Piersma, T., Verkuil, Y. 1996. Food, Feeding and Refuelling of Red Knots during Northward Migration at San Antonio Oeste, Rio Negro, Argentina. Journal of Field Ornithology 67: 575-591

González, R. 2000. Notas y comentarios sobre el proceso de transformación del sector pesquero rionegrino en el período 1990-1998. Documento Técnico, IBMyP Almirante Storni, Rio Negro, Argentina 04/00.

González, R., Gaspar, C., Curtolo, L., Sangiuliano, I., Osovnikar, P., Borsetta, N. 2004. Fishery and Oceanographic monitoring system (FOMS): A new technological tool base on remote sensing, with applications in ecosystem management of coastal fisheries in Patagonia. Gayana Concepción 68: 234-238.

González, R., Narvarte, M., Caille, G.M. 2007. An assessment of the sustainability of the hake *Merluccius hubbsi* artisanal fishery in San Matías Gulf, Patagonia, Argentina. Fisheries Research 87: 58-67.

Hammond, P.S., Bearzi, G., Bjørge, A., Forney, K.A., Karkzmarski, L., Kasuya, T., Perrin, W.F., Scott, M.D., Wang, J.Y. , Wells, R.S., Wilson, B. 2012. *Tursiops truncatus*. *In*: IUCN 2013. IUCN Red List of Threatened Species. Version 2013.2. < www.iucnredlist.org>. Downloaded on 18 March 2014.

Hersh, S.L. and Duffield, D.A. 1990. Distinction between northwest Atlantic offshore and coastal bottlenose dolphins based on haemoglobin profile and morphometry. *In*: Leatherwood, S. and Reeves, R.R. (Eds.), The bottlenose dolphin. Academic Press, San Diego, CA, pp. 129-139.

Hershkovitz, P. 1966. A catalogue of living whales. Bulletin of the US Natural Museum 246: 1-259.

Hoelzel, A.R., Potter, C.W., Best, P.B. 1998. Genetic differentiation between parapatric ‘nearshore’ and ‘offshore’ populations of the bottlenose dolphin. Proceedings of the Royal Society of London. Series B: Biological Sciences 265: 1177-1183.

Janik, V.M. and Thompson, P.M. 1996. Changes in surfacing patterns of bottlenose dolphins in response to boat traffic. Marine Mammals Science 12: 597-602.

Krepper, C.M. and Bianchi, A. 1982. Balance Cal6rico del Mar Epicontinental Argentino. Acta Oceanografica, Argentina 3: 1.

Lasta, M.L., Iribarne, O.O., Pascual, M.S., Zampatti, E.A., Vacas, H.C. 1988. La pesquería del Golfo San Matías: una aproximación al manejo experimental. Informe Unesco Ciencia del Mar 47: 168-175.

Leatherwood, S. and Reeves, R.R. 1990. The bottlenose dolphin. Academic Press, San Diego, CA, 653 pp.

Lemos, L.S., de Moura, J.F., Hauser-Davis, R.A., de Campos, R.C., Siciliano, S. 2013. Small cetaceans found stranded or accidentally captured in southeastern Brazil : Bioindicators of essential and non-essential trace elements in the environment. Ecotoxicology and Environmental Safety 97: 166-175.

Lucas, A.J., Guerrero, R.A., Mianzán, H.W., Acha, E.M., Lasta, C.A. 2005. Coastal oceanographic regimes of the Northern Argentine Continental Shelf (34-43°S). Estuarine, Coastal and Shelf Science 65: 405-420.

LeDuc, R.G., Perrin, W.F., Dizon, A.E. 1999. Phylogenetic relationships among the Delphinid cetaceans based on fall cytochrome *b* sequences. Marine Mammal Science 15: 619-648.

Lusseau, D., Schneider, C., Boisseau, O.J., Haase, P., Slooten, E., Dawson, S.M. 2003. The bottlenose dolphin community of Doubtful Sound features a large proportion of long-lasting associations. Can geographic isolation explain this unique trait? Behavioral Ecology and Sociobiology 54: 396-405.

Lusseau, D. 2006. Quantifying the influence of sociality on population structure in bottlenose dolphins. Journal of Animal Ecology 75: 14–24.

Lütkebohle, T. 1995. Dolphin movements and behaviour in the Kessock Channel and how these are influenced by boat traffic. Scottish Natural Heritage, Scotland.

Machado-Schiaffino, G., Juanes, F., García-Vázquez, E. 2011. Identifying unique populations in long-dispersal marine species: Gulfs as priority conservation areas. Biological Conservation 144: 330-338.

Mann, J. and Smuts, B. 1999. Behavioural development in wild bottlenose dolphin newborns (*Tursiops sp*.). Behaviour 136: 529-566.

Mann, J., Connor, R.C., Barre, L.M., Heithaus, M.R. 2000. Female reproductive success in bottlenose dolphins (*Tursiops* sp.): life history, habitat, provisioning, and group-size effects. Behavioral Ecology 11: 210-219.

Marcovecchio, J., Moreno, V., Bastida, R., Gerpe, M., Rodriguez, D. 1990. Tissue distribution of heavy metals in small cetaceans from the Southwestern Atlantic Ocean. Marine Pollution Bulletin 21: 299-304.

Marcovecchio, J.E., Gerpe, M.S., Bastida, R.O. Rodriguez, D.H., Moron, S.G. 1994. Environmental contamination and marine mammals in coastal waters from Argentina: an overview. Science of the Total Environment 154: 141-151.

Maza, I. 2008. Pedido de Informe al Codema respecto al cumplimiento del control ambiental de la empresa ALPAT. Informe Prensa Bloqe encuentro FG, Río Negro, Argentina.

Maze, K.S. and Würsig, B. 1999. Bottlenose dolphins of San Luis Pass, Texas: occurrence patterns, site-fidelity, and habitat use. Aquatic Mammals 25: 91–103.

Mendes, S., Turrell, W., Lükebohle, T., Thompson, P. 2002. Influence of the tidal cycle and a tidal intrusion front on the spatio-temporal distribution of coastal bottlenose dolphins. Marine Ecology Progress Series 239: 221-229.

Millán, D., 2011. Anuario de Estadísticas Pesqueras de la Provincia de Río Negro. Departamento Policía de Pesca, Dirección de Pesca, Reporte 2007. San Antonio Oeste.

Minchin, D., Oehlmann, J., Duggan, C.B., Stroben, E., Keatinge, M. 1995. Marine TBT antifouling contamination in Ireland, following legislation in 1987. Marine Pollution Bulletin 30: 633-639.

Möller, L.M., Bilgmann, K., Charlton-Robb, K., Beheregaray, L. 2008. Multi-gene evidence for a new bottlenose dolphin species in southern Australia. Molecular Phylogenetic Evolution 49: 674–681.

Moreira, D., Simionato, C.G., Dragani, W. 2011. Modelling ocean tides and their energetics in the North Patagonia Gulfs of Argentina. Journal of Coastal Research 27: 87-102.

Ocampo-Reinaldo M. 2010. Evaluación pesquera integral de la merluza común (*Merluccius hubbsi* Marini, 1933) del Golfo San Matías y efectos de la explotación de esta especie sobre otros componentes de la trama trófica. Dissertation, National University of Córdoba, Argentina, 164 pp.

Ocampo-Reinaldo, M., González, R., Williams, G., Storero, L.P., Romero, M.A., Narvarte, M., Gagliardini, D.A. 2013. Spatial patterns of the Argentine hake *Merluccius hubbsi* and oceanographic processes in a semi-enclosed Patagonian ecosystem. Marine Biology Research 9: 394-406.

Panebianco, M.V., Negri, M.F., Botté, S.E., Marcovecchio, J.E., Cappozzo, H.L. 2011. Metales pesados en el riñón del delfín franciscana, *Pontoporia blainvillei* (*Cetacea: Pontoporiidae*), y su relación con parámetros biológicos. Latin American journal of aquatic research 39: 526-533.

Parsons, E.C. and Chan, H.M. 2001. Organochlorine and trace element contamination in bottlenose dolphins (*Tursiops truncatus*) from the South China Sea. Marine Pollution Bulletin 42: 780-786.

Perier, M.R. 1994. La fauna íctica en el litoral de la Bahía de San Antonio (Golfo San Matias, Provincia de Río Negro). Dissertation, Facultad de Ciencias naturales y Museo, Universidad Nacional de La Plata, Argentina.

Perier, M.R. and Di Giacomo, E.E. 2002. El savorin *Seriolella porosa* como un recurso estacional en el Golfo San Matias, Republica Argentina. Revista de Investigación de Desarrollo Pesquero 15: 15-26.

Piola, A.R. and Scasso, L.M. 1988. Circulación en el Golfo San Matías. Geoacta 15: 33–51.

Pisoni, J.P. and Rivas, A. 2006. Frentes térmicos sobre la PCA por medio de imágenes satelitales. Proceedings of the VI Jornadas Nacionales de Ciencias del Mar and XIV Coloquio de Oceanografía. Puerto Madryn, Argentina.

Reddy, M.L., Dierauf, L.A., Gulland, F.M.D. 2001. Marine mammals as sentinels of ocean health. *In*: Dierauf, L. and Gulland, F. (Eds.), Marine Mammal Medicine. CRC Press, Boca Raton, FL, pp. 3–13.

Reeves, R.R. and Leatherwood, S. 1994. 1998 Action plan for the conservation of cetaceans: dolphins, porpoises, and whales. Gland and Cambridge, IUCN/SSC Cetacean Specialist Group, 91 pp.

Reeves, R.R., Smith, B.D., Crespo, E.A., Notarbartolo di Sciara, G. 2003. Dolphins, whales and porpoises: 2002-2010 conservation plan for the world's cetaceans. Gland and Cambridge, IUCN/SSC Cetacean Specialist Group, 139 pp.

Reynolds, J.E., Wells, R.S., Eide, S.D. 2000. The bottlenose dolphin: biology and conservation. Gainesville, University Press of Florida, USA, 288 pp.

Rivas, A.L. and Beier, E.J. 1990. Temperature and salinity fields in the Northpatagonic Gulfs. Oceanologica Acta 13: 15-20.

Roditi-Elasar, M., Kerem, D., Hornung, H., Kress, N., Shoham-Frider, E., Goffman, O., Spanier, E. 2003. Heavy metal levels in bottlenose and striped dolphins off the Mediterranean coast of Israel. Marine Pollution Bulletin 46: 503-512.

Romero, S.I., Piola, A.R., Charo, M., García, C.A.E. 2006. Chlorophyll-a variability off Patagonia based on SeaWiFS data. Journal of Geophysical Research 111 DOI:10.1029/ 2005JC003244.

Romero, M.A., González, R., Ocampo-Reinaldo, M. 2010. When conventional fisheries management measures are not effective to reduce the catch and discard of juvenile fish: A case study of Argentine hake trawl fishery in San Matías Gulf (Patagonia, Argentina). North American Journal of Fisheries Management 30: 702-712.

Romero, M.A., Ocampo-Reinaldo, M., Williams, G., Narvarte, M., Gagliardini, D.A., González, R. 2013. Understanding the dynamics of an enclosed trawl demersal fishery in Patagonia (Argentina): A holistic approach combining multiple data sources. Fisheries Research 140: 73-82.

Ross, G.J.B. 1977. The taxonomy of bottlenosed dolphins *Tursiops* species in South African waters, with notes on their biology. Cape Province Museum of Natural History 11: 135-194.

Ross, G.J.B. and Cockcroft, V.G. 1990. Comments on Australian bottlenose dolphins and the taxonomic status of *Tursiops aduncus* (Ehrenberg, 1832). *In*: Leatherwood, S. and Reeves, R.R. (Eds.), The bottlenose dolphin. Academic Press, San Diego, CA, pp. 101–128.

Sabatini, M.E. 2004. Características ambientales, reproducción y alimentación de la merluza (*Merluccius hubbsi*) y la anchoíta (*Engraulis anchoíta*) en su hábito reproductivo patagónico, síntesis y perspectivas. Revista de Investigación y Desarrollo Pesquero 16: 5-25.

Sardella, N. and J. Timi. 2004. Parasites of Argentine hake in the Argentine Sea: Population and infra-community structure as evidence for host stock discrimination. Journal of Fish Biology 65: 1472-1488.

Scasso, L.M.L. and Piola, A.R. 1988. Intercambio neto de agua entre el mar y la atmósfera en el Golfo San Matías. Geoacta 15: 13-31.

Smolker, R.A., Richards, A.F., Connor, R.C., Pepper, J.W. 1992. Sex differences in patterns of associations among Indian Ocean bottlenose dolphins. Behaviour 123: 38-69.

Stavros, H.C.W., Bossart, G.D., Hulsey, T.C., Fair, P.A. 2007. Trace element concentrations in skin of free-ranging bottlenose dolphins (*Tursiops truncatus*) from the southeast Atlantic coast. Science of the Total Environment 388: 300-315.

Tolosa, I., Readman, J.W., Blaevoet, A., Ghilini, S., Bartocci, J., Milena, H. 1996. Contamination of Mediterranean (Côte D'Azur) Coastal Waters by Organotins and Irgarol 1051 Used in Antifouling Paints. Marine Pollution Bulletin 32: 335-341.

Van Waerebeek, K., Reyes, J.C., Read, A.J., McKinnon, J.S. 1990. Preliminary observations of bottlenose dolphins from the Pacific coast of South America. *In*: Leatherwood, S. and Reeves, R.R. (Eds.), The bottlenose dolphin. Academic Press, San Diego, CA, pp. 143–154.

Vázquez, N.N., Gil, M.A., Esteves, J.L., Narvate, M.A. 2007. Monitoring Heavy Metal Pollution in San Antonio Bay, Río Negro, Argentina. Bulletin of environmental contamination and toxicology 79: 121-125.

Vázquez-Medina, J.P., Cantu-Medellin, N., Medina-Rodriguez, M., Mendez-Rodriguez, L.C., Zenteno-Savin, T. 2007. Oxidative stress indicators and heavy metal levels in bottlenose dolphin (*Tursiops truncatus*) tissues from Bahía de La Paz, Mexico. Free Radical Biology and Medicine 43: S123.

Vidal, M.L. 2004. Contaminación ambiental y salud humana. IBMP Serie Publicaciones 3: 67-69.

Villarino, F.M., Lasta, M.L., Pájaro, M. 2002. Exploring alternative management policies: a preliminary ecological approach for the San Matías Gulf fishery, Argentina. Fisheries Centre Research Reports 10: 109.

Wang, J.Y., Chou, L.S., White, B.N. 2000. Differences in the external morphology of two sympatric species of bottlenose dolphins (genus *Tursiops*) in the waters of China. Journal of Mammalogy 81: 1157-1165.

Wells, R.S. 1986. The population structure of bottlenose dolphins. Dissertation, University of California Santa Cruz, Santa Cruz, CA, 234 pp.

Wells, R.S., Scott, M.D., Irvine, A.B. 1987. The social structure of free-ranging bottlenose dolphins. *In*: Genoways, H.H (Ed.), Current Mammalogy Vol. 1. Plenum Press, New York, pp. 247-305.

Wells, R.S. and Scott, M.D. 1990. Estimating bottlenose dolphin population parameters from individual identification and capture-release techniques. *In*: Hammond, P.S., Mizroch, S.A., Donovan, G.P. (Eds.), Individual recognition of cetaceans: Use of photo-identification and other techniques to estimate population parameters. Report of the International Whaling Commission Special Issue 12, pp. 407-415.

Wells, R.S. and Scott, M.D. 1994. Bottlenose dolphins. *In*: Ridgway, S.H. and Harrison, F.R.S. (Eds.), Handbook of Marine Mammals: Small Cetaceans. Academic Press, London, pp. 1-55.

Wells, R.S., Scott, M.D. 1999. Bottlenose dolphin - *Tursiops truncatus* (Montagu, 1821) *In*: Ridgway, S.H. and Harrison, S.R. (Eds.), Handbook of Marine Mammals Vol. 6: The second book of dolphins and porpoises, pp. 137-182.

Wells, R.S., Rhinehart, H.L., Hansen, L.J., Sweeney, J.C., Townsend, F.I., Stone, R., Casper, D.R., Scott, M.D., Hohn, A.A., Rowles, T.K. 2004. Bottlenose dolphins as marine ecosystem sentinels: developing a health monitoring system. EcoHealth 1: 246-254.

Whitehead, H. and Connor, R. 2005. Alliances I. How large should alliances be? Animal Behaviour 69: 117-126.

Willers, V., Naravate, M., Gil, M., Esteves, J.L. 2004. Imposex en *Buccinanops globulosum* y su utilización como bioindicado de contaminación por triburil estaño (TBT) en la Bahía de San Antonio (Río Negro, Patagonia Argentina). IBMP – Serie Publicaciones 3: 61-62.

Williams, J.A., Dawson, S.M., Slooten, E. 1993. The abundance and distribution of bottlenose dolphins (*Tursiops truncatus*) in Doubtful Sound, New Zealand. Canadian Journal of Zoology 71: 2080-2088.

Wilson, B. 1995. The ecology of bottlenose dolphins in the Moray Firth, Scotland: a population at the northern extreme of the species' range. Dissertation, Faculty of Biological Science, University of Aberdeen, Scotland, UK.

Wöhler, O.C., Hansen, J.E., Cordo, H.D., Giussi, A.R. 1999. Evaluación del estado de explotación y recomendaciones para el manejo de la merluza de cola, *Macruronus magellanicus*, del Atlántico Sudoccidental. Período 1985–1997. Informe Interno INIDEP 6, pp. 16.

Würsig, B. and Würsig, M. 1977. The photographic determination of group size, composition and stability of coastal porpoises (*Tursiops truncatus*). Science 198: 755-756.

Würsig, B. 1978. Occurrence and group organization of Atlantic bottlenose porpoise (*Tursiops truncatus*) in an Argentine bay. Biological Bulletin 154: 348-359.

Würsig, B. and Würsig, M. 1979. Behaviour and ecology of bottlenose porpoises, *Tursiops truncatus*, in the South Atlantic. Fishery Bulletin 77: 399-442.

2

FRAMEWORK AND AIM

1. FRAMEWORK

Although the bottlenose dolphin is believed to be the best-studied cetacean species in the world, most information comes from captive studies, whereas much less appears to be known about wild population structures and trends (see Table 7), and ecological needs. Indeed, the global population trend is currently unknown even though the global population status is listed by the IUCN as of least concern. The largest gaps of information for this species exist in Africa and South America.

Bottlenose dolphins have been among the most frequently observed cetacean species in Argentine coastal waters for decades. This is revealed by preliminary studies conducted on the species in the 1970s and by e.g., the frequently reoccurring references to these animals in names of older towns, streets and buildings, and in the slang of older people, especially fishermen (pers. comm.).
However, since the 1980s this situation has changed, and today only occasional sightings are possible in places where they were once common. Despite the noted disappearance of bottlenose dolphins, the species has been largely ignored in this country for research and/or conservation purposes in the past 40 years. Consequently, there is almost no knowledge of the wild populations in this part of the Southwestern Atlantic, also an important gap of information when attempting to assess the global situation of the species.

The information gathered over the course of this research contains the first data on the demography and first recent data on the ecology of the species in Argentina. Furthermore, it is among the first thorough studies on bottlenose dolphins in the larger Southwestern Atlantic Ocean.
Considering that the Atlantic coastline of South America is in continuous human development, the results of the present study may help lead to accurate conservation measures for bottlenose dolphins to ensure the ecologically sustainable and responsible coastal urbanisation and development of this part of the world.

2. AIM OF THE STUDY

The general objective of this research is to study the population ecology of bottlenose dolphins in Bahía San Antonio, Northern Patagonia, Argentina. Furthermore, this thesis evaluates the obtained results within the larger context of their conservation status in their southernmost range of the Southwestern Atlantic Ocean. Based on these data, new and improved directives are proposed to enhance current marine conservation measures and ensure the accurate preservation of the bottlenose dolphin in Argentina.

For conservation biology, demographic studies are an essential starting point to gain insight into the status of a population and to evaluate its likely ability to persist in the future. Therefore, **demographic parameters** of bottlenose dolphins in Northern Patagonia were assessed, including the estimation of their **abundance, adult survival rate** and **birth demographics**. As gene flow enhances the evolutionary potential of small populations, it was considered to be important to study the connectivity between populations and/or communities. Therefore, **social structure** and **ranging patterns** of the dolphins were investigated in detail.

When creating detailed management plans to improve the conservation status of a regional population, it is essential to understand the ecological needs such as the availability of resources, shelter from predators and access to mates. For this reason, core-use areas were identified through the study of **residency patterns**. **Activity patterns** were studied within the core area together with **habitat selection**. This information may help to identify when and where these animals perform biologically important behaviours such as feeding, and how they respond to perturbations in their habitat. Moreover, as **association patterns** are good indicators for the ecological constraints bottlenose dolphins experience, data on the variation of their **fission-fusion dynamics** were analysed in response to a changing environment.

3

MATERIALS AND METHODS

1. DEFINITIONS

A bottlenose dolphin group was defined as all individuals within a 100 m radius of each other, interacting or engaged in similar activities (Irvine et al., 1981; Wells et al., 1987; Wilson, 1995; Lusseau et al., 2005).

Each individual in the group was categorised as belonging to one of the following age classes:

- **Neonates** were defined by their small size (less than 1⁄3 the length of an adult), their foetal folds (Mann and Smuts, 1999) and their close association with an adult (Shane, 1990)
- **Calves** were categorised by being between 1/3 and 2⁄3 of the length of an adult, without foetal folds and mostly swimming in close association with an adult
- **Immatures** were defined as individuals of similar size to an adult (Cockcroft and Ross, 1990; Wilson et al., 1999) but with lighter colouration and an overall lack of severe scars and marks on their dorsal fins and flanks (Würsig and Jefferson, 1990). Furthermore, they were clearly no longer in a close association with an adult
- **Adults** were defined by their larger size, darker colouration and higher number of permanent scars and marks on the edge of their dorsal fins and flanks. Dolphins identified to be closely accompanied by a calf or neonate on at least two different occasions were assumed to be **females** (Grellier et al., 2003; Mann and Smuts, 1999)

The group size and age classes were later verified through photo-identification analyses.

Seasons were defined as follows:

- **Summer**: January-February-March
- **Autumn**: April-May-June
- **Winter**: July-August-September
- **Spring**: October-November-December

To indicate the tidal phase, the complete tide cycle was divided into four observational periods of approximately three hours each:

- **High tide** period included the hour of high tide plus the hour prior and subsequent to it
- **Low tide** period included the hour of low tide plus the hour prior and subsequent to it
- **Flood tide** was the 3 h between low and high tide periods
- **Ebb tide** was the 3 h between high and low tide periods

The behavioural categories used in behavioural observations are defined in Table 1. Dives longer than 30 sec were categorised in the behavioural state ‘diving’ as they were longer than the mean dive duration of 21.8 sec measured for coastal bottlenose dolphins in Argentine waters (Würsig, 1978).

Table 1 – Categories used to record behaviour and group cohesion (adapted Shane, 1990; Bearzi et al., 1999; Bearzi, 2005)

Behaviour	**Observed events**
Travel	Moving steadily in one direction
Surface feeding	Obvious feeding activities performed close to the water surface, typical fast moving in circles at the surface. Fish are often seen to jump out of the water (usually with birds concentrating over the dolphins). No clear physical contact between individuals can be observed
Diving	No steady directional movements, tail-out dives longer than 30 sec occurring during the 5-min sample
Socialising	At least some of the group members are in frequent physical contact, no steady directional movement, displaying surface behaviours. Playful behaviour, defined as any activity involving a foreign object e.g., kelp tossing was included in this category (Shane et al., 1986)
Milling	Moving in varying directions in one general location, no obvious surface behaviours, no apparent physical contact
Resting	Lying motionless or moving slowly at the surface
Not classified	When none of the above categories could be assigned correctly
Group cohesion	
Tight	All dolphins are less than one body length apart from each other
Loose	At least one dolphin is between 1 and 5 body lengths from the others
Disperse	At least one dolphin is more than 5 body lengths from the others

2. FIELD TECHNIQUES

2.1. BEHAVIOURAL SAMPLING

Data on behaviour and group cohesion were recorded using a focal group 5-min point sampling mode (Altmann, 1974; Mann, 1999), during which the predominant activity of the majority of the group and its cohesion was noted every 5 minutes. A dolphin group was followed until it was lost out of sight, or until it became clear that the animals were being disturbed in their normal behaviour (e.g., being attracted by or avoiding the research vessel). When the dolphin group split, observations continued for the largest part of the group when possible.

Altmann (1974) has been cited in favour of the focal group sampling mode, however only under the condition that all individuals of the sample group are continuously visible throughout the sample period, a condition that will be inevitably violated in cetacean research. In fact, Mann (1999) does not recommend the focal group sampling mode to investigate cetacean behaviour, as it might bias towards the most conspicuous behaviours, therefore overestimating their relative importance in a group. Nonetheless, keeping in mind these limitations, the focal group sampling mode was still chosen for several reasons. In the study area, groups were inclined to be small and individuals always engaged in similar behaviour (included in the used definition of ‘dolphin group’). This minimises potential biases stated above. Further, using a focal follow sampling mode could potentially bias observations towards certain age and sex classes, for example, as individuals that are visually easier identifiable by their markings tend to be males (e.g., Wilson, 1995) and/or older individuals (the acquisition of marks and scars on small cetaceans is cumulative over time; Würsig and Jefferson, 1990). Furthermore, difficulties in distinguishing among unmarked animals could potentially bias sampling methods such as scan sampling (Mann, 1999), where individuals should be sampled sequentially.

2.2. LAND-BASED SURVEYS

Land-based surveys were conducted between August 2006 and October 2010 in BSA during daylight hours (between 0800h and 1800h), and had a minimum length of 4 consecutive hours. These surveys were performed from various pre-determined elevated points, spread strategically around the bay, using binoculars Nikon 8x40, a Kowa scope TSN-822 20-60x82 and a Kenko Volare scope 20x50. All surveys were conducted in good weather conditions (≤ 3 Beaufort scale).

Regardless of the presence of dolphins, data were recorded on a prepared observation schedule (see Appendix 3) that included the name of the observers, date and time, observation area, tide and weather conditions. The latter included wind direction, wind strength, air temperature, sea state and cloud cover. Weather conditions such as wind direction, wind strength and temperature were measured using a hand-held anemometer.

When dolphins were seen, group size was determined and groups were labelled as ‘groups with calves’ or ‘groups without calves’. When possible, age categories were assigned, limited to two categories: young (incl. neonates, calves and immatures) and adults. Group size and age classes were later verified through photo-identification analysis. The distance from the coast was estimated (when possible) by eye using various reference points (buoys) at known distances. Four categories were used: (1) ≤ 100 m; (2) 100 - 500 m; (3) 500 – 1,000 m and (4) 1,000 – 1,500 m.

When dolphins were observed, data on their behaviour were recorded every 5 min (Table 1). Only the dolphin groups close enough to the shore were observed, in order to ensure the quality of the behavioural observations. When dolphins were too far from the shore to determine their behaviour accurately, solely their presence was recorded. Dorsal fins of all individuals in the group were photographed when possible, regardless of the presence of clear marks. All dolphin groups were followed until they were out of sight.

When the observation of different dolphin groups during a land-based survey was separated by at least half an hour, they were categorised as belonging to a different ‘sighting period’ (SP). On the contrary, if a dolphin group was observed within a half hour from the last observation of the previous dolphin group, both dolphin groups were categorised as belonging to the same SP.

2.3. BOAT-BASED SURVEYS

Boat-based surveys were conducted between August 2008 and December 2011 in BSA, from a small outboard-powered inflatable boat (outboard motor Suzuki 40 HP). All surveys were conducted in good weather conditions (≤ 3 Beaufort). Due to logistic limitations, the course of the boat-based survey could not be standardised; the area was surveyed until a dolphin group was found. During each survey, the boat was maintained at a steady speed of 4 - 5 knots, with always the same 2 - 3 observers maintaining a continuous visual search for dolphins. The effort of these surveys was logged using the automatic tracking system of an on-board GPS (WGS84; Figure 5). Regardless of the presence of dolphins, data were noted on a prepared observation schedule (see Appendix 3) that included the name of the observers, date and time, tidal phase and weather conditions. This latter included wind direction, wind strength, outside temperature, sea state, cloud cover and SST. Wind direction, wind strength and outside temperature were measured using a hand-held anemometer, whereas SST was measured using the boat’s echo sounder that was equipped with a thermometer (Garmin Fishfinder 140).

Once a bottlenose dolphin group was encountered, the speed of the vessel was altered to match the pace of the group. The dolphins were approached in a slow and parallel way within a range of 5 to 10 m. Changes in speed and direction of the boat were kept to an absolute minimum during the encounter as not to disturb the animals. However, the course of the boat was changed when it was necessary for the vessel to be positioned on different sides of the group, as required by the photographer for photo-identification purposes. In those cases, the boat navigated slowly behind the dolphin group to ensure than disturbance was kept to a minimum.

In the presence of a dolphin group, group size was determined and groups were decided to be either ‘groups with calves’ or ‘groups without calves’. The number of individuals in each age category was noted as accurately as possible, and was later verified during photo-identification analysis. Along with behavioural data (Table 1), exact GPS positions and exact depths were registered every 5 min in the presence of dolphins using a hand-held GPS Garmin Etrex and the vessel’s echo sounder (Garmin Fishfinder 140), respectively.

2.4. PHOTO-IDENTIFICATION

The naturally occurring markings on the dorsal fins of bottlenose dolphins can be used to identify individual animals. Würsig and Würsig (1977) were among the first researchers to use this technique referred to as photo-identification. These natural marks need to be recognisable over time, be unique to the animal and have nearly equal probability of being sighted and re-sighted in order for this technique to be useful (Würsig and Jefferson, 1990).

Therefore, during each encounter, as many high-quality photographs of the dorsal fins of all individuals in the group were taken as possible using a digital SLR camera Nikon D90 with a 70 – 200 mm F: 2.8 Nikor lens. Pictures of dolphins were taken regardless of the obvious presence of clear marks, and were obtained preferably from both sides. When possible, it was aimed to obtain photographs from all individuals in the group.

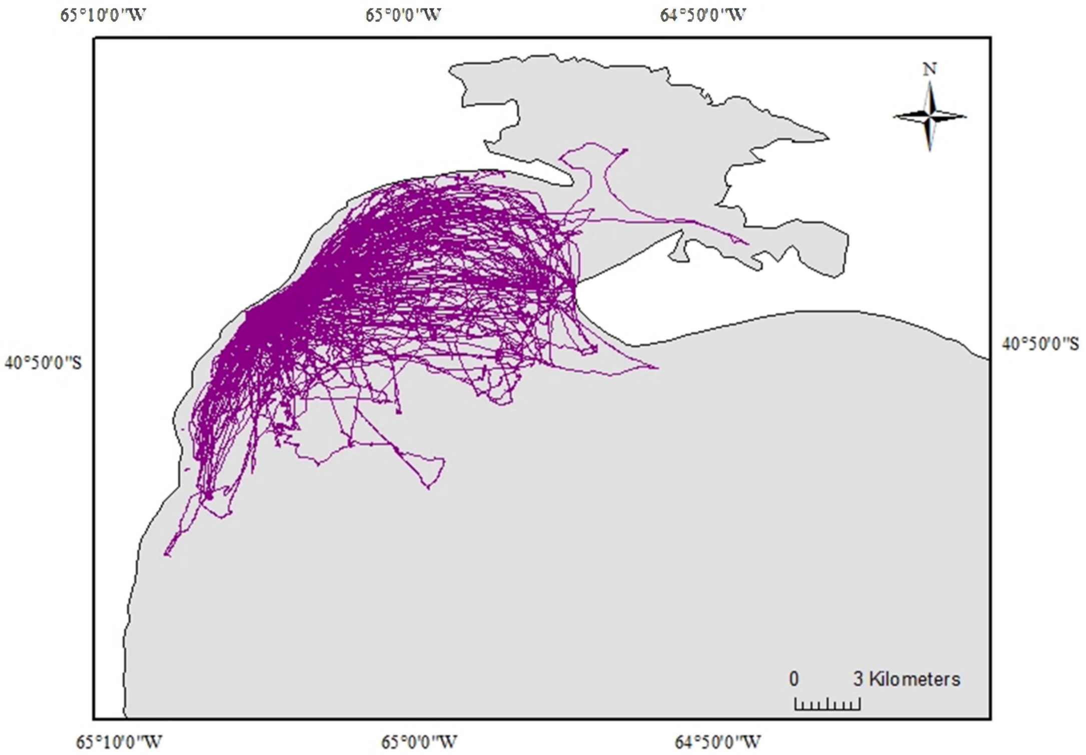

Figure 5 - Map of the primary study area, BSA, indicating boat-based survey effort tracks

3. TOTAL EFFORT

In total, 356 systematic photo-identification surveys of bottlenose dolphins were conducted between 2006 and 2011 in BSA. Of these surveys, 227 were land-based and 129 were conducted from a small outboard-powered rigid-hull inflatable boat.

Table 2 – Hours of land- and boat-based survey effort over the seasons and years (h). Additionally, the number of opportunistic photo-identification surveys of unknown duration per season (Opp.), expressed in days

	Summer			**Autumn**			**Winter**			**Spring**		
	Land based (h)	boat based (h)	Opp. (days)	Land-based (h)	boat based (h)	Opp. (days)	Land based (h)	boat based (h)	Opp. (days)	Land based (h)	boat based (h)	Opp. (days)
2006	0	0	0	0	0	0	81	0	0	0	0	0
2007	27	0	0	175	0	0	123	0	0	42	0	0
2008	178	0	0	45	0	1	34	31	4	12	53	3
2009	20	67	0	80	40	3	12	37	9	0	18	1
2010	0	31	0	0	14	3	51	143	2	5	22	0
2011	0	78	1	0	33	0	0	20	0	0	0	3
TOTAL	225	176	1	300	87	7	301	231	15	59	93	7

The total field effort equalled 1472 h, and resulted in 215 h of observation of 415 dolphin groups (260 and 155 from land- and boat-based observations respectively). Another 30 land-based surveys of unknown duration were conducted in an opportunistic way with the sole purpose of photo-identification. Table 2 presents the distribution of effort during the land-based, boat-based and opportunistic surveys. Table 3 summarises the total survey effort, the total amount of time observing bottlenose dolphins and the number of dolphin groups observed per season.

Table 3 – Total survey effort (h) over the different seasons (land- and boat-based summed). The number of hours observing bottlenose dolphins and the number of dolphin groups observed per season is also given

	Summer	Autumn	Winter	Spring	TOTAL
Number of observation hours	401	387	532	152	1472
Number of hours observing dolphins	61	33	100	21	215
Number of observed dolphin groups	117	128	134	36	415

4. PHOTO-IDENTIFICATION ANALYSIS

Picture selection was based on recommendations provided by Read et al. (2003), using consistent criteria (i.e., entire dorsal fin visible, fin perpendicular to camera, in focus, unobscured, no water spray masking fin profile). All selected photographs of dorsal fins were analysed using the computer-assisted identification systems *FinEx* and *FinMatch* (EC EuroPhlukes Initiative, University of Leiden, The Netherlands) (e.g., Figure 6).

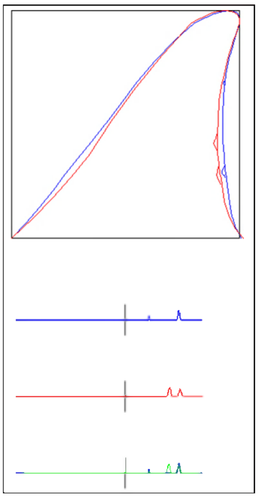

Figure 6 – Example of matching two dorsal fin shapes and cuts using the software FinMatch

The natural occurring marks used in this study to identify individuals were:

- Dorsal fin cuts: Pieces of tissue missing from the edge of the dorsal fin
- Unusual dorsal fin shapes: Distinctive dorsal fins
- Major scars: Large scars and scratches on the dorsal fin or flank
- Areas of depigmentation: Areas on the dorsal fin or flank with a distinctive lighter colouration
- Deformations: Alterations of the normal body contour

These marks are considered to be unique and permanent.

Animals were catalogued as:

- Newly-identified: When no match could be found and marks were clear enough to newly identify the individual
- Re-identified: When marks were clear enough to be certain
- Unknown: When no sufficient data were present to newly- or re-identify the individual

Every newly identified dolphin was catalogued with the code RN-BSA-(n°)/yr standing for 'Rio Negro – Bahía San Antonio – (ID N°) / year of first identification'. As a result of these analysis, a total of 67 bottlenose dolphins could be individually identified (Appendix 2) and re-identified in BSA up to 44 times on separate days (median = 16; mean = 17.6; SD = 11.1). Most individuals were identified for the first time in the first two years after which the identification of new individuals gradually levelled off. By the end of 2009, all adult dolphins in the bay appeared to have been identified; i.e., the virtual lack of additions in the photo-identification catalogue since 2009 (1 adult and 2 immature individuals in 2009, 1 immature dolphin in 2010 and none in 2011) is believed to be largely explained by the recruitment of all available, i.e., surviving, calves into the marked population (Figure 7).

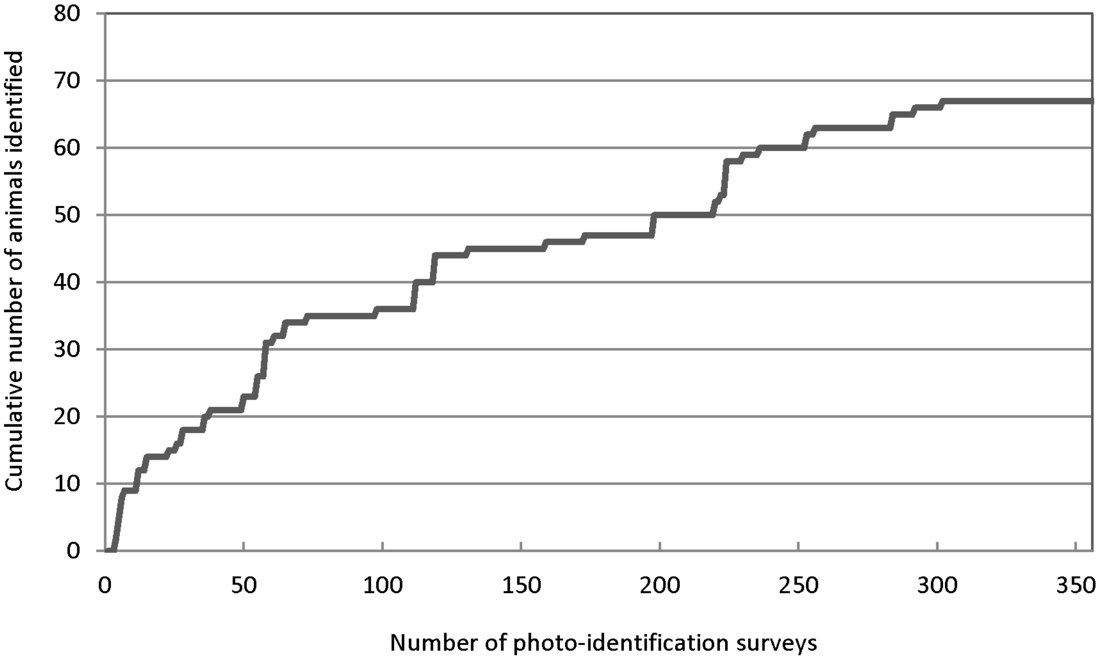

Figure 7 – Discovery curve: cumulative number of individual bottlenose dolphins identified over 356 systematic photo-identification surveys conducted in BSA

Fourteen of the catalogued dolphins (21%) were reproducing females defined by their repeated close association with at least one calf. Ten of the identified individuals were assumed to be immatures. Furthermore, the gender of 2 additional non-reproductive females (adults) and 12 males (10 adults, 2 immatures) was determined through genetic methods from biopsy samples of identified individuals (see Fruet et al., 2014 for details; Appendix 1).

In summary, by the end of 2011, the identification catalogue of BSA contained 67 individuals including 14 reproducing females, 2 adult non-reproductive females, 10 adult males, 2 immature males, 8 immatures of unknown sex and 31 adults of unknown sex (Appendix 2).

During the study period, a total of 5 carcasses were recovered (3 adults, 1 immature individual and 1 calf), amongst which two were previously identified adults and a known calf of approximately 2 years of age.

5. REFERENCES

Altmann, J. 1974. Observational study of behaviour: sampling methods. Behaviour 49: 227-265.

Bearzi, G., Politi, E., Notarbartolo di Sciara, G. 1999. Diurnal behavior of free-ranging bottlenose dolphins in the Kvarneric (northern Adriatic Sea). Marine Mammal Science 15: 1065–1097.

Bearzi, M. 2005. Aspects of ecology and behaviour of bottlenose dolphins (*Tursiops truncatus*) in Santa Monica Bay, California. Journal of Cetacean Research and Management 7: 75-83.

Cockcroft, V.G. and Ross, G.J.B. 1990. Food and feeding of the Indian Ocean bottlenose dolphin off Southern Natal, South Africa. *In*: Leatherwood, S. and Reeves, R.R. (Eds.), The bottlenose dolphin. Academic Press, San Diego, CA, pp. 295-308.

Fruet, P.F., Secchi, E.R., Daura-Jorge, F., Vermeulen, E., Flores, P.A.C., Simões-Lopes, P.C., Genoves, R.C., Laporta, P., Di Tullio, J.C., Freitas, T.R.O., Dalla Rosa, L., Valiati, V.H., Beheregaray, L., Möller, L.M. 2014. Remarkably low genetic diversity and strong population structure in common bottlenose dolphins (*Tursiops truncatus*) from coastal waters of the Southwestern Atlantic Ocean. Conservation Genetics 10.1007/s10592-014-0586-z.

Grellier, K., Hammond, P.S., Wilson, B., Sanders-Reed, C.A., Thompson, P.M. 2003. Use of photo-identification data to quantify mother-calf association patterns in bottlenose dolphins. Canadian Journal of Zoology 81: 1421-1427.

Irvine, A.B. and Wells, R.S. 1972. Results of attempts to tag Atlantic bottlenose dolphins, *Tursiops truncatus*. Cetology 13: 1-5.

Lusseau, D., Wilson, B., Hammond, P., Grellier, K., Durban, J.W., Parsons, K.M., Barton, T.R., Thompson, P.M. 2005. Quantifying the influence of sociality on population structure in bottlenose dolphins. Journal of Animal Ecology 75: 14-24.

Mann, J. 1999. Behavioural sampling methods for cetaceans: a review and critique. Marine Mammal Science 15: 102-122.

Mann, J. and Smuts, B. 1999. Behavioural development in wild bottlenose dolphin newborns (*Tursiops sp.*). Behaviour 136: 529-566.

Read, A.J., Urian, K.W., Wilson, B., Waples, D.M. 2003. Abundance of bottlenose dolphins in the bays, sounds and estuaries of North Carolina. Marine Mammal Science 19: 59-73.

Shane, S.H., Wells, R.S., Würsig, B. 1986. Ecology, behavior and social organization of the bottlenose dolphins: A review. Marine Mammal Science 2: 34-63.

Shane, S.H. 1990. Behaviour and ecology of the bottlenose dolphin at Sanibel Island, Florida. *In*: Leatherwood, S. and Reeves, R.R. (Eds.), The bottlenose dolphin. Academic Press, San Diego, CA, pp. 653.

Wells, R.S., Scott, M.D., Irvine, A.B. 1987. The social structure of free-ranging bottlenose dolphins. *In*: Genoways, H.H. (Ed.), Current Mammalogy Vol. 1. Plenum Press, New York, pp. 247-305.

Wilson, B. 1995. The ecology of bottlenose dolphins in the Moray Firth, Scotland: a population at the northern extreme of the species' range. Dissertation, Faculty of Biological Science, University of Aberdeen, Scotland, UK.

Wilson, B., Hammond, P.S., Thompson, P.M. 1999. Estimating size and assessing trends on a coastal bottlenose dolphin population. Ecological Applications 9: 288-300.

Würsig, B. and Würsig, M. 1977. The photographic determination of group size, composition and stability of coastal porpoises (*Tursiops truncatus*). Science 198*:* 755-756.

Würsig, B. 1978. Occurrence and group organization of Atlantic bottlenose porpoise (*Tursiops truncatus*) in an Argentine bay. Biological Bulletin 154: 348-359.

Würsig, B. and Jefferson, T.A. 1990. Methods of photo-identification for small cetaceans. Report to the International Whaling Commission Special Issue 12: 43-52.

4

DEMOGRAPHICS

After

Vermeulen, E. and Bräger, S. submitted. Demographics of the disappearing bottlenose dolphin in Argentina: a common species on its way out? PLoS-One.

ABSTRACT - Populations of the once common bottlenose dolphin (*Tursiops truncatus*) in Argentina have precipitously declined throughout the country in the past decades. Unfortunately, local declines of common species are easily overlooked when establishing priorities for conservation. In this study, demographics of what may well be the last remaining resident population in the country were assessed using mark-recapture analysis (Pollock's Robust Design) of a photo-identification dataset collected between 2006 and 2011 in Bahía San Antonio (Patagonia, Argentina).

Total abundance ranged from 40 (95%CI: 16 - 99) to 83 (95%CI = 46 - 152) individuals. Adult survival rates varied between 0.97 (SE = 0.04) and 0.99 (SE = 0.01). Average calving interval equalled 3.5 ± 1.0 years, with 3.5 births/year in the entire population and a minimum annual birth rate of 4.2%. However, data suggest that calves may have been born and lost before being documented, underestimating birth rate, calf mortality and possibly the number of reproductive females. Either way, the recruitment rate of calves appears to be insufficient to compensate the overall mortality in the population.

This population is relatively small and possibly declining. Considering the disappearance of populations north and south of the study area, an incessant decline will have severe consequences for the continuous existence of this species in Argentina, indicating an urgent need for serious conservation efforts. This study provides insight into how the failure to recognise local population declines can threaten the national (and eventually the international) status of a common species like the bottlenose dolphin.

KEYWORDS - Argentina, bottlenose dolphin, demographics, population dynamics, priorities of conservation

1. INTRODUCTION

Coastal bottlenose dolphin (*Tursiops truncatus*) populations in Argentina have declined notably in the past decades, with sightings being extremely rare nowadays in regions where they were once common (Bastida and Rodríguez, 2003; Coscarella et al., 2012). Unfortunately, these declines have been ignored continuously resulting in possibly a single resident population remaining in the country (Vermeulen and Cammareri, 2009).

It occurs frequently that threatened populations of common species are overlooked when priorities for biodiversity conservation are established. However, the failure to recognise local population declines, and thus the failure to apply the necessary conservation measures, may cause once-common species slide towards extinction (e.g., Casey and Myers, 1998). The common bottlenose dolphin is a species believed to be common and widespread with its global conservation status listed as of least concern (Hammond et al., 2012). Nonetheless, an ever-increasing number of coastal populations have been reported to be declining over the past decades and to be seriously threatened by human activities, thus becoming endangered in many regions worldwide (e.g., Currey et al., 2009; Birkun, 2002). Such population declines will not only affect the global status of the species, but will also have subsequent ecological effects given the general role of the bottlenose dolphin as an apex predator.

In this study, demographics of what may be one of the last remaining resident coastal populations in Argentina were assessed using mark-recapture analysis (Pollock's Robust Design) of a photo-identification dataset collected between 2006 and 2011 in BSA (Province of Río Negro). Although the species is known to be among the best-studied cetacean species in the world, our results provide only the second robust estimates for bottlenose dolphins in the Southwestern Atlantic (cf. Daura-Jorge et al., 2013), and are the first estimates for the species from Argentine waters.

Therefore, the obtained information appears to be critical for any attempt to avoid the looming disappearance of the bottlenose dolphin along the coasts of Argentina, indicating the urgent need for serious conservation efforts. Furthermore, this study provides an example on how the failure to recognise local population declines can threaten the national (and eventually the international) status of a once common marine species.

2. MATERIALS AND METHODS

2.1. PHOTO-IDENTIFICATION

In order to minimise misidentification, individual identification was primarily based on long-lasting natural marks on the dorsal fin (Würsig and Jefferson, 1990; Williams et al., 1993; Daura-Jorge et al., 2013). Photographs were graded either as 'good', 'moderate' or 'poor' according to their sharpness, contrast, size and angle of the dorsal fin relative to the frame. Only 'good' quality pictures were used in this analysis to avoid misidentifications, as poor-quality photographs are known to lead to biased estimates (Yoshizaki et al., 2009; Mansur et al., 2011).

Some dorsal fins are not sufficiently marked to be unmistakably recognisable and thus cannot be included in capture-recapture analyses that only pertain to the distinctly marked proportion of the population (Wilson et al., 1999; Read et al., 2003). Therefore, all individuals with no or few distinct marks were not used for any further analysis in this study (see details below). Calves and neonates were excluded from all analyses related to abundance and survival not only because they usually do not possess sufficient markings to ensure their future recognition without error, but also because their movements depend on their mothers' movements. Immature individuals, calves and neonates were only used in the estimation of the proportion of well-marked individuals in the population. Since the acquisition of marks and scars on small cetaceans is cumulative over time (Würsig and Jefferson, 1990), all distinctly marked individuals used in the analysis were assumed to be adults.

2.2. ANALYSIS

2.2.1 Modelling procedures

The mark-recapture histories were compiled for each distinctly marked dolphin and then analysed using Pollock's Robust Design (Pollock, 1982; Kendall et al., 1995; 1997) within the program MARK (White and Burnham, 1999) to estimate abundance, adult survival probabilities and temporary emigration rates. Data were structured in temporarily closed (i.e., without gain or loss due to immigration or emigration, birth or death) secondary sampling periods within primary periods that are separated by a longer time interval and assumed to be open.

The following parameters were estimated under the full-likelihood parameterisation: apparent survival probability (φ) being the probability of surviving and staying in the study area (this is the sum of true survival and fidelity to the study area), abundance of marked individuals (N), the probability of temporary emigration (γ'') or being unavailable for capture given that the individual was available during the previous sampling occasion, the probability that an emigrated individual remained outside the study area or unavailable for capture during subsequent sampling (γ') (Kendall et al., 1995; 1997), and capture probability (p). The probability of recapture (c) was set to equal the capture probability (p) as photo-identification is known not to provoke a trap response ($p = c$).

From the closed and open population models (Otis et al., 1978; Lebreton et al., 1992), a set of models were considered; without time-dependent effect (.), with time-dependent effect between primary periods (*t*), with time-dependent effect within primary periods (*s*), with time-dependent effect between and within primary periods (*t*s*), with time-dependent effect over the different season (*season*), with time-dependent effect over the different years (*annual*), and with the combination of all these effects.

After selecting the most parsimonious model, three temporary emigration patterns were considered in the model set being (1) no temporary emigration ($\gamma'' = \gamma' = 0$) where there is no emigration at all,

(2) random temporary emigration (γ″ = γ′) where the probability of an individual being present in the study area is independent on whether or not it was present in the study area during the previous sampling period, and (3) Markovian temporary emigration (γ″γ′) where the probability of an individual being present in the study area is conditional on whether it was present in the study area during the previous sampling period or not (Kendall and Nichols, 1995; Kendall et al., 1997; Williams et al., 2002; Nicholson et al., 2012). The model with no emigration (γ″ = γ′ = 0) was used as a basis to investigate the time-dependence of the estimated parameters. To explore the effects of heterogeneity in capture probabilities, additional models within Pollock's Robust Design were fitted to the data using Pledger's (2000) mixture models, with a maximum of 2 mixtures. However, heterogeneity in capture probabilities has not been included in the models that incorporated temporary emigration as, according to Kendall et al. (1997), full-likelihood estimators have not yet been developed for these models.

2.2.2 Model selection procedure

As there is no goodness-of-fit (GOF) test available in MARK for Robust Designs (White and Burnham, 1999), the model with the lowest AICc (Akaike's Information Criterion) value was selected as the most parsimonious model (Anderson et al., 1994). AICc is a transformation of the maximised log-likelihood that has been adjusted for the relatively small ratio of estimated parameters to sample size (Akaike, 1973; Hurvich and Tsai, 1991). However, models within two AICc units have support from the data and should not be dismissed (Burnham and Anderson, 2002). Therefore, final parameter estimates and respective SEs were averaged across all models in the candidate set based on the AICc weights, to account for model uncertainty (Burnham and Anderson, 2002). Further, the Likelihood Ratio Test (LRT) was used to test specific biological hypotheses between nested models.

2.2.3 Model assumptions and validation

The assumptions of Pollock's Robust Design can be summarised as follows (Pollock, 1982; Pollock et al., 1990; Williams et al., 2002; Nicholson et al., 2012): (1) all individuals have an equal capture probability within a sampling occasion, (2) capture and recapture probabilities are equal; there is no trap response, (3) marks are unique, permanent and correctly identified, (4) sampling is instantaneous, (5) the population is closed within primary periods, (6) all individuals have equal probability of survival and (7) each individual's probability of capture is independent of all others.

In order to meet the terms of these assumptions, the following precautions were taken: (1) One of the causes of heterogeneity in capture probability when using photo-identification is the degree to which individuals are marked when compared to others. This heterogeneity due to mark-distinctiveness was minimised by including only data from good quality pictures of distinctly marked individuals. However, regardless of this correction, the assumption of all individuals having equal probability of capture is rarely met for any cetacean population (Hammond, 1986) as capture probability may vary with age, sex or social status of the animal. Although the Robust Design is robust for capture heterogeneity when estimating survival rates (Pollock, 1982), it is not for the estimation of abundance. To explore the possible effects of these heterogeneous capture probabilities on the resulting estimates, Pledger's mixture model for heterogeneity (Pledger, 2000) was also fitted to the data. (2) The assumption of equal capture and recapture probability can be considered valid, as photo-identification is non-invasive and thus does not provoke a trap-response. (3) As correct identification of individuals is a requirement for unbiased parameter estimates (Evans and Hammond, 2004; Yoshizaki et al., 2009; Nicholson et al., 2012), only good quality pictures and distinctly marked dorsal fins were used for individual identification, minimising the possibility of misidentification. Misidentifications due to mark changes were also believed to be unlikely in this study, as data were collected in consecutive years and most individuals were captured each year, making mark changes likely to be tracked successfully. (4) The assumption of instantaneous sampling refers to static population dynamics during the sampling period. It is expected that this assumption is met as the secondary sampling periods are chosen short enough to assume population closure (i.e., no gain or loss due to immigration or emigration, birth or death) for the duration of this period (see next). (5) In order to ensure closure of the population within a primary period, secondary samples were taken over a short period of time (varying between 2 to 30 days). The rate at which new bottlenose dolphins were identified in the study area is asymptotic (see Figure 7). It is believed that the virtual lack of additions in the photo-identification catalogue since 2009 (1 adult and 2 immature individuals in 2009, only 1 immature dolphin in 2010 and 0 in 2011) can be explained by the recruitment of surviving calves into the marked population alone. This suggests a low to non-existent immigration of adults from a possible outside community into the study area. Furthermore, previous studies have indicated that bottlenose dolphins show a high degree of residency in this region (Vermeulen and Cammareri, 2009; Vermeulen et al., submitted) and that the studied population constitutes a low genetic diversity comprising of only one haplotype (Fruet et al*.,* 2014; Appendix 1). As a result, the assumption of demographic closure within short primary periods in this study appears reasonable. In any case, under the random movement model, violation of the closure assumption should not introduce a bias to the abundance estimates, although the estimates may be less precise (Kendall, 1999). (6) It is difficult to fully satisfy the assumption of equal probability of survival, as survival rates will vary with age. In order to minimise violation of this assumption, only adults were included in the analysis. However, survival may still vary within this broad age class (Nicholson et al*.,* 2012), and therefore this assumption may not be fully met. Nevertheless, the estimation of survival probabilities is generally robust in terms of heterogeneity (Pollock et al., 1990). (7) As coastal bottlenose dolphin populations are socially structured in a way that capturing a particular individual increases the chance of its closest associates being captured over other individuals (Connor et al*.,* 2000), the assumption of independent capture probabilities will be violated. However, according to Williams et al. (2002), this is unlikely to cause a bias in the estimates and only the standard errors may be underestimated to some extent (Nicholson et al., 2012).

2.2.4 Total abundance

The estimated abundance (*N*) only provides an index of the size of the distinctively marked population. There is, however, a proportion of the population that is not or only slightly marked and thus 'uncatchable'. In order to estimate the total abundance (N_{total}) of bottlenose dolphins in the study area, it was thus necessary to assess what proportion of the population was marked (θ). This was done by calculating the proportion of unmarked individuals (1 - θ) (including immature individuals, calves and neonates) by dividing the total number of unmarked individuals by the total number of individual dolphins observed per dolphin group (Williams et al., 1993; Stensland et al., 2006; Bearzi et al., 2008; 2011). This was achieved for all encounters where it was believed that all individual dolphins were photographed. The values of 1 - θ were averaged over all dolphin groups encountered within a primary period to obtain a single value per primary period. The total abundance (N_{total}) and confidence intervals were then corrected by inflating *N* with the correction factor (1 - θ). The standard error (SE) of the total abundance (N_{total}) was calculated using the delta method (Williams et al., 2002) as:

$$\mathrm{SE}(Ntotal) = \sqrt{Ntotal^2\left(\frac{SE(N)^2}{N^2} + \frac{1-\theta}{n\theta}\right)}$$

where θ is the proportion of marked individuals in the population, 1 - θ is the proportion of unmarked individuals in the population, and *n* is the total number of dolphin groups used to estimate θ. Log-normal 95% confidence intervals were calculated following Burnham et al. (1987), with a lower limit of *N* (low 95%CI) = N_{total}/C and upper limit of *N* (up 95%CI) = $N_{\text{total}} \times C$

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

2.2.5 Birth demographics

Birth demographics were assessed from data obtained between 2006 and 2011 from the 14 identified reproducing females with their closely associated calves. Calving intervals were assessed and averaged for all reproducing females. Deaths of calves were inferred from the abrupt disappearance of a calf from its mother's side within the first 3 years of its life, because calves are assumed to depend on and thus be closely associated with their mothers for at least this period of time (Scott et al., 1990; Read et al., 1993; Haase and Schneider, 2001). The birth season was estimated for each newly observed calf taking into account its size and the presence/absence of foetal folds, assuming foetal folds would be discernable up to an age of 6 - 8 months (Mann and Smuts, 1999). The minimum annual birth rate was estimated by dividing the average number of calves born per year by the estimated maximum population size (Wilson et al., 1999).

3. RESULTS

3.1. MODELLING PROCEDURES

Through the selection of only adult individuals with highly distinctive marked dorsal fins, the encounter histories of 45 individuals were used as a subset for the estimation of abundance and survival rates. In total, 12 primary periods were chosen within all 12 seasons of 2009, 2010 and 2011, with daylong survey trips within each season as secondary samples. The secondary samples were separated by short time periods, ranging between 2 and 30 days to ensure closure of the population, whereas primary periods were separated by at least 1.5 months (Table 4).

Table 4 - Duration of primary periods (consecutive days) and the number of secondary samples (survey trips) within each primary period used in Pollock's Robust Design. The number of adult dolphins identified or re-identified within each primary period is also given

		Duration primary period (days)	Number of secondary samples (survey trips)	Individuals identified within the primary period
2009	Summer	29	7	35
	Autumn	24	6	14
	Winter	26	7	40
	Spring	9	3	28
2010	Summer	15	3	24
	Autumn	2	2	14
	Winter	22	12	38
	Spring	7	3	21
2011	Summer	8	3	23
	Autumn	9	4	10
	Winter	30	5	30
	Spring	20	3	5

According to AICc, the most parsimonious model had constant survival probability, random emigration probability (not time-dependent) and a capture probability varying between and within primary periods (Table 5). The model accounting for heterogeneity with 2 mixtures had little or no support (model 45).

Although all the models with no emigration were rejected in the LRT in favour of models with migration (Random: $\chi^2 = 5.49$, $p < 0.05$; Markovian: $\chi^2 = 6.28$, $p < 0.05$), the model with Markovian emigration could not be rejected in favour of a random emigration ($\chi^2 = 0.79$, $p = 0.37$). None of the models with annual, seasonal and full time dependence of γ could be rejected (annual: $\chi^2 = 3.07$, $p = 0.21$; seasonal: $\chi^2 = 1.01$, $p = 0.79$; full time dependence: $\chi^2 = 9.35$, $p = 0.406$). The constant survival probability was not favoured in the LRT when compared to annual, seasonal and full time dependent variation (annual: $\chi^2 = 2.61$, $p = 0.28$; seasonal: $\chi^2 = 1.18$, $p = 0.76$; full time dependence: $\chi^2 = 5.45$, $p = 0.86$). Time-dependence of capture probability between and within primary periods did contribute significantly to the model fitting (between primary periods; $\chi^2 = 344.06$, $p < 0.01$; within primary periods: $\chi^2 = 281.03$, $p < 0.01$).

Table 5 – Robust Design candidate models for survival probability (s), capture probability (p), temporary emigration probability (γ) and abundance (N). Models are ranked by their AICc values. Δ AICc is the difference in the AICc of a model from that of the minimum AICc model. AICc weight indicates the support of the selected model over the others. Deviance is a measure of model fit. At all times, recapture probability (c) was set equal to capture probability (p) and is therefore not mentioned. Notations: (.) constant, (t) time-dependence between primary periods, (s) time-dependence within primary periods, (γ”) probability of temporal emigration, (γ') probability of remaining outside the study area, (γ” = γ' = 0) no emigration, (γ” = γ') random emigration, (γ” γ') Markovian emigration

Model nr in Program Mark	Model	AICc	Δ AICc	AICc Weights	Deviance	Number of parameters
1	s(.) γ”(.) = γ'(.) p(t*s) N(t)	768.4	0.00	0.40	1349.1	73
2	s(annual) γ” = γ' = 0 p(t*s) N(t)	770.3	1.87	0.16	1351.0	73
3	s(.) γ”‘(.) γ '(.) p(t*s) N(t)	770.7	2.29	0.13	1348.3	74
4	s(.) γ” = γ' = 0 p(t*s) N(t)	770.9	2.43	0.12	1354.6	72
5	s(.) γ”(annual) = γ'(annual) p(t*s) N(t)	771.6	3.11	0.08	1346.0	75
6	s(annual) γ”(.) = γ'(.) p(t*s) N(t)	772.0	3.57	0.07	1346.5	75
7	s(.) γ”(annual) γ'(.) p(t*s) N(t)	774.6	6.17	0.02	1345.9	76
8	s(seasonal) γ”(.) = γ'(.) p(t*s) N(t)	776.6	8.13	0.01	1347.9	76
9	s(.) γ”(season) = γ'(season) p(t*s) N(t)	776.7	8.29	0.01	1348.1	76
10	s(.) γ”(.) γ'(season) p(t*s) N(t)	778.2	9.80	0.00	1346.4	77
11	s(season) γ” = γ' = 0 p(t*s) N(t)	778.7	1.02	0.00	1353.1	75
45	s(.) γ” = γ' = 0 pi(t) p(t)	990.5	222.02	0.00	1698.6	25

3.2. Adult survival and Temporal emigration

Adult survival probability was very similar in all the candidate models, and the resulting average survival rate (weighted over the best fitting models) varied between 0.97 (SE = 0.04) and 0.99 (SE = 0.01). The probability of temporal emigration was equal to the probability of remaining outside the area (γ” = γ’), and averaged 0.047 (95%CI: 0.004 - 0.637) over the models. The derived return rate of temporary emigrants (1 - γ’) was 0.953, equal to the probability of remaining in the area (1 – γ”). Capture probability varied between 0.02 and 0.66.

To verify whether the high survival probability was caused by models overestimating emigration rates, survival probability was re-estimated using the best fitting models with no emigration (model 2 and 4). Survival rates for model 2 varied annually between 0.93 (SE = 0.05) and 0.99 (SE = 0.01), whereas survival rate for model 4 remained constant at an estimated 0.99 (SE = 0.01).

3.3. ABUNDANCE ESTIMATES

The total abundance of dolphins in the study area, corrected for unmarked individuals, varied over time, between the lowest value of 40 individuals (95%CI: 16 - 99) in autumn 2011 and the highest value of 83 individuals (95%CI: 46 - 152) in summer 2010 (Figure 8; Table 6). The proportion of marked individuals in the population averaged 0.65 (SD = 0.05).

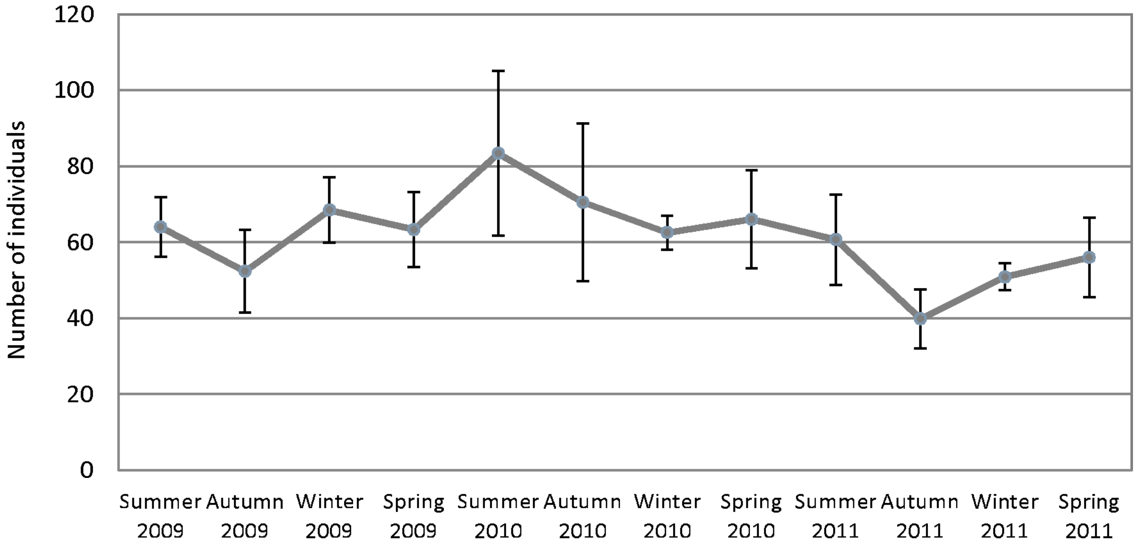

Figure 8 - Total abundance estimates (with SD) for the study area of 2009, 2010 and 2011, corrected for the proportion of unmarked individuals in the population

Table 6 - Seasonal abundance estimates of bottlenose dolphins in the study area. N_{marked}: abundance estimate of marked individuals, SE: standard error, Proportion of marked dolphins: seasonal average (± SD) of the proportion of marked individuals in the dolphin groups encountered, N_{total}: total abundance estimate (marked and unmarked individuals), Low 95%CI: lower limit of 95% confidence intervals, Up 95%CI: upper limit of 95% confidence intervals

		N_{marked}	SE	Proportion of marked dolphins	N_{total}	SE	Low 95%CI	Up 95%CI
2009	Summer	40	5.8	0.63±0.09	64	12.3	44	93
	Autumn	38	13.9	0.73±0.14	52	20.9	25	111
	Winter	44	6.1	0.64±0.08	68	12.5	48	98
	Spring	44	9.3	0.69±0.03	63	15.6	39	102
2010	Summer	52	13.9	0.62±0.07	83	26.1	46	152
	Autumn	40	14.0	0.57±0.09	71	29.5	32	155
	Winter	39	1.1	0.63±0.12	63	7.1	50	78
	Spring	42	10.2	0.63±0.05	66	19.6	37	117
2011	Summer	36	10.0	0.60±0.08	61	19.6	33	112
	Autumn	28	12.6	0.71±0.09	40	19.5	16	99
	Winter	35	3.1	0.69±0.09	51	7.0	39	67
	Spring	36	1.9	0.65±0.05	56	18.6	30	106

3.4. BIRTH DEMOGRAPHICS

During the entire study period (2006 - 2011), a total of 25 calves were known to have been born alive to only 14 reproducing females in the population, 21 of which were born after 2006. The other 4 calves were assumed to have been born probably in spring of 2005, approximately 10 months before the start of this study.

Over the years, 4 calves disappeared abruptly at an age < 2 yrs suggesting that they had died. Only the carcass of one of these calves was recovered. In total, 14 calves are known to have survived the first 3 years of life, of which at least five could be included into the photo-identification catalogue due to their first distinct marks and scars. By the end of 2012, 7 calves were still present in close association with their mother and were thus assumed to be still at pre-weaning age. When these dependent calves are excluded from calculation, it can be concluded that 14 out of the 18 calves (78% i.e., 25 calves minus 7 pre-weaning calves) of known age, survived to post-weaning age.

The birth season could be determined for 18 of the 25 calves, of which 83% (n = 15) were born in late spring/early summer. During the study period, the average calving interval equalled 3.5 ± 1.0 years (n = 14), ranging from 2 to 5 years, with an estimated 3.5 births/yr (21 births in 6 years) in the entire population. Accounting for a maximum estimated population size of 83 individuals, this results a minimum annual birth rate of 4.2%.

4. DISCUSSION

4.1. MODEL ASSUMPTIONS

Pollock's Robust Design (Pollock, 1982; Pollock et al., 1990) was chosen to estimate seasonal abundance and annual survival while taking into account possible temporary emigrations, as the study area does not comprise the entire home range of many of these dolphins (Failla et al., in press; Vermeulen et al., 2008). Additionally, Pollock's Robust Design allows for multiple capture occasions between survival intervals, which is also of benefit as it is not always possible to photograph all individuals in the study area during one survey trip. Furthermore, the model's two levels of sampling allow for a finer control over the relative precision of each parameter (Kendall and Pollock, 1992). Another advantage of this model design is that survival estimates are less biased by heterogeneity in capture probability.

When using photo-identification data for capture-recapture analysis, it is important to consider how the model assumptions can be satisfied to ensure unbiased parameter estimates. As in other cetacean field studies, it is virtually impossible to guarantee that none of the standard mark-recapture assumptions were violated (Hammond et al., 1990; Wilson et al., 1999). Probably the most difficult assumption to satisfy is the one of equal capture probability for all individuals at any sampling occasion. The obtained estimates for capture probability varied notably over time, and might be a reflection of the heterogeneity in individual capture probabilities. The fluctuation in sampling effort, for example, might have influenced the number of dolphins identified within each period, as well as their capture probability, which might affect the precision of each abundance estimate. However, an extra analysis allowing for individual heterogeneity in capture probability suggested that any possible bias was small as the obtained abundance estimates were almost identical for a model that did allow for capture heterogeneity.

4.2. ADULT SURVIVAL PROBABILITY

The presented estimate of apparent adult survival ($\varphi_{(2009\ -\ 2011)}$ = 0.97 - 0.99) represents the first available estimate for bottlenose dolphins in Argentina, and only the second such estimate for the species in the Southwestern Atlantic (Daura-Jorge et al., 2013). They are slightly higher than those reported for other regions which range from 0.92 to 0.97 (Wells and Scott, 1990; Corkrey et al., 2008; Currey et al., 2008a; Silva et al., 2009; Nicholson et al., 2012; Daura-Jorge et al., 2013). The model that fitted the data best suggests a constant survival rate. Nevertheless, time dependency of survival could not be rejected, but even estimates obtained by models accounting for time dependency of survival rates (annual, seasonal and full time dependency) never dropped below 0.93 (SE = 0.05).

The estimated value of apparent survival is the sum of true survival and permanent emigration, as Pollock's Robust Design cannot distinguish between the two. The estimate would only be a measure of true survival, if permanent emigration was assumed to be zero. Despite the fact that immigration of adult individuals into the study area is suggested to be non-existing, it is not possible to determine whether the population is geographically isolated, especially since a neighbouring community is known to exist further north (Vermeulen et al., submitted). Nonetheless, as adult survival rates are estimated to be high and permanent immigration is suggested to be virtually non-existent, the number of permanent emigrants is likely to be very low.

4.3. BIRTH DEMOGRAPHICS

The calving interval of 3.5 ± 1.0 years appears to be common among bottlenose dolphins and has been reported previously for several coastal populations of this species (Mann et al., 2000; Haase and Schneider, 2001; Kogi et al., 2004). Differences in calving intervals among different populations may be indicative for body size, nutrition levels and calf mortality (Connor et al., 2000), suggesting that nutrition levels for reproductive females in the study provided good conditions and at least the registered calf mortality lies within the values common for bottlenose dolphins. However, the minimum annual birth rate was estimated to be 4.2%, which is somewhat lower than values reported for other bottlenose dolphin populations (Wells and Scott, 1990: 5.5%; Wilson et al., 1999: 4.5% - 5.6%; Haase and Schneider, 2001: 5.6% - 13.8%; Kogi et al., 2004: 7%). Consistent with the reported low birth rate, it is noteworthy that the average proportion of unmarked individuals in the population was considerably lower in the study period (0.35) compared to 2008 (0.47; Vermeulen and Cammareri, 2009), most likely due to recruitment of calves and their acquisition of permanent marks and scars at a faster rate than the addition of new calves into the population.

Considering a normal calving interval, the low minimum annual birth rate should be related to a low number of successfully reproducing females in the entire population rather than to a low number of calves born from the known reproducing females. As such, considering a photo-identification catalogue containing minimum 57 adults and supposing a 1:1 ratio of males vs. females at birth, twice as many than the reported 14 reproducing females would be expected within this population. The small proportion of documented calves dying before being weaned from their mothers (22%) suggests a low calf mortality (Wells and Scott, 1990; Mann et al., 2000). However, only 38% of the calves born after 2006 were documented with foetal folds, suggesting that most calves were only observed for the first time when they were already over 6 - 8 months old (Mann and Smuts, 1999). It is therefore likely calves were born and lost before being documented, suggesting birth rate, calf mortality and possibly number of reproductive females are underestimated. Presented information would thus only reflect data of successful females with calves around long enough to be documented. In terms of population dynamics, an equal underestimation of birth rate and calf mortality may cancel each other out. Nonetheless, values suggest the recruitment rate of calves appears to be insufficient to compensate for the mortality within the population: the recorded calf mortality amounts to 0.7 animals / year (4 calves in 6 years), which represents a minimum annual mortality rate of 1% of the registered population or a third of the total estimated mortality. At an estimated adult mortality rate of 2%, a population growth of 1.2% per year is possible only when ignoring the mortality of immature dolphins (considering the minimum annual birth rate of 4.2%). If their mortality rate is equivalent to that of adults or higher, this population is declining.

An underestimated calf mortality and/or unsuccessful reproduction in certain females might be caused by inexperienced primiparous females, predation or another factor reducing the reproductive success of female bottlenose dolphins in this population. The predation pressure in the study area is suggested to be low according to the lack of visual predatory scars from shark or killer whale bite marks. Limited toxicological research in Argentina, however, indicated elevated levels of heavy metals in bottlenose dolphins in various regions along the Argentinean coast (Marcovecchio et al., 1990; 1994). Within our study area, research on the accumulation of heavy metals in crustaceans (*Chasmagnathus granulate*), molluscs (*Brachydontes rodriguezi*), sea lions (*Otario flavescens*) and even in children living near the study area revealed elevated levels of lead, copper, zinc and cadmium in their systems, assumed to be related to a former mining activity in the region that left waste piles still leaching various metals into the environment more than two decades after closure of the mines (Gil et al., 1999; 2006; Bonuccelli et al., 2004; Vázquez et al., 2007). Most of these pollutant levels are elevated considerably (up to 3 orders of magnitude) compared to levels reported for other coastal regions of Argentine Patagonia. The values in crustaceans and molluscs in the bay were up to 6 times higher than the upper limits allowed for human consumption (Gil et al., 2006). As apex predators, bottlenose dolphins are known to accumulate heavy metals, and negative health effects have been shown or are presumed also in other parts of the world, including in the South Atlantic (e.g., Parsons and Chan, 2001; Roditi-Elasar et al., 2003; Carballo et al., 2004; Stavros et al., 2007; Vázquez-Medina et al., 2007; Lemos et al., 2013). Elevated levels of lead in the study area are known to have affected not only fertility in women, but also caused mental disabilities and delayed mental development in children of the localities surrounding the study area (Claps, 2005). Vázquez et al. (2007) raised concerns about the consequences of the reported high levels of heavy metals in molluscs at a higher trophic level in the study area, suggesting that ‘although future studies should be pursued, enough is already known to require immediate action’. Claps (2005) adds that ‘the high levels of accumulation in mussels of lead, zinc, copper and cadmium in the bay of San Antonio might pose a contamination risk throughout the food chain, proving a great threat to larger predators’. Frodello et al. (2002) indicated that metal pollutants pass from the tissue to the milk in lactating bottlenose dolphins. Lead is also known to pass the placenta affecting the nervous system of the foetus (Vos et al., 2003). Contaminants passed down from the mother as well as other health related stresses may compromise the immune response of newborn dolphins (Stolen and Barlow, 2003). Cockcroft et al. (1989) found that an adult female might transfer as much as 70% of her pollutant load to her first calf, with consequently primiparous females having an increased risk of reproductive failure (Wells et al., 2005).

It is suggested that the reported levels of pollution should be regarded as a major concern for the health and reproduction of the bottlenose dolphins residing in the region.

4.4. POPULATION AT RISK?

This population of bottlenose dolphins is relatively small and likely to be declining. The reported high contamination with heavy metals (Gil et al., 1999; Vidal, 2004) and possibly overfishing in the area (Cauhépé, 1999) might be among the causes of this decline and need to be investigated further. Considering the genetic isolation and low genetic diversity of the studied population (Fruet et al., 2014; Appendix 1), and the continuously increasing urbanisation in the country, results suggest this population is highly vulnerable and at risk, as cetacean populations of less than 100 individuals are considered to have higher extinction risks due to stochastic events (Thompson et al., 2000). The toxicology of the population should be monitored, and measures need to be taken to protect this species and its habitat, including a controlled management of rural, urban and industrial wastes, protective laws to limit harassment, as well as educational projects to increase public awareness (for an example see Appendix 4). Understanding that the species has nearly disappeared from the regions north and south of the study area (Bastida and Rodríguez, 2003; Coscarella et al., 2012), continuous failure in their conservation could have a devastating effect on the presence of coastal bottlenose dolphins in this South American country.

4.5. A COMMON SPECIES?

The coastal lifestyle and site-fidelity of coastal bottlenose dolphins may have obfuscated the need for more extensive research and conservation efforts in Argentina in former years. It is suggested that this misconception about the status of coastal bottlenose dolphin populations might also be wide-spread on an international scale, exacerbated by a global attitude towards the *Tursiops* species. As human urbanisations increase along coastlines, coastal bottlenose dolphins are particularly vulnerable to ensuing anthropogenic impacts (Sutherland, 2000). Additionally, research increasingly indicates coastal bottlenose dolphin populations are more isolated than previously believed, a finding that makes them even more vulnerable. To test our assumption, I reviewed the available literature and found an ever-increasing number of coastal bottlenose dolphin populations worldwide have been reported to be vulnerable or declining (Table 7). Not a single population, however, was described to be increasing.

Therefore it is suggested that the misconception about the global wellbeing of coastal bottlenose dolphin needs to be re-evaluated while leaving behind the 'one species, one assessment' approach for a more fine-scale approach based on improved scientific collaboration.

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Table 7 - List of regional coastal bottlenose dolphin populations (*Tursiops* sp.) reported to be declining or vulnerable (defined as containing fewer than 1000 mature individuals; IUCN 2012)

Region	Population	Population size	Population trend	Possible threats	Reference
Europe	Moray Firth, Scotland, UK	~130	- 5% pa	Pipeline construction, dumping of dredge spoils, commercial fishing, dolphin-watching	Reid et al., 2003; Sanders-Reed et al., 1999; Thompson et al., 2000; Wilson et al., 1999
	Sound of Barra, Scotland, UK	~15	n/a	Fishing industry, gas- and oil-related activities, coastal developments	Grellier and Wilson, 2003
	Cornwall, SW England, UK	~30	n/a	Bycatch, disease, prey depletion	Wood, 1998; Doyle et al., 2007; Pikesley et al., 2012
	Cardigan Bay, UK	~200	n/a	Boat traffic	Grellier et al., 1995; Baines et al., 2002; Parsons et al., 2002; Evans et al., 2003
	Shannon Estuary, Ireland	113	n/a	Pollution, habitat degradation, bycatch, dolphin watching	Ingram et al., 1999; Rogan et al., 2000
	Channel Islands, France	66	n/a	n/a	Lahaye and Mauger, 2001
	Molène Archipelago, Brittany, France	~50	n/a	n/a	Evans et al., 2003
	Ile de Sein, France	~20	n/a	n/a	Evans et al., 2003
	Southern Galicia, Spain	123-664	n/a	Fishing industry, contamination	López, 2003; López et al., 2004; Fernández et al., 2011
	Sado Estuary, Portugal	~25	n/a	Habitat degradation	Gaspar, 2003; Silva, 2008
	Asinara Island National Park, Italy	22	n/a	Interaction with fisheries	Lauriano et al., 2004
	Lampedusa Island, Italy	249-446	n/a	Interaction with fisheries, boat traffic	Pace et al., 1999; La Manna et al., 2013; Pulcini et al., 2013

	Gulf of Trieste, Slovenia	47	n/a	Contamination, recreational boats, fishing industry, habitat degradation	Genov et al., 2008
	Kvarnerić, Croatia	~200	-50% in past 50 yrs	Historical killing, habitat degradation, nautical tourism, fishing activities	Bearzi et al., 2004; Pleslić et al., 2013; Rako et al., 2013
	Ionian Sea, Greece	48	n/a	Overfishing	Bearzi et al., 2005
	Amvrakikos Gulf, Greece	148	n/a	Contamination, habitat degradation, overfishing	Bearzi et al., 2008
	Israeli Mediterranean Sea, Israel	85	n/a	Fishing industry	Scheinin et al., 2005
	Kerch Strait, Black sea	127	n/a	Noise pollution, habitat degradation	Birkun, 2002; Birkun et al., 2004
Australasia	Fiordland, New Zealand (3 subpopulations)	205	- 2.8% pa (Doubtful Sound)	Freshwater discharge, dolphin-watching	Lusseau et al., 2006; Currey et al., 2007; 2008b; 2009
	Bay of Island, New Zealand	483	- 5.8-7.5% pa	Dolphin-watching	Tezanos-Pinto et al., 2013
	Hauraki Gulf, New Zealand	162	n/a	Shipping traffic	Berghan et al., 2008
	Marlborough Sounds, New Zealand	195-232	n/a	Recreational vessel traffic, ecotourism, aquaculture, contamination from runoffs	Merriman, 2007
	Moreton Bay, Queensland, Australia	446+193 (North+South)	n/a	Urban development	Ansmann et al., 2013
	Port Stephens, NSW, Australia	~160	n/a	Dolphin watching, contamination	Möller et al., 2002; Steckenreuter et al., 2012
	Jervis Bay, NSW, Australia	108	n/a	Dolphin watching, contamination	Möller et al., 2002
	Clarence River Estuary, NSW, Australia	71	n/a	Fishing activities	Fury and Harrison, 2011
	Richmond River Estuary, NWS, Australia	34	n/a	Fishing activities	Fury and Harrison, 2011

	Useless Loop, Shark Bay, WA, Australia	~208	n/a	Dolphin based tourism, habitat degradation	Bejder et al., 2006; Nicholson et al., 2012
	Bunburry, WA, Australia	139	n/a	Contamination, prey depletion	Smith, 2012
	Pilbara, WA, Australia	n/a	n/a	Commercial trawl fishery	Allen et al., 2013
	Mirura Island, Japan	~220	n/a	Dolphin based tourism	Kogi et al., 2004
Africa	Kwazulu-Natal, South Africa	~ 900	n/a	By-catch in shark nets	Cockcroft et al., 1990; Peddemors, 1999; Natoli et al., 2008
	West Africa	n/a	n/a	Incidental and directed takes	Van Waerebeek et al., 2008
	Zanzibar, Tanzania	136-179	n/a	Historic hunting, bycatch, dolphin watching,	Stensland et al., 2006
	São Tomé Island, Democratic Republic of São Tomé and Príncipe	37	n/a	(Illegal) Fishing activities	Pereira et al., 2013
Central America	Bocas del Toro, Panama	~150	n/a	Dolphin watching	Barragán-Barrera et al., 2013
	Drowned Cayes, Belize	122	n/a	Overfishing, contamination	Kerr et al., 2005
	Turneffe Atoll, Belize	~86	n/a	Tourism, fishing activities	Campbell et al., 2002
	Tamiahua, Mexico	177	n/a	Artisanal fishing	Valdes-Arellanes et al., 2011
	Tuxpan, Mexico	161	n/a	Artisanal fishing	Valdes-Arellanes et al., 2011
	Coast of Tabasco, Mexico	300-573	n/a	n/a	López-Hérnandez, 1997
South America	Margarita Island & Los Frailes Archipelago, Venezuela	< 60	n/a	Directed catches, tourism	Oviedo and Silva, 2005
	Gulf of Guayaquil, Ecuador	115	n/a	Bycatch	Félix, 1994; Van Waerebeek et al., 1997
	Chañaral, Damas, Choros and Gaviota Islands, Chile	30-35	n/a	Dolphin based tourism, bycatch	González et al., 1989; Sanino and Van Waerebeek, 2008; Sanino and Yáñez, 2000
	Cagarras Archipelago, Brazil	n/a	n/a	Fishing activities, marine traffic, contamination	Lodi and Monteiro-Neto, 2012; Lodi et al., 2014; Lemos et al., 2013

Mirim, Imaruí & St. Antônio Lagoons, Brazil	~54	n/a	Incidental catch, contamination	Simões-Lopez and Daura-Jorge, 2008; Daura-Jorge et al., 2013
Patos Lagoon Estuary, Brazil	~84	n/a	Incidental catch, collisions with fishing boats	Fruet et al., 2011 ; 2012; Zappes et al., 2013
Coast of Uruguay	~55	n/a	Overfishing, habitat degradation, incidental catch	Laporta, 2008
Buenos Aires, Argentina	n/a	n/a	Overfishing, habitat degradation	Bastida and Rodríguez, 2003
Península Valdés, Argentina	n/a	n/a	Overfishing, habitat degradation	Coscarella et al., 2012
Bahía San Antonio, Argentina	83	n/a	Contamination, overfishing	This study

5. REFERENCES

Akaike, H. 1973. Information theory and an extension of the maximum likelihood principle. *In*: Petran, B.N. and Csaki, F. (Eds.), International Symposium on Information Theory, Budapest, pp. 267-281.

Allen, S.J., Pollock, K., Krützen, M., Tyne, J., Jaiteh, V., McElligott, D., Loneragan, N. 2013. Incidental dolphin capture and bycatch mitigation in a Western Australian trawl fishery. Abstract 20th Biennial conference on the Biology of Marine Mammals, 9-13 December 2013, Dunedin, New Zealand.

Anderson, D.R., Burnham, K.P., White, G.C. 1994. AIC model selection in overdispersed capture–recapture data. Ecology 75: 1780–1793.

Ansmann, I.C., Lanyon, J.M., Seddon, J.M., Parra, G.J. 2013. Monitoring Dolphins in an Urban Marine System: Total and Effective Population Size Estimates of Indo-Pacific Bottlenose Dolphins in Moreton Bay, Australia. PLoS-One. 8: e65239.

Baines, M.E., Reichelt, M., Evans, P.G.H., Shepherd, B. 2002. Comparison of the Abundance and Distribution of Harbour Porpoises (*Phocoena phocoena*) and Bottlenose Dolphins (*Tursiops truncatus*) in Cardigan Bay, UK. Abstract, 16th Annual Conference of the European Cetacean Society, 7-11 April 2002, Liège, Belgium.

Barragán-Barrera, D.C., May-Collado, L.J., Quiñones-Lebrón, S.G., Caballero, S. 2013. Population at risk: low genetic diversity in bottlenose dolphins of Bocas del Toro, Panama. Report to the International Whaling Commission SC/65a/SM15.

Bastida, R. and Rodríguez, D. 2003. Mamíferos Marinos Patagonia Antartida. Vazquez Mazzini Editors, Buenos Aires, Argentina, 206 pp.

Bearzi, G., Holcer, D., Notarbartolo di Sciara, G. 2004. The role of historical dolphin takes and habitat degradation in shaping the present status of northern Adriatic cetaceans. Aquatic Conservation 14: 363-379.

Bearzi, G., Politi, E., Agazzi, S., Bruno, S., Costa, M., Bonizzoni, S. 2005. Occurrence and present status of coastal dolphins (*Delphinus delphis* and *Tursiops truncatus*) in the eastern Ionian Sea. Marine Freshwater Ecosystems 15: 243-257.

Bearzi, G., Agazzi, S., Bonizzoni, S., Costa, M., Azzellino, A. 2008. Dolphins in a bottle: Abundance, residency patterns and conservation of common bottlenose dolphins *Tursiops truncatus* in the semi-closed eutrophic Amvrakikos Gulf, Greece. Aquatic Conservation 18: 130-146.

Bearzi, G., Bonizzoni, S., Agazzi, S., Gonzalvo, J., Currey, R.C. 2011. Striped dolphins and short-beaked common dolphins in the Gulf of Corinth, Greece: Abundance estimates from dorsal fin photographs. Marine Mammal Science 27: 165-184.

Bejder, L., Samuels, A., Whitehead, H., Gales, N., Mann, J., Connor, R., Heithaus, M. Watson-Capps, J., Flaherty, C., Krützen, M. 2006. Decline in relative abundance of bottlenose dolphins exposed to long-term disturbance. Conservation Biology 20: 1791-1798.

Berghan, J., Algie, K.D., Stockin, K.A., Wiseman, N., Constantine, R., Tezanos-Pinto, G., Mourão, F. 2008. A preliminary photo-identification study of bottlenose dolphin (*Tursiops truncatus*) in Hauraki Gulf, New Zealand. New Zealand Journal of Marine and Freshwater Research 42: 465-472.

Birkun, A.A. 2002. Disturbance to cetaceans in the Black Sea. *In*: Notarbartolo di Sciara, G. (Ed.), Cetaceans of the Mediterranean and Black Seas: state of knowledge and conservation strategies. A report to the ACCOBAMS Secretariat, Monaco, Section 14, pp. 7.

Birkun, A.A., Krivokhizhin, S.V., Glazov, D.M., Shpak, O.V., Zanin, A.V., Mukhametov, L.M. 2004. Abundance estimates of cetaceans in coastal waters of the northern Black Sea: Results of boat surveys in August-October 2003. *In*: Marine Mammals of the Holarctic: Collection of Scientific Papers after the 3rd Internat. Conf. Koktebel, Ukraine, 11-17 October 2004, Moscow, pp. 64-68.

Bonuccelli, R., Malan, J., Luna, L.I., Torres, L. 2004. Contaminación por metales pesados derivados de la lixiviación de escorias de fundición San Antonio Oeste-Río Negro. IBPM – Serie Publicaciones 3: 63-66.

Burnham, K.P., Anderson, D.R., White, G.C., Brownie, C., Pollock, K.H. 1987. Design and analysis methods for fish survival experiments based on release-recapture. American Fisheries Society Monograph No. 5. Bethesda, Maryland, 437 pp.

Burnham, K.P. and Anderson, D.R. 2002. Model Selection and Multimodel Inference: a Practical Information-theoretic Approach. 2nd Edition. Springer-Verlag, New York, New York, 488 pp.

Campbell, G.S., Bilgre, B.A., Defran, R.H. 2002. Bottlenose dolphins (*Tursiops truncatus*) in Tuneffe Atoll, Belize: occurrence, site fidelity, group size, and abundance. Aquatic Mammals 28: 170-180.

Carballo, M., De la Peña, E., Fernández, A., Aguayo, S., Esperón, F., De la Torre, A., Muñoz, M.J. 2004. Accumulation of persistent organic chemicals and metals in stranded bottlenose dolphins (*Tursiops truncatus*) in Canary Islands (Spain). Toxicology and Applied Pharmacology 197: 235.

Casey, J.M. and Myers, R.A. 1998. Near extinction of a large, widely distributed fish. Science 281: 690-692.

Cauhépé, M.E. 1999. Management of the Argentine hake. Final project UNU Fisheries Training Program, Reykjavic, Iceland.

Claps, E.L. 2005. A Heavy Legacy: lead contamination in San Antonio Oeste, Argentina. Mines and Communities, http://www.minesandcommunities.org/article.php?a = 5363. Downloaded on 11 June 2013.

Cockcroft, V.G., de Kock, A.C., Lord, D.A., Ross, G.J.B. 1989. Organochlorines in bottlenose dolphins *Tursiops truncatus* from the east coast of South Africa. South African Journal of Marine Science 8: 207-217.

Cockcroft, V.G., Ross, G.J.B., Peddemors, V.M. 1990. Bottlenose dolphin *Tursiops truncatus* distribution in Natal's coastal waters. South African Journal of Marine Science 9: 1-10.

Connor, R.C., Wells, R.S., Mann, J., Read, A.J. 2000. The bottlenose dolphin: social relationships in a fission–fusion society. *In*: Mann, J. Connor, R.C., Tyack, P.L., Whitehead, H. (Eds.), Cetacean Societies: Field Studies of Dolphins and Whales. The University of Chicago Press, Chicago, IL, pp. 91-126.

Corkrey, R., Brooks, S., Lusseau, D., Parsons, K., Durban, J.W., Hammond, P.S., Thompson, P.M. 2008. A Bayesian capture-recapture population model with simultaneous estimation of heterogeneity. Journal of the American Statistical Association 103: 948-960.

Coscarella, M., Dans, S.L., Degrati, M., Garaffo, G.V., Crespo, E.A. 2012. Bottlenose dolphins at the southern extreme of the Southwestern Atlantic: local population decline? Journal of the Marine Biological Association of the United Kingdom 92: 1843-1849.

Currey, R.J.C., Dawson, S.M., Slooten, E. 2007. New abundance estimates suggest Doubtful Sound bottlenose dolphins are declining. Pacific Conservation Biology 13: 265-273.

Currey, R.J.C., Dawson, S.M., Slooten, E., Schneider, K., Lusseau, D., Boisseau, O., Haase, P., Williams, J.A. 2008a. Survival rates for a declining population of bottlenose dolphins in Doubtful Sound, New Zealand: An information theoretic approach to assessing the role of human impacts. Aquatic Conservation 19: 658-670.

Currey, R.J.C., Rowe, L.E., Dawson, S.M., Slooten, E. 2008b. Abundance and demography of bottlenose dolphins in Dusky Sound, New Zealand, inferred from dorsal fin photographs. New Zealand Journal of Marine and Freshwater research 42: 439-449.

Currey, R.J.C., Dawson, S.M., Slooten, E. 2009. An approach for regional threat assessment under IUCN Red List Criteria that is robust for uncertainty: The Fiordland bottlenose dolphins are critically endangered. Biological Conservation 142: 1570-1579.

Daura-Jorge, F.G., Ingram S.N., Simões-Lopez, P.C. 2013. Seasonal abundance and adult survival of bottlenose dolphins (*Tursiops truncatus*) in a community that cooperatively forages with fishermen in southern Brazil. Marine Mammal Science 29: 293-311.

Doyle, J., Goodwin, L., Loveridge, J.E. 2007. The Decline of Inshore Bottlenose Dolphins (*Tursiops truncatus*) in Southwest England. Abstract, 21th Annual Conference of the European Cetacean Society, 22-25 April 2007, San Sebastian, Spain.

Evans, P.G.H. and Hammond, P.S. 2004. Monitoring cetaceans in European waters. Mammal Review 34: 131–156.

Evans, P.G.H., Anderwald, P., Baines, M.E. 2003. UK cetacean status review. Report to English Nature & Countryside Council for Wales, 160 pp.

Failla, M., Seijas, V.A., Vermeulen, E. in press. Occurrence of Bottlenose dolphins (*Tursiops truncatus*) in the Río Negro Estuary, Argentina, and their mid-distance movements along the Northeast Patagonian coast. Latin American Journal of Aquatic Mammals.

Félix, F. 1994. Ecology of the coastal bottlenose dolphin *Tursiops truncatus* in the Gulf of Guayaquil, Ecuador. Investigations on Cetacea 25: 235-256.

Fernández, R., Santos, M.B., Pierce, G.J., Llavona, Á., López, A., Silva, M.A., Ferreira, M., Carrillo, M., Cermeño, P., Lens, S., Piertney, S.B. 2011. Fine-scale genetic structure of bottlenose dolphins, *Tursiops truncatus*, in Atlantic coastal waters of the Iberian Peninsula. Hydrobiologia 670: 111-125.

Frodello, J.P., Viale, D., Marchand, B. 2002. Metal concentrations in the milk and tissues of a nursing *Tursiops truncatus* female. Marine Pollution Bulletin 44: 551-554.

Fruet, P.F., Secchi, E.R., Di Tullo, J.C., Kinas, P.G. 2011. Abundance of bottlenose dolphins, *Tursiops truncatus* (Cetacea: Delphinidae), inhabiting the Patos Lagoon estuary, southern Brazil: Implications for conservation. Zoologia 28: 23-30.

Fruet, P.F., Kinas, P.G., Da Silva, K.G., Di Tullio, J.C., Monteiro, D.S., Dalla Rosa, L., Estima, S.C., Secchi, E.R. 2012. Temporal trends in mortality and effects of by-catch on common bottlenose dolphins *Tursiops truncatus*, in southern Brazil. Journal of the Marine Biological Association of the United Kingdom 92: 1865-1876.

Fruet, P.F., Secchi, E.R., Daura-Jorge, F., Vermeulen, E., Flores, P.A.C., Simões-Lopes, P.C., Genoves, R.C., Laporta, P., Di Tullio, J.C., Freitas, T.R.O., Dalla Rosa, L., Valiati, V.H., Beheregaray, L., Möller, L.M. 2014. Remarkably low genetic diversity and strong population structure in common bottlenose dolphins (*Tursiops truncatus*) from coastal waters of the Southwestern Atlantic Ocean. Conservation Genetics 10.1007/s10592-014-0586-z.

Fury, C.A. and Harrison, P.L. 2011. Seasonal variation and tidal influences on estuarine use by bottlenose dolphins (*Tursiops aduncus*). Estuarine and Coastal Shelf Science 93: 389-395.

Gaspar, R. 2003. Status of the resident bottlenose dolphin population in the Sado estuary: past, present and future. Dissertation, St Andrews University, Scotland, UK.

Genov, T., Kotnjek, P. Lesjak, J., Hace, A., Fortuna, C.M. 2008. Bottlenose dolphins (*Tursiops truncatus*) in Slovenian and adjacent waters (northern Adriatic Sea). Annales, Series Historia Naturalis 18: 227-244.

Gil, M.N., Harvey, M.A., Esteves, J.L. 1999. Heavy metals in intertidal sediments from Patagonian coast, Argentina. Bulletin of Environmental Contamination and Toxicology 63: 52-58.

Gil, M.N., Torres, A., Harvey, M., Esteves, J.L. 2006. Metales pesados en organismos marinos de la zona costera de la Patagonia argentina continental. Revista de Biología Marina y Oceanografía 41: 167-176.

González, J., Capella, J., Gibbons, J. 1989. Delfines nariz de botella *Tursiops truncatus* (Montagu, 1821) habitando frente a isla Chañaral, Provincia de Huasco, Chile. Estudios Oceanológicos 8: 67-71.

Grellier, K., Arnold, H., Thompson, P., Wilson, B., Curran, S. 1995. Management recommendations for the Cardigan Bay bottlenose dolphin population. A report to the Countryside Council for Wales, 68 pp.

Grellier, K. and Wilson, B. 2003. Bottlenose dolphins using the Sound of Barra, Scotland. Aquatic Mammals 29: 378-382.

Haase, P.A. and Schneider, K. 2001. Birth demographics of bottlenose dolphin, *Tursiops truncatus*, in Doubtful Sound, Fiordland, New Zealand - preliminary findings. New Zealand Journal of Marine and Freshwater Research 35: 675-680.

Hammond, P.S. 1986. Estimating the size of naturally marked whale populations using capture–recapture techniques. Report to the International Whaling Commission Special Issue 8: 252-282.

Hammond, P.S., Mizroch, S.A., Donovan, G.P. 1990. Individual recognition of cetaceans: use of photo-identification and other techniques to estimate population parameters. Report to the International Whaling Commission Special Issue 12: 3-17.

Hammond, P.S., Bearzi, G., Bjørge, A., Forney, K.A., Karkzmarski, L., Kasuya, T., Perrin, W.F., Scott, M.D., Wang, J.Y. , Wells, R.S., Wilson, B. 2012. *Tursiops truncatus*. *In*: IUCN 2012. IUCN Red List of Threatened Species. Version 2012.2, www.iucnredlist.org. Downloaded on 11 June 2013.

Hurvich, C.M. and Tsai, C. 1991. Bias of the corrected AIC criterion for underfitted regression and time series models. Biometrika 78: 499-509.

Ingram, S., Rogan, E., O'Flanagan, C. 1999. Population estimates and seasonal changes in abundance of resident bottlenose dolphins (*Tursiops truncatus*) in the Shannon Estuary, Ireland. European Research on Cetaceans 13: 328.

IUCN. 2012. IUCN Red List Categories and Criteria: Version 3.1. Second edition. Gland, Switzerland and Cambridge, UK: IUCN. iv + 32 pp. http://www.iucnredlist.org/technical-documents/categories-and-criteria.

Kendall, W.L. and Pollock, K.H. 1992. The robust design in capture-recapture studies: a review and evaluation by monte carlo simulation. *In*: McCullough, D.R. and Barrett, R.H. (Eds.), Wildlife 2001: Populations. Elsevier, London, UK, pp. 31-43.

Kendall, W.L. and Nichols, J.D. 1995. On the use of secondary capture–recapture samples to estimate temporary emigration and breeding proportions. Journal of Applied Statistics 22: 751-762.

Kendall, W.L., Pollock, K.H., Brownie, C. 1995. A likelihood based approach to capture recapture estimation of demographic parameters under the robust design. Biometrics 51: 293-308.

Kendall, W.L., Nichols, J.D., Hines, J.E. 1997. Estimating temporary emigration using capture-recapture data with Pollock's robust design. Ecology 78: 563-578.

Kendall, W.L. 1999. Robustness of closed capture–recapture methods to violations of the closure assumption. Ecology 80: 2517-2525.

Kerr, K.A., Defran, R.H., Campbell, G.S. 2005. Bottlenose dolphins (*Tursiops truncatus*) in the Drowned Cayes, Belize: Group size, site fidelity and abundance. Caribbean Journal of Science 41: 172-177.

Kogi, K., Hishii, T., Imamura, A., Iwatai, T., Dudzinski, K.M. 2004. Demographic parameters of indo-pacific bottlenose dolphins (*Tursiops aduncus*) around Mikura Island, Japan. Marine Mammal Science 20: 510-526.

Lahaye, V. and Mauger, G. 2001. Site fidelity, movement patterns and group mixing of Normandy bottlenose dolphins (*Tursiops truncatus*). European Research on Cetaceans 14: 335-338.

La Manna, G., Manghi, M., Pavan, G., Lo Mascolo, F. Sarà, G. 2013. Behavioural strategy of common bottlenose dolphins (*Tursiops truncatus*) in response to different kinds of boats in the waters of Lampedusa Island (Italy). Aquatic Conservation: Marine and Freshwater Ecosystems 23: 745-757.

Laporta, P. 2008. Abundância, distribução e uso de habitat do boto (*Tursiops truncatus*) em Cabo Polonio e La Coronolla (Rocha, Uruguay). Dissertation, Universidade Federal do Rio Grande, Brasil.

Lauriano, G., Fortuna, C.M., Moltedo, G., Notarbartolo di Sciara, G. 2004. Interactions between common bottlenose dolphins (*Tursiops truncatus*) and the artisanal fishery in Asinara Island National Park (Sardinia): assessment of catch damage and economic loss. Journal of Cetacean Research and Management 6: 165-173.

Lebreton, J.D., Burnham, K.P., Clobert, J., Anderson, D.R. 1992. Modelling survival and testing biological hypotheses using marked animals: A unified approach with case studies. Ecological Monographs 62: 67-118.

Lemos, L.S., de Moura, J.F., Hauser-Davis, R.A., de Campos, R.C., Siciliano, S. 2013. Small cetaceans found stranded or accidentally captured in southeastern Brazil : Bioindicators of essential and non-essential trace elements in the environment. Ecotoxicology and Environmental Safety 97: 166-175.

Lodi, L. and Monteiro-Neto, C. 2012. Group size and composition of *Tursiops truncatus* (*Cetacea: Delphinidae*) in a coastal insular habitat off southeastern Brazil. Biometas 25: 157-164.

López, A. 2003. Estatus dos pequenos cetáceos da plataforma de Galicia. Dissertation, Universidade de Santiago de Compostela, Spain.

López, A., Pierce, G.J., Valeiras, X., Santos, M.B., Guerra, Á. 2004. Distribution patterns of small cetaceans in Galician waters. Journal of the Marine Biological Association of the United Kingdom 84: 283-294.

López-Hernández, I. 1997. Ecología poblacional de las toninas *Tursiops truncatus* en la costa de Tabasco, México. Dissertation, Facultad de Ciencias, Universidad Nacional Autónoma de México, México, 77 pp.

Lusseau, D., Slooten, L., Currey, R.J. 2006. Unsustainable dolphin-watching tourism in Fiordland, New Zealand. Tourism in Marine Environments 3: 173-178.

Mann, J. and Smuts, B. 1999. Behavioural development in wild bottlenose dolphin newborns (*Tursiops sp.*). Behaviour 136: 529-566.

Mann, J., Connor, R.C., Barre, L.M., Heithous, M.R. 2000. Female reproductive success in bottlenose dolphins (*Tursiops sp.*): Life history, habitat, provisioning and group-size effects. Behavioural Ecology 11: 210-219.

Mansur, R.M., Strindberg, S., Smith, B.D. 2011. Mark-resight abundance and survival estimation of Indo-Pacific bottlenose dolphins, *Tursiops aduncus*, in the Swatch-of-No-Ground, Bangladesh. Marine Mammal Science 28: 561-578.

Marcovecchio, J.E., Moreno, V.J., Bastida, R.O., Gerpe, M.S., Rodriguez, D.H. 1990. Tissue distribution of heavy metals in small cetaceans from the Southwestern Atlantic Ocean. Marine Pollution Bulletin 21: 299-304.

Marcovecchio, J.E., Gerpe, M.S., Bastida, R.O. Rodriguez, D.H., Moron, S.G. 1994. Environmental contamination and marine mammals in coastal waters from Argentina: an overview. Science of the Total Environment 154: 141-151.

Merriman, M.G. 2007. The occurrence and behavioural ecology of bottlenose dolphins (*Tursiops truncatus*) in the Marlborough Sounds, New Zealand. Dissertation, Massey University, Auckland, New Zealand.

Möller, L.M., Allen, S.J., Harcourt, R.G. 2002. Group characteristics, site fidelity and seasonal abundance of bottlenose dolphins *Tursiops aduncus* in Jervis Bay and Port Stephens, South-Eastern Australia. Australian Mammalogy 24: 11-21.

Natoli, A., Peddemors, V.M., Hoelzel, R.A. 2008. Population structure of bottlenose dolphins (*Tursiops truncatus*) impacted by bycatch along the east coast of South Africa. Conservation Genetics 9: 627-636.

Nicholson, K., Bejder, L., Allen, S.J., Krützen, L., Pollock, K.H. 2012. Abundance, survival and temporary emigration of bottlenose dolphins (*Tursiops truncatus*) off Useless Loop in the western gulf of Shark Bay, Western Australia. Marine and Freshwater Research 63: 1059-1068.

Otis, D.L., Burnham, K.P., White, G.C., Anderson, D.R. 1978. Statistical inference for capture data on closed animal populations. Wildlife Monographs 62: 1-135.

Oviedo, L. and Silva, N. 2005. Sighting frequency and relative abundance of bottlenose dolphins (*Tursiops truncatus*) along the northeast coast of Margarita Island and Los Frailes Archipelago, Venezuela. Revista de Biología Tropical 53: 595-600.

Pace, D.S., Pulcini, M., Triossi, F., Cerioni, S. 1999. *Tursiops truncatus* population at Lampedusa Island (Italy): preliminary results. European Research on Cetaceans 12: 165-69.

Parsons, E.C. and Chan, H.M. 2001. Organochlorine and trace element contamination in bottlenose dolphins (*Tursiops truncatus*) from the South China Sea. Marine Pollution Bulletin 42: 780-786.

Parsons, K.M., Noble, L.R., Reid, R.J., Thompson, P.M. 2002. Mitochondrial genetic diversity and population structuring of UK bottlenose dolphins (*Tursiops truncatus*): is the NE Scotland population demographically and geographically isolated? Biological Conservation 108: 175-182.

Peddemors, V.M. 1999. Delphinids of southern Africa: a review of their distribution, status and life history. Journal of Cetacean Research and Management 1: 157-165.

Pereira, A., Martinho, F., Brito, C., Carvalho, I. 2013. Bottlenose dolphin *Tursiops truncatus* at São Tomé Island (São Tomé and Príncipe) - relative abundance, site fidelity and social structure. African Journal of Marine Science 35: 501-510.

Pikesley, S.K., Witt, M.J., Hardy, T., Loveridge, J., Williams, R., Godley, B.J. 2012. Cetacean sightings and strandings: evidence for spatial and temporal trends? Journal of the Marine Biological Association of the United Kingdom 92: 1809-1820.

Pledger, S. 2000. Unified maximum likelihood estimates for closed capture–recapture models using mixtures. Biometrics 56: 434-442.

Pleslić, G., Rako Gospić, N., Mackelworth, P., Wiemann, A., Holcer, D., Fortuna, C. 2013. The abundance of common bottlenose dolphins (*Tursiops truncatus*) in the former special marine reserve of the Cres-Lošinj Archipelago, Croatia. Aquatic Conservation: Marine and Freshwater Ecosystems DOI: 10.1002/aqc.2416.

Pollock, K.H. 1982. A capture-recapture design robust to unequal probability of capture. Journal of Wildlife Management 46: 757-760.

Pollock, K.H., Nichols, J.D., Brownie, C., Hines, J.E. 1990. Statistical inference for capture–recapture experiments. Wildlife Monographs 107: 3-97.

Pulcini, M., Pace, D.S., La Manna, G., Triossi, F., Fortuna, C.M. 2013. Distribution and abundance estimates of bottlenose dolphins (*Tursiops truncatus*) around Lampedusa Island (Sicily Channel, Italy): implications for their management. Journal of the Marine Biological Association of the United Kingdom 1-10.

Rako, N., Fortuna, C.M., Holcer, D., Mackelworth, P., Nimak-Wood, M., Pleslić, G., Sebastianutto, L., Vilibic, I., Wiemann, A., Picciulin, M. 2013. Leisure boat noise as a trigger for the displacement of the bottlenose dolphins of the Cres-Losinj archipelago (northern Adriatic Sea, Croatia). Marine Pollution Bulletin 68: 77-84.

Read, A.J., Wells, R.S., Hohn, A.A., Scott, M.D. 1993. Patterns of growth in wild bottlenose dolphins, *Tursiops truncatus*. Journal of Zoology 231: 107-123.

Read, A.J., Urian, K.W., Wilson, B., Waples, D.M. 2003. Abundance of bottlenose dolphins in the bays, sounds and estuaries of North Carolina. Marine Mammal Science 19: 59-73.

Reid, J.B., Evans, P.G.H., Northridge, S.P. 2003. Atlas of cetacean distribution in north-west European waters. Joint Nature Conservation Committee (JNCC), Peterborough, 76 pp.

Roditi-Elasar, M., Kerem, D., Hornung, H., Kress, N., Shoham-Frider, E., Goffman, O., Spanier, E. 2003. Heavy metal levels in bottlenose and striped dolphins off the Mediterranean coast of Israel. Marine Pollution Bulletin 46: 503-512.

Rogan, E., Ingram, S., Holmes, B., O’Flanagan, C. 2000. A survey of bottlenose dolphins (*Tursiops truncatus*) in the Shannon Estuary. Marine Resource Series, Dublin.

Sanders-Reed, C.A., Hammond, P.S., Grellier, K., Thompson, P.M. 1999. Development of a population model for bottlenose dolphins. Survey and Monitoring Rep. No. 156, Scottish Natural Heritage, Battleby, Redgorton, Perth.

Sanino, G.P. and Van Waerebeek, K. 2008. A note on the southern distribution range of inshore and offshore common bottlenose dolphins *Tursiops truncatus* in the Southeast Pacific. Report to the International Whaling Commission SC/60/SM18.

Sanino, G.P. and Yáñez, J.L. 2000. Efectos del turismo de observación de cetáceos en punta de Choros, IV Región, Chile. Revista Gestión Ambiental 6: 41-53.

Scheinin, A., Kerem, D., Markovich, M., Goffman, O., Spanier, E. 2005. First summary of coastal sea surveys done off the Mediterranean coast of Israel between the years 1999-2005. Abstract presented at the 16th Biennial Conference on the Biology of Marine Mammals, 12-16 December 2005, San Diego, California.

Scott, M.D., Wells, R.S., Irvine, A.R. 1990. A long- term study of bottlenose dolphins on the west coast of Florida, in: Leatherwood, S. and Reeves, R.R. (Eds.), The bottlenose dolphin. Academic Press, San Diego, CA, pp. 235-244.

Silva, C. 2008. A populaçaõ residente de *Tursiops truncatus* num quadro de gestaõ integrada do estuário do Sado: Proposta de um acordo voluntário. Dissertation, Faculdade de Ciências da Universidade de Lisboa, Portugal.

Silva, M.A., Magalhaes, S., Prieto, R., Santos, R.S., Hammond, P.S. 2009. Estimating survival and abundance in a bottlenose dolphin population taking into account transience and temporary emigration. Marine Ecology Progress Series 392: 263-276.

Simões-Lopes, P.C. and Daura-Jorge, F.G. 2008. Os Parceiros da Sobrevivência: A interação entre botos e pescadores no sul do Brasil. Florianópolis Insular 52.

Smith, H. 2012. Population dynamics and habitat use of bottlenose dolphins (*Tursiops aduncus*), Bunbury, Western Australia. Dissertation, Murdoch University, Australia.

Stavros, H.C.W., Bossart, G.D., Hulsey, T.C., Fair, P.A. 2007. Trace element concentrations in skin of free-ranging bottlenose dolphins (*Tursiops truncatus*) from the southeast Atlantic coast. Science of the Total Environment 388: 300-315.

Steckenreuter, A., Möller, L., Harcourt, R. 2012. How does Australia's largest dolphin-watching industry affect the behaviour of a small and resident population of Indo-Pacific bottlenose dolphins? Journal of Environmental Management 97: 14-21.

Stensland, E., Carlen, I., Sarnblad, A., Bignert, A., Bergrenn, P. 2006. Population size, distribution, and behavior of indo-pacific bottlenose (*Tursiops aduncus*) and humpback (*Sousa chinensis*) dolphins off the south coast of Zanzibar. Marine Mammal Science 22: 667-682.

Stolen, M.K. and Barlow, J. 2003. A model life table for bottlenose dolphins (*Tursiops truncatus*) from the Indian river lagoon system, Florida, USA. Marine Mammal Science 19: 630-649.

Sutherland, W.J. 2000. The conservation handbook: Research, management and policy. Blackwell, Hoboken, NJ.

Thompson, P.M., Wilson, B., Grellier, K., Hammond, P.S. 2000. Combining power analysis and population viability analysis to compare traditional and precautionary approaches to conservation of coastal cetaceans. Biological Conservation 14: 1253–1263.

Tezanos-Pinto, G., Constantine, R., Brooks, L., Jackson, J.A., Mourão, F., Wells, S., Baker, S.C. 2013. Decline in local abundance of bottlenose dolphins (*Tursiops truncatus*) in the Bay of Islands, New Zealand. Marine Mammal Science 29: 390-410.

Valdes-Arellanes, M.P., Serrano, A., Heckel, G., Schramm, Y., Martínez-Serrano, I. 2011. Abundancia de dos poblaciones de toninas (*Tursiops truncatus*) en el norte de Veracruz, México Revista Mexicana de Biodiversidad 82.

Van Waerebeek, K., Van Bressem, M.F., Félix, F., Alfaro-Shigueto, J., García-Godos, A., Chávez-Lisambart, L., Ontón, K., Montes, D., Bello, R. 1997. Mortality of dolphins and porpoises in coastal fisheries off Peru and southern Ecuador in 1994. Biological Conservation 81: 43-49.

Van Waerebeek, K., Bamy, I., Jiddou, A.M., Sequeira, M., Diop, M., Ofori-Danson, P.K., Tchibozo, S., Campredon, P. 2008. Indeterminate status of West African populations of inshore common bottlenose dolphins *Tursiops truncatus* cautions against opportunistic live-capture schemes. Report to the Fondation Internationale du Banc 'Arguin, 9 pp.

Vázquez, N.N., Gil, M.A., Esteves, J.L., Narvate, M.A. 2007. Monitoring Heavy Metal Pollution in San Antonio Bay, Río Negro, Argentina. Bulletin of Environmental Contamination and Toxicology 79: 121-125.

Vázquez-Medina, J.P., Cantu-Medellin, N., Medina-Rodriguez, M., Mendez-Rodriguez, L.C., Zenteno-Savin, T. 2007. Oxidative stress indicators and heavy metal levels in bottlenose dolphin (*Tursiops truncatus*) tissues from Bahía de La Paz, Mexico. Free Radical Biology and Medicine 43: S123.

Vermeulen, E., Cammareri, A., Failla, M., Holsbeek, L. 2008. An identification study on bottlenose dolphins (*Tursiops truncatus*) in Northeast Patagonia, Argentina. Abstract, XIII Reunion de trabajo de Especialistas en Mamíferos Aquaticos del Sur y 7° congreso SOLAMAC, 13-17 November 2008, Montevideo, Uruguay, pp. 209.

Vermeulen, E. and Cammareri, A. 2009. Residency Patterns, Abundance and Social composition of bottlenose dolphins (*Tursiops truncatus*) in Bahía San Antonio, Patagonia, Argentina. Aquatic Mammals 35: 379-386.

Vermeulen, E., Balbiano, A., Belenguer, F., Colombil, D., Failla, M., Intrieri, E., Bräger, S. submitted. Limited ranging patterns of a highly mobile marine species: conservation implications for bottlenose dolphins (*Tursiops truncatus*) in Argentina. Biodiversity and Conservation.

Vidal, M.L. 2004. Contaminación ambiental y salud humana. IBMP Serie Publicaciones 3: 67-69.

Vos, J.G., Bossart, G.D., Fournier, M., O'Shea, T.J. 2003. Toxicology of Marine Mammals. Taylor and Francis, London, UK.

Wells, R. and Scott, M.D. 1990. Estimating bottlenose dolphin population parameters from individual identification and capture–release techniques. Report to the International Whaling Commission Special Issue 12: 407-415.

Wells, R.S., Tornero, V., Borrell, A., Aguilar, A., Rowles, T.K., Rhinehart, H.L., Hofmann, S., Jarman, W., Hohn, A.A., Sweeney, J.C. 2005. Integrating life-history and reproductive success data to examine potential relationship with organochlorine compounds for bottlenose dolphins (*Tursiops truncatus*) in Sarasota Bay, Florida. Science of the Total Environment 249: 106-119.

White, G.C. and Burnham, K.P. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46: 120-138.

Williams, J.A., Dawson, S.M., Slooten, E. 1993. The abundance and distribution of bottlenose dolphins (*Tursiops truncatus*) in Doubtful Sound, New Zealand. Canadian Journal of Zoology 71: 2080-2088.

Williams, B.K., Nichols, J.D., Conroy, M.J. 2002. Analysis and Management of Animal Populations. Academic Press: San Diego, CA.

Wilson, B., Hammond, P.S., Thompson, P.M. 1999. Estimating size and assessing trends on a coastal bottlenose dolphin population. Ecological Applications 9: 288-300.

Wood, C.J. 1998. Movement of bottlenose dolphins around the south-west coast of Britain. Journal of Zoology 246: 155-163.

Würsig, B. and Jefferson, T.A. 1990. Methods of photo-identification for small cetaceans. Report to the International Whaling Commission Special Issue 12: 43-52.

Yoshizaki, J., Pollock, K.H., Brownie, C., Webster, R.A. 2009. Modelling misidentification errors in capture–recapture studies using photographic identification of evolving marks. Ecology 90: 3-9.

Zappes, C.A., Pinto de Sá Alves, L.C., da Silva, C.V., de Freitas Azevedo, A., Madeira Di Beneditto, A.P., Andriolo, A. 2013. Accidents between artisanal fisheries and cetaceans on the Brazilian coast and Central Amazon: Proposals for integrated management. Ocean and Coastal Management 85: 45-57.

5

SOCIAL STRUCTURE

After

Vermeulen, E. submitted. Effect of prey availability on fission-fusion dynamics of bottlenose dolphins (Tursiops truncatus) *in Northern Patagonia. Behavioral Ecology and Sociobiology.*

ABSTRACT - The social structure of bottlenose dolphins (*Tursiops truncatus*) is believed to be a good indicator of the ecological constraints of their habitat. This species has been reported frequently to live in fission-fusion societies with varying intensities of associations among populations. However, the dynamics of the fission and fusion behaviour within a population may be a more useful way to describe the true nature of these dolphins' social structure. Furthermore, it may reflect more accurately their response to fluctuating ecological pressures.

Here, the temporal variation in fission-fusion dynamics of one of the last remaining populations of bottlenose dolphins in Argentina is examined. Although the overall association rate was high, HWI 0.30 ± 0.08, it appeared to contain of a large seasonal and behavioural fluctuation in fission and fusion behaviour. Dolphins had a high yet random association rate (high rate of fusion) when prey was expected to form dense spawning shoals. When prey was not aggregated and more limited, they associated only with few preferred companions and avoided most others (high rate of fission). Despite the small size and apparent isolation of this population, the fluctuation in prey density and availability appeared to be the most important factor determining their fission-fusion dynamics. A combination of aspects inherent to the species and this habitat, such as low cost of locomotion, low predation pressure and food predictability, appears to have helped reduce the costs of fission in response to intraspecific competition.

KEYWORDS - bottlenose dolphin, ecological constraints, fission-fusion dynamics, intraspecific competition, prey availability, social structure

1. INTRODUCTION

Being an easily accessible coastal species, the social ecology of bottlenose dolphin (*Tursiops truncatus*) communities has been studied in many regions around the world (reviewed by Connor et al., 2000). These studies indicated that this dolphin has a fluid social structure (Würsig and Würsig, 1979; Balance, 1990; Smolker et al., 1992; Williams et al. 1993; Wilson, 1995) often referred to as a fission-fusion society (Würsig and Würsig, 1977; Wells et al., 1987; Smolker et al., 1992; Connor et al., 2000). However, although often invoked, the term 'fission-fusion society' does little to specify the nature of the social organisation of dolphins. In fact, this term has been applied to a diverse set of social systems ranging from, for example, the hierarchically organised societies of hamadryas and gelada baboons (Kummer, 1971) to the random associations within some ungulate herds (Hillamn, 1987). Instead, it appears to be more useful to describe these species' social structure through the dynamics of their fission-fusion behaviour.

Bottlenose dolphins, like many other mammals, are known to show a high degree of fission-fusion dynamics (Aureli et al., 2008), where opposing pressures related to mating, predation risk and food availability provide underlying costs and benefits of grouping (Würsig, 1978; Lehmann, 2007). Habitat specific variation in these pressures is known to cause fine-scale differences in the social organisation of different bottlenose dolphin populations (Connor et al., 2000). Consequently, association patterns may be good indicators of the local ecological constraints a population experiences, although it remains unclear exactly how these ecological factors influence a population's social structure (Ramos-Fernández et al., 2006). So far, only few studies have been carried out to investigate temporal variations in the social organisation within a single population (e.g., Heithaus and Dill, 2002; Pearson, 2009). Nonetheless, association-related indicators may reveal fluctuating ecological pressures within a specific habitat, irrespective of whether or not they are induced by human activities.

The social structure of bottlenose dolphins was studied first in Argentina some 40 years ago (Würsig and Würsig, 1977). In the meantime, this population and many others have been reported to be nearly vanished from the Argentine coastline (Bastida and Rodriguez, 2003; Coscarella et al., 2012). This decline may have resulted in the population studied here to be one of the last remaining resident populations of bottlenose dolphins in the country (Vermeulen and Cammareri, 2009; Vermeulen and Bräger, submitted). This population was estimated to be small and isolated (Vermeulen and Bräger, submitted), with Bahía San Antonio suggested as the core area within their larger home range (Vermeulen et al., submitted a).

Predation risk is hypothesised to be the main driver of sociality in odontocetes (Whitehead, 2003). Due to the low predation pressure in the study area (Vermeulen and Bräger, submitted), it is believed prey availability might be the main factor determining the social structure in this population of dolphins. This study thus aims to describe the temporal variation in the fission-fusion dynamics of this community of bottlenose dolphins in response to seasonal fluctuations of prey density and availability in the bay. Additionally, as the looming disappearance of the species from Argentina may be related to overfishing (Cauhépé, 1999, Coscarella et al., 2012), the data presented here may serve as a baseline for future insight into the effects of increasing prey depletion. This in turn will be vital in the design and implementation of effective conservation measures, specifically in terms of (commercial and artisanal) fishing activities in the area.

2. MATERIALS AND METHODS

2.1. DATA SELECTION

All individuals within a group were considered to be associated with each other, a spatial definition of association commonly used in studies of vertebrate social structure (Whitehead and Dufault, 1999). The more frequently two dolphins were sighted together in the same group, the closer they were associated. To accurately estimate the association of identified animals, 66 encounters with dolphin groups between 2008 and 2011 were selected for analysis. During these encounters more than 50% of the individuals in the group were positively identified, with all sightings at least a day apart from each other to ensure some independence of association (Bejder et al., 1998). Out of these, 60 identified dolphins seen ≥ 5 times were selected for social association analysis. Twelve of these individuals were males while 15 were females and the remaining 33 individuals were of unknown sex. Calves were not included in these analyses, because their associations depend on their mothers' associations. A monthly sampling period was chosen to calculate the association index value for each dyad (pair of individuals).

2.2. DEFINING ASSOCIATIONS

Half-weight index (HWI) values were calculated using *SocProg 2.4*, a program developed for *Matlab* to analyse the social organisation of animal communities (Whitehead, 2009a,b). The HWI was chosen as a measure of association, because it tends to correct for missed identifications of one member of a pair, which is inherent in photo-identification techniques including within-group sampling errors and within-community sampling errors (Cairns and Schwager, 1987; Smolker et al., 1992; Ginsberg and Young, 1992). The HWI was originally used by Dice (1945) and is calculated as follows:

$$HWI = \frac{x}{(x + ½\,(Ya + Yb)}$$

Where x is the total number of encounters that included both dolphins *a* and *b*, *Ya* the total number of encounters that included dolphin *a* but not dolphin *b* and *Yb* the total number of encounters that included dolphin *b* but not dolphin *a*. The HWI, which can vary from 0.0 for individuals never seen together to 1.0 for individuals always seen together, has been applied at various times previously to evaluate the association patterns of bottlenose dolphins (e.g., Wells et al., 1987; Weller, 1991; Connor et al., 1992; Smolker et al., 1992; Bräger et al., 1994; Lott, 2004).

2.3. SOCIAL ORGANISATION

The social organisation of the population was analysed using the average linkage hierarchical cluster analysis (Morgan et al., 1976; Colgan, 1978). This method clusters individuals not only by preferred associations but also by using the least preferred associations (Lusseau et al., 2003). The possibility that the population was divided into such clusters was assessed using modularity, with generally high association index values among individuals in the same cluster, and generally low association index values between individuals of different clusters (Newman, 2004). The modularity is a scalar value that measures the quality of a particular division of a network into communities. It is an eigenvector-based method that compares differences between the total proportions of associations in the real cluster with those in the expected randomly distributed cluster (Wiszniewski et al., 2009). Modularity around 0.3 indicates a useful division of the population into separate communities, with lower modularity indicating a fission-fusion structure (Wiszniewski et al., 2009).

The Monte Carlo randomisation technique was employed to measure the significance of all possible dyads of animals within the sample by comparing any association pattern in real data with a distribution of random data (Manly, 1995; Bejder et al., 1998). The permutation tests performed (of groups within samples) tests the hypothesis that the distribution of association index values from the empirical data was not significantly different from a randomly expected one (the permuted data sets). During this test, the number of groups in which each animal was observed as well as their group sizes were kept constant for each sampling period (Whitehead, 2009a,b). While this test takes into account that individuals sighted in many groups might associate at random, it also accounts for situations in which not all individuals are present during each sampling interval (for example, due to death or migration; Whitehead, 2009b). Within this permutation test, short-term (within sampling periods) preferred/avoided associations are indicated by a significantly lower mean of the observed *vs*. random association index (Whitehead et al., 2005; Whitehead, 2008). This is because in that case there will be proportionally more pairs of individuals repetitively grouped, thus reducing the proportion of non-zero dyads and the overall mean. Additional proof for the presence of avoided associations is found when this decrease of the proportion of non-zero association index values is significant when comparing the observed *vs*. random data (Whitehead, 2008). Long-term (between sampling periods) preferred/avoided associations are indicated by a significantly higher standard deviation (SD) of the observed *vs*. random association index values (Whitehead et al., 2005; Whitehead, 2008). This is caused by a wider range of associations between the sampling periods than expected if dolphins associated at random (dyads with respectively higher and lower HWI). However, the latter appears more prone to false positive readings when short-term preferred/avoided associates are also present, as a lower mean association index value (see above) will tend to lower the SD as well. A proposed solution is the additional use of the coefficient of variation (CV) of the association index values as a test statistic for long-term preferences (Whitehead et al., 2005). Following the methods of Bejder et al. (1998) and Whitehead (1999), the number of permutations performed in this test was increased until the *p* value obtained from the Monte Carlo simulation stabilised and the confidence intervals decreased. This occurred at 20,000 permutations with 1,000 trials per permutation.

In order to assess differences in association by gender, a Mantel test (Mantel, 1967) was carried out. The statistical significance of each Mantel test was tested against the null hypothesis in which the number of preferred associations was unrelated to the age class or gender, using 1,000 random permutations.

Gregariousness, being an individual's tendency to associate with others, was tested in order to search for individuals that may be consistently found in groups larger or smaller than the typical (Jarman, 1974; Whitehead et al., 2005). The null hypothesis is that all individuals are found in groups with a similar size distribution, and it is rejected when the SD of the typical group size (tgs = mean group size for any given individual) is unexpectedly high and significantly different from the permutated data (Whitehead, 2009b).

In order to examine the temporal stability of associations between individuals further and thus the permanency of the observed associations, one may consider the time between dyad sightings. The program *SocProg 2.4* was used to calculate the probability of two animals remaining associated after various time lags (Whitehead, 2009a,b). It thus estimates the probability of two individuals that are associating now, still to be associated various time lags later (lagged association rate). Hence, the proportion of companions an individual had at time *t* that remained companions at time *t + d* (where *d* is the time lag) was calculated for each individual, and averaged over all individuals. The precision of this process was estimated by jackknifing over the sampling periods (Efron and Stein, 1981). The resulting proportion was then compared to the null association rate (Whitehead, 1995) which represents the lagged association rate if individuals were associating at random with no preferred companions. The rate of decay of the lagged association rate was then compared with a number of mathematical models describing different rates of exponential decay (Whitehead, 1995). These models consist of three components and any combination of those; constant companionships (who stay together permanently), rapid disassociation (associate and disassociate very quickly, within one time period), and casual acquaintances (who associate for some time, disassociate, and may re-associate). The best fitting model was then selected using the Akaike Information Criteria (AIC) (Burnham and Anderson, 1998).

3. RESULTS

3.1. ASSOCIATION PATTERNS

The HWI value for all possible dyads (n = 1770) averaged 0.30 (SD = 0.08; Figure 9), whereas the maximum HWI value averaged 0.67 (SD = 0.13) (Table 8). The values varied only slightly over the years, but fluctuated notably among seasons. The lowest average HWI value could be found in summer and the highest one in winter. Associations also fluctuated according to the behaviour dolphins engaged in, with the highest values of association being found during surface-feeding and the lowest for diving. Associations between and within gender were not significantly different (Mantel test: *t* = -1.41; *p* = 0.07) (Table 8).

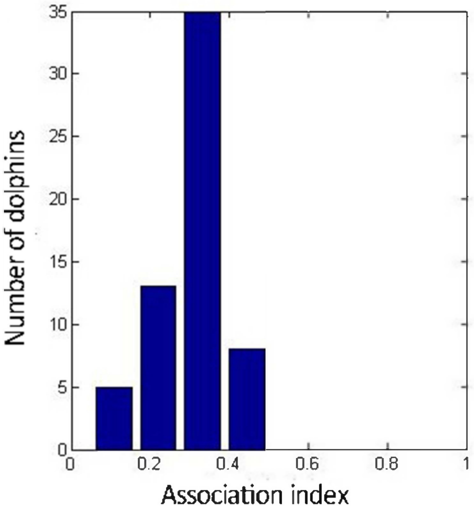

Figure 9 – Average HWI values for all pair-wise comparisons of 60 bottlenose dolphins selected for analysis (n = 1770 possible dyads)

Table 8 – Average and maximum HWI (with SD) for all individuals calculated over the various years, seasons and behavioural states, and between and within the gender classes. The number of possible dyads and the number of dyads for which the HWI > 0 (number of non-zero dyads) is also given

	Average HWI for all dyads	SD	Average of maximum HWI of all dyads	SD	Number of non-zero dyads	Number of possible dyads
Total	0.30	0.08	0.67	0.13	1628	1770
2008	0.38	0.14	0.91	0.12	1010	1485
2009	0.25	0.10	0.86	0.15	991	1770
2010	0.40	0.13	0.91	0.12	1021	1326
2011	0.36	0.14	0.92	0.13	909	1378
Summer	0.20	0.08	0.81	0.15	574	1275
Autumn	0.22	0.11	0.83	0.15	267	703
Winter	0.46	0.16	0.90	0.12	1575	1770
Spring	0.26	0.11	0.96	0.10	570	1326
Male-male	0.46	0.06	0.74	0.14	66	66
Female-female	0.29	0.08	0.54	0.13	98	105
Female-male	0.34	0.04	0.67	0.16	173	180
Surface feeding	0.37	0.11	0.86	0.11	1369	1711
Resting	0.27	0.12	0.82	0.16	909	1540
Diving	0.20	0.11	0.96	0.11	200	741
Travel	0.27	0.11	0.86	0.11	1369	1711

3.2. SOCIAL ORGANISATION

The observed mean association index was not significantly different from the random mean (observed mean = 0.30; random mean = 0.30; $p = 0.75$), suggesting there were no short-term preferred companion. There were however indications of the presence of long-term preferred and avoided associations (observed SD = 0.18; random SD = 0.17; $p > 0.99$; proportion of non-zero association index values: observed = 0.90; random = 0.91; $p < 0.01$; SD of non-zero association index values: observed = 0.15; random = 0.14; $p > 0.99$).

All individuals had a similar tendency to associate with others (gregariousness), as the SD of the tgs was relatively low and showed no difference when compared to the permuted data (real SDtgs = 3.8; random SDtgs = 3.5; $p = 0.82$). The cluster analysis did not show a clear division in the community (modularity = 0.09), nor for the different years nor seasons. Low modularity was also found in the cluster analysis of known males and females separately (0.09 and 0.12 respectively).

Only 37 dyads (2.1% of all possible dyads or 2.3% of all non-zero dyads) associated significantly more or less than expected at random over the total duration of the study (Table 9). Of the dyads that associated more than expected, 3 refer to relationships between known mothers and their independent offspring. No significant difference in dyad distribution (association pattern) could be found among years, seasons or behaviours.

Table 9 – Number of dyads associating significantly different from random over the entire study period, depending on gender classes. The total number of possible dyads and the number of dyads for which the HWI > 0 (number of non-zero dyads) is also given

	Less than expected ($p < 0.025$)	More than expected ($p > 0.975$)	Total possible dyads	Number of non-zero dyads
Male-male	0	2	66	66
Female-female	0	2	105	98
Male-female	3	3	180	173
Male-unknown gender	4	4	396	380
Female-unknown gender	6	5	495	436
Unknown gender-unknown gender	7	1	528	470
TOTAL	20	17	1770	1628

When the dataset was permuted for each study year, the observed trend in associations remained the same: associations did not differ from random associations, except for a few long-term preferred and avoided associates. However, when the dataset was permuted randomly for each season (e.g., summer associations of all study years combined), a variable trend became visible:

- In autumn and winter, dolphins appeared to associate completely at random, with no proof for preferred or avoided companions (autumn: observed mean = 0.22; random mean = 0.22; $p = 0.38$; observed SD = 0.30; random SD = 0.30; $p = 0.60$; proportion non-zero association index values: observed = 0.38; random = 0.39; $p = 0.15$; SD of non-zero association index values: observed = 0.18; random = 0.18; $p = 0.33$; winter: observed mean = 0.46; random mean = 0.45; $p = 0.88$; observed SD = 0.25; random SD = 0.25; $p = 0.52$; proportion non-zero association index values: observed = 0.89; random = 0.88; $p = 0.88$; SD of non-zero association index values: observed = 0.20; random = 0.19; $p = 0.94$).

- In spring and summer, however, dolphins associated non-randomly. Indications were found for both short- and long-term preferred/avoided associates (summer: observed mean = 0.20; random mean = 0.21; $p < 0.01$; observed SD = 0.25; random SD = 0.24; $p > 0.99$; observed CV = 1.3; random CV = 1.1; $p > 0.99$; proportion non-zero association index values: observed = 0.45; random = 0.49; $p < 0.01$; SD of non-zero association index values: observed = 0.18; random = 0.16; $p > 0.99$; spring: observed mean = 0.26; random mean = 0.27; $p < 0.01$; observed SD = 0.32; random SD = 0.32; $p = 0.56$; observed CV = 1.3; random CV = 1.2; $p > 0.99$; proportion non-zero association index values: observed = 0.43; random = 0.44; $p < 0.01$; SD of non-zero association index values: observed = 0.17; random = 0.17; $p = 0.65$).

The dataset was further permuted to check for behaviour-specific preferred associations, using the most frequent behavioural states that remained after data selection (i.e., surface-feeding, resting, diving and traveling). During surface-feeding, resting and travel, dolphins appeared to continue to associate at random, with no evidence for preferred or avoided companions. However, during diving behaviour, dolphins showed a reduced number of dyads (HWI: observed mean = 0.19; random mean = 0.21; $p < 0.01$) indicating the presence of short-term preferred/avoided companionships. Furthermore, proof was found for long-term preferred/avoided associates (observed SD = 0.33; random SD = 0.34; $p = 0.03$; observed CV = 1.7; random CV = 1.6; $p > 0.99$; proportion non-zero association index values: observed = 0.27; random = 0.30; $p < 0.01$; SD of non-zero association index values: observed = 0.19; random = 0.19; $p = 0.74$).

3.3. TEMPORAL ASSOCIATION PATTERN

The lagged association rate was similar to, but consistently above the null association rate during the entire study period. The best fitting model represents a population of rapid dissociations, constant companions and casual acquaintances (represented by the function a2+a3*exp(-a1*td) where 'a' represents the different parameters of the models, thus the different levels of associations, and 'td' represents the time lag, Figure 10).

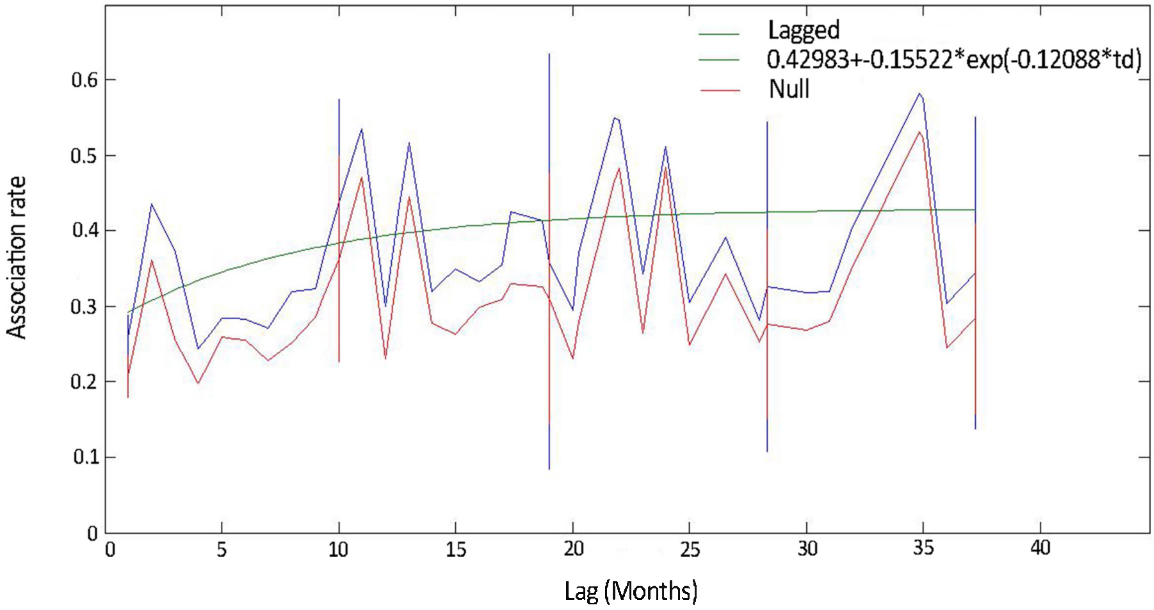

Figure 10 - Lagged association rate for pairs of bottlenose dolphins associated within groups in BSA; the plot shows the probability of associations persisting after increasing time lags between observations (Lagged). The null association rate (Null) is the expected value of the lagged association rate if there are no preferred associations. The best-fit curve (represented by a2+a3*exp(-a1*td)) represents a population of rapid dissociations, constant companions and casual acquaintances. Error bars were obtained by jackknifing

4. DISCUSSION

In small dolphin communities, cohesiveness increases (Augusto et al., 2011) as there are only a small number of possible associates for each individual (Bräger, 1999). Furthermore, high encounter rates of animals that show a high site-fidelity to a small core area may facilitate familiarity to a larger number of individuals (Connor et al., 2000). This is especially true in gregarious animals that are capable of individual recognition, such as the bottlenose dolphin (Ramos-Fernández et al., 2006; Wolf et al., 2007), possibly aiding in the formation of strong bonds. The combination of these factors explains the high association index values recorded in this population compared to other populations worldwide (Smolker et al., 1992; Bräger et al., 1994; Wilson, 1995; Rossbach and Herzing, 1999; Connor et al., 2000; Ingram, 2000; Lott, 2004). However, this high overall association rate contains a large seasonal fluctuation, with considerably higher values observed in winter.

Whitehead (2008) emphasised that associations (due to their definition as membership of the same group) are also influenced by the tgs. This correlates with, but is usually slightly higher than the mean group size as it is the arithmetic mean of crowding measures averaged across all individuals in a group (Reiczigel et al., 2008). Vermeulen et al. (submitted b) showed that bottlenose dolphin group sizes in the study area vary significantly with seasons and behaviour, and correlated this with the seasonal fluctuation in prey density and availability. The association rates among these dolphins seemed to vary accordingly.

In winter, association rates were higher on average, albeit at random, with 89% of the possible dyads formed. High random association rates were also found during surface-feeding, a behaviour mostly observed in winter (Vermeulen et al., submitted b). This high rate of fusion is interpreted to suggest that dolphins aimed to increase their food capture efficiency by grouping together in response to the arrival of dense shoals of spawning fish (*sensu* Würsig, 1986; Wells et al., 1980; Defran et al., 1999; Wells and Scott, 2002). It is in accordance with the large group sizes generally observed during this season, probably related to cooperative foraging (Vermeulen et al., submitted b), and may thus confirm a reduced intraspecific competition at that time.

On the other hand, association rates dropped to a minimum during summer and while diving. Diving was connected to a tail out/peduncle-dive foraging behaviour almost exclusively observed during summer (Vermeulen et al., submitted b). It thus appears that in summer, dolphins choose to forage individually or with only a few (long- and short-term) preferred companions while avoiding others. This high rate of fission indicates a temporally higher cost of grouping. It is suggested to be a response to more evenly and perhaps less densely distributed prey and to the decreasing availability of prey species in the area at that time (Perier, 1994). These findings are in accordance with the very small group sizes observed in summer, especially during diving (Vermeulen et al., submitted b), believed to increase the individual rate of food intake when prey is not aggregated or limited (Würsig, 1986; Meynier et al., 2008). It was previously suggested that an increased time spent alone (or in very small groups) is a strategy to reduce scramble competition in bottlenose dolphins (Pearson, 2009). This means individuals distribute themselves among patches of resources to minimise competition (Gowans et al., 2007) and lower their time travelling between patches of food (Pearson, 2009). This way intraspecific competition is reduced and individual fitness increased (Würsig, 1986). Additionally, the spatial and temporal predictability of food availability may enable bottlenose dolphins to have an intimate knowledge on where and when food can be found (Gowans et al., 2007), leading to a diminished need of social foraging at times food is limited (Overington et al., 2008).

In summary, it is suggested that a combination of factors related to the species and this core habitat may have helped reduce the costs of fission, ensuring it remained a viable ecological option to reduce intraspecific competition. These factors may include, among others, the local low predation pressure, predictability of food and a low cost of locomotion.

The random associations observed in autumn, when prey is reported to be least available (Perier, 1994), appear counter-intuitive in terms of an even stronger intraspecific competition. However, the observed pattern may be related to previous formulated suggestions on the ranging of bottlenose dolphins out of BSA triggered by the very low availability of prey (Failla et al., in press; Vermeulen et al., submitted a; b).

4.1. CONCLUSION

Despite the small size and isolation of this population, dolphins were able to maintain flexible fission-fusion dynamics in response to considerable and predictable fluctuations in prey density and availability within their core habitat. A combination of factors related to the species and this local habitat may have helped to diminish the costs of fission in response to intraspecific competition. Nonetheless, it appears valuable to further study in detail these fluctuating costs and benefits of group living within BSA and how they may affect other aspects such as reproduction (e.g., mate access, increased risk to calf survival during times of fission).

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5. REFERENCES

Augusto, J.F., Rachinas-Lopes, P., Dos Santos, M.E. 2011. Social structure of the declining resident community of common bottlenose dolphins in the Sado Estuary, Portugal. Journal of the Marine Biological Association of the United Kingdom 1-10. DOI:10.1017/S0025315411000889.

Aureli, F., Schaffner, C.M., Boesch, C., Bearder, S.K., Call, J., Chapman, C.A., Connor, R., Di Fiore, A., Dunbar, R.L.M., Henzi, P.S., Holekamp, K., Korstjens, A.H., Layton, R., Lee, P., Lehmann, J., Manson, J.H., Ramos-Fernandez, G., Strier, K.B., Van Schaik, C.P. 2008. Fission-Fusion Dynamics. Current Anthropology 49: 627-654.

Ballance, L.T., 1990. Residence patterns, group organization, and surfacing associations of bottlenose dolphins in Kino Bay, Gulf of California, Mexico. *In*: Leatherwood, S. and Reeves, R.R. (Eds.), The bottlenose dolphin. Academic Press, San Diego, CA, pp 267-283.

Bastida, R. and Rodríguez, D. 2003. Mamíferos Marinos Patagonia Antartida. Vázquez Mazzini Editors, Buenos Aires, Argentina, 206 pp.

Bejder, L., Fletcher, D., Bräger, S. 1998. A method for testing association patterns of social animals. Animal Behaviour 56: 719-725.

Bräger, S., Würsig, B., Acevedo, A., Henningsen, T. 1994. Association patterns of bottlenose dolphins (*Tursiops truncatus*) in Galveston Bay, Texas. Journal of Mammalogy 75: 431–437.

Bräger, S. 1999. Association patterns in three populations of Hector's dolphin, *Cephalorynchus hectori*. Canadian Journal of Zoology 77: 13-18.

Burnham, K.P. and Anderson, D.R. 1998. Model Selection and Inference: A Practical Information-Theoretical Approach. Springer-Verlag, NY.

Cairns, S.J. and Schwager, S.J. 1987. A comparison of association index values. Animal Behaviour 35: 1454-1469.

Cauhépé, M.E. 1999. Management of the Argentine hake. Final project UNU Fisheries Training Program, Reykjavic, Iceland.

Colgan, P.W. 1978. Hierarchical cluster analysis. *In*: Colgan, P.W. (Ed.), Quantitative ethology. J. Wiley and Sons, NY, pp. 116-144.

Connor, R.C., Smolker, R.A., Richards, A.F. 1992. Two levels of alliance formation among male bottlenose dolphins (*Tursiops sp.*). Proceedings of the National Academy of Sciences 89: 987-990.

Connor, R.C., Wells, R.S., Mann, J., Read, A.J., 2000. The bottlenose dolphin. Social relationships in a fission-fusion society. *In*: Mann, J., Connor, R.C., Tyack, P.L., Whitehead, H. (Eds.), Cetacean Society, Field studies of dolphins and whales. University of Chicago Press, Chicago and London, pp. 91-126.

Coscarella, M., Dans, S.L., Degrati, M., Garaffo, G.V., Crespo, E.A. 2012. Bottlenose dolphins at the southern extreme of the southwestern Atlantic: local population decline? Journal of the Marine Biological Association of the United Kingdom 92: 1843-1849.

Defran, R.H., Weller, D.W., Kelly, D.L., Espinosa, M.A. 1999. Range characteristics of Pacific coast bottlenose dolphins (*Tursiops truncatus*) in the Southern California bight. Marine Mammal Science 15: 381–393.

Dice, L.R. 1945. Measures of the amount of ecologic association between species. Journal of Ecology 26: 297-302.

Efron, B. and Stein, C. 1981. The jackknife estimate of variance. The Annals of Statistics 9: 586-596.

Failla, M., Seijas, V.A., Vermeulen, E. in press. Occurrence of bottlenose dolphins (*Tursiops truncatus*) in the Río Negro Estuary, Argentina, and their mid-distance movements along the Northeast Patagonian coast. Latin American Journal of Aquatic Mammals.

Ginsberg, J.R. and Young, T.P. 1992. Measuring association between individuals or groups in behavioural studies. Animal Behaviour 44: 377-379.

Gowans, S., Würsig, B., Karczmarski, L. 2007. The social structure and strategies of Delphinids: predictions based on an ecological framework. Advances in Marine Biology 53: 195-294.

Heithaus, M.R. and Dill, L.M. 2002. Food availability and tiger shark predation risk influence bottlenose dolphin habitat use. Ecology 83: 480-491.

Hillman, J.C. 1987. Group size and association patterns of the common eland (*Tragelaphus oryx*). Journal of Zoology 213: 641-663.

Ingram, S.N. 2000. The ecology and conservation of bottlenose dolphins in the Shannon estuary, Ireland. Dissertation, University College Cork, Ireland.

Jarman, P.J. 1974. The social organization of antelope in relation to their ecology. Behaviour 48: 215-267.

Kummer, H. 1971. Primate societies: Group techniques of ecological adaptation. Arlington Hights, AHM Publishing Corporation, IL.

Lehmann, J., Korstjens, A.H., Dunbar, R.I.M. 2007. Fission-fusion social systems as a strategy for coping with ecological constraints: a primate case. Evolutionary Ecology 21: 613-634.

Lott, R. 2004. Group size, social associations and resident patterns of bottlenose dolphins (*Tursiops truncatus*) in Cardigan Bay, Wales. Dissertation, University of Wales, Bangor.

Lusseau, D., Schneider, C., Boisseau, O.J., Haase, P., Slooten, E., Dawson, S.M. 2003. The bottlenose dolphin community of Doubtful Sound features a large proportion of long-lasting associations. Can geographic isolation explain this unique trait? Behavioral Ecology and Sociobiology 54: 396-405.

Manly, B.F.J. 1995. A note on the analysis of species co-occurrences. Ecology 76: 1109-1115.

Mantel, N.A. 1967. The detection of disease clustering and a generalized regression approach. Cancer Research 27: 209-220.

Meynier, L., Pusineri, J.C., Spitz, M.B., Santos, Pierce, G.J., Ridoux, V. 2008. Intraspecific dietary variation in the short-beaked common dolphin *Delphinus delphis* in the Bay of Biscay: Importance of fat fish. Marine Ecology Progress Series 354: 277–287.

Morgan, B.J.T., Simpson, M.J.A., Hanby, J.P., Hall-Craggs, J. 1976. Visualizing interaction and sequential data in animal behaviour: theory and application of cluster-analysis methods. Behaviour 56: 1-43.

Newman, M.E.J. 2004. Fast algorithm for detecting community structure. European Physical Journal 38: 321-330.

Overington, S.E., Dubois, F., Lefebvre, L. 2008. Food unpredictability drives both generalism and social foraging: a game theoretical model. Behavioural Ecology 19: 836-841.

Pearson, H.C. 2009. Influences on dusky dolphin (*Lagenorhynchus obscurus*) fission-fusion dynamics in Admiralty Bay, New Zealand. Behavioral Ecology and Sociobiology 63: 1437-1446.

Perier, M.R. 1994. La fauna íctica en el litoral de la Bahía de San Antonio (Golfo San Matias, Provincia de Río Negro). Dissertation, Facultad de Ciencias naturales y Museo, Universidad Nacional de La Plata, Argentina.

Ramos-Fernández, G., Boyer, D., Gómez, V.P. 2006. A complex social structure with fission-fusion properties can emerge from a simple foraging model. Behavioral Ecology and Sociobiology 60: 536-549.

Reiczigel, J., Lang, Z., Rózsa, L., Tóthmérész, B. 2008. Measures of sociality: two different views of group size. Animal Behaviour 75: 715-721.

Rossbach, K.A. and Herzing, D.L. 1999. Inshore and offshore bottlenose dolphin (*Tursiops truncatus*) communities distinguished by association patterns near Grand Bahama Island, Bahamas. Canadian Journal of Zoology 77: 581-593.

Smolker, R.A., Richards, A.F., Connor, R.C., Pepper, J.W. 1992. Sex differences in patterns of associations among Indian Ocean bottlenose dolphins. Behaviour 123: 38-69.

Vermeulen, E. and Cammareri, A. 2009. Residency Patterns, Abundance and Social composition of Bottlenose Dolphins (*Tursiops truncatus*) in Bahía San Antonio, Patagonia, Argentina. Aquatic Mammals 35: 379-386.

Vermeulen, E., Balbiano, A., Belenguer, F., Colombil, D.J., Failla, M., Intrieri, E., Bräger, S. submitted a. Limited ranging patterns of a highly mobile marine species: conservation implications for bottlenose dolphins (*Tursiops truncatus*) in Argentina. Biodiversity and Conservation.

Vermeulen, E and Bräger, S. submitted. Demographics of the disappearing bottlenose dolphin in Argentina: a common species on its way out? PLoS-One.

Vermeulen, E., Holsbeek, L., Das, K. submitted b. Diurnal and seasonal variation in the behaviour of bottlenose dolphins (*Tursiops truncatus*) in Bahía San Antonio, Patagonia, Argentina. Mammalian Biology.

Weller, D.W. 1991. The social ecology of Pacific coast bottlenose dolphins. Dissertation, San Diego State University, San Diego, CA, 93 pp.

Wells, R.S., Irvine, A.B., Scott, M.D. 1980. The social ecology of inshore odontocetes. *In*: Herman, L.M. (Ed.), Cetacean behaviour: Mechanisms and processes. John Wiley and Sons, NY, pp. 263-317.

Wells, R.S., Scott, M.D., Irvine, A.B. 1987. The social structure of free-ranging bottlenose dolphins. *In*: Genoways, H.H. (Ed.), Current Mammalogy. Plenum Press, NY, pp. 247-305.

Wells, R.S., Scott, M.D. 2002. Bottlenose dolphins, *Tursiops truncatus* and *T. aduncts*. *In*: Perrin, W.F., Würsig, B., Thewissen, J.G.M. (Eds.), Encyclopaedia of Marine Mammals. Academic Press, San Diego, pp. 122-128.

Whitehead, H. 1995. Investigating structure and temporal scale in social organizations using identified individuals. Behavioural Ecology 6: 199-208.

Whitehead, H. and Dufault, S. 1999. Techniques for analysing vertebrate social structure using identified individuals: Review and recommendations. Advanced Study of Behaviour 28: 33-74.

Whitehead, H. 2003. Sperm Whales: Social Evolution in the Ocean. University of Chicago Press, Chicago.

Whitehead, H., Bejder, L., Ottensmeyer, C.A. 2005. Testing association patterns: issues arising and extensions. Animal Behaviour 69: e1–e6.

Whitehead, H. 2008. Analysing animal societies: quantitative methods for vertebrate social analysis. University of Chicago Press, Chicago.

Whitehead, H. 2009a. SOCPROG programs: Analyzing animal social structures. Behavioral Ecology and Sociobiology 63: 765-778.

Whitehead, H. 2009b. SOCPROG 2.4 Programs for analyzing social structure. Dalhousie University, Nova Scotia. http://myweb.dal.ca/hwhitehe/social.htm.

Williams, J.A., Dawson, S.M., Slooten, E. 1993. The abundance and distribution of bottlenose dolphins (*Tursiops truncatus*) in Doubtful Sound, New Zealand. Canadian Journal of Zoology 71: 2080-2088.

Wilson, B. 1995. The ecology of bottlenose dolphins in the Moray Firth, Scotland: a population at the northern extreme of the species' range. Faculty of Biological Science. Dissertation, University of Aberdeen, Aberdeen, Scotland, UK.

Wiszniewski, J., Allen, S.J., Möller, L.M. 2009. Social cohesion in a hierarchically structured embayment population of Indo-Pacific bottlenose dolphins. Animal Behaviour 77: 1449-1457.

Wolf, J.B., Mawdsley, D., Trillmich, F., James, R. 2007. Social structure in a colonial mammal: unravelling hidden structural layers and their foundations by network analysis. Animal Behaviour 74: 1293-1302.

Würsig, B. and Würsig, M. 1977. The photographic determination of group size, composition and stability of coastal porpoises (*Tursiops truncatus*). Science 198: 755-756.

Würsig, B. 1978. Occurrence and group organization of Atlantic bottlenose porpoise (*Tursiops truncatus*) in an Argentine bay. Biological Bulletin 154: 348-359.

Würsig, B. and Würsig, M. 1979. Behavior and ecology of the bottlenose dolphin (*Tursiops truncatus*) in the south Atlantic. Fishery Bulletin 77: 399-412.

Würsig, B. 1986. Delphinid foraging strategies. *In*: Schusterman, R.J., Thomas, J.A., Wood, F.G. (Eds.), Dolphin cognition and behaviour: a comparative approach. Lawrence Erlbaum Association, Hillsdale, NJ, pp. 347-359.

6

ACTIVITY PATTERNS

After

Vermeulen, E. and Cammareri, A. 2009. Residency, abundance and social composition of bottlenose dolphins (Tursiops truncatus) *in Bahía San Antonio, Patagonia Argentina. Aquatic Mammals 35: 379-386.*

Vermeulen, E., Holsbeek, L., Das, K. submitted. Diurnal and seasonal variation in the behaviour of bottlenose dolphins (Tursiops truncatus) *in Bahía San Antonio, Patagonia, Argentina. Mammalian Biology.*

ABSTRACT - Diurnal and seasonal patterns in the behaviour of a small population of bottlenose dolphins were assessed in Bahía San Antonio, Patagonia, Argentina, between 2006 and 2011. Dolphins appeared to use the study area mainly to rest, travel and forage, with a marked diurnal and seasonal pattern in their activity. During the early morning, most dolphin groups were resting while towards the afternoon and evening surface feeding and social activities peaked. During winter, social activities and surface feeding increased notably, whereas during summer diving behaviour reached its peak, presumably associated with a tail out/peduncle-dive foraging strategy. The observed seasonal variation in foraging activities is hypothesised to be related to the seasonal behavioural changes of the fish species present in the area.

Data indicate that the study area forms a safe habitat for this bottlenose dolphin community, where they can rest, forage and nurture their young. These data serve as vital baseline information for future monitoring of the impact of the increasing human activities in this bay, known to be the core area of this vulnerable community of dolphins.

KEYWORDS - bottlenose dolphins, behaviour, diurnal, habitat, prey species, seasonal

1. INTRODUCTION

Many animals display daily and seasonal variations in their behavioural patterns (Bräger, 1993), presumed to balance costs and benefits of expending energy (Boness, 1984). As this balance changes, activity patterns may also change, reaching a complex compromise between needs related to feeding, resting, reproduction (Nielsen, 1983) and avoidance of predators (Mann et al., 2000). The more time animals spend in one behavioural state will decrease the amount of time devoted to other behaviours that may nonetheless be crucial to an animal's survival. This highlights the importance of determining an animal's activity patterns and the main factors affecting them.

The quantitative description of dolphin behaviour, however, can often be ambiguous, as they are visible at the surface only during a small proportion of their time (Bearzi et al., 1999). For bottlenose dolphins (*Tursiops sp*.), it can be even more challenging as they show great behavioural flexibility in response to different ecological constraints. Additionally, this can vary significantly depending on the habitat they live in (Shane, 1990a), a feature that has contributed greatly to the survival success of this species (Shane et al., 1986; Bearzi et al., 1997; Reynolds et al., 2000).

In Argentina, the bottlenose dolphin lives in coastal waters from the Province of Buenos Aires to the Province of Chubut (also possibly in offshore waters). Infrequent records have been made as far south as the Provinces of Santa Cruz and Tierra del Fuego (Bastida and Rodríguez, 2003).

The behavioural studies conducted on bottlenose dolphins in Argentina (Würsig and Würsig, 1979; Coscarella and Crespo, 2009) were discontinued in the 1980s due to the noted population declines and the subsequent lack of sightings in the study areas (Bastida and Rodríguez, 2003). One of the last remaining resident populations of the country is suggested to reside in Bahía San Antonio (Vermeulen and Cammareri, 2009; Vermeulen and Bräger, submitted). Research conducted in this area described this population as small, essentially closed (Vermeulen and Bräger, submitted) and highly resident in the study area, indicating this bay as the core region of this population's larger home range (Vermeulen and Cammareri, 2009).

This study aims to provide a better understanding of the activity patterns of this vulnerable population of bottlenose dolphins. It was aimed to detect potential diurnal and seasonal patterns and formulate hypothesis on the main factors affecting these patterns. Results will serve as vital baseline information for future monitoring of the effect of increasing human activities in this bay, as e.g., fishing and the recently initiated dolphin-based tourism.

2. MATERIALS AND METHODS

From land-based observations, the observation of different groups of dolphins had to be separated by at least half an hour to be categorised as a different sighting period (SP), and thus one SP could contain observations of several dolphin groups. The sighting frequency (SF) of bottlenose dolphins in BSA was then obtained by dividing the number of SP by the amount of effort of land-based observations, expressed per time units. To reduce the error, land-based survey efforts less than 4h/day was excluded from analysis.

Behavioural data of sightings < 30 min were disregarded for the analysis of activity patterns, in order to comply with the definition of a group follow stated by Mann (1999). This data selection resulted in the behavioural observation of 265 dolphin groups (DG) to be included in analysis (Table 10). In order to obtain independent samples, only one behaviour sample of each dolphin group was selected at random to construct the activity pattern and perform subsequent statistical analysis. The obtained values thus represent the frequencies of observed activities.

Table 10 – The number of observed dolphin groups (#DG) and the number of observed dolphin groups used in analysis after selecting those that were followed ≥ 30 min (Mann, 1999) (#DG used in analysis)

	Summer (15 months)	Autumn (15 months)	Winter (18 months)	Spring (12 months)	TOTAL
# DG observed	117	128	134	36	415
#DG used in analysis	98	49	89	29	265

Due to the limited number of samples per season for each year, no accurate seasonal comparison could be made for the different survey years. For the analysis of the daily variation of behaviour, the day was divided in 5 periods of equal duration: (1) Early morning (0800h-1000h), (2) Morning (1000h-1200h), (3) Noon (1200h-1400h), (4) Afternoon (1400h-1600h) and (5) Evening (1600h-1800h). This time span was chosen as a balance between reflecting detailed information vs. acceptable sample size in each category. To visualise the diurnal and seasonal variation in behaviour, the relative frequencies of each observed behaviour was plotted for each analysed 2-hour period or season respectively. To test the significance of both the diurnal and seasonal variation in behaviour, contingency tables were created and a Chi-square test was applied. Kruskal-Wallis tests were used to test the variation in group composition, the number of calves and group sizes. Separate Mann-Whitney U tests with Bonferroni corrections were used to further determine individual differences. To investigate the correlation between the number of calves in a group and the group size, a linear regression analysis was performed.

All statistical analyses were conducted using the software *Statistica 7.0* (StatSoft, Inc. 2004) as well as Zar (1996).

3. RESULTS

3.1. SIGHTING FREQUENCY

Based on land-based observations, bottlenose dolphins could be observed from the shore every four hours on average (SF = 0.24/h; SD = 0.11). This frequency stayed relatively constant over the different seasons (Table 11). Sighting periods (possibly containing multiple dolphin groups) ranged between 5 min - 4 h (quartile values: Q1 = 15 min; Q2 = 30 min; Q3 = 55 min) whereas the duration of an observation of a single dolphin group ranged between 5 min - 4 h (Q1 = 15 min; Q2 = 25 min; Q3 = 45 min). A Kruskal-Wallis test indicated that these durations did not fluctuate significantly among the different seasons (sighting periods: $p = 0.06$ - DG: $p = 0.07$). A SP had on average 1.3 DGs (SD = 0.4), which stayed relatively constant over the different seasons.

Table 11 – Average sighting frequency (SF) (Sighting Period/hour) with Standard Deviation (SD), and median (Q2) duration of sighting periods (SP) and observation of dolphin groups (DG) per season (expressed in minutes), including quartile values Q1 and Q3

	SP/h (SF)	SD	Median duration SP (min)	Q1 (min)	Q3 (min)	Median duration DG (min)	Q1 (min)	Q3 (min)
Summer	0.20	0.08	35	20	60	28	15	47
Autumn	0.24	0.08	25	15	45	20	10	35
Winter	0.24	0.09	35	20	60	28	15	50
Spring	0.26	0.17	30	20	40	20	15	30
TOTAL	0.24	0.11	30	15	55	25	15	45

3.2. SEASONAL AND DAILY VARIATIONS IN BEHAVIOUR

Analysis of behavioural data showed that most observed dolphin groups were resting (28%), followed by travel (27%) and surface feeding (15%). Overall, less dolphin groups were found diving (12%), milling (5%) and socialising (6%) (n = 265). In 7% of the observed dolphin groups, the behaviour could not be accurately classified.

The relative frequencies of observed behavioural patterns varied significantly among different periods of the day ($\chi2 = 40.8$; d.f. = 24; $p < 0.02$) (Figure 11). Resting clearly occurred mostly in the early morning (0800h-1000h), decreased during the day and slowly increased again in the evening (1600h-1800h). Social activity increased in the afternoon (1400h-1600h) and evening (1600h-1800h), whereas surface feeding clearly peaked in the evening (1600h-1800h). This diurnal trend remained relatively constant over the different years. Due to the limited amount of data, diurnal patterns per season were assessed using only two categories: 0800h-1300h and 1300h-1800h. A similar diurnal trend was found for all seasons, with increased resting before noon (0800h-1300h) and increased feeding activities during the afternoon (1300h-1800h).

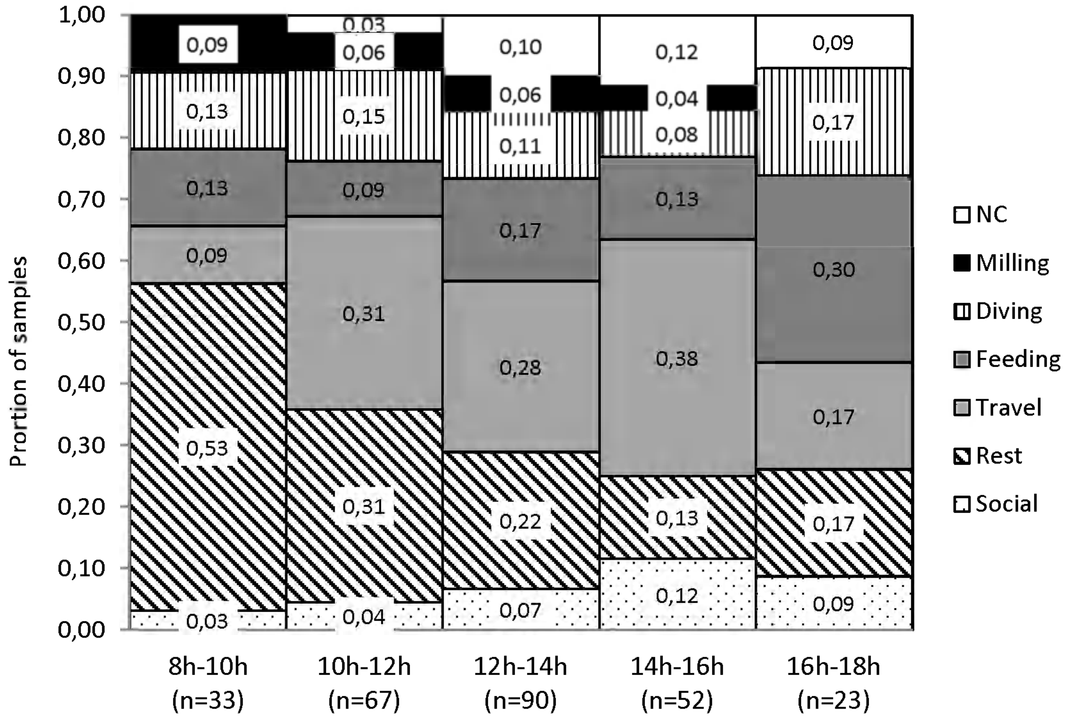

Figure 11 - Daily variation in behaviour of observed bottlenose dolphin groups in BSA (total n = 265 DG)

The relative frequencies of observed behavioural patterns also varied significantly among the different seasons (χ2 = 83.7; d.f. = 18; *p* < 0.01). Socialising and surface feeding clearly peaked during winter and spring. During summer, diving reached its maximum, after which it declined drastically in autumn and could not be observed during winter or spring (Figure 12).

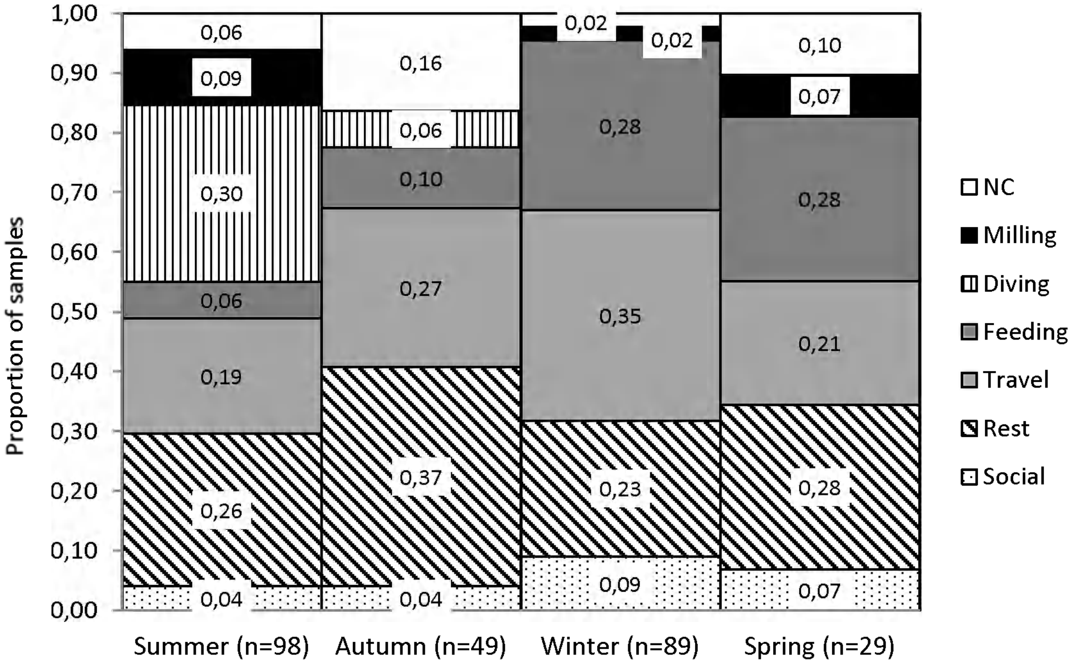

Figure 12 - Seasonal variation in behaviour of observed bottlenose dolphin groups in BSA (total n = 265 DG)

3.3. GROUP COHESION AND SIZE

Dolphin groups were significantly more frequent in a dispersed group formation than in any other cohesion state (59%; loose = 24%; tight = 17%; Kruskal-Wallis: $p < 0.01$; n = 265). These values remained constant over the different seasons (Kruskal-Wallis: $p = 0.3$) and behavioural states (Kruskal-Wallis: $p = 0.8$). Median dolphin group size ($\tilde{x}$) was 4 (Q1 = 2; Q3 = 8; n = 265) ranging from 1 to 50 individuals. Group size frequencies were 16% for pairs, 12% for trios, 20% for groups of 4 to 6, 18% for 7 to 10, 11% for groups of 11 to 20 and 8% for larger groups. Lone individuals accounted for 15% of the sightings (n = 265). The size of the dolphin groups remained rather constant over the years (Kruskal-Wallis: $p = 0.7$) and did not vary significantly over the course of the day (Kruskal-Wallis: $p = 0.4$). Group size did vary significantly among the different seasons (Kruskal-Wallis: $p < 0.01$), with group sizes being significantly larger in winter ($\tilde{x}$ = 7; n = 89) than during spring ($\tilde{x}$ = 4; n = 29), summer ($\tilde{x}$ = 3; n = 98) and autumn ($\tilde{x}$ = 3; n = 49) (separate Mann-Whitney U tests with Bonferroni correction $\alpha = 0.0125$: summer-autumn: $p = 0.5$; summer-winter: $p < 0.01$; summer-spring: $p = 0.09$; autumn-winter: $p < 0.01$; autumn-spring: $p < 0.05$; winter-spring: $p < 0.01$).

Dolphin group sizes were also analysed according to the behaviour the groups were engaged in (n = 265). This indicated that groups were significantly larger when surface feeding ($\tilde{x}$ = 10; n = 37) and socialising ($\tilde{x}$ = 8; n = 18) than during all other classified behaviours (Figure 13; Kruskal-Wallis: $p < 0.01$; Diving: $\tilde{x}$ = 2, n = 32; Resting: $\tilde{x}$ = 4, n = 74; Travelling: $\tilde{x}$ = 4, n = 71; milling: $\tilde{x}$ = 3.5, n = 14). Groups of which the behaviour could not be classified had a median size of 2 individuals (n = 19). More specifically, dolphin groups surface feeding during winter ($\tilde{x}$ = 27.5) were significantly larger than dolphin groups surface feeding during all other seasons (spring: $\tilde{x}$ = 8; summer: $\tilde{x}$ = 4; autumn: $\tilde{x}$ = 7; Kruskal-Wallis: $p < 0.01$).

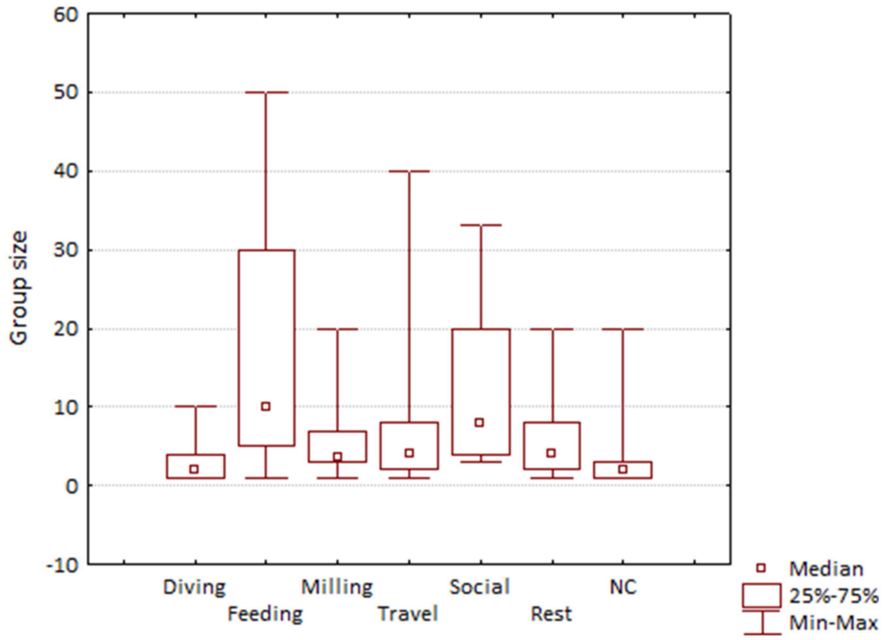

Figure 13 - Median group size of bottlenose dolphins in BSA vs. behaviour, indicating the median, quartile values and non-outlier range (total n = 265; diving: n = 32; feeding: n = 37; milling: n = 14; travel: n = 71; social: n = 18; rest: n = 74; not classified: n = 19)

Overall, 75% of the dolphin groups encountered contained calves (between 1 and 8 calves per group; n = 265). Group size seemed positively correlated with the presence of calves ($R^2 = 0.49$; $p < 0.01$). Groups containing calves, excluding mothers and calves from analysis ($\tilde{x} = 8$), were significantly larger than groups without calves ($\tilde{x} = 3$; Mann-Whitney U-test: $p < 0.05$).

4. DISCUSSION

This study showed that bottlenose dolphins used the study area mainly to rest, travel and forage. The large amount of resting behaviour suggests Bahía San Antonio is a safe habitat for the bottlenose dolphins in North Patagonia. Resting has been defined as one of the most dangerous behaviours because of reduced vigilance (Würsig et al., 1994; Connor and Heithaus, 1996) and the lack of refuge from predators (Heithaus and Dill, 2002). As dolphins have low travel costs (Williams et al., 1992), they will most likely rest in the safest habitats (Heithaus, 2001). The bay is indeed characterised by its shallowness and lack of strong currents. Furthermore, predation risk in the area has been considered to be very low (Vermeulen and Bräger, submitted). The hypothesis of a safe habitat appears to be supported by the large amount of dolphin groups observed with calves. The group size of bottlenose dolphins in BSA was also positively correlated with the amount of calves in the group. This tendency has been reported before in other bottlenose dolphin populations (dos Santos and Lacerda, 1987; Wells et al., 1987; Weigle, 1990; Weller, 1991; Bearzi et al., 1997) and was associated with the better calf assistance and protection, a reduced maternal investment and the benefits of learning (Norris and Dohl, 1980; Johnson and Norris, 1986).

Behavioural data further indicated the area is not only used as a shelter, but also as a foraging site. Overall, the proportions of travelling and feeding are comparable to those found for other bottlenose dolphin populations in inshore waters (e.g., Shane, 1990b; Hansen and Defran, 1993; Lynn, 1995; Neumann, 2001), but varied on a diurnal and seasonal basis.

4.1. DIURNAL VARIATION

It is believed that feeding habits have a largest effect in shaping the behavioural patterns of bottlenose dolphins (Shane et al., 1986), a species that is known to have a broad feeding taste and to take advantage of a number of prey items (Leatherwood, 1975; Barros and Odell, 1990). Therefore, a diurnal variation in their behaviour is to be expected if prey behaviour or availability varies during the day. The increased amount of foraging in the evening might be indicative for an increased amount of prey availability during this period of the day. This could be related to a diurnal pattern of the pelagic fish species in the region and could be supported by the decreased amount of travelling during this time of day. Considering that travelling has the primary function of locating food and conspecifics (Shane, 1990b), a decrease in travelling might indicate less time is needed to be spend searching for food. The large amount of resting in the early morning is suggested to be caused by a decrease in prey availability in the morning. It could also be a reflection of a satisfaction of the nutritional needs, as it has been stated that only then other activities will only become frequent (Doenier et al., 1997; Neumann, 2001). The low amount of travelling during that time of day further suggests that dolphins seemed less likely to be actively looking for food. This could reconfirm a satisfaction of nutritional needs and thus be indicative of an increased foraging at night. However, no information is available on the dolphins' behaviour during night-time hours.

The diurnal trend related to feeding activities showed remarkable similarities with a study conducted previously on this species in Península Valdés, Argentina (Würsig and Würsig, 1979). However, it differed from diurnal patterns found in Bahía Engaño, Argentina (Coscarella and Crespo, 2009), Galvestone, Texas (Bräger, 1993), South Africa (Saayman et al., 1973), North San Diego (Hansen and Defran, 1993) and Cardigan Bay, Wales (Bristow and Rees, 2001). These studies found a general but variable trend towards an increased feeding activity in early morning and late afternoon. However, some bottlenose dolphin populations show no diurnal cycle in their behavioural patterns, e.g., in the Adriatic Sea (Bearzi et al., 1999) and in Sarasota Bay (Irvine et al., 1981; Scott et al., 1990). According to Bearzi et al. (1999), the lack of a diurnal pattern in his study population was linked to a large amount of time dedicated to foraging, including searching for food in places with limited food resources. However, as was indicated previously by Shane (1990b) and Bearzi et al. (1999), comparison of behavioural patterns between regions is complicated. Dolphin behaviour will be influenced by a wide range of factors depending on the habitat in which they live. Furthermore, methodological differences in data collection will make comparisons challenging.

4.2. OPTIMAL GROUP SIZE

Median group size varied significantly over the different behaviours although no variation could be found over the different analysed day-time periods. These variations in optimal group size over short periods of time is a clear reflection the bottlenose dolphin's tendency to live in fission-fusion societies (Würsig and Würsig, 1977; Wells et al., 1987) in which the group size and composition will change to maximise behaviourally specific benefits (Gero et al., 2005). Ecological aspects (e.g., habitat characteristics, prey availability and predation) are considered to be important in shaping the social interactions within cetacean communities (Lusseau et al., 2003). Bearing this in mind, the small median group size observed during resting behaviour, considered to be the most dangerous behaviour (Würsig et al., 1994; Connor and Heithaus, 1996), seems to reconfirm the low predation risk in the study area. Fission-fusion societies are also known to improve the regulation of feeding competition and offer greater flexibility in exploiting resources (Lehmann and Boesch, 2004). This indicates that the group size and composition will be adapted to be optimal according to the variation in prey species, abundance, density and availability.

4.3. SEASONAL VARIATION IN FORAGING BEHAVIOUR

Winter and spring - Dolphins were more engaged in surface feeding during winter and spring, which possibly indicates a higher energy demand during colder seasons caused by lower water temperatures (Shane, 1990a). Although possibly true for winter, this could not solely explain the variation in time spent surface feeding in spring vs. autumn when average water temperatures are similar. Bräger (1993) suggested that an increased amount of time foraging might indicate more time is needed to obtain the required energy when less food is available. Bearzi et al. (1999) also related the large amount of foraging behaviour to a limited amount of prey. However in the latter study, foraging comprised more than 80% of the dolphin's activity budget. On the other hand, Cornick and Horning (2003) showed that in some marine mammal species, an increased foraging time and efficiency was caused by an increase in prey encounter rate. McFadden (2003) indicated similar results for dusky dolphins (*Lagenorhynchus obscurus*), where an increased feeding bout length was related to successful foraging in cooperative hunting groups.

The hypothesis of an increased prey availability during winter and spring in this study would further be supported by the clear increase in group size during surface feeding activities, especially in winter ($\tilde{x}$ = 27.5), often related to increased food capture efficiencies when prey is abundant (e.g., Wells et al., 1980; Würsig and Würsig, 1980). Also in spinner dolphins (*Stenella longirostris*) increased group size and cooperation was particularly evident when they were foraging in high prey densities (Benoit-Bird and Au, 2003). The increased group size during foraging also suggests a patchy prey distribution (Defran and Weller, 1999), and suggests dolphins were targeting the dense spawning shoals that form in winter (Perier, 1994). Cooperative feeding in larger groups is expected to improve individual fitness when prey is aggregated and abundant (Wells et al., 1980; Defran et al., 1999; Wells and Scott, 2002).

Summer - As shown, surface feeding was very low during summer. Over the seasons, prey shifts may occur requiring more time to search for other types of prey (Bräger, 1993), which might also result in a shift in foraging strategy. As surfacing patterns characterised by long dives have been related to feeding activities (Gunter, 1954; Norris and Prescott, 1961; Hussenot, 1980; dos Santos and Lacerda, 1987; Bearzi et al., 1999), the diving behaviour observed during summer may be related to 'tail out/peduncle-dive' foraging strategy. In other regions, long dive durations have been related to resting (Lynn, 1995). Although no underwater observations were possible during this study to confirm our hypothesis, the very little amount of time dedicated to surface feeding behaviour in summer suggests that the diving behaviour may be foraging related. It is suggested this foraging strategy is related to the behavioural tendency of local prey species to seek shelter from predators under rocks and in caves, making them less easy available thus requiring more time of the dolphins near the bottom (Perier, 1994). The significantly smaller group sizes during the observed diving behaviour further indicates that prey targeted while diving was not aggregated and probably limited, as small groups of dolphins are believed to increase their individual rate of food intake when prey is limited (Würsig, 1986). It is clear that if the benefit of foraging individually is greater than that of foraging in a group, social foraging will not be a stable strategy (Caraco, 1987). It is said that preying on schooling species is the most energetically profitable foraging tactic for a cooperative predator (Meynier et al., 2008), suggesting that during summer fewer schooling prey species were available.

4.4. PREY COMPOSITION

Since dead bottlenose dolphins are rarely encountered, very few data on stomach contents of this species are available in Argentina. The limited results from along the coast of the Province of Buenos Aires indicated ingestion of whitemouth croaker (*Micropogonias furnieri*), Brazilian codling (*Urophysis brasiliensis*), striped weakfish (*Cynoscion guatucupa*), king weakfish (*Macrodon ancylodon*) and Atlantic squid (*Loligo sanpaulensis*) (Bastida and Rodríguez, 2003). The limited data available for central Patagonia includes species such as pouched lamprey (*Geotria australis*), Patagonian squid (*Loligo gahi*), Patagonian octopus (*Octopus tehuelchus*), Argentine seabass (*Acanthistius brasilianus*), Argentine Hake (*Mercluccius hubbsi*), different species of crabs and shrimps (Crespo et al., 2008), the Patagonian blenny (*Eleginops maclovinus*), Silverside (*Odonthestes sp*.) and the South American silver porgy (*Diplodus argenteus*) (Els Vermeulen, pers. obs.) Many of these species have also been confirmed to be part of the diet of the South American sea lion (*Otaria flavescens*) and of other dolphin species living in the SMG such as the common dolphin (*Delphinus delphis*) and dusky dolphin (*Lagenorhynchus obscurus*) (Romero et al., 2011a,b). Overall, very few interactions between bottlenose dolphins and fisheries have been documented in Argentina (Bastida and Rodriguez, 2003).

4.5. CONCLUSION

Data suggest that the study area forms a safe habitat for this bottlenose dolphin population, where they can rest, nurture their young and forage. It is furthermore believed that the seasonal variation in activity is mainly a reflection of the predictable seasonal variation of prey density and availability.

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5. REFERENCES

Barros, N.B. and Odell, D.K. 1990. Food habits of bottlenose dolphins in the southeastern United States. *In*: Leatherwood, S. and Reeves, R.R. (Eds.), The Bottlenose Dolphin. Academic Press, San Diego, CA, pp. 309-328.

Bastida, R. and Rodríguez, D. 2003. Mamíferos Marinos Patagonia Antartida. Vázquez Mazzini Editors, Buenos Aires, Argentina, 206 pp.

Bearzi, G., Notarbartolo di Sciara, G., Politi, E. 1997. Social ecology of bottlenose dolphins in Kvarneric (Northern Adriatic Sea). Marine Mammal Science 13: 650-668.

Bearzi, G., Politi, E., Notarbartolo di Sciara, G. 1999. Diurnal behavior of free-ranging bottlenose dolphins in the Kvarneric (Northern Adriatic Sea). Marine Mammal Science 15: 1065-97.

Benoit-Bird, K.J. and Au, W.W. 2003. Prey dynamics affect foraging by a pelagic predator (*Stenella longirostris*) over a range of spatial and temporal scales. Behavioral Ecology and Sociobiology 53: 364-373.

Boness, D.J. 1984. Activity budget of male grey seals, *Halichoerus grypus*. Journal of Mammalogy 65: 291-297.

Bräger, S. 1993. Diurnal and seasonal behaviour patterns of bottlenose dolphins (*Tursiops truncatus*). Marine Mammal Science 9: 434-438.

Bristow, T. and Rees, E.I.S. 2001. Site fidelity and behaviour of bottlenose dolphins (*Tursiops truncatus*) in Cardigan Bay, Wales. Aquatic Mammals 27: 1-10.

Caraco, T. 1987. Foraging games in a random environment. *In*: Kamil, A.C., Krebs, J.R., Pulliam, H.R. (Eds.), Foraging Behavior. Plenum Press, NY, pp. 389-414.

Connor, R.C. and Heithaus, M.R. 1996. Great white shark approach elicits flight response in bottlenose dolphins. Marine Mammal Science 12: 602-606.

Cornick, L.A. and Horning, M. 2003. A test of hypotheses based on optimal foraging considerations for a diving mammal using a novel experimental approach. Canadian Journal of Zoology 81: 1799-1807.

Coscarella, M.A. and Crespo, E.A. 2009. Feeding aggregation and aggressive interaction between bottlenose (*Tursiops truncatus*) and Commerson's dolphins (*Cephalorhynchus commersonii*) in Patagonia, Argentina. Journal of Ethology 28: 183-187.

Crespo, E.A., García, N.A., Dans, S.L., Pedraza, S.N. 2008. Mamíferos marinos. *In*: Boltovskoy, D. (Ed.), Atlas de Sensibilidad Ambiental de la Costa y el Mar Argentino. Secretaría de Ambiente y Desarrollo Sustentable de la Nación (Proyecto ARG 02/018 'Conservación de la Diversidad Biológica y Prevención de la Contaminación Marina en Patagonia'). Available from: http://atlas.ambiente.gov.ar/index.htm.

Defran, R.H., Weller, D.W., Kelly, D.L., Espinosa, M.A. 1999. Range characteristics of Pacific coast bottlenose dolphins (*Tursiops truncatus*) in the southern California bight. Marine Mammal Science 15: 381-393.

dos Santos, M. and Lacerda, M. 1987. Preliminary observations of bottlenose dolphin (*Tursiops truncatus*) in the Sado estuary (Portugal). Aquatic Mammals 13: 65-80.

Doenier, P.B., Delgiudice, G.D., Riggs, M.R. 1997. Effects of winter supplemental feeding on browse consumption by white-tailed deer. Wildlife Society Bulletin 25: 235-243.

Gero, S., Bejder, L., Whitehead, H., Mann, J., Connor, R.C., 2005. Behaviourally specific preferred associations in bottlenose dolphins, *Tursiops spp*. Canadian Journal of Zoology 83: 1566-1573.

Gunter, C. 1954. Mammals of the Gulf of Mexico. Fishery Bulletin 55: 543-551.

Hansen, L. and Defran, R.H. 1993. The behaviour and feeding ecology of the Pacific coast bottlenose dolphin, *Tursiops truncatus*. Aquatic Mammals 19: 127-142.

Heithaus, M.R. 2001. Predator–prey and competitive interactions between sharks (Order *Selachii*) and dolphins (Suborder *Odontoceti*): a review. Journal of Zoology 253: 53-68.

Heithaus, M.R. and Dill, L.M. 2002. Food availability and tiger shark predation risk influence bottlenose dolphin habitat use. Ecology 83 : 480-491.

Hussenot, E. 1980. Le grand dauphin *Tursiops truncatus* en Bretagne: types de fréquentation. Penn ar Bed 12: 355-380.

Irvine, A.B., Scott, M.D., Wells, R.S., Kaufmann, J.H. 1981. Movements and activities of the Atlantic bottlenose dolphin, *Tursiops truncatus*, near Sarasota, Florida. Fishery Bulletin 79: 671-688.

Johnson, C.M. and Norris, K.S. 1986. Delphinid social organisation and social behaviour. *In*: Schusterman, R.J., Thomas, J.A., Wood, F.G. (Eds.), Dolphin cognition and behaviour: A comparative approach. Lawrence Erlbaum, Hillsdale, NJ, pp. 335-346.

Leatherwood, S. 1975. Some observation of feeding behavior of bottle-nosed dolphins (*Tursiops truncatus*) in the northern Gulf of Mexico and (*Tursiops cf. T. gilli*) off southern California, Baja California, and Nayarit, Mexico. Marine Fisheries Review 37: 10-16.

Lehmann, J. and Boesch, C. 2004. To fission or to fusion: Effects of community size on wild chimpanzee (*Pan troglodytes versus*) social organization. Behavioral Ecology and Sociobiology 56: 207-216.

Lusseau, D., Schneider, C., Boisseau, O.J., Haase, P., Slooten, E., Dawson, S.M. 2003. The bottlenose dolphin community of Doubtful Sound features a large proportion of long-lasting associations. Can geographic isolation explain this unique trait? Behavioral Ecology and Sociobiology 54: 396-405.

Lynn, S.K. 1995. Movements, site fidelity and surfacing patterns of bottlenose dolphins on the central Texas coast. Dissertation, Texas A&M University, Galveston, TX, 92 pp.

Mann, J. 1999. Behavioural sampling methods for cetaceans: A review and critique. Marine Mammal Science 19: 102-122.

Mann, J., Connor, R.C., Barre, L.M., Heithaus, M.R. 2000. Female reproductive success in bottlenose dolphins (*Tursiops sp.*): life history, habitat, provisioning, and group-size effects. Behavioral Ecology 11: 210-219.

McFadden, C.J. 2003. Behavioral flexibility of feeding dusky dolphins. Dissertation, Texas A&M University, TX.

Meynier, L., Pusineri, J.C., Spitz, M.B., Santos, M.B., Pierce, G.J., Ridoux, V. 2008. Intraspecific dietary variation in the short-beaked common dolphin *Delphinus delphis* in the Bay of Biscay: Importance of fat fish. Marine Ecology Progress Series 354: 277–287.

Neumann, D.R. 2001. Activity budget of free-ranging common dolphins (*Delphinus delphis*) in the northwestern Bay of Plenty, New Zealand. Aquatic Mammals 27: 121-136.

Nielsen, E.T. 1983. Relation of behavioral activity rhythms to the changes of day and night. A revision of views. Behaviour 89: 147–173.

Norris, K.S. and Dohl, T.P. 1980. The structure and function of cetacean schools. *In*: Herman, L.M. (Ed.), Cetacean Behaviour: Mechanisms and Functions. John Wiley and Sons, NY, pp. 211-261.

Norris, K.S. and Prescott, J.H. 1961. Observations on Pacific cetaceans of Californian and Mexican waters. University of California Publications in Zoology 63: 291-402.

Perier, M.R. 1994. La fauna íctica en el litoral de la Bahía de San Antonio (Golfo San Matias, Provincia de Río Negro). Dissertation, Facultad de Ciencias naturales y Museo, Universidad Nacional de La Plata, Argentina.

Reynolds, J.E., Wells, R.S., Eide, S.D. 2000. The bottlenose dolphin: Biology and conservation. University Press, Florida, 289 pp.

Romero, M.A., Dans, S.L., González, R., Svendsen, G.M., García, N., Crespo, E.A. 2011a. Solapamiento trófico entre el lobo marino de un pelo Otaria flavescens y la pesquería de arrastre demersal del golfo San Matías, Patagonia, Argentina. Latin American Journal of Aquatic Research 39: 344-358.

Romero, M.A., Dans, S.L., García, N., Svendsen, G.M., González, R., Crespo, E.A. 2011b. Feeding habits of two sympatric dolphin species off North Patagonia, Argentina. Marine Mammal Science DOI: 10.1111/j.1748-7692.2011.00477.

Saayman, G.S., Tayler, C.K., Bower, D. 1973. Diurnal activity cycles in captive and free-ranging Indian Ocean bottlenose dolphins (*Tursiops adunctus* Ehrenburg). Behaviour 44: 212-233.

Scott, M.D., Wells, R.S., Irvine, A.B. 1990. A long-term study of bottlenose dolphins on the West coast of Florida. *In*: Leatherwood, S. and Reeves, R.R. (Eds.), The Bottlenose Dolphin. Academic Press, San Diego, CA, pp. 235-244.

Shane, S.H., Wells, R.S., Würsig, B. 1986. Ecology, behavior and social organization of the bottlenose dolphin: a review. Marine Mammal Science 2: 34-63.

Shane, S.H. 1990a. Behavior and ecology of the bottlenose dolphin at Sanibel Island, Florida. *In*: Leatherwood, S. and Reeves, R.R. (Eds.), The Bottlenose Dolphin. Academic Press, San Diego, CA, pp. 245-266.

Shane, S.H. 1990b. Comparison of bottlenose dolphin behaviour in Texas and Florida, with a critique of methods studying dolphin behaviour. *In*: Leatherwood, S. and Reeves, R.R. (Eds.), The Bottlenose Dolphin. Academic Press, San Diego, CA, pp. 541-558.

StatSoft, Inc. 2004. STATISTICA (data analysis software system), version 7. www.statsoft.com.

Vermeulen, E. and Cammareri, A. 2009. Residency Patterns, Abundance and Social Composition of Bottlenose Dolphins (*Tursiops truncatus*) in Bahía San Antonio, Patagonia, Argentina. Aquatic Mammals 35: 379-386.

Vermeulen, E. and Bräger, S. submitted. Demographics of the disappearing bottlenose dolphin in Argentina: a common species on its way out? PLoS-One.

Weigle, B. 1990. Abundance, distribution and movements of bottlenose dolphins (*Tursiops truncatus*) in lower Tampa Bay, Florida. *In*: Hammond, P.S., Mizroch, S.A., Donovan, G.P. (Eds.), Individual recognition of cetaceans: Use of photo-identification and other techniques to estimate population parameters. Cambridge: International Whaling Commission Special Issue 12, pp. 195-202.

Weller, D.W. 1991. The social ecology of Pacific coast bottlenose dolphins. Dissertation, San Diego State University, San Diego, CA, 93 pp.

Wells, R.S., Irvine, A.B., Scott, M.D. 1980. The social ecology of inshore odontocetes. *In*: Herman, L.M. (Ed.), Cetacean behaviour: Mechanisms and processes. John Wiley & Sons, NY, pp. 263-317.

Wells, R.S., Scott, M.D., Irvine, A.B. 1987. The social structure of free-ranging bottlenose dolphins. *In*: Genoways, H.H. (Ed.), Current Mammalogy. Plenum Press, NY, pp. 247-305.

Wells, R.S. and Scott, M.D. 2002. Bottlenose dolphins, *Tursiops truncatus* and *T. adunctus*. *In*: Perrin, W.F., Würsig, B., Thewissen, J.G.M. (Eds.), Encyclopaedia of Marine Mammals. Academic Press, San Diego, pp. 122-128.

Williams, T.M., Friedlander, A.W., Fong, M.L., Yamada, R.M., Sedivy, P., Haun, J.E. 1992. Travel at low energetic cost by swimming and wave-riding bottlenose dolphins. Nature 355: 821–823.

Würsig, B. 1986. Delphinid foraging strategies. *In*: Schusterman, R.J., Thomas, J.A., Wood, F.G. (Eds.), Dolphin cognition and behaviour: a comparative approach. Lawrence Erlbaum Assoc: Hillsdale, NJ, pp. 347-359.

Würsig, B. and Würsig, M. 1977. The photographic determination of group size, composition and stability of coastal porpoises (*Tursiops truncatus*). Science 198: 755-756.

Würsig, B. and Würsig, M. 1979. Behavior and ecology of bottlenose porpoises, *Tursiops truncatus*, in the South Atlantic. Fishery Bulletin 77: 399-442.

Würsig B. and Würsig M. 1980. Behavior and ecology of the dusky dolphin, *Lagenorhynchus obscurus*, in the South Atlantic. Fishery Bulletin 77: 871-890

Würsig, B., Wells, R.S., Norris, K.S., Würsig, M. 1994. A spinner dolphin's day. *In*: Norris, K.S., Würsig, B., Wells, R.S., Würsig, M. (Eds.), The Hawaiian spinner dolphin. University of California Press, Berkeley, California, pp. 65–102.

Zar, J.H. 1996. Biostatistical analysis (3rd ed.). Upper Saddle River, Prentice Hall, NJ.

7

HABITAT SELECTION

After

Vermeulen, E. submitted. A shared habitat for humans and dolphins: conservation implications of the intertidal habitat selection of bottlenose dolphins. Aquatic Conservation: Marine and Freshwater Ecosystems.

ABSTRACT - Although one of the best-studied cetacean species in the world, no information is available on bottlenose dolphin (*Tursiops truncatus*) habitat selection in Argentina. There is, however, a notable decline in their abundance, with questions on the exact causes still to be answered.

In this study, bottlenose dolphin habitat selection was assessed in Bahía San Antonio, the core area of what could be one of the last remaining populations of the species in Argentina. This area is known for its large tidal amplitude, leaving 86% of its surface exposed during low tide. It was aimed to provide a deeper insight in the ecology of the species in this country, allowing for predictions on how they might respond to continuing changes in their environment.

Although defined as their core habitat, dolphins appeared to use only 51% of the surveyed area. There was a clear preference for the shallower waters and dolphins appeared to move in and out with the tide to remain in the intertidal zone as long as possible, including to forage.

The invertebrate community inhabiting the intertidal zone is known to be of great biological importance in Bahía San Antonio, providing resources to many species up the food chain. However, due to the large-scale and fast coastal development in this area, urgent conservation measures are required to protect these natural resources. Actions should include an improved urban planning and waste management at a minimum.

KEYWORDS - bottlenose dolphin, environmental degradation, habitat selection, intertidal zone, rocky flats, water depth

1. INTRODUCTION

Animals are believed to show positive habitat selection by using certain habitats disproportionately to their availability (Allen et al., 2001). Within ecology, it is important to understand the patterns of habitat selection, as it is a function of the habitat heterogeneity and the biological requirements of a species (Rosenzweig, 1981). Furthermore, understanding these habitat preferences can aid in formulating predictions on how animals will respond to changes in their environment (Karczmarski et al., 2000; Heithaus and Dill, 2002), an important factor in terms of conservation.

Cetaceans, including bottlenose dolphins (*Tursiops truncatus*), live in complex habitats with a dynamic regime of physical and chemical properties (Bräger et al., 2003). They are known to interact with their environment on a wide scale of spatial and temporal variations, making these interactions even more complex at times (Allen et al., 2001). The relationship between bottlenose dolphins and their habitat can differ largely among different regions. Some coastal populations were shown to perform seasonal movements from deeper channels to shallow waters (e.g., Waples, 1995), whereas others indicated preferences for estuarine habitats and/or structural features (e.g., Shane, 1990; Ballance, 1992; Hanson and Defran, 1993; Scott et al., 1996). Nonetheless, most studies indicated that habitat selection by bottlenose dolphins was mainly driven by prey distribution and abundance, sometimes in combination with predation risk (e.g., Shane, 1990; Ballance, 1992; Hanson and Defran, 1993; Waples, 1995; Scott et al., 1996).

So far, only a single study related to bottlenose dolphin habitat use was conducted in Argentina (Würsig and Würsig, 1979). However, today such studies would be of great value in the attempt to explain the causes of the precipitous population declines observed over the past decades (Bastida and Rodríguez, 2003; Coscarella et al., 2012). These declines may have resulted in the studied population to be one of the last remaining resident populations of bottlenose dolphins in the country (Vermeulen and Cammareri, 2009; Vermeulen and Bräger, submitted). However, this population is estimated to be small and isolated (Vermeulen and Bräger, submitted), with Bahía San Antonio suggested as the core area within their larger home range (Vermeulen et al., submitted a). This study is aimed to provide an insight into the habitat selection of this community. As coastal developments and human activities are increasing notably in this region, the presented information is of critical importance for accurate conservation management in times of increased coastal urban and industrial developments.

2. MATERIALS AND METHODS

2.1. ARCGIS SETUP

The software programme ESRI ArcGIS 10.1 was used to subdivide the study area into grid cells of 1 km² (1 km x 1 km). Cells with a total survey effort lower than a cell's diagonal (1414 m) were excluded from subsequent analyses. This resulted in a total of 245 grid cells (or 233 km² after excluding grids overlapping land) surveyed. In total, 155 bottlenose dolphin groups were initially sighted inside 66 of these grid cells (64.7 km²) and were followed over a total of 127 grid cells or 121 km² (51% of surveyed area; Figure 14). The commonly used World Geodetic System of 1984 (UTM zone 20S) was used as the projected coordinate system.

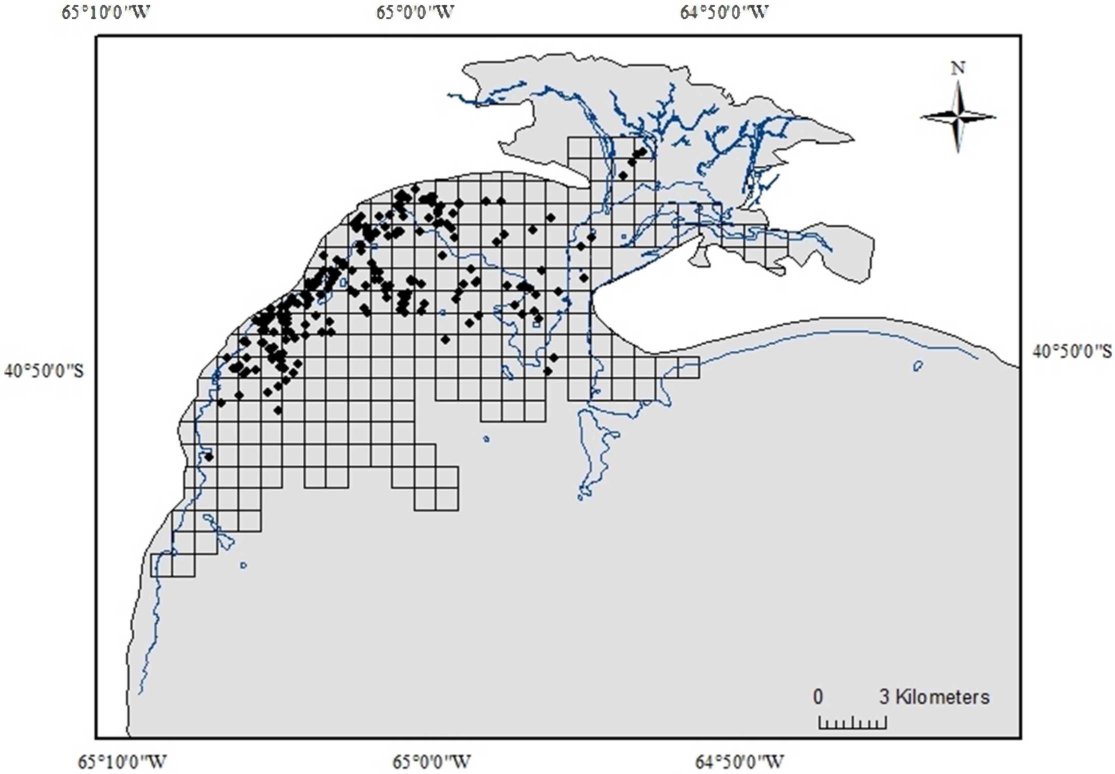

Figure 14 – Map of the study area, BSA, indicating 245 surveyed grid cells and the initial sightings of bottlenose dolphin groups. The isobath indicates the shoreline at low tide

A detailed electronic bathymetrical chart was obtained from the Naval Hydrographical Service of Argentina, indicating the mean depth at mid-tide (further referred to as MDMT) and the substrate. Utilising this chart within ArcGIS, each cell of the grid was characterised by the environmental variables MDMT, slope and substrate:

(1) *Depth*: The value of MDMT for each cell was obtained by averaging all MDMT values for each cell. The value of MDMT reflects a depth range ± 4.75 m depending on tide, with the intertidal zone thus consisting of cells with a MDMT < 5 m.

Additionally, exact depth measurements were also registered in the field when possible using the boat's echo sounder. Due to logistical limitations this could only be done during the observation of 41 dolphin groups.

(2) *Slope:* Slope was calculated as $(D_{max} - D_{min})/DI$ where D_{max} is the maximum depth recorded in a given cell and D_{min} is the minimum depth recorded in the same cell, and DI marks the distance between the points of maximum and minimum depth of the cell (Cañadas et al., 2002; Garaffo et al., 2007). Slope was expressed in degrees.

(3) *Substrate:* The kind of substrate appointed to each cell was according to the majority of substrate found in each cell. Substrate included sand, rocky flats, gravel and shells.

As depth (MDMT from the chart as well as measured depth) and slope are considered to be continuous variables, Kruskal-Wallis tests were employed to evaluate differences among these variables. As substrate is considered to be a categorical variable, χ^2 of independence was used to test for differences.

Annual mean measured SST was 14.9°C ± 4.0 (n = 82; Figure 15). For analysis, each survey year was divided in two temperature periods: warm (monthly average above annual mean; January, February, March, October, November, December) and cold (monthly average below annual mean; April, May, June, July, August, September). Additionally, each survey year was also divided into four seasons: summer (January-March; average SST = 18.4°C; SD = 1.4; n = 18), autumn (April-June; average SST = 12.8°C; SD = 2.0; n = 24), winter (July-September; average SST = 9.4°C; SD = 1.3; n = 20), spring (October-December; average SST = 17.4°C; SD = 2.8; n = 20).

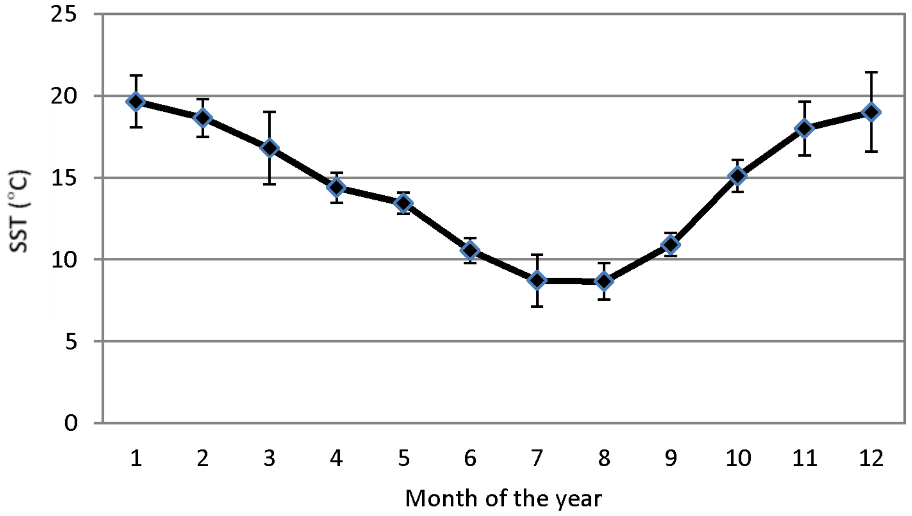

Figure 15 – Average sea surface temperature per month of the year (measured over the study period) with SD error bars (n_{total} = 82)

2.2. ANALYSIS

2.2.1 Encounter rate

The encounter rate (ER) of dolphin groups (DG) was calculated as n/L where n is the number of DG sighted in each cell and L the total number of kilometres spent on effort in each cell (Bearzi et al., 2005; 2008). To test whether cells were spatially auto-correlated, and thus not independent, Moran's I index was calculated for the DG encounter rates using the Spatial Statistics Tool in ArcGIS 10.1.

To investigate a temporal variation in the overall ER, differences were investigated between survey years, seasons, temperature periods, tidal phases and stages of high tidal current (ebb and flood tide) *vs.* low tidal current (high and low tide). A log-linear analysis was used to investigate the relationship between ER and the environmental factors (1) MDMT (≤ 5 m; > 5 m), (2) slope (< 0.1°; 0.1° - 0.2°; > 0.2°), (3) substrate (sand, rocky flats, gravel, shells).

2.2.2 Variation in spatial use

Environmental variables were compared between grid cells where dolphin groups were initially observed *vs.* those surveyed cells where dolphins had never been seen. The observed distribution of MDMT (< 10 m; 10 - 15 m; > 15 m), slope (< 0.1°; 0.1° - 0.2°; > 0.2°) and substrate was also investigated in relation to their expected distribution (total distribution) from the surveyed cells utilising a Chi-square analysis (Siegel and Castellan, 1995; Conover, 1999; Garaffo et al., 2007).

A variation in spatial use was further analysed between different group sizes (≤ 5 individuals; 6 - 10 individuals; > 10 individuals) and composition (groups with calves *vs.* group without calves) utilising only the initial sighting of each group. To investigate the temporal variation of the dolphin's spatial use, the environmental variables of the cells where dolphins were observed initially were compared between survey years, seasons, temperature periods, tidal phases and stages of high tidal current *vs.* low tidal current.

To investigate a variation in spatial use related to behaviour, the environmental variables of cells where dolphin groups were observed were compared among the different behavioural categories, using only the initial behaviour of each dolphin group. Furthermore, a variation in the spatial distribution of surface feeding behaviour was analysed specifically: the environmental variables of the cells where surface feeding was observed initially were compared between the different seasons, temperature periods, tidal phase and stages of high tidal current (ebb and flood tide) *vs.* those of low tidal current (high and low tide). For this analysis, the different survey years were pooled together to increase the amount of data.

All statistical analyses were conducted using the software *Statistica 7.0* (StatSoft, Inc. 2004) as well as Zar (1996).

3. RESULTS

3.1. ENCOUNTER RATE

The median ER amounted to approximately 2 DG per 100 km surveyed (Q1 = 1.3; Q3 = 2.8) or 6 dolphins every 100 km (Q1 = 1.5; Q3 = 14.1). Moran's I index calculated for the encounter rates was not significantly different from zero (z = 0.12; $p > 0.05$) indicating that cells were not spatially auto-correlated.

The ER of groups remained similar across all temporal variables. However, a significant difference could be found in the ER of dolphins across the different seasons and temperature periods, with a higher value found in the cold winter months (Kruskal-Wallis: H = 16.8; $p < 0.01$). A log-linear analysis indicated that only substrate had a significant effect on ER (Table 12). This analysis further showed that the three environmental variables were not interrelated in the areas where dolphin groups were observed.

Table 12 – Log-linear analysis of data classified by encounter rate (ER), MDMT, slope and substrate. Star (*) marks the significant relation

	d.f.	χ^2	*p*
ER - MDMT	4	2.3	0.69
ER - Slope	4	10.0	0.06
ER - Substrate	4	17.0	0.001*
MDMT - Slope	4	6.5	0.17
MDMT - Substrate	4	2.5	0.65
Slope - Substrate	4	4.2	0.38

3.2. VARIATION IN SPATIAL USE

Dolphin groups were initially sighted in cells that were significantly more shallow (n = 66 cells; MDMT = 3.5 m; Q1 = 0.13 m; Q3 = 6.9 m) than the surveyed cells where dolphins were never seen (n = 118 cells; MDMT = 6.9 m; Q1 = 0.06 m; Q3 = 12.3 m; Wilcoxon Matched Pair test: z = 4.79; $p < 0.01$). Accordingly, a significant difference could be found in the observed *vs.* the total expected distribution of MDMT (n = 245 cells; $\chi^2 = 56.8$; $p < 0.01$), indicating that dolphins preferred areas with MDMT < 5 m (intertidal zone), and were never observed in areas with a MDMT > 15 m (areas with a depth of approximately 10 m at the lowest tide). Accordingly, depth values measured in the presence of dolphins never exceeded 10 m (median depth = 5.8 m; Q1 = 4.1 m; Q3 = 7.2 m; range: 0.8 m - 10 m).

The median slope of cells where dolphin groups were initially observed equalled 0.15° (n = 66 cells; Q1 = 0.10°; Q3 = 0.28°), being significantly steeper than the slope of the surveyed cells where dolphins were never seen (n = 118 cells; median slope = 0.08°; Q1 = 0.05°; Q3 = 0.18°; Wilcoxon Matched Pair test: z = 6.13; $p < 0.01$). Analysis further confirmed that dolphins used steeper slopes more so than expected ($\chi^2 = 44.9$; $p < 0.01$).

In total, 69% of the cells where dolphin groups were sighted initially had a sandy substrate, 20% had a rocky flat substrate, 10% had gravel and only 1% had shells. When compared to those surveyed cells where dolphins were never seen, a significant difference could be found (n = 118 cells; $\chi^2 = 9.14$; $p < 0.05$) with the latter containing almost exclusively sandy substrate. Further analysis confirmed dolphins used more rocky flats than expected ($\chi^2 = 9.14$; $p < 0.01$).

Groups with calves (n = 113) showed no significant variation in spatial use when compared to groups without calves (n = 42). Further analysis showed that the largest groups occurred mostly over a sandy substrate and rocky flats, whereas the smallest groups were found almost exclusively over sand ($\chi^2 = 11.2$; $p < 0.05$).

The only temporal variation found in the dolphin's spatial use related to depth values measured in the field, which indicated that dolphin groups were encountered in deeper waters during the colder months (Mann-Whitney: U = 1408; $p < 0.01$).

When relating spatial use to behaviour, results showed that diving occurred in deeper waters (MDMT*:* Kruskal-Wallis: H = 26.3; $p < 0.01$; measured depths: Kruskal-Wallis: H = 61.9; $p < 0.01$; Figure 16). Separate Mann-Whitney tests indicated a significant increase in depth during diving behaviour *vs.* all other behaviours. Furthermore, resting, milling and socialising were observed in significantly shallower regions than all other behaviours. Cells where diving occurred had a significant steeper slope than all other behaviours (Kruskal-Wallis: H = 17.6; $p < 0.01$). There was no significant variation in substrate for the different behaviours ($\chi^2 = 17.3$; $p = 0.50$).

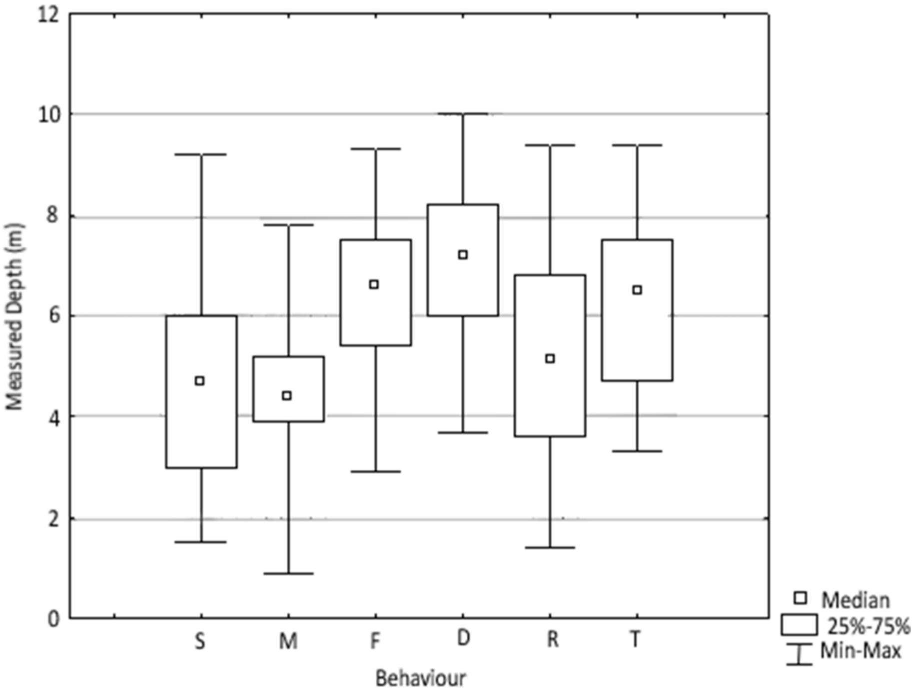

Figure 16 - Median depth values measured in the field during different behavioural states (n = 41 DG). S = socialising, M = milling, F = surface feeding, D = diving, R = resting, T = travel

However, when surface feeding behaviour was analysed separately (n = 42 cells), data showed that dolphins were performing this behaviour more frequently over rocky flats and gravel substrate in winter than in all other seasons ($\chi^2 = 21.8$; $p < 0.01$). Exact depth measurements taken on the field further showed dolphins engaged in surface feeding behaviour in deeper waters during the colder months (n = 32 DG; Mann-Whitney: U = 82; $p < 0.01$). During flood tide dolphins seemed to feed in cells with a deeper MDMT (Mann-Whitney: U = 4509.5; $p < 0.01$). Additionally, they seemed to forage more so over rocky flats during flooding tide and over sandy substrate during ebbing tide ($\chi^2 = 9.89$; $p < 0.01$).

4. DISCUSSION

Bottlenose dolphins could be observed in only 51% of the surveyed area in BSA, clearly preferring the shallower waters. It is common for some coastal bottlenose dolphins to remain in very shallow waters (Würsig and Würsig, 1979; dos Santos and Lacerda, 1987; Ballance, 1992; Wilson et al., 1997; Defran and Weller, 1999; Allen et al., 2001; Ingram and Rogan, 2002) which has often been related to a trade-off between food availability and predation risk (Heithaus and Dill, 2002). As predation risk is believed to be low inside BSA (Vermeulen and Bräger, submitted), food availability is believed to be the primary trigger for the dolphin's spatial distribution within the bay. This idea is further supported by a similar habitat selection of dolphin groups with calves *vs.* dolphin groups without calves.

Bottlenose dolphins appeared to respond to the large tidal fluctuations in BSA by moving in and out with the tide, remaining in the intertidal zone most of the time. Many invertebrate species are known to inhabit this intertidal zone, and serve as an important food source for many fish species (Perier, 1994; González, 1993; García et al., 2010) potentially preyed on by bottlenose dolphins. Additionally, Perier (1994) indicated several fish species use the structural features along the coast of BSA also as a nursery ground, attracting predators up the food chain. On the other hand, when these rocky flats are uncovered during low tide, many species of shorebirds come to feed, especially on the abundant mussel *Brachidontes rodriguezi* (e.g., González, 1993; Sitters et al., 2001; García et al., 2010). The importance of these rocky flats for migrating shorebirds is reflected in the declaration of BSA as a BirdLife International Important Bird Area (Di Giacomo, 2005) and a Western Hemisphere Shorebird Reserve Network Site (González et al., 1996).

This study showed dolphins preferred to feed over the rocky flats at flooding tide during the day, whereas during ebbing tide they preferred sandy substrates. It could be that during flooding tide, an increased amount of predators is attracted to the remnants of the shorebirds' feeding activity, with consequences throughout the food chain.

During winter, bottlenose dolphins were observed more frequently in deeper waters although no temporal difference could be found for MDMT values. Also during winter, surface feeding activities were found to occur even more over rocky flats. Their feeding activities in this season have previously been related to cooperative feeding (Vermeulen et al., submitted b) on shoals of spawning fish (Perier, 1994; Di Giacomo et al., 1993; Perier and Di Giacomo, 2002). Accordingly, González

(1993) indicated that spawning fish in this bay use the structural features near the coasts to deposit their gametes during the colder months. Furthermore, as echolocation is known to be less efficient in very shallow waters (Heithaus and Dill, 2002), dolphins might prefer slightly deeper waters to perform a cooperative foraging strategy.

In any case, the use of structural features during feeding activities has been reported previously for coastal bottlenose dolphins and was related to prey distribution and abundance (e.g., Hanson and Defran, 1993).

Conservation implications - Coastal bottlenose dolphins appear to show a preference for the intertidal zone of BSA. This intertidal region is known to be of high importance for the provision of resources for many species up the food-chain. However, despite of being declared a 'Natural Reserve' in 1993, anthropogenic pressures in this coastal area increase considerably with the increasing coastal developments. For example, eutrophication caused by the discharge of wastewater from the coastal towns produces periodic macroalgae blooms in this region, shown to affect the intertidal invertebrate community and consequently predation by shorebirds (Garcia et al., 2010). Furthermore, in BSA severe elevated levels of heavy metals (Pb, Cu, Zn, Hg and Cd) were found in the soil and molluscs (*Brachydontes rodriguezi*), the most abundant invertebrate species on the rocky flats (Gil et al., 1999; for more information see Chapter 1 – 2.3.3). As apex predators, bottlenose dolphins are known to accumulate heavy metals, and negative health effects have been shown or are presumed also in other parts of the world, including the South Atlantic (e.g., Parsons and Chan, 2001; Roditi-Elasar et al., 2003; Carballo et al., 2004; Stavros et al., 2007; Vázquez-Medina et al., 2007; Lemos et al., 2013). Additionally, the intertidal zone is degrading rapidly due to direct removal of parts for building intertidal swimming pools, damage by vehicles and pollution (Gil et al., 2006).

How these anthropogenic pressures on the intertidal zone might affect directly or indirectly the dolphins in the area remains undetermined. Nonetheless, as Carbone et al. (2011) reported, the area is in risk of environmental degradation due increased urbanisation, these effects should be monitored more in detail. It is therefore recommended that improved conservation measures are implemented in BSA that will limit direct human impact to the intertidal zone, including an improved urbanisation planning and waste management.

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5. REFERENCES

Allen, M.C., Read, A.J., Gaudet, J., Sayigh, L.S. 2001. Fine-scale habitat selection of foraging bottlenose dolphins *Tursiops truncatus* near Clearwater, Florida. Marine Ecology Progress Series 222: 253-264.

Balance, L.T. 1992. Habitat use patterns and ranges of the bottlenose dolphin in the Gulf of California, Mexico. Marine Mammal Science 8: 262-274

Bastida, R. and Rodríguez, D. 2003. Mamíferos Marinos Patagonia Antartida. Vázquez Mazzini Editors, Buenos Aires, Argentina, 206 pp.

Bearzi, M. 2005. Aspects of ecology and behaviour of bottlenose dolphins (*Tursiops truncatus*) in Santa Monica Bay, California. Journal of Cetacean Research and Management 7: 75-83.

Bearzi, G., Azzellino, A., Politi, E., Costa, M., Bastianini, M. 2008. Influence of seasonal forcing on habitat use by bottlenose dolphins *Tursiops truncatus* in the Northern Adriatic Sea. Ocean Science Journal 43: 175-182.

Bräger, S., Harraway, J.A., Manly, B.F.J. 2003. Habitat selection in a coastal dolphin species (*Cephalorhynchus hectori*). Marine Biology 143: 233-244.

Cañadas, A., Sagarminaga, R., García-Tiscar, S. 2002. Cetacean distribution related with depth and slope in Mediterranean waters off southern Spain. Deep-Sea Research 49: 2053-2073.

Carballo, M., De la Peña, E., Fernández, A., Aguayo, S., Esperón, F., De la Torre, A., Muñoz, M.J. 2004. Accumulation of persistent organic chemicals and metals in stranded bottlenose dolphins (*Tursiops truncatus*) in Canary Islands (Spain). Toxicology and Applied Pharmacology 197: 235.

Carbone, M.E., Piccolo, M.C., Perillo, G.M.E. 2011. Zonificación ambiental de la reserva natural Bahía San Antonio, Argentina: aplicación del índice de calidad ambiental. Investigaciones Geográficas 56: 49-67.

Conover, W.J. 1999. Practical nonparametric statistics, 3rd edition. Wiley, New York.

Coscarella, M., Dans, S.L., Degrati, M., Garaffo, G.V., Crespo, E.A. 2012. Bottlenose dolphins at the southern extreme of the Southwestern Atlantic: local population decline? Journal of the Marine Biological Association of the United Kingdom 92: 1843-1849.

Defran, R.H. and Weller, D.W. 1999. Occurrence, distribution, site fidelity, and school size of bottlenose dolphins (*Tursiops truncatus*) off San Diego, California. Marine Mammal Science 15: 366-380.

Di Giacomo, E.E., Calvo, J., Perier, M.R., Morriconi, E. 1993. Spawning aggregations of *Merluccius hubbsi* in Patagonian waters: evidence for a single stock? Fisheries Research 16: 9-16.

Di Giacomo, A.S. 2005. Áreas importantes para la conservación de las aves en la Provincia de Río Negro. *In*: Di Giacomo, A.S. (Ed.), Áreas Importantes para la conservación de las Aves en la Argentina Aves Argentinas and Asociación Ornitológica del Plata, Buenos Aires, Argentina, pp. 334-349.

dos Santos, M.E. and M. Lacerda. 1987. Preliminary observations of the bottlenose dolphins (*Tursiops truncatus*) in the Sado estuary (Portugal). Aquatic Mammals 13: 65-80.

Garaffo, G.V., Dans, S.L., Pedraza, S.N., Crespo, E.A., Degrati, M. 2007. Habitat use by dusky dolphin in Patagonia: how predictable is their location? Marine biology 152: 165-177.

García, G.O., Isacch, J.P., Laich, A.G., Albano, M., Favero, M., Cardoni, D.A., Luppi, T., Iribarne, O. 2010. Foraging behaviour and diet of American Oystercatchers in a Patagonian intertidal area affected by nutrient loading. Emu 110: 146-154.

Gil, M.N., Harvey, M.A., Esteves, J.L. 1999. Heavy metals in intertidal sediments from Patagonian coast, Argentina. Bulletin of Environmental Contamination and Toxicology 63: 52 – 58.

Gil, M.N., Torres, A., Harvey, M., Esteves, J.L. 2006. Metales pesados en organismos marinos de la zona costera de la Patagonia argentina continental. Revista de Biología Marina y Oceanografía 41: 167-176.

González, P.M., Piersma, T., Verkuil, Y. 1996. Food, Feeding, and Refuelling of Red Knots during Northward Migration at San Antonio Oeste, Rio Negro, Argentina. Journal of Field Ornithology 67: 575-591.

González, R.A. 1993. Variaciones en la abundancia de las especies ícticas durante un ciclo anual, en una restinga del submareal costero nortpatagónico. Actas Jornada Nacional de Ciencias Del Mar 1: 118-128.

Hanson, M.T. and Defran, R.H. 1993. The behaviour and feeding ecology of the Pacific coast bottlenose dolphin, *Tursiops truncatus*. Aquatic Mammals 19: 127-142.

Heithaus, M.R. and Dill, L.M. 2002. Food availability and tiger shark predation risk influence bottlenose dolphin habitat use. Ecology 83: 480-491.

Ingram, S.N. and Rogan, E. 2002. Identifying critical areas and habitat preferences of bottlenose dolphins *Tursiops truncatus.* Marine Ecology Progress Series 224: 247-255.

Karczmarski, L., Cockcroft, V.G., McLachlan, A. 2000. Habitat use and preferences of Indo-Pacific humpback dolphins *Sousa chinensis* in Algoa Bay, South Africa. Marine mammal science 16 : 65-79.

Lemos, L.S., de Moura, J.F., Hauser-Davis, R.A., de Campos, R.C., Siciliano, S. 2013. Small cetaceans found stranded or accidentally captured in southeastern Brazil : Bioindicators of essential and non-essential trace elements in the environment. Ecotoxicology and Environmental Safety 97: 166-175.

Parsons, E.C. and Chan, H.M. 2001. Organochlorine and trace element contamination in bottlenose dolphins (*Tursiops truncatus*) from the South China Sea. Marine Pollution Bulletin 42: 780-786.

Perier, 1994. La fauna ictica en el litoral de la Bahía de San Antonio (Golfo San Matías, Provincia de Río Negro). Dissertation, Facultad de Ciencias naturales y Museo, Universidad Nacional de La Plata, Argentina.

Perier, M.R. and Di Giacomo, E.E. 2002. El savorin Seriolella porosa como un recurso estacional en el Golfo San Matías, Republica Argentina. Revista de Investigación de Desarrollo Pesquero 15: 15-26.

Roditi-Elasar, M., Kerem, D., Hornung, H., Kress, N., Shoham-Frider, E., Goffman, O., Spanier, E. 2003. Heavy metal levels in bottlenose and striped dolphins off the Mediterranean coast of Israel. Marine Pollution Bulletin 46: 503-512.

Rosenzweimg, L. 1981. A theory of habitat selection. Ecology 62: 327-335.

Shane, S.H. 1990. Behaviour and ecology of the bottlenose dolphin at Sanibel Island, Florida. *In:* Leatherwood, S. and Reevers, R.R. (Eds.), The Bottlenose Dolphin. Academic Press, San Diego, CA, pp. 245-266.

Scott, M.D., Wells, R.S., Irvine, A.B. 1996. Long-term studies of bottlenose dolphins in Florida. IBI Rep 6: 73–80.

Siegel, S. and Castellan, N.J. 1995. Estadística no paramétrica aplicada a la ciencia de la conducta. 4 Edición, México.

Sitters, H.P., González, P.M., Piersma, T., Baker, A.J., Price, D.J. 2001. Day and night feeding habitat of Red Knots in Patagonia: Profitability versus safety? Journal of Field Ornithology 72: 86-95.

StatSoft, Inc. 2004. STATISTICA (data analysis software system), version 7. www.statsoft.com.

Stavros, H.C.W., Bossart, G.D., Hulsey, T.C., Fair, P.A. 2007. Trace element concentrations in skin of free-ranging bottlenose dolphins (*Tursiops truncatus*) from the southeast Atlantic coast. Science of the Total Environment 388: 300-315.

Vázquez-Medina, J.P., Cantu-Medellin, N., Medina-Rodriguez, M., Mendez-Rodriguez, L.C., Zenteno-Savin, T. 2007. Oxidative stress indicators and heavy metal levels in bottlenose dolphin (*Tursiops truncatus*) tissues from Bahía de La Paz, Mexico. Free Radical Biology and Medicine 43: S123.

Vermeulen, E. and Cammareri, A. 2009. Residency Patterns, Abundance and Social composition of Bottlenose Dolphins (*Tursiops truncatus*) in Bahía San Antonio, Patagonia, Argentina. Aquatic Mammals 35: 379-386.

Vermeulen, E., Balbiano, A., Belenguer, F., Colombil, D.J., Failla, M., Intrieri, E., Bräger, S. submitted a. Limited ranging patterns of a highly mobile marine species: conservation implications for bottlenose dolphins (*Tursiops truncatus*) in Argentina. Biodiversity and Conservation.

Vermeulen, E. and Bräger, S. submitted Demographics of the disappearing bottlenose dolphin in Argentina: a common species on its way out? PLoS-One.

Vermeulen, E., Holsbeek, L., Das, K. submitted b. Diurnal and seasonal activity budgets of bottlenose dolphins (*Tursiops truncatus*) in Bahía San Antonio, Patagonia, Argentina. Mammalian Biology.

Waples, D.M. 1995. Activity budgets of free-ranging bottlenose dolphins (*Tursiops truncatus*) in Sarasota Bay, Florida. Dissertation, University of California Santa Cruz, USA.

Wilson, B., Thompson, P.M., Hammond, P.S. 1997. Habitat use by bottlenose dolphins: seasonal distribution and stratified movement patterns In Moray Firth, Scotland. Journal of Applied Ecology 34: 1365-1374.

Würsig, B. and Würsig, M. 1979. Behaviour and ecology of bottlenose porpoises, *Tursiops truncatus*, in the South Atlantic. Fishery Bulletin 77: 399-442.

Zar, J.H. 1996. Biostatistical analysis (3rd ed.). Upper Saddle River, Prentice Hall, NJ.

8

RESIDENCY AND MOVEMENTS

After

*Vermeulen, E., Balbiano, A., Belenguer, F., Colombil, D.J., Failla, M., Intrieri, E., Bräger, S. submitted. Limited ranging patterns of a highly mobile marine species: conservation implications for bottlenose dolphins (*Tursiops truncatus*) in Argentina. Biodiversity and Conservation.*

*Failla, M., Seijas, V., Vermeulen, E. in press. Occurrence of bottlenose dolphins (*Tursiops truncatus*) in the Río Negro Estuary, Argentina, and their mid-distance movements along the Northeast Patagonian coast. Latin American Journal of Aquatic Mammals.*

Vermeulen, E. and Cammareri, A. 2009. Variation in external morphology of resident bottlenose dolphins in Bahía San Antonio, Patagonia, Argentina. Journal of Marine Animals and Their Ecology Vol2 N°2.

1. RESIDENCY AND RANGING PATTERNS

After

*Vermeulen, E., Balbiano, A., Belenguer, F., Colombil, D.J., Failla, M., Intrieri, E., Bräger, S. submitted. Limited ranging patterns of a highly mobile marine species: conservation implications for bottlenose dolphins (*Tursiops truncatus*) in Argentina. Biodiversity and Conservation.*

ABSTRACT – Highly mobile marine species, such as the bottlenose dolphin (*Tursiops truncatus*), can show significant population structuring over short geographical distances, affecting their population viability and conservation status. Coastal bottlenose dolphins in central Argentina were recently classified as an Evolutionary Significant Unit within the larger Southwestern Atlantic (Fruet et al., 2014; Appendix 1). Additionally, severe population declines have been reported for this area, revealing the need for a better understanding and more accurate conservation measures. Therefore, fine-scale population structures were identified through the analysis of residency and ranging patterns. A community of bottlenose dolphins displayed a year-round site-fidelity in Bahía San Antonio while ranging up to 200 km along the northern coastline of the San Matías Gulf (SMG). Although the species is capable of covering larger distances, ranging patterns of this community to the north did not appear to extend beyond this distance. Therefore, the existence of a separate community in the south of the Province of Buenos Aires is proposed. Environmental discontinuities between two adjacent oceanic regimes in SMG and El Rincón are hypothesised to promote their co-existence. Although genetic differentiation and connectivity remains undetermined, these results call for caution when making assumptions about the degree of genetic connectivity along the country's coastline. At this stage, it is suggested that the two communities in central Argentina are to be viewed as distinct ecological management units.

KEYWORDS - bottlenose dolphin, communities, conservation strategies, ranging patterns, population structure, residency, site-fidelity

1.1. INTRODUCTION

All individuals of a species that interact with each other in overlapping home ranges and share aspects of their residency and association patterns are defined as a community (Goodall, 1986; Wells, 1986). Communities are not necessarily closed demographic units, however, as gene flow may occur across community boundaries (Wells, 1986; Connor et al., 2000). Assessing residency patterns may thus help to identify distinct communities and to reveal trends between them (Würsig and Jefferson, 1990).

Despite the social fluidity of bottlenose dolphins and their potential for long distance dispersal (e.g., Wells et al., 1990; Würsig and Harris, 1990), Natoli et al. (2004) indicated the high potential for speciation of the genus *Tursiops* based on high levels of genetic differentiation between regional populations. Indeed, coastal bottlenose dolphins are increasingly reported to show significant population structuring over short geographical distances (e.g., Wells, 1986; Hoelzel et al., 1998; Chilvers and Corkeron, 2001; Rosel et al., 2009). Such revelations of significant population differentiation of this highly mobile species have major conservation management implications and reveal the need for accurate and detailed information of the species in any given region.

Although being among the best-studied dolphin species in the world, information about the structures of bottlenose dolphin populations in the Southwestern Atlantic is extremely limited (Fruet et al., 2014; Appendix 1). Such information on population fragmentation and connectivity, however, is essential for the identification and conservation of relevant biological units. A preliminary description of the population structure of coastal bottlenose dolphins in the Southwestern Atlantic was prepared for the late 1980s and - based on their morphology - suggested the existence of two coastal populations (Bastida and Rodríguez, 2003). A northern population was described to range along the coasts of Southern Brazil, Uruguay and the Province of Buenos Aires (Argentina). It included a resident community of about 100 individuals, known to reside in the region of Mar del Plata with a range extending to Bahía Samborombón (Figure 3; Bastida and Rodríguez, 2003). A southern population was reported to range along the coast of the Province of Chubut and included a resident community of at least 53 individuals in the San José Gulf in Península Valdés (Figure 3; Würsig and Würsig, 1977).

A recent genetic study indicated that the proposed population differentiation within Argentine coastal waters was still accurate, as sampled individuals from southern and northern populations are genetically very different in both mitochondrial and nuclear DNA markers (P. Fruet, unpublished data). This is also reflected in their distinct morphology (Bastida and Rodríguez, 2003; Vermeulen and Cammareri, 2009b). Additionally, the coastal bottlenose dolphins of central Argentina were classified as a distinct ESU when compared to those of Southern Brazil and Uruguay (Fruet et al., 2014; Appendix 1; for definitions see Funk et al., 2012).

Within Argentina, however, bottlenose dolphins have been described as nearly vanished from the coasts of the Provinces of Buenos Aires and Chubut since the 1980s (Bastida and Rodríguez, 2003;

Coscarella et al., 2012). Only infrequent and isolated observations are reported nowadays for areas where they were once very common, suggesting already an apparent population fragmentation in the country (Bahía Samborombón: Bastida and Rodríguez, 2003; Península Valdés: Coscarella et al., 2012; Bahía Engaño: Coscarella and Crespo, 2009; Figure 3). Consequently, Bahía San Antonio (Province of Río Negro) was recently suggested to be home to one of the last remaining resident communities of the country (Vermeulen and Cammareri, 2009a; Vermeulen and Bräger, submitted). However, this community was reported to be small and highly vulnerable (Vermeulen and Bräger, submitted). Although bottlenose dolphins in central Argentina were classified as a separate ESU in the larger Southwestern Atlantic, the local population structure within this region remains unclear. The present study aims to provide insight into the residency and site-fidelity of the bottlenose dolphins in Bahía San Antonio as well as into their ranging patterns connecting them with other regions. Photographic mark-recapture data are a powerful tool to identify distinct communities and to reveal connections among them (Würsig and Jefferson, 1990). This assessment is therefore believed to be essential for continued research on the fine-scale population structure of bottlenose dolphins in this region and to provide critical information for the design of effective management plans within Argentina.

1.2. MATERIALS AND METHODS

1.2.1 Sites of opportunistic photo-identification

Photo-identification data were collected opportunistically in several sites other than BSA, briefly introduced in the following (Figure 17):

The Río Negro Estuary (RNE, 41°04' S, 63°50' W) is an area with turbid waters, islands, sandbars, channels and saltmarshes, located at the north-eastern border of the SMG. The Río Negro river discharges into this region and politically separates the Provinces of Buenos Aires and Río Negro from each other.

Bahía San Blas (BSB, 40°40’ S, 62°10’ W) is located in the most southern part of the Province of Buenos Aires. It is a coastal marsh zone that also includes a group of five islands and sand embankments. The water in the area is turbid as it is influenced by the sediments and freshwater from the Río Colorado river. The area is famous for its fishing activities, related to a high productivity in the area (Lucifora, 2003). The targeted species include large sharks such as grey nurse shark (*Carcharias taurus*), copper shark (*Carcharhinus brachyurus*), school shark (*Galeorhinus galeus*) and the broadnose sevengill shark (*Notorynchus cepedianus*) (Lucifora, 2003).

Bahía Blanca Estuary (BBE, 39°25’ S, 61°15’ W) is located in the south of the Province of Buenos Aires. It is a large and complex estuary system with periods of high freshwater inflow from the Río Colorado river (Piccolo and Perillo, 1990) and mean tidal amplitude of approx. 2 m (Servício Hidrografía Naval de Argentina). It is the second largest deep-water port and biggest petrochemical pole of Argentina, and the second largest but most complex estuary system in the country. A large number of channels separated by islands and wide tidal flats give it physical characteristics that vary significantly from all other estuary systems in South America (Picolo and Perillo, 1990).

BSA, RNE, BSB and BBE are located in two different oceanographic regimes, delineated by salinity distributions (Lucas et al., 2005):

(1) El Rincón estuary system (Figure 17) separates an area extending from the RNE up to BBE, with low salinity year-round (approx. 30 ppm) due to the influxes of the Río Negro and Río Colorado rivers. Overall, the waters in this region are homogenous and turbid, due to the large mixing produced by river discharge and tides (Ancha et al., 2004; Sardiña 2004). Additionally, the characteristics of these waters differ so much from to those of the adjacent waters north and south that it is frequently referred to as the 'El Rincón Front' (Piola and Rivas, 1997; Volpedo and Cirelli, 2006).

(2) San Matías Gulf: a gulf (including BSA) with high salinity year-round (> 34 ppm) as the result of a combined effect of net evaporation and increased residence time caused by decreased advection imposed by the geomorphology of the area (Scasso and Piola, 1988; Rivas and Beier, 1990; Lucas et al., 2005). Due to its isolation, the waters in the gulf are typically warmer than adjacent waters (Krepper and Bianchi, 1982). The gradient in salinity and SST creates a density field which separates the denser waters of the SMG from adjacent less dense waters from the El Rincón region and CSW (Lucas et al., 2005). There is, however, a seasonal variation in its surface extension. During winter and autumn, the regime of the SMG extends across almost the entire El Rincón area. During spring and summer, however, the influence of the gulf waters diminishes and allows the expansion of the El Rincón estuarine low salinity signal. This latter is caused primarily by an increased discharge from the Río Negro and Río Colorado streams (Lucas et al., 2005).
In the SMG, tidal currents are known to be larger than the residual currents. Consequently, there is and increasing tendency towards stratification of the water column (Moreira et al., 2011). The currents increase in strength towards the northeast and southeast parts of the mouth of the gulf, where the tide appears to have enough kinetic energy to overcome stratification and produce a tidal front (Moreira et al., 2011). In the northeast, this tidal front extends from the RNE up the area of BSB (Bogazzi et al., 2005; Moreira et al., 2011). Such a tidal front it is known to be related to high primary production (Sabatini, 2004; Pisoni and Rivas, 2006; Romero et al., 2006), and is often used by marine top predators (Mendes et al., 2002) such as bottlenose dolphins and sharks for foraging.

1.2.2 Opportunistic survey effort

A total of 4,356 opportunistic photo-identification pictures were obtained outside of BSA, of which 110 were taken in BBE, 46 in BSB and 4,200 in RNE (Figure 17). The number of opportunistic daily surveys of unknown duration during which these pictures were gathered is shown in Table 13.

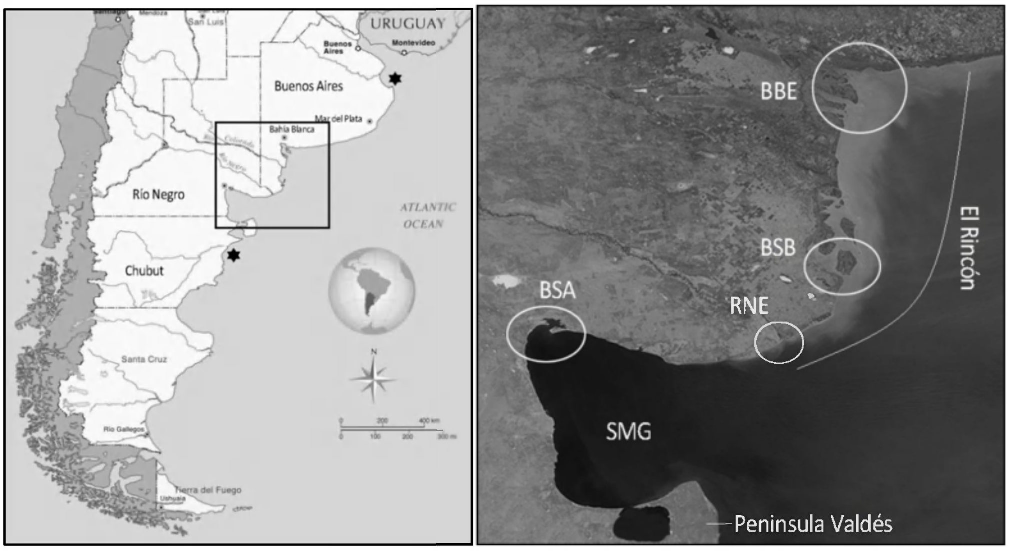

Figure 17 - Map indicating the primary study area BSA and locations where additional photo-identification data were obtained: Río Negro Estuary (RNE), Bahía San Blas (BSB) and Bahía Blanca Estuary (BBE). The geographical extent of the oceanographic regimes El Rincón and San Matías Gulf (SMG) is indicated. Distances along the coastline: BSA – RNE: approx. 200 km; RNE –BSB: approx. 90 km; BSB –BBE: approx. 180 km. Additional localities where bottlenose dolphins can be observed, although only rarely and in low numbers, are indicated with a star (i.e., Bahía Samborombón (in the Northeast), Península Valdés and Bahía Engaño (in the South))

Table 13 – Total opportunistic photo-identification surveys of unknown duration conducted in the Río Negro Estuary (RNE), Bahía San Blas (BSB) and Bahía Blanca Estuary (BBE) over the seasons

	Summer			Autumn			Winter			Spring		
	BBE	BSB	RNE	BBE	BSB	RNE	BBE	BSB	RNE	BBE	BSB	RNE
2007						3						
2008			1			4				1		
2009				2		3	1			1		
2010			2	1		22			2	1		
2011						11	1					
2012	1			1		4	1					
2013				1	1			1		2	1	
TOTAL	1	0	3	5	1	47	3	1	2	5	1	0

1.2.3 Analysis

Categories of residency were adapted from definitions by Zolman (2002) as (1) residents: dolphins identified in the study area during all four seasons (regardless of year, i.e., not necessarily in consecutive seasons), (2) partial residents: dolphins identified in the study area in 2 or 3 seasons in each of the study years, (3) transients: dolphins identified on various occasions but always in the same season in some of the study years. Dolphins seen only once or twice during the entire study were defined as non-residents. Furthermore, the proportion of months with survey effort (with a minimum of three fieldtrips) in which an individual was photo-identified was calculated. This was referred to as a Residency Index (RI) (Koelsh, 1997; Simões-Lopes and Fabian, 1999; Quintana-Rizzo and Wells, 2001; Lusseau, 2005; Lodi et al., 2008) and was calculated for each individual dolphin. This proportion was considered as high between 1 and 0.7, as moderate between 0.6 and 0.4 and as low when < 0.4 (Simões-Lopes and Fabian, 1999).

Ranging patterns were assessed through the re-identification of individuals in different regions. In order to assess the extent of movements, the distance along the coastline between the different locations were measured using ESRI ArcGIS 10.1.

All statistical analyses were conducted using the software *Statistica 7.0* (StatSoft, Inc. 2004) as well as Zar (1996).

1.3. RESULTS

1.3.1 Residency patterns in Bahía San Antonio

Almost all individuals (98%) of the identification catalogue (n = 67; Appendix 2) were observed at least once every year (2007 – 2011) in the study area after their initial identification. According to the definitions used, 38 individuals (57%) were classified as residents, 22 (33%) as partial residents and 6 (9%) individuals as transients present only during the winter season. Only one individual was never re-identified and thus defined as a non-resident, although it could not be excluded the animal had died. The Residency Index (RI) for all identified dolphins in the study area (n = 67; 2007 - 2011) had a median of 0.24 (Q1 = 0.11; Q3 = 0.36; ranging between 0 and 0.56), with no significant difference among research years (Table 14: Kruskal-Wallis: $p = 0.6$). Overall, the RI for 12 individuals was considered moderate (18% of identified individuals consisting of 6 reproducing females, 3 adult males and 3 adults of unknown sex), whereas the RIs for all other individuals were considered low, i.e., sighted in less than 40% of the surveyed months.

Table 14 - Median Residency Index of the identified bottlenose dolphins in BSA, including quartile values (2007 – 2011). n = number of dolphins in the identification catalogue

	Median (Q2)	Q1	Q3	n
2007	0.20	0.10	0.40	44
2008	0.21	0.11	0.33	61
2009	0.30	0.10	0.40	64
2010	0.22	0.11	0.44	66
2011	0.29	0.14	0.43	67

When summing up respective seasons, individual dolphins were significantly more often present in winter than in any other season (Kruskal-Wallis: $p < 0.01$). In total, 28 individuals (43% of the total number of identified individuals), were present in the study area during each winter season since their first identification. Another 13 individuals were present in the study area during all but one winter season since their first identification. Only two individuals were seen in only one winter season since their first identification (although more would have been possible). These data clearly indicate a high return rate of bottlenose dolphins to BSA in winter.

Immatures were significantly less often re-sighted in the study area than the adults (adults: median RI = 0.24; Q1 = 0.13; Q3 = 0.36; n = 57; immatures: median RI = 0.11; Q1 = 0.1; Q3 = 0.2; n = 10; Mann-Whitney U test: U = 147.5; *p* < 0.01), a difference that remained significant over all the different seasons. Although females associated with dependent calves appeared to be more frequently sighted in the study area (median RI = 0.36; Q1 = 0.18; Q3 = 0.43; n = 14), there was no significant difference from all other adults (median RI = 0.24; Q1 = 0.14; Q3 = 0.36; n = 43) (Mann-Whitney U test: U = 210.5; *p* = 0.16). However, only in summer and autumn, females associated with calves were significantly more often present than all other adults (summer: Mann-Whitney U test: U 90; *p* < 0.05; autumn: Mann-Whitney U test: U = 183; *p* < 0.05; Figure 18).

Reproducing females were not significantly more often present in the study area in the years they gave birth (Mann-Whitney U test: U = 429.5; *p* = 0.9).

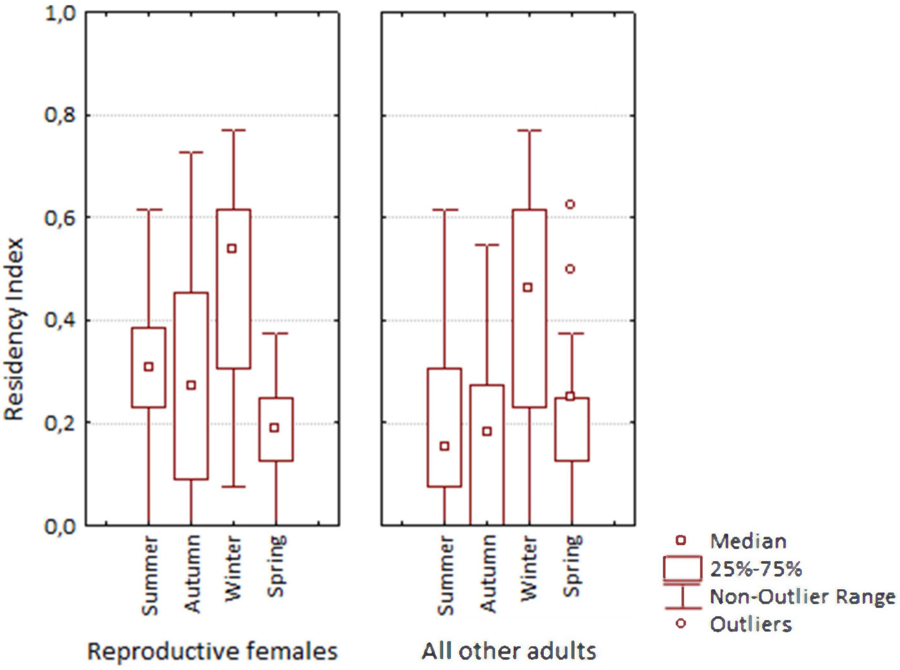

Figure 18 - Median Residency Index for the reproducing female bottlenose dolphins (n = 14) vs. all other adult dolphins (n = 43) in BSA across the seasons (2007 - 2011)

1.3.2 Ranging patterns

In BBE, opportunistic photographs allowed for the identification of 17 individual bottlenose dolphins. One of these could be re-identified in three different years within BBE and another one was re-identified in BSB.

In BSB, opportunistically taken photographs allowed for the identification of two new individuals and the re-identification of three others. Of the latter, one individual was previously identified in BBE and the other two were previously identified in BSA and RNE (both adults of unknown sex defined as partial residents in BSA).

In RNE, opportunistically taken photographs allowed for the identification of one individual (seen only once) as well as the re-identification of 20 individual dolphins previously identified in BSA. The majority of these re-identifications occurred in autumn, the season commonly known for increased bottlenose dolphin sightings in this region. Most of these (n = 17) were subsequently re-identified on various occasions in both areas, with a minimum difference of 8 days between sightings in both areas. Three of these individuals were reproductive females with associated calves, four were adult males and one individual was an older non-reproductive female. All other individuals were adults of unknown sex. Eight of the individuals were classified as year-round residents in BSA, 10 as partial residents (of which two were also re-identified in BSB) and two as transients. Figure 19 provides an overview.

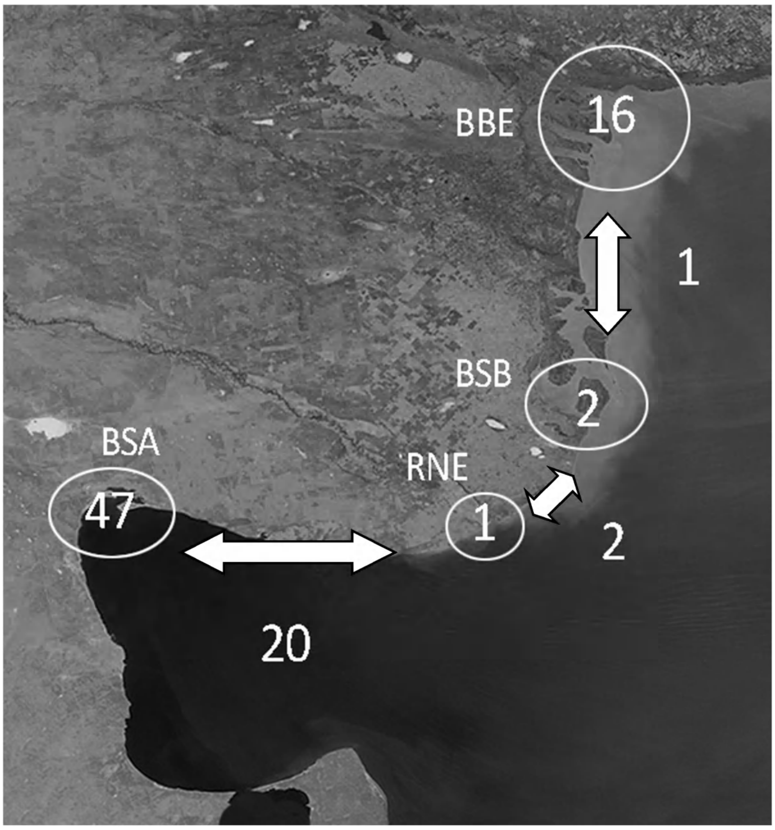

Figure 19 - Connectivity among the study areas. Encircled numbers indicate the number of identified individuals unique to each area (individuals never re-identified in any other area). The numerals next to the arrows indicate the number of individuals known to have ranged between the two adjacent areas. Note that the two individuals ranging between RNE and BSB also ranged to BSA

1.4. DISCUSSION

1.4.1 Residency

Bottlenose dolphins living in protected coastal environments are often reported to display a high degree of residency and long-term site-fidelity, while belonging to relatively small communities (e.g., Wells et al. 1987; Bearzi et al. 2008). Gowans et al. (2008) predicted that the residency of dolphins in relatively small areas is caused by spatially and temporally predictable resource availability. Such is the case in Bahía San Antonio, indicating that it may be the core habitat within a larger home range.

The dolphins' tendency to reside in BSA appeared to be consistent with the local predictable fluctuation in prey abundance and availability. Many bottlenose dolphin populations living in cold waters are known to migrate seasonally, apparently to avoid waters below their thermo-neutral zone (e.g., True, 1890; Mead, 1975; Mead and Potter, 1990; Barco et al., 1999; Zolman, 2002; Torres et al., 2005) (defined as the temperature range within which they spend little or no energy to maintain their core temperature; Schmidt-Nielsen, 1990). However, dolphins in BSA could clearly compensate for the increased energetic requirements in winter caused by the low SST most likely due to the availability of sufficient prey (Barco et al., 1999). Despite the overall residency decreasing in summer and autumn when prey is less densely distributed and more limited (Perier, 1994), females with calves had the highest tendency to remain in the area. Female mammals are known to be more likely to remain philopatric as they benefit more than males from a familiarity with surrounding food resources (Greenwood, 1980) for reasons of energetic efficiency (Sandell, 1989). Furthermore, as predation on bottlenose dolphins appears to concentrate on females and calves (Corkeron et al., 1987), female philopatry to sheltered areas may improve reproductive success. The females' decreasing tendency to remain resident in spring, the population's mating season (Vermeulen and Bräger, submitted), may be related to an avoidance behaviour towards males, sometimes known to harass females (Connor et al., 2000) and even kill calves (e.g., Patterson et al., 1998; Dunn et al., 2002; Möller and Beheregaray, 2004).

Contrary to mothers with calves, immature dolphins appeared more to range outside of this core habitat, as is the case in many young mammals (Greenwood, 1980). However, as immatures often have fewer marks, their identification is more difficult. Therefore, no strong conclusion can be drawn from the residency or movement patterns of younger, poorly marked individuals.

1.4.2 Ranging patterns

This community of bottlenose dolphins appears to range along the entire northern coastline of the SMG to the RNE (approx. 200 km). Survey effort in the RNE revealed the ranging pattern to be consistent with the seasonal migration of potential prey species out of BSA (Perier, 1994). Furthermore, it appears to coincide with an increased influence of the SMG regime over the El Rincón regime (Lucas et al., 2005). Return rates of identified individuals indicate long-term site fidelity to both areas, a characteristic found in many other coastal bottlenose dolphin populations (e.g., Wells et al., 1987; Smolker et al., 1992; Maze-Foley and Würsig, 2002) (see Chapter 8 - 2 for further information).

The recorded ranging distances to the north appear to be limited for this high mobile species capable to range over 500 km (Wells et al., 1990; Mate et al., 1995; Defran and Weller, 1999; Hwang et al., 2014) or even >1,000 km (Wood, 1998; Wells et al., 1999). As such, despite an apparent continuous distribution of the species in this region, this community seems to be largely isolated from an adjacent community inhabiting the region of El Rincón. So far, it remains undetermined what may be the underlying factor promoting the formation of this population structure of bottlenose dolphins in central Argentina. However, ranging patterns and population structures of mobile marine species, including bottlenose dolphins, are known to be influenced by environmental discontinuities (Mendez et al., 2011). As the dispersal of coastal bottlenose dolphins residing in embayments is often restricted (Krützen et al., 2004; Sellas et al., 2005; Parsons et al., 2006; Möller et al., 2007), their population structure may be dependent on the type of environment they inhabit (Wiszniewski et al., 2010). Hoelzel (1998) suggested that successful adaptations of coastal bottlenose dolphins to local ecological conditions and resources can lead to increased site-fidelity and potentially may be an evolutionary mechanism to promote fine-scale population structures. Therefore, it is presumed that the environmental discontinuities between the two adjacent oceanographic regimes may play an important role.

The observed ranging pattern of two individuals (possibly males due to the lack of an accompanying calf) raises doubts regarding the genetic connection of the two communities. In most mammal species, males tend to disperse farther (Greenwood, 1980). In many bottlenose dolphin populations, sporadic forays of individuals outside their core areas have been observed, possibly promoting genetic exchange between adjacent dolphin communities (Wells, 1991; Möller et al., 2002). Dispersal appears advantageous for males when their breeding prospects are greater in other areas and/or when the likelihood of inbreeding is reduced (Dobson, 1982; Dobson and Jones, 1985). In some resident populations of bottlenose dolphins, males and females appear to display the same levels of natal site philopatry (Wells, 1991; Connor et al., 2000). However, other studies contradict this hypothesis of bisexual natal philopatry for the species (Möller and Beheregaray, 2004; Bearzi et al., 2010). It is believed that a very limited genetic exchange is sufficient to prevent the development of separate units (Perrin and Mazalov, 1999), and that this exchange usually remains undetected by a photo-identification study. On the other hand, the community of bottlenose dolphins in the SMG shows an extremely low genetic diversity (Fruet et al., 2014; Appendix 1). This finding supports the unlikelihood of genetic exchange between the two communities. Additionally, or alternatively, it might suggest that only a low number of females reproduce successfully in the community of SMG thus effectively constituting a genetic bottleneck. This is a disconcerting possibility also pointed out by Vermeulen and Bräger (submitted).

Several genetic studies around the world have reported some genetic differentiation among regional populations of bottlenose dolphins, despite some reproductive exchange (e.g., Sellas et al., 2005; Rosel et al., 2009; Tezanos-Pinto et al., 2009; Urian et al., 2009; Mirimin et al., 2011). Therefore, regardless of the possible reproductive connectivity between these two communities, the observed division and low reported genetic diversity of the bottlenose dolphins inhabiting the SMG (Fruet et al., 2014; Appendix 1) stresses the importance of population structure in conservation management.

1.4.3 Conservation implications

Recent studies in Argentina (e.g., Vermeulen and Cammareri, 2009b; Coscarella et al., 2012; Fruet et al., 2014; this study) reveal a progressive population fragmentation for the species within the country, possibly limiting the gene flow needed for the long-term survival of small populations. Due to a lack of continuous research, no information is available about the underlying causes of the reported bottlenose dolphin population declines in the country (Coscarella et al., 2012). It can be hypothesised, however, that any population fragmentation, whether occurring naturally or induced by anthropogenic activities, would have aggravated the effects of local anthropogenic pressures on the marine environment. Furthermore, a lack of knowledge may have led to the ineffectiveness of previous marine conservation measures to preserve the bottlenose dolphin in Argentina (e.g., the creation of Marine Protected Areas; Campagna et al., 2007). Based on the presented findings, the two described communities need to be viewed as distinct ecological management units for conservation management. Further detailed research on the fine-scale population structure of bottlenose dolphins in Argentina is necessary for an accurately evaluated and newly implemented conservation strategy to ensure the survival of the species in this country.

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1.5. REFERENCES

Ancha, E.M., Mianzan, H.W., Guerrero, R.A., Favero, M., Bava, J. 2004. Marine fronts at the continental shelves of austral South America. Physical and ecological processes. Journal of Marine Systems 44: 83-105.

Barco, S.G., Swingle, W.M., Mellan, W.A., Harris, R.N., Pabst, D. 1999. Local abundance and distribution of bottlenose dolphins (*Tursiops truncatus*) in the nearshore waters of Virginia Beach, Virginia. Marine Mammal Science 15: 394-408.

Bastida, R. and Rodríguez, D. 2003. Mamíferos Marinos Patagonia Antartida. Vázquez Mazzini Editors, Buenos Aires, Argentina, 206 pp.

Bearzi, G., Agazzi, S., Bonizzoni, S., Costa, M., Azzellino, A. 2008. Dolphins in a bottle: Abundance, residency patterns and conservation of common bottlenose dolphins *Tursiops truncatus* in the semi-closed eutrophic Amvrakikos Gulf, Greece. Aquatic Conservation: Marine and Freshwater Ecosystems 18: 130-146.

Bearzi, G., Bonizzoni, S., Gonzalvo, J. 2010. Mid-distance movements of common bottlenose dolphins in the coastal waters of Greece. Journal of ethology 29: 369-374.

Bogazzi, E., Baldoni, A., Rivas, A., Martos, P., Reta, R., Orenzanz, J.M., Lasta, M., Dell'Arciprete, P., Werner, F. 2005. Spatial correspondence between areas of concentration of Patagonian scallop (*Zygochlamys patagonica*) and frontal systems in the Southwestern Atlantic. Fisheries Oceanography 14: 359-376.

Campagna, C., Falabella, V., Tagliorette, A., Sapoznikow, A., Quintana, F. 2007. El mar des-protegido: Zonificación y conservación de la biodiversidad. *In*: Boltovskoy, D. (Ed.), Atlas de sensibilidad ambiental de la costa y el Mar Argentino. www.atlas.ambiente.gov.ar

Chilvers, B.L. and Corkeron, P.J. 2001. Trawling and bottlenose dolphins' social structure. Proceedings of the Royal Society of London. Series B: Biological Sciences 268: 1901-1905.

Connor, R.C., Wells, R.S., Mann, J., Read, A.J. 2000. The bottlenose dolphin: Social relationships in a fission-fusion society. *In*: Mann, J., Connor, R.C., Tyack, P.L., Whitehead, H. (Eds.), Cetacean societies: Field studies of dolphins and whales. University of Chicago Press, Chicago, IL, pp 91-126.

Corkeron, P.J., Morris, R.J., Bryden, M.M. 1987. Interactions between bottlenose dolphins and sharks in Moreton Bay, Queensland. Aquatic Mammals 13: 109-113.

Coscarella, M.A. and Crespo, E.A. 2009. Feeding aggregation and aggressive interaction between bottlenose (*Tursiops truncatus*) and Commerson's dolphins (*Cephalorhynchus commersonii*) in Patagonia, Argentina. Journal of Ethology 28: 183-187.

Coscarella, M., Dans, S.L., Degrati, M., Garaffo, G.V., Crespo, E.A. 2012. Bottlenose dolphins at the southern extreme of the Southwestern Atlantic: local population decline? Journal of the Marine Biological Association of the United Kingdom 92: 1843-1849.

Defran, R.H. and Weller, D.W. 1999. The occurrence, distribution, and site fidelity of bottlenose dolphins (*Tursiops truncatus*) in San Diego, California. Marine Mammal Science 15: 366-380.

Dobson, F.S. 1982. Competition for mates and predominant juvenile mate dispersal in mammals. Animal Behaviour 30: 1183-1192.

Dobson, F.S. and Jones, W.T. 1985. Multiple causes of dispersal. The American Naturalist 126: 855-858.

Dunn, D.G., Barco, S.G., Pabst, D.A., McLellan, W.A. 2002. Evidence for infanticide in bottlenose dolphins of the Western North Atlantic. Journal of Wildlife Diseases 38: 505-510.

Failla, M., Seijas, V.A., Vermeulen, E. in press. Occurrence of Bottlenose dolphins (*Tursiops truncatus*) in the Río Negro Estuary, Argentina, and their mid-distance movements along the Northeast Patagonian coast. Latin American Journal of Aquatic Mammals.

Fruet, P., Secchi, E.R., Daura-Jorge, F., Vermeulen, E., Flores, P.A.C., Simões-Lopes, P.C., Genoves, R.C., Laporta, P., Di Tullio, J.C., Freitas, T.R., Dalla Rosa, L., Valiati, V.H., Behereharay, L.B., Möller, L.M. 2014. Remarkably low genetic diversity and strong population structure in common bottlenose dolphins (*Tursiops truncatus*) from coastal waters of the Southwestern Atlantic Ocean. Conservation Genetics DOI: 10.1007/s10592-014-0586-z.

Funk, W.C., McKay, J.K., Hohenlohe, P.A., Allendorf, F.W. 2012. Harnessing genomics for delineating conservation units. Trends in Ecology and Evolution 27: 489-496.

Goodall, J. 1986. The chimpanzees of Gombe: Patterns of behavior. The Belknap Press of Harvard University Press, Cambridge, MA.

Gowans, S., Würsig, B., Karczmarski, L. 2008. The social structure and strategies of Delphinids: predictions based on an ecological framework. Advances in Marine Biology 53: 195-294.

Greenwood, P.J. 1980. Mating systems, philopatry and dispersal in birds and mammals. Animal Behaviour 28: 140-162.

Hoelzel, A.R. 1998. Genetic structure of cetacean populations in sympatry, parapatry, and mixed assemblages: implications for conservation policy. Journal of Heredity 89: 451-458.

Hoelzel, A.R., Potter, C.W., Best, P.B. 1998. Genetic differentiation between parapatric 'nearshore' and 'offshore' populations of the bottlenose dolphin. Proceedings of the Royal Society of London. Series B: Biological Sciences 265: 1177-1183.

Hwang, A., Defran, R.H., Bearzi, M., Maldini, D., Saylan, C.A., Lang, A.R., Dudzik, K.J., Guzón-Zatarain, O.R., Kelly, D.L., Weller, D.W. 2014. Coastal range and movements of common bottlenose dolphins off California and Baja California, Mexico. Bulletin of the Southern California Academy of Sciences 113: 1-13.

Koelsh, J.K. 1997. The seasonal occurrence and ecology of Florida manatees (*Trichechus manatus latirostris*) in coastal waters near Sarasota, Florida. Dissertation, University of South Florida, Tampa, 121 pp.

Krepper, C.M. and Bianchi, A. 1982. Balance Cal6rico del Mar Epicontinental Argentino. Acta Oceanográfica, Argentina 3: 1-7.

Krützen, M, Sherwin, W.B., Berggren, P., Gales, N. 2004. Population structure in an inshore cetacean revealed by microsatellite and mtDNA analysis: bottlenose dolphins (*Tursiops sp.*) in Shark Bay, Western Australia. Marine Mammal Science 20: 28-47.

Lodi, L., Wedekin, L., Rossi-Santos, M.R., Marcondes, M.C. 2008. Movements of the bottlenose dolphin (*Tursiops truncatus*) in the Rio de Janeiro State, Southeastern Brazil. Biota Neotropica 8: 205-209. Available on CJO 2011 DOI:10.1590/S1676-06032008000400020.

Lucas, A.J., Guerrero, R.A., Mianzán, H.W., Acha, E.M., Lasta, C.A. 2005. Coastal oceanographic regimes of the Northern Argentine Continental Shelf (34-43°S). Estuarine, Coastal and Shelf Science 65: 405-420.

Lucifora, L.O. 2003. Ecología y conservación de los grandes tiburones costeros de Bahía Anegada, Provincia de Buenos Aires, Argentina. Dissertation, University of Mar del Plata, Argentina, 410 pp.

Lusseau, D. 2005. Residency pattern of bottlenose dolphins Tursiops spp. in Milford Sound, New Zealand, is related to boat traffic. Marine Ecology Progress Series 295: 265-272.

Mate, B.R., Rossbach, K.A., Nieukirk, S.L., Wells, R.S., Irvine, A.B., Scott, M.D., Read, A.J. 1995. Satellite-monitored movements and dive behavior of a bottlenose dolphin (*Tursiops truncatus*) in Tampa Bay, Florida. Marine Mammal Science 11: 452–463.

Maze-Foley, K. and Würsig, B. 2002. Patterns of social affiliation and group composition for bottlenose dolphins (*Tursiops truncatus)* in San Luis Pass, Texas. Gulf of Mexico Science 20: 122-134.

Mead, J.G. 1975. Preliminary report on the former net fisheries for *Tursiops truncatus* in the western North Atlantic. Journal of Fisheries Research Board Canada 32: 1155-1160.

Mead, J.G. and Potter, C.W. 1990. Natural History of bottlenose dolphins along the central Atlantic coast of the United States. *In:* Leatherwood, S. and Reeves, R.R. (Eds.), The Bottlenose Dolphin. Academic Press, San Diego, CA, pp. 165-195.

Mendes, S.*,* Turrell, W., Lüktebohle, T., Thompson, P. 2002. Influence of the tidal cycle and a tidal intrusion front on the spatio-temporal distribution of coastal bottlenose dolphins. Marine Ecology Progress Series 239: 221-229.

Mendez, M., Subramaniam, A., Collins, T., Minton, G., Baldwin, R., Berggren, P., Särnblad, A., Amir, O.A., Peddemors, V.M., Karczmarski, L., Guissamulo, A., Rosenbaum, H.C. 2011. Molecular ecology meets remote sensing: environmental drivers to population structure of humpback dolphins in the Western Indian Ocean. Heredity 107: 349-361.

Mirimin, L., Miller, R., Dillane, E., Berrow, S.D., Ingram, S., Cross, T.F., Rogan, E. 2011. Fine-scale population genetic structuring of bottlenose dolphins in Irish coastal waters. Animal Conservation 14: 342-353.

Möller, L.M., Allen, S.J., Harcourt, R.G. 2002. Group characteristics, site fidelity and seasonal abundance of bottlenose dolphins (*Tursiops aduncus*) in Jervis Bay and Port Stephens, South-Eastern Australia. Australian Mammalogy 24: 11-22.

Möller, L.M. and Beheregaray, L.B. 2004. Genetic evidence for sex-biased dispersal in resident bottlenose dolphins (*Tursiops aduncus*). Molecular Ecology 13: 1607-1612.

Möller, L.M., Wiszniewski, J., Allen, S.J., Beheregaray, L.B. 2007. Habitat type promotes rapid and extremely localized genetic differentiation in dolphins. Marine and Freshwater Research 58: 640-648.

Moreira, D., Simionato, C.G., Dragani, W. 2011. Modelling ocean tides and their energetics in the North Patagonia Gulfs of Argentina. Journal of Coastal Research 27: 87-102.

Natoli, A., Peddemors, V.M., Hoelzel, R.A. 2004. Population structure and speciation in the genus *Tursiops* based on microsatellite and mitochondrial DNA analyses. Journal of evolutionary biology 17: 363-375.

Parsons, K.M., Durban, J.W., Claridge, D.E., Herzing, D.L., Balcomb, K.C., Noble, L.R. 2006. Population genetic structure of coastal bottlenose dolphins (*Tursiops truncatus*) in the northern Bahamas. Marine Mammal Science 22: 276-298.

Patterson, I.A.P., Reid, R.J., Wilson, B., Grellier, K., Ross, H.M., Thompson, P.M. 1998. Evidence for infanticide in bottlenose dolphins: an explanation for violent interactions with harbour porpoises? Proceedings of the Royal Society London B 265: 1167-1170.

Perier, M.R. 1994. La fauna íctica en el litoral de la Bahía de San Antonio (Golfo San Matias, Provincia de Río Negro). Dissertation, Facultad de Ciencias naturales y Museo, Universidad Nacional de La Plata, Argentina.

Perrin, N. and Mazalov, V. 1999. Dispersal and inbreeding avoidance. The American Naturalist 154: 282-292.

Piccolo, M.C. and Perillo, G.M. 1990. Physical characteristics of the Bahía Blanca estuary (Argentina). Estuarine, Coastal and Shelf Science 31: 303-317.

Piola, A.R. and Rivas, A.L. 1997. Corrientes en la plataforma continental. *In*: Boschi, E.E. (Ed.), El Mar Argentino. Instituto Nacional de Investigación y Desarrollo Pesquero, Mar del Plata, Argentina, pp. 119-132.

Pisoni, J.P. and Rivas, A. 2006. Frentes térmicos sobre la PCA por medio de imágenes satelitales. Proceedings of the VI Jornadas Nacionales de Ciencias del Mar and XIV Coloquio de Oceanografía. Puerto Madryn, Argentina.

Quintana-Rizzo, E. and Wells, R.S. 2001. Resighting and association patterns of bottlenose dolphins (*Tursiops truncatus*) in the Cedar Keys, Florida: insights into social organization. Canadian Journal of Zoology 79: 447-456.

Rivas, A.L. and Beier, E.J. 1990. Temperature and salinity fields in the Northpatagonic Gulfs. Oceanologica Acta 13: 15-20.

Romero, S.I., Piola, A.R., Charo, M., García, C.A.E. 2006. Chlorophyll-a variability off Patagonia based on SeaWiFS data. Journal of Geophysical Research 111 DOI:10.1029/ 2005JC003244.

Rosel, P., Hansen, L., Hohn, A.A. 2009. Restricted dispersal in a continuously distributed marine species: common bottlenose dolphins *Tursiops truncatus* in coastal waters of the western North Atlantic. Molecular Ecology 18: 5030-5045.

Sabatini, M.E. 2004. Características ambientales, reproducción yalimentación de la merluza (*Merluccius hubbsi*) y la anchoíta (*Engraulis anchoíta*) en su hábito reproductivo patagónico, síntesis y perspectivas. Revista de Investigación y Desarrollo Pesquero 16: 5-25.

Sandell, M. 1989. The mating tactics and spacing patterns of solitary carnivores. *In*: Gittleman, J.L. (Ed.), Carnivore behaviour, ecology, and evolution. Cornell University Press, Ithaca, NY, pp. 164-182.

Sardiña, P. 2004. Ecología trófica de estadios juveniles de los esciénidos dominantes en el estuario de Bahía Blanca. Pescadilla de red (*Cynoscion guatucupa*) y corvina rubia (*Micropogonias furnieri*). Dissertation, Universidad Nacional del Sur, Argentina.

Scasso, L.M.L. and Piola, A.R. 1988. Intercambio neto de agua entre el mar y la atmósfera en el Golfo San Matías. Geoacta 15: 13-31.

Sellas, A.B., Wells, R.S., Rosel, P.E. 2005. Mitochondrial and nuclear DNA analyses reveal fine scale geographic structure in bottlenose dolphins (*Tursiops truncatus*) in the Gulf of Mexico. Conservation Genetics 6: 715-728.

Schmidt-Nielsen, N. 1990. Animal physiology: Adaptation and environment. 4th ed. Cambridge University Press, New York, NY.

Simões-Lopes, P.C. and Fabian, M.E. 1999. Residence patterns and site fidelity in bottlenose dolphins (*Tursiops truncatus*) (Montagu) (*Cetacea, Delphinidae*) off Southern Brazil. Revista Brasilera de Zoologia 16: 1017-1024.

Smolker, R.A., Richards, A.F., Connor, R.C., Pepper, J.W. 1992. Sex differences in patterns of associations among Indian Ocean bottlenose dolphins. Behaviour 123: 38-69.

StatSoft, Inc. 2004. STATISTICA (data analysis software system), version 7. www.statsoft.com.

Tezanos-Pinto, G., Baker, C.S., Russell, K., Martien, K., Baird, R.W., Hutt, A., Stone, G., Mignucci-Giannoni, A.A., Caballero, S., Endo, T., Lavery, S., Oremus, M., Olavarría, C., Garrigue, C. 2009. A worldwide perspective on the population structure and genetic diversity of bottlenose dolphins (*Tursiops truncatus*) in New Zealand. Journal of Heredity 100: 11-24.

Torres, L.G., McLellan, W.A., Meagher, E., Pabst, D.A. 2005. Seasonal distribution and relative abundance of bottlenose dolphins, *Tursiops truncatus*, along the US mid-Atlantic Coast. Journal of Cetacean Research Management 7: 153-161.

True, F.W. 1890. Observations on the life history of the bottlenose porpoise. Proceedings of the U.S. National Museum 13: 197-203.

Urian, K.W., Hofmann, S., Wells, R.S., Read, A.J. 2009. Fine-scale population structure of bottlenose dolphins (*Tursiops truncatus*) in Tampa Bay, Florida. Marine Mammal Science 25: 619-638.

Vermeulen, E., Cammareri, A., Failla, M., Holsbeek, L. 2008. An identification study on bottlenose dolphins (*Tursiops truncatus*) in Northeast Patagonia, Argentina. Abstract XIII Reunion de trabajo de Especialistas en Mamíferos Aquaticos del Sur y 7° congreso SOLAMAC, 13-17 November 2008, Montevideo, pp. 209.

Vermeulen, E. and Cammareri, A. 2009a. Residency Patterns, Abundance and Social composition of Bottlenose Dolphins (*Tursiops truncatus*) in Bahía San Antonio, Patagonia, Argentina. Aquatic Mammals 35: 379-386.

Vermeulen, E. and Cammareri, A. 2009b. Variation in external morphology of resident bottlenose dolphins (*Tursiops truncatus*) in Bahía San Antonio, Patagonia, Argentina. Journal of Marine Animals and Their Environment 2: 3-6.

Vermeulen, E. and Bräger, S. submitted Demographics of the disappearing bottlenose dolphin in Argentina: a common species on its way out? PLoS-One.

Volpedo, A.V. and Cirelli, A.F. 2006. Otolith chemical composition as a useful tool for sciaenid stock discrimination in the Southwestern Atlantic. Scientia Marina 70: 325-334.

Wells, R.S. 1986. Population structure of bottlenose dolphins: Behavioral studies along the central west coast of Florida. Contract Report to National Marine Fisheries Service, Southeast Fisheries Center. Contract No.45-WCNF-5–00366. 58 pp.

Wells, R.S., Scott, M.D., Irvine, A.B. 1987. The social structure of free-ranging bottlenose dolphins. *In:* Genoways, H.H. (Ed.), Current mammalogy: Vol. 1, Plenum Press, NY, pp. 247-305.

Wells, R.S., Hansen, L.J., Baldridge, A., Dohl, T.P., Kelly, D.L., Defran, R.H. 1990. Distribution, movements and abundance. *In:* Leatherwood, S. and Reeves, R.R. (Eds.), The bottlenose dolphin. Academic Press, San Diego, CA, pp. 369-434.

Wells, R.S. 1991. The role of long-term study in understanding the social structure of a bottlenose dolphin community. *In:* Pryor, K. and Norris, K.S. (Eds.), Dolphin societies: Discoveries and puzzles. University of California Press, Berkeley, CA, pp. 199-225.

Wells, R.S., Rhinehart, H.L., Cunningham, P., Whaley, J., Baran, M., Koberna, C., Costa, D.P. 1999. Long distance offshore movements of bottlenose dolphins. Marine Mammal Science 15: 1098-1114.

Wiszniewski, J., Beheregaray, L.B., Allen, S.J., Möller, L.M. 2010. Environmental and social influences on the genetic structure of bottlenose dolphins (*Tursiops aduncus*) in Southeastern Australia. Conservation Genetics 11: 1405-1419.

Wood, C.J. 1998. Movement of bottlenose dolphins around the southwest coast of Britain. Journal of Zoology 246: 155–163.

Würsig, B. and Würsig, M. 1977. The photographic determination of group size, composition, and stability of coastal porpoises (*Tursiops truncatus*). Science 198: 755-756.

Würsig, B. and Harris, G. 1990. Site and association fidelity of bottlenose dolphins off Argentina. *In:* Leatherwood, S. and Reeves, R.R. (Eds.), The bottlenose dolphin. Academic Press, San Diego, CA, pp. 361-365.

Würsig, B. and Jefferson, T.A. 1990. Methods of photo-identification for small cetaceans. Report of the International Whaling Commission, Special Issue 12: 43-52.

Zar, J.H. 1996. Biostatistical analysis (3rd ed.). Upper Saddle River, Prentice Hall, NJ.

Zolman, E.S. 2002. Residence patterns of bottlenose dolphins (*Tursiops truncatus*) in the Stono River Estuary, Charleston County, South Carolina, U.S.A. Marine Mammal Science 18: 879-892.

2. BOTTLENOSE DOLPHINS IN THE RÍO NEGRO ESTUARY

After

Failla, M., Seijas, V., Vermeulen, E. in press. Occurrence of bottlenose dolphins (Tursiops truncatus) *in the Río Negro Estuary, Argentina, and their mid-distance movements along the Northeast Patagonian coast. Latin American Journal of Aquatic Mammals.*

ABSTRACT - A systematic study on the presence of bottlenose dolphins (*Tursiops truncatus*) was carried out in the Río Negro Estuary (RNE), Patagonia Argentina, between the months March – July from 2008 to 2011. Data on the dolphin's activity patterns were gathered via an *ad libitum* focal group sampling mode accompanying dorsal fin images taken for identification and re-identification of individuals. A total effort of 188 h resulted in 58 h of observation of 124 dolphin groups (sightings per unit effort (SPUE) = 0.66 DG/h). Data analysis showed two main activity states for the observed groups, travelling (65%) and foraging (26%). The remaining 9% of the groups were involved in other activities.

The photo-identification effort, which started opportunistically in 2006, resulted in a catalogue of 21 individual dolphins, with a total mean re-identification rate of 9 days (max = 24 days). When comparing these pictures to the existing catalogue of Bahía San Antonio (approximately 200 km west from the study area) dorsal fins of 20 individuals could be positively matched and most (n = 17) could be subsequently re-identified in both areas, indicating their long distance movements along the north Patagonian coast during the austral autumn months. This season coincides with the lowest amount of feeding activity observed in Bahía San Antonio.

This study suggests that bottlenose dolphins enter RNE, mainly during autumn, to forage. It appears that the search for food resources may be the trigger for their movement patterns along the north Patagonian coast during this season, at least for certain individuals. More research is needed to accurately confirm this hypothesis.

KEYWORDS - bottlenose dolphin, behaviour, photo-identification, movement patterns

2.1. INTRODUCTION

The bottlenose dolphin (*Tursiops truncatus*) inhabits warm and temperate coastal regions worldwide and is one of the best-studied cetacean species in the world (Leatherwood and Reeves, 1990; Reynolds et al., 2000; Bearzi, 2005). In Argentina, they are known to occur mainly from the Province of Buenos Aires south to the Province of Chubut, although some records have been made as far south as the Province of Tierra del Fuego (Perrin et al., 2002; Bastida and Rodríguez, 2003; Goodall et al., 2008). The first studies in Argentina were made between 1970 and 1980 (Würsig, 1978; Würsig and Würsig, 1979; Bastida and Rodríguez, 2003) but these studies were discontinued due to a significant decrease in sightings. No clear explanation can be given on the reason for this apparent decline in bottlenose dolphin occurrence although suggestions include resource depletion (Coscarella et al., 2012). More recently, the regular observations of the species in Northeast Patagonia have caused systematic studies to be initiated in this region in 2006, with an increased effort in Bahía San Antonio (BSA; Vermeulen and Cammareri, 2009). The latter was recently suggested to be one of the last remaining areas in Argentina where bottlenose dolphins show a high degree of residency year-round (Vermeulen and Cammareri, 2009; Vermeulen et al., submitted a) .

The present study aims to investigate the occurrence and activity patterns of bottlenose dolphins in the Río Negro Estuary (RNE), located approximately 200 km east of BSA. Furthermore, photo-identification effort was initiated to gain a better understanding on the movements of the species throughout the larger area of Northeast Patagonia. Despite the fact that this species is considered the most extensively studied dolphin species, information on movements and home ranges in the Southwestern Atlantic Ocean are still scarce. However, insight into the movement patterns of these dolphins is vital to comprehend ecological aspects of the population (Silva et al., 2008).

2.2. MATERIALS AND METHODS

2.2.1 Fieldwork

Data were gathered in the RNE, North Patagonia, Argentina (Figure 3). This estuary and its surrounding areas contain warm turbid waters (visibility < 1 m, mean annual temperature 19°C; M. Failla, pers. obs.), islands, sandbars, channels and saltmarshes. Generally, the coast drops off steeply with depths of up to 2 m at the distance of only 5 m from the coastline. The annual mean tidal amplitude is approximately 2.2 m (M. Failla, pers. comm.). The Río Negro river, which terminates in this estuary, is the longest river in Patagonia. The water flow of this river is regulated 500 km upstream by a dam, varying its discharge between 500 - 2,000 m^3/sec (M. Failla, pers. comm.).
Systematic land-based surveys were conducted inside the estuary by two observers (always the same) during the months March - July of 2008 till 2011. When dolphins were seen, their overall activity pattern was observed and recorded by means of an Ad libitum focal group sampling mode (Altmann, 1974; Mann, 1999) using the categories travelling, feeding, other.

Dolphin group sizes were classified into the following ranges: 1 - 5 individuals, 6 - 10, 11 - 15, 16 - 20 and so on. When the number of animals could not be estimated accurately, group size was labelled as ‘Not Classified’ (NC).

2.2.2 Analysis

All observations of dolphin groups that lasted ≤ 15 min or were beyond 500 m from the shore were not included in this study, as they were considered to be too short or too distant for accurate determination of the group’s activity pattern and size. The field effort, time of actual dolphin observations, number of dolphin groups and number of sightings per unit effort (SPUE) was calculated in total and over the different survey years (SPUE was defined as the number of dolphin groups observed per hour of survey effort). The proportion of dolphin groups in each activity state was calculated and represented graphically. To study the movement patterns of this species in Northeast Patagonia, good quality pictures were selected for comparison with the existing photo-identification catalogue of BSA (Appendix 2).

2.3. RESULTS

2.3.1 Survey effort

A total of 71 days (188 h) were spent looking for dolphins in the study area. This survey effort resulted in 58 h of observation of 124 dolphins groups. The overall SPUE was 0.66 DG/h (Table 15).

Table 15 – Total survey effort (days and hours), time observing dolphins (hours), number of dolphin groups (DG) observed and SPUE (dolphin groups/hour) in RNE (2008 - 2011)

	Total effort (days)	Total effort (h)	Time observing dolphins (h)	DG (#)	SPUE (DG/h)
2008	11	33.5	6.3 (19%)	15	0.45
2009	8	18.0	5.1 (28%)	12	0.67
2010	30	68.9	16.8 (24%)	49	0.71
2011	22	68.0	20.4 (30%)	48	0.71
TOTAL	71	188.4	48.6	124	0.66

2.3.2 Activity patterns and group size

Most groups were seen travelling (65%; n = 124), whereas 26% were seen feeding in the study area. Other activity states could only be observed in 9% of the sightings (Figure 20).

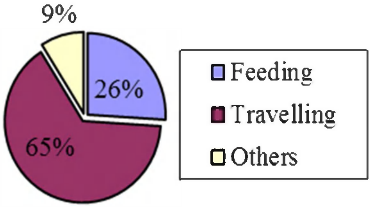

Figure 20 - Proportion of DG observed in the different activity states (n = 124) in the RNE

Most of the groups observed contained between 1-5 individuals (37%), although occasional aggregations of up to 20 dolphins per group (2%) were recorded (Figure 21). In total, 31% of the observed groups had calves, with never more than 1 calf per group. Nevertheless, in 30% of the sightings, the presence of calves could not be accurately determined.

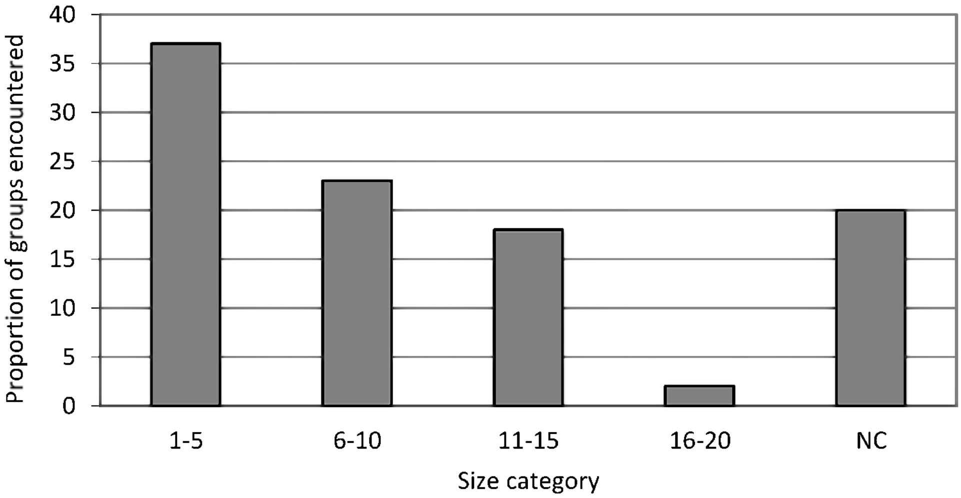

Figure 21 - Proportion of different size categories recorded for bottlenose dolphin groups observed in the RNE (n = 124; NC = not classified)

2.3.3 Photo-identification

A total of 4,200 digital pictures of dorsal fins were analysed from opportunistic and systematic photo-identification surveys (2006 - 2011). These pictures resulted in an identification catalogue of 21 individuals, with a maximum re-identification rate of 24 days (mean = 9). Most re-identifications occurred during the austral autumn months (April - June), and the majority of the individuals (n = 17) were re-identified within the study area in successive years with 1 individual present during all six annual survey periods.

When comparing these pictures to the existing catalogue from BSA, dorsal fins of 20 individuals could be positively matched and most (n = 17) could subsequently be re-identified in both areas (example Figure 22). Six identified dolphins were re-sighted during the same month in RNE and BSA, with a minimum time of 8 days between sightings.

Figure 22 - Example of a dorsal fin profile of a bottlenose dolphin (RN-BSA-43/07) photo-identified on various occasions in BSA (left) and the RNE (right)

2.4. DISCUSSION

The results from this study clearly indicate that bottlenose dolphins enter the RNE between March and July. The sizes of the dolphin groups observed during this study were relatively small, similar to those previously described for BSA (Vermeulen and Cammareri, 2009) and Patos Lagoon, an estuary in Southern Brazil (Mattos et al., 2007). These small group sizes could indicate a relative low predation pressure in the study area (Wells et al., 1987).

The recorded activities of the observed bottlenose dolphin groups suggest that the study area is regularly used for feeding activities, similar to the Río Chubut Estuary, Argentina (Coscarella and Crespo, 2009) and the Patos Lagoon Estuary, Brazil (Mattos et al., 2007). Furthermore, bottlenose dolphins have been recorded to travel 30 km upstream in the river (near the city of Viedma, 40° 48′ S, 62° 58′ W), where they have been seen foraging in fresh and turbid waters with low visibility (M. Failla, pers. obs.). This suggests that besides the estuary itself, dolphins also use the river's fresher waters upstream as a foraging site, possibly in relation to the abundance of several fish species, such as the southern flounder (*Paralichthys sp.*), liza (*Mugil liza*), silverside (*Odonthestes sp.*) and eels

(*Chlopsis sp.*), known to transit up and down the river with the tide. All these species are caught in the area by local fishermen year-round (Curtolo and Di Giacomo, 2002) and are suggested prey species of the dolphins (M. Failla, pers. obs.). In general, estuarine areas and river mouths have repeatedly been reported as sites of high bottlenose dolphin occurrence (Scott et al., 1990; Berrow et al., 1996; Gubbins, 2002; Zolman, 2002), and are often characterised by high levels of primary production and prey abundance (Acevedo, 1991).

The re-identification of several individuals in both BSA and RNE, approximately 200 km apart, indicates that these bottlenose dolphins move along the whole northern coastline of SMG. Overall, movements of coastal populations of bottlenose dolphins are known to range between short-distances of up to 100 km (Ballance, 1992; Lodi et al., 2008) and mid-distances of up to 300 km (Würsig, 1978; Simões-Lopes and Fabián, 1999; Defran et al., 1999; Bearzi et al., 2011). Occasionally, long-distances of more than 500 km (Wells et al., 1990; Mate et al., 1995; Defran and Weller, 1999) or even > 1,000 km (Wood, 1998; Wells et al., 1999) have been recorded for the species. The re-sighting of several individuals in both areas within the same month, and one individual within 8 days, indicates furthermore that these long distance movements can occur in a relatively short time frame. Bottlenose dolphins have been recorded previously to travel large distances in relative short time frames, with records of up to 50 km/day (Mate et al., 1995).

The analysis of ranging patterns of dolphins is crucial to understand several aspects of the ecology of a population (Silva et al., 2008), as dispersion is a biologically important behaviour that is triggered by a range of key functions as feeding, mating and finding shelter (e.g., Bearzi et al., 2011). Generally, bottlenose dolphins living in less protected waters display extensive ranging patterns, whereas dolphins residing in protected coastal environments show a higher degree of site fidelity and residency (Wells et al., 1987).

Among coastal populations of bottlenose dolphins, males seem to have a wider home range than females, related to their mating strategy (Wells et al., 1987). On the other hand, female ranging patterns are considered to be minimal for reasons of energetic efficiency (Sandell, 1989) and are usually thought to be more directly affected by ecological parameters such as the availability of resources and predation risk (Silva et al., 2008). Accordingly, females associated with a calf were determined as being more resident in BSA than individuals without calves (Vermeulen et al., submitted a). However, in the present study, both males and female/calf pairs were re-identified in both areas, and such a lack of differences in ranging patterns among sexes is considered to be related to environmental productivity (Fisher and Owens, 2000; Silva et al., 2008). In practice, an increase in home range size with decreasing food availability/density seems to be a general result in mammals (Sandell, 1989).

The present study shows that, while bottlenose dolphins in North Patagonia seem to display a year-round residency in BSA, their home range may include the whole northern coastline of the SMG. It further suggests that a variation in productivity and prey availability may be an important factor influencing the ranging patterns of these dolphins, suggesting their range increases in order to feed in RNE when food availability appears to decrease in their core area (Vermeulen et al., submitted b).

However, it is known that a general lack of information on the dolphin's movement patterns could bias the assessment of site fidelity and residence in certain core areas, as ranges could easily be interpreted from the perspective of the study area covered by the researchers (Bearzi et al., 2011). This could in turn insufficiently weigh the use of alternative areas. Furthermore, McLoughlin and Ferguson (2000) stated home rang size is not determined by a single factor but is more likely to be the result of the combination of several variables working simultaneously. It is thus possible that other factors as e.g., social learning of foraging techniques, social affiliations and potential other feeding grounds, play a yet unknown role in the ranging patterns of the bottlenose dolphins in the region. Up to now, limited survey effort has been made in RNE during the winter, spring and summer months, mostly due to financial limitations and the general knowledge that bottlenose dolphins are rarely seen in the area during these seasons. Nevertheless, a year-round systematic study is recommended.

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2.5. REFERENCES

Acevedo, A. 1991. Behaviour and movements of bottlenose dolphins, *Tursiops truncatus*, in the entrance to Ensenda De La Paz, Mexico. Aquatic Mammals 17: 137-147.

Altmann, J. 1974. Observational study of behaviour: Sampling methods. Behaviour 49: 227-265.

Ballance, L.T. 1992. Habitat use patterns and ranges of the bottlenose dolphin in the Gulf of California, México. Marine Mammal Science 8: 262-274.

Bastida, R. and Rodríguez, D. 2003. Mamíferos Marinos Patagonia Antartida. Vázquez Mazzini Editors, Buenos Aires, Argentina, 206 pp.

Bearzi, M. 2005. Aspects of ecology and behaviour of bottlenose dolphins (*Tursiops truncatus*) in Santa Monica Bay, California. Journal of Cetacean Research and Management 7: 75-83.

Bearzi, G., Bonizzoni, S., Gozalvo, J. 2011. Mid-distance movements of common bottlenose dolphins in the coastal waters of Greece. Journal of Ethology 29: 369-374.

Berrow, S.D., Holmes, B., Kiely, O. 1996. Distribution and abundance of Bottle-nosed dolphins *Tursiops truncatus* (Montagu) in the Shannon estuary, Ireland. Biology and Environment. Proceedings of the Royal Irish Academy 96: 1-9.

Coscarella, M.A. and Crespo, E.A. 2009. Feeding aggregation and aggressive interaction between bottlenose (*Tursiops truncatus*) and Commerson's dolphins (*Cephalorhynchus commersonii*) in Patagonia, Argentina. Journal of Ethology 28: 183-187.

Coscarella, M.A., Dans, S.L., Degrati, M., Garaffo, G.V., Crespo, E.A. 2012. Bottlenose dolphins at the southern extreme of the south-west Atlantic : local population decline? Journal of the Marine Biological Association of the United Kingdom 92: 1843-1849.

Curtolo, L. and Di Giacomo, E. 2002. Potencial pesquero de la desembocadura del Río Negro. Informe Técnico del Instituto de Biología Marina y Pesquera Almirante Storni. San Antonio Oeste, Argentina, 60 pp.

Defran, R.H. and Weller, D.W. 1999. The occurrence, distribution, and site fidelity of bottlenose dolphins (*Tursiops truncatus*) in San Diego, California. Marine Mammal Science 15: 366-380.

Defran, R.H., Weller, D.W., Kelly, D.L., Espinosa, M.A. 1999. Range characteristics of the Pacific coast bottlenose dolphins (*Tursiops truncatus*) in the southern California bight. Marine Mammal Science 15: 381-393.

Fisher, D.O. and Owens, I.P.F. 2000. Female home range size and the evolution of social organization in macropods marsupials. Journal of Animal Ecology 69: 1083-1098. Available on CJO 2011 DOI:10.1046/j.1365-2656.2000. 00450.x

Goodall, R.N.P., Dellabianca, N., Boy, C.C., Benegas, L.G., Pimper, L.E., Riccialdell, L. 2008. Review of small cetaceans stranded or incidentally captured on the coasts of Tierra del Fuego, Argentina, over 33 years. Report of International Whaling Commission SC/60/SM21.

Gubbins, C. 2002. Use of home ranges by resident bottlenose dolphins (*Tursiops truncatus*) in a South Carolina Estuary. Journal of Mammology 83: 178-187.

Irvine, A.B., Scott, M.D., Wells, R.S., Kaufmann, J.H. 1981. Movements and activities of the Atlantic bottlenose dolphin, *Tursiops truncatus*, near Sarasota, Florida. Fishery Bulletin 79: 671-688.

Leatherwood, S. and Reeves, R.R. 1990. The Bottlenose Dolphin. Academic Press, San Diego, CA.

Lodi, L., Liberali Wedekin, L., Rossi-Santos, M.R., Marcondes, M.C. 2008. Movements of the bottlenose dolphin (*Tursiops truncatus*) in the Rio de Janeiro State, Southeastern Brazil. Biota Neotropica 8: 205-209. Available on CJO 2011 DOI:10.1590/S1676-06032008000400020.

Lusseau, D., Wilson, B., Hammond, P., Grellier, K., Durban, J.W., Parsons, K.M., Barton, T.R., Thompson, P.M. 2005. Quantifying the influence of sociality on population structure in bottlenose dolphins. Journal of Animal Ecology 1: 1-11.

McLoughlin, P.D. and Ferguson, S.H. .2000. A hierarchical pattern of limiting factor helps explain variation in home range size. Ecoscience 7: 123–130.

Mann, J. 1999. Behavioural sampling methods for cetaceans: A review and critique. Marine Mammal Science 15: 102-122.

Mate, B.R., Rossbach, K.A., Nieukirk, S.L., Wells, R.S., Irvine, A.B., Scott, M.D., Read, A.J. 1995. Satellite-monitored movements and dive behavior of a bottlenose dolphin (*Tursiops truncatus*) in Tampa Bay, Florida. Marine Mammal Science 11: 452–463.

Mattos, P.H., Rosa, L.D., Fruet, P.F. 2007. Activity budgets and distribution of bottlenose dolphins (*Tursiops truncatus*) in the patos lagoon estuary, Southern Brazil. Latin American Journal of Aquatic Mammals 6: 161-169.

Perrin, W.F., Würsig, B., Thewissen, J.G.M. 2002. Encyclopaedia of marine mammals. Academic Press, San Diego, CA.

Reynolds, J.E., Wells, R.S., Eide, S.D. 2000. The Bottlenose Dolphin: Biology and Conservation. University Press of Florida, Gainesville.

Sandell, M. 1989. The mating tactics and spacing behaviour of solitary carnivores. *In:* Gittleman, J.L. (Ed.), Carnivore behaviour, ecology and evolution. Cornell University Press, NY, pp. 164-182.

Scott, M.D., Wells, R.S., Irvine, A.B. 1990. A long-term study of bottlenose dolphins on the West coast of Florida. *In*: Leatherwood, S. and Reeves, R.R. (Eds.), The Bottlenose Dolphin. Academic Press, San Diego, CA, pp. 235-244.

Shane, S.H. 1990. Behaviour and ecology of the bottlenose dolphin at Sanibel Island, Florida. *In:* Leatherwood, S. and Reeves, R.R. (Eds.), The Bottlenose Dolphin. Academic Press, San Diego, CA, pp. 245-266.

Silva, M.A., Prieto, R., Magalhães, S., Seabra, M.I., Santos, R.S., Hammond, P.S. 2008. Ranging patterns of bottlenose dolphins living in oceanic waters: implications for population structure. Marine Biology 156: 179-192.

Simões-Lopes, P.C. and Fabián, M.E. 1999. Residence patterns and site fidelity in bottlenose dolphins, *Tursiops truncatus* (Montagu) (Cetacea, Delphinidae) off Southern Brazil. Revista Brasilera de Zoologia 16: 1017-1024.

Vermeulen, E. and Cammareri, A. 2009. Residency Patterns, Abundance, and Social Composition of Bottlenose Dolphins (*Tursiops truncatus*) in Bahía San Antonio, Patagonia, Argentina. Aquatic Mammals 35: 379-386.

Vermeulen, E., Balbiano, A., Belenguer, F., Colombil, D., Failla, M., Intrieri, E., Bräger, S. submitted a. Limited ranging patterns of a highly mobile marine species: conservation implications for bottlenose dolphins (*Tursiops truncatus*) in Argentina. Biodiversity and Conservation.

Vermeulen, E., Holsbeek, L., Das, K. submitted b. Diurnal and seasonal activity budgets of bottlenose dolphins (*Tursiops truncatus*) in Bahía San Antonio, Patagonia, Argentina. Mammalian Biology.

Wells, R.S., Scott, M.D., Irvine, A.B. 1987. The social structure of free-ranging bottlenose dolphins. *In:* Genoways, H.H. (Ed.), Current mammalogy. Plenum Press, NY, pp. 247-305.

Wells, R.S., Hansen, L.J., Baldridge, A., Dohl, T.P., Kelly, D.L., Defran, R.H. 1990. Northward extension of the range of bottlenose dolphins along the California coast. *In:* Leatherwood, S. and Reeves, R.R. (Eds.), The bottlenose dolphin. Academic Press, San Diego, CA, pp. 421-431.

Wells, R.S., Rhinehart, H.L., Cunningham, P., Whaley, J., Baran, M., Koberna, C., Costa, D.P. 1999. Long distance offshore movements of bottlenose dolphins. Marine Mammal Science 15: 1098-1114.

Wilson, B. 1995. The ecology of bottlenose dolphins in the Moray Firth, Scotland: A population at the northern extreme of the species' range. Dissertation, University of Aberdeen, Aberdeen, Scotland, UK.

Wood, C.J. 1998. Movement of bottlenose dolphins around the southwest coast of Britain. Journal of Zoology 246: 155–163.

Würsig, B. 1978. Occurrence and group organization of Atlantic bottlenose porpoises (*Tursiops truncatus*) in an Argentine bay. The Biological Bulletin 154: 348-359.

Würsig, B. and Würsig, M. 1979. Behaviour and ecology of bottlenose dolphin, *Tursiops truncatus*, in the South Atlantic. Fishery Bulletin 77: 399-442.

Zolman, E.S. 2002. Residence patterns of bottlenose dolphins (*Tursiops truncatus*) in the Stono River Estuary, Charleston County, South Carolina, U.S.A. Marine Mammal Science 18: 879-892.

3. VARIATION IN EXTERNAL MORPHOLOGY OF RESIDENT BOTTLENOSE DOLPHINS

After

Vermeulen, E. and Cammareri, A. 2009. Variation in external morphology of resident bottlenose dolphins in Bahía San Antonio, Patagonia, Argentina. Journal of Marine Animals and Their Ecology Vol2 N°2.

ABSTRACT - A photo-identification study carried out in Bahía San Antonio showed a variation in the external morphology among year-round resident bottlenose dolphins. Out of all the individually identified bottlenose dolphins, three of the year-round residents show variations in external morphology: they have a more falcate dorsal fin, darker colouration and shorter beak, characteristics described for the bottlenose dolphins present in the more southern Province of Chubut. The three morphologic distinct individuals, with one associated calf, could be re-identified in the study area in all the different seasons and up to now, no other bottlenose dolphins with similar characteristics could be observed in the area. These dolphins swam always in close association with each other and on many occasions also in close association with other individuals of the catalogue. Recent genetic analysis revealed both forms are strongly differentiated in both mitochondrial and nuclear DNA markers (P. Fruet, unpublished data).

So far it was believed that the two regional forms of bottlenose dolphins present in Argentina were geographically isolated. This communication is meant to document the residency and interaction of both regional forms in the same area.

KEYWORDS - bottlenose dolphin, morphology, residency

3.1. INTRODUCTION

The taxonomy of bottlenose dolphins has been a debate for a long time. At this moment two species of *Tursiops* are recognised being *T. truncatus* the common bottlenose dolphin and *T. aduncus* the Indo-Pacific bottlenose dolphin. In South America, the species *Tursiops gephyreus* was originally used for bottlenose dolphins from the South Atlantic coast. However, its use gradually decreased when the morphological plasticity of the genus was recognised (Barreto, 2004). Nowadays, up to 20 morphotypes are described worldwide but geographic variation of the species remains poorly understood.

In Argentina, two geographic variations of bottlenose dolphins were described by Bastida and Rodriguez (2003). The bottlenose dolphins living along the coasts of the Province of Buenos Aires are characterised by their triangular dorsal fin shape whereas bottlenose dolphins living more south along the coasts of the Province of Chubut are characterised by their falcate dorsal fin shape. Bastida and Rodriguez (2003) further stated that 'their clear difference would indicate that both geographic forms are isolated'. This communication is meant to document the residency and interaction of both geographic variations in Bahía San Antonio (Province of Río Negro).

3.2. MATERIAL AND METHODS

Land- and boat-based observations were made with the attempt to photograph the dorsal fins of all individuals in the group, regardless the presence of clear marks. Residency patterns were analysed regarding the presence or absence of dolphins in different seasons. Residency was defined according to Zolman (2002) (see Chapter 8 - 1 for further information on the analysis of residency).

3.3. RESULTS

Three of the year-round residents and an associated calf (RN-BSA-55, RN-BSA-56 + calf, RN-BSA-57; appendix 2) were noted to show variations in external morphology when compared to the other catalogued dolphins, being distinguishable by a more falcate dorsal fin (Figure 23), a darker colouration (Figure 23) and a notably shorter beak (Figure 24).

Figure 23 - Variation in dorsal fin shape of year-round resident bottlenose dolphins. Left: RN-BSA-39 and RN-BSA-57. Right: adults RN-BSA-56 and RN-BSA-6

Figure 24 - Comparison of external morphology of two year-round resident bottlenose dolphins in BSA. Left: bottlenose dolphin RN-BSA-55. Right: bottlenose dolphin RN-BSA-31

This group of four morphological distinct bottlenose dolphins (#55, #56 + calf and #57) were first observed inside BSA in September 2008 and were since then defined as year-round residents in the study area. They were always seen in close association with each other, and often in close association with other catalogued bottlenose dolphins. No other bottlenose dolphin with similar characteristics could be observed in the area. An additional recapture of these 4 falcate dorsal fin shaped bottlenose dolphins could also be made in Puerto Lobos, 150 km south of the study area and at the border of the Province of Chubut.

3.4. DISCUSSION

Four of the frequently observed bottlenose dolphins in BSA show variations in external morphology when compared to all the other bottlenose dolphins observed in the study area. Similar characteristics were described for the bottlenose dolphins present in the area of the Province of Chubut (Bastida and Rodriguez, 2003), studied by Würsig in the 1970 - 1980 (Würsig and Würsig, 1977; 1979; Würsig, 1978; 1984; Figure 25). Würsig and Würsig (1977) were able to identify up to 53 bottlenose dolphins in the Province of Chubut, all falcate dorsal fin shaped, and described these bottlenose dolphins as 'coastal' as they appeared 92% of their time in waters < 10 m deep (Würsig and Würsig, 1979). In this case, the variation in external morphology is not of the type 'inshore vs. offshore'.

Figure 25 - Comparison of external morphology of bottlenose dolphins in the area of Península Valdés and BSA. Left: picture from Würsig (1984) of a bottlenose dolphin in the area of Península Valdés. Middle: bottlenose dolphin RN-BSA-55, year-round resident in BSA. Left: bottlenose dolphin RN-BSA-11, year-round resident in BSA

It seems also remarkable that only four of these individuals could be observed in BSA and that they were always observed in close association with each other. Up to now, on all occasions a clear differentiation could be made between the two variations.

Although both forms show variations in external morphology, the extent to which this phenotypic variation is genetically correlated was unknown. Only recently a genetic differentiation between these two morphotypes was detected; individuals #55, #56 and #57 are strongly genetically differentiated in both mitochondrial and nuclear DNA markers from all other sampled individuals in BSA (P. Fruet, unpublished data). The clear insight on the differentiation between these regional forms might have important conservation implications for the bottlenose dolphin in Argentina.

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3.5. REFERENCES

Barreto, A.S. 2004. *Tursiops* in Atlantic South America: Is *Tursiops gephyreus* a valid species? Abstract at the Symposium on Cetacean Systematics, La Jolla, California.

Bastida, R. and Rodríguez, D. 2003. Mamíferos Marinos Patagonia Antartida. Vázquez Mazzini Editors, Buenos Aires, Argentina, 206 pp.

Würsig, B. and Würsig, M. 1977. The photographic determination of group size, composition and stability of coastal porpoises (*Tursiops truncatus*). Science 198: 755-756.

Würsig, B. 1978. Occurrence and group organization of Atlantic bottlenose porpoise (*Tursiops truncatus*) in an Argentine bay. The Biological Bulletin 154: 348-359.

Würsig, B. and Würsig, M. 1979. Behaviour and ecology of bottlenose porpoises, *Tursiops truncatus*, in the South Atlantic. Fishery Bulletin 77: 399-442.

Würsig B. 1984. Aspects of the natural history of bottlenose and dusky dolphins. National Geographic Society, Research reports 1975 projects, pp. 759-768.

Zolman, E.S. 2002. Residence patterns of bottlenose dolphins (*Tursiops truncatus*) in the Stono River Estuary, Charleston County, South Carolina, U.S.A. Marine Mammal Science 18: 879-892.

9

DISCUSSION AND CONCLUSIONS

1. DISCUSSION AND CONCLUSIONS

The aim of this study was to investigate the population ecology of coastal bottlenose dolphins (*Tursiops truncatus*) in Northern Patagonia in order to contribute to their conservation. With this objective, a photo-identification survey was conducted between 2006 and 2011 to assess demographic parameters, as well as core areas, ranging and activity patterns, and possible community divisions.

Results indicated that a small community of bottlenose dolphins ranges along the northern coastline of the San Matías Gulf. Due to the dolphins' long-term site-fidelity to Bahía San Antonio, this protected coastal environment is suggested to be a core area within their larger home range. While adult survival is high, the low reproductive output, possibly due to the low number of successfully reproducing females, appears to be insufficient to sustain the community at its present size. Furthermore, these dolphins were recently classified as an Evolutionary Significant Unit within the larger Southwestern Atlantic, stressing their apparent isolation and low genetic diversity (Fruet et al., 2014; Appendix 1). It can therefore be concluded that this community is highly vulnerable to anthropogenic impacts and possibly at risk of extinction.

A small neighbouring community of bottlenose dolphins exists in the southern part of the Province of Buenos Aires. Both communities are largely isolated from each other, and their separation is thought to be governed by environmental discontinuities between the two adjacent oceanographic regimes they inhabit.

Despite having been one of the most common coastal cetacean species in Argentina (Bastida and Rodríguez, 2003), currently only rare and isolated observations of few individual bottlenose dolphins can be made in areas where they were once very common. This creeping disappearance of the species is most likely related to serious population declines.

- A community of bottlenose dolphins was known to reside in the Province of Buenos Aires, between Mar del Plata and Bahía Samborombón (Figure 3). Studies in the early 1980s estimated a local abundance of approx. 100 individuals (Bastida and Rodríguez, 2003). However, these studies were discontinued due to the disappearance of the species (R. Bastida, pers. comm.). Although no recent abundance estimates are available, currently bottlenose dolphins can be sighted only on very rare occasions in Bahía Samborombón (Bastida and Rodríguez, 2003).

- Another community was known to reside in the Province of Chubut (Figure 3), where studies conducted in the 1970s resulted in an identification catalogue of 53 individuals in the San José Gulf (Figure 3; Würsig and Würsig, 1977). This number was not regarded as a total abundance estimate, however, as at the same time unidentified bottlenose dolphins were sighted outside the core study area (B. Würsig, pers. comm. in Coscarella et al., 2012). The individuals of this community are morphologically distinct from the bottlenose dolphins occurring elsewhere in the country, and have proven to be genetically differentiated in both mitochondrial and nuclear DNA markers (P. Fruet, unpublished data). Recently, aerial surveys failed to record hardly any bottlenose dolphin in the San José Gulf (Coscarella et al., 2012). Even more, a recent estimate indicated an abundance of only 34 (95%CI = 22 – 51) remaining bottlenose dolphins spread over the larger area of central Patagonia (Península Valdés to Bahía Engaño; Figure 3) (Coscarella et al., 2012). Although this estimate is reported to be merely indicative, it suggests a drastic population decline since the 1970s.

Despite the generally recognised taxonomical uncertainty in the species *Tursiops truncatus*, local populations of coastal bottlenose dolphins are usually believed to be part of larger regional metapopulations, defined as a group of spatially separated populations of the same species which interact at some level (Levins, 1969). The metapopulation theory states that each population cycles in relative independence of other populations and eventually becomes extinct as a consequence of demographic stochasticity (with smaller populations being more prone to extinction) (Levins, 1969). This theory thus emphasises the importance of connectivity between apparently isolated populations to maintain gene flow and genetic diversity, and hence the evolutionary potential or ability of a species to adapt to environmental changes (Hanson, 1991; Hamner et al., 2012). Therefore, in terms of species preservation, there is an interest in determining not only the size but also the proximity of and the exchange among populations.

Bottlenose dolphins are a highly mobile marine species (e.g., Wells et al., 1990). Nevertheless, Natoli et al. (2004) showed a high potential for speciation in the genus *Tursiops* based on high levels of genetic differentiation between regional populations. Indeed, coastal bottlenose dolphins are increasingly reported to show significant genetic population structuring over short geographical distances (e.g., Wells, 1986; Hoelzel, 1998; Chilvers and Corkeron, 2001; Rosel et al., 2009). According to Hoelzel (1998), ecological specialisation and/or geographic separation are the main underlying evolutionary mechanisms.

Population fragmentation can occur naturally and may be a mere reflection of the heterogeneity in the environment and distribution of resources (Rodríguez and Delibes, 2003). However, population fragmentation may be induced and/or aggravated by anthropogenic activities. Based on the genetic and demographic evidence of strong philopatry in coastal bottlenose dolphins (e.g., Wells, 1991; Connor et al., 2000; Möller and Beheregaray, 2004; Bearzi et al., 2010), it is likely that gene flow will occur mostly between adjacent communities. Consequently, human activities that result in the loss of local populations will increase the likelihood of population fragmentation and isolation, with potentially severe consequences for the long-term survival of the species in the region.

The notable decrease in coastal bottlenose dolphin observations in Argentina over the past 40 years appears to have been largely ignored so far. Consequently, no verifiable information is available about the possible underlying causes. However, as bottlenose dolphin populations have disappeared both from areas with and without significant urbanisations (e.g., compare the large city of Mar del Plata vs. San José Gulf, see below), hypothesis have been formulated about the wide-ranging effects of increasing environmental pressures, for example, through overfishing and contamination (Bastida and Rodríguez, 2003; Coscarella et al., 2012).

Cauhépé (1999) indicated that the fishing sector in Argentina is in a critical state due to a severe decline of some of its major resources and that the situation may be difficult to resolve (see Chapter 1 – 2.3.1 for additional information). Moreover, pollution has proven to be a growing worry in Argentina. Especially metal pollution has reached levels of considerable concern (Gil et al., 1999). Due to bio-accumulation, high concentrations of trace elements such as Cd and Cu have been found in several piscivorous marine mammal species along the Argentine coast including the bottlenose dolphin (Marcovecchio et al., 1990; 1994). Contamination in Argentina is not restricted to toxic metals; it also includes polycyclic aromatic hydrocarbons and TBTs among others (see Chapter 1 – 2.3.3 for additional information). In general, the effects of prey depletion and pollution on bottlenose dolphins can vary, and may lead to emigration to other areas, reduced health condition, reproductive failure or even to increased mortality (e.g., Green et al., 1997; Kannan, 1997; Pfeiffer et al., 2000). The risk of direct removal due to intentional or unintentional killing (e.g., in bycatch) is assumed to be small for bottlenose dolphins in Argentina (Crespo et al., 1997).

Despite anthropogenic pressures on the marine environment in Argentina, a total of 44 Marine Protected Areas (MPA) exist along the Argentine coastline, individually relatively small but in total covering 7927 km^2 of sea surface (Campagna et al., 2007). Most of these protected areas were created in the 1990s and at least 24 of them are located in known (past and present) distribution areas of bottlenose dolphins along the coasts of the Provinces of Buenos Aires, Río Negro and Chubut (Campagna et al., 2007). Nevertheless, population declines of bottlenose dolphins appear to have continued at the same time. For example, within the area of the Province of Chubut, the local population decline occurred almost simultaneously with the creation of one of the largest MPAs in Argentina (San José Gulf). This gulf was declared a 'Provincial Marine Park' in 1975 and subsequently declared, within the larger area of Península Valdés, as a Natural World Heritage Site in 1999 by UNESCO (Coscarella et al., 2012). Its conservation measures restricted nearly all human activities, especially within the San José Gulf. Although these measures were primarily taken to protect an important breeding ground of southern right whales (*Eubalaena australis*), it was expected to contribute also to the preservation of other marine species such as the bottlenose dolphin. The only activity that continued to increase in the San José Gulf was recreational and artisanal fishing, including in areas previously used as foraging sites by bottlenose dolphins (Coscarella et al., 2012). Although the extent of the impact remains undetermined, local abundance and body size of several fish species have decreased notably since the 1970s (Venerus, 2006). This in turn was mentioned as a contributing cause for the local disappearance of bottlenose dolphins by Coscarella et al. (2012).

Generally, the creation of MPAs is a widely recommended and used tool to protect and preserve marine wildlife. However, despite its frequent use, currently there is very little evidence that MPAs have been effective in preserving marine mammal populations (e.g., Gormley et al., 2012). It appears that the creation of protected areas along the Argentine coast has been ineffective so far to preserve the local bottlenose dolphin populations. For a future attempt to improve the conservation status of the species in the country, the following measures are proposed:

- Considering the importance of population connectivity to retain the evolutionary potential of small populations, the protection of discrete local populations will not be sufficient. Instead, corridors for individual dispersal need to be considered during conservation management. Indeed, Hoelzel (1994) indicated that typical MPAs are too small to offer effective protection for cetaceans, which often have high dispersal capabilities. This in mind, one might consider the possibility to increase the area covered by the existing MPAs, however, only when ensuring the actual capacity for law enforcement. These larger areas should be evaluated carefully, as they could contain different levels of protection and management at varying spatial and temporal scales. Continuous monitoring will be vital to ensure the effectiveness of any existing MPAs or other conservation measures (Hoyt, 2005).

- Currently existing limitations on fishing activities in the country should be re-evaluated for their effectiveness, improved where necessary and at all times strictly enforced. Furthermore, despite the existence of some levels of restriction on commercial fisheries in Argentina, artisanal and recreational fishing activities are still permitted and increasing inside MPAs. The effects of these activities should be evaluated, monitored and managed accordingly.

- Considering the apparent effect of pollution also on human health in several localities in Argentina (e.g., Claps, 2005), an improved management scheme for rural, urban and industrial wastes appears much needed, as well as an improved urbanisation planning and an increased public awareness for conservation issues. In this context, it may also be advisable to ensure the strict enforcement of current regulations related to waste management as well as a continuous monitoring of their effectiveness. Monitoring the effects of organic and inorganic pollutants should take place within nationwide stranding and necropsy schemes. Areas with high levels of contamination, such as Bahía San Antonio, should evaluate the possibility for large-scale removal or safe storage of contaminated materials such as mine tailings.

- For a recently initiated dolphin watching activity based on bottlenose dolphins, protective regulations should be created and enforced to ensure as small an impact as possible on the dolphin behaviour. As tourism has been shown to cause negative effects on bottlenose dolphin populations elsewhere in the world (e.g., Constantine et al., 2003; Bejder et al., 2006), it is prudent to manage this new form of tourism sustainably. If managed appropriately, it might not only be educational, but also improve the socio-economic situation and lead to an increased public awareness. Therefore, management policies guided by research need to create an educational, sustainable and economically viable industry with the least possible impact on the dolphins.

- Educational projects are needed to increase the awareness of the general public and of decision makers alike, to improve the capacity to take responsible decisions at all levels concerning the conservation and exploitation of natural resources. Within environmental education projects, the needs of many different stakeholders should be recognised and engaged in order to address the current environmental issues. Foremost, however, it should be acknowledged that the people's perception of and interaction with the environment depends on the culture they live in. For an example see appendix 4.

- In order to ensure the accuracy of any conservation measure, there is a need for continued and expanded research efforts on the bottlenose dolphins along the entire Argentine coastline, including e.g., abundance and demographics, distribution and population structure (including management units). Furthermore, continued monitoring of the species is vital to confirm the effectiveness of conservation measures.

In general, the coastal bottlenose dolphin is believed to the best-studied dolphin species in the world. Nonetheless, most information about the species comes from captive studies, whereas much less appears to be known about wild population structures and trends, as well as ecological needs. Indeed, although their global population status is listed as of least concern by the IUCN, the global population trend is listed as unknown (Hammond, 2012). As human urbanisations continue to increase along the world's coastlines, coastal bottlenose dolphins are often particularly susceptible to the ensuing anthropogenic pressures (Sutherland, 2000). Therefore, it is not surprising that in recent years an ever-increasing number of coastal bottlenose dolphin populations has been reported to be vulnerable or declining worldwide (Table 7).

To conclude, despite having been one of the most common coastal cetacean species in Argentina, bottlenose dolphins have been reported as nearly vanished now from many regions along the country's coastline (Bastida and Rodríguez, 2003; Coscarella et al., 2012). Nowadays, only infrequent and isolated observations can be made in areas where they were once common. However, this notable decrease in observations, most likely related to drastic population declines, has been largely ignored over the past 40 years. It appears that the coastal lifestyle and strong site-fidelity of these dolphins as well as the general belief of them being a 'common' species have obfuscated the need for more extensive research and conservation efforts in the past. Today, possibly only a few small and largely isolated communities remain to exist.

It is apparent that increased research in Argentina reveals a progressive population fragmentation for the species within the country, possibly limiting the gene flow needed for the evolutionary potential of small populations and thus the regional survival of a species. Considering additionally the low abundance and declining trend along with an extremely low genetic diversity (Fruet et al., 2014; Appendix 1), this study reveals a major concern for the survival of the coastal bottlenose dolphin within their southernmost range of the Southwestern Atlantic Ocean. It furthermore provides an example of how local population declines can threaten the regional status of a once common and robust species such as the bottlenose dolphin.

2. REFERENCES

Bastida, R. and Rodríguez, D. 2003. Mamíferos Marinos Patagonia Antartida. Vázquez Mazzini Editors, Buenos Aires, Argentina, 206 pp.

Bearzi, G., Bonizzoni, S., Gonzalvo, J. 2010. Mid-distance movements of common bottlenose dolphins in the coastal waters of Greece. Journal of ethology 29: 369-374.

Bejder, L., Samuels, A., Whitehead, H., Gales, N., Mann, J., Connor, R., Heithaus, M., Watson-Capps, J., Flaherty, C., Kruetzen, M. 2006. Decline in relative abundance of bottlenose dolphins exposed to long-term disturbance. Conservation Biology 20: 1791-1798.

Campagna, C., Falabella, V., Tagliorette, A., Sapoznikow, A., Quintana, F. 2007. El mar des-protegido: Zonificación y conservación de la biodiversidad. *In*: Boltovskoy, D. (Ed.), Atlas de sensibilidad ambiental de la costa y el Mar Argentino. www.atlas.ambiente.gov.ar

Cauhépé, M.E. 1999. Management of the Argentine hake. Final project UNU Fisheries Training Program, Reykjavic, Iceland.

Chilvers, B.L. and Corkeron, P.J. 2001. Trawling and bottlenose dolphins' social structure. Proceedings of the Royal Society of London. Series B: Biological Sciences 268: 1901-1905.

Claps, E.L. 2005. A Heavy Legacy: lead contamination in San Antonio Oeste, Argentina. Mines and Communities, http://www.minesandcommunities.org/article.php?a = 5363. Downloaded on 11 June 2013.

Connor, R.C., Wells, R.S., Mann, J., Read, A.J. 2000. The bottlenose dolphin: Social relationships in a fission-fusion society. *In*: Mann, J., Connor, R.C., Tyack, P.L., Whitehead, H. (Eds.), Cetacean societies: Field studies of dolphins and whales. University of Chicago Press, Chicago, IL, pp. 91-126.

Constantine, R., Brunton, D.H., Dennis, T. 2003. Dolphin-watching tour boats change bottlenose dolphin (*Tursiops truncatus*) behaviour. Biological conservation 117: 299-307.

Coscarella, M., Dans, S.L., Degrati, M., Garaffo, G.V., Crespo, E.A. 2012. Bottlenose dolphins at the southern extreme of the Southwestern Atlantic: local population decline? Journal of the Marine Biological Association of the United Kingdom 92: 1843-1849.

Crespo, E.A., Pedraza, S.N., Dans, S.L., Alonso, M.K., Reyes, L.M., García, N.A., Coscarella, M., Schiavini, A.C.M. 1997. Direct and indirect effects of the highseas fisheries on the marine mammal populations in the northern and central Patagonian coast. Journal of Northwest Atlantic Fisheries Science 22: 189–207.

Fruet, P., Secchi, E.R., Daura-Jorge, F., Vermeulen, E., Flores, P.A.C., Simões-Lopes, P.C., Genoves, R.C., Laporta, P., Di Tullio, J.C., Freitas, T.R., Dalla Rosa, L., Valiati, V.H., Behereharay, L.B., Möller, L.M. 2014. Remarkably low genetic diversity and strong population structure in common bottlenose dolphins (*Tursiops truncatus*) from coastal waters of the Southwestern Atlantic Ocean. Conservation Genetics DOI: 10.1007/s10592-014-0586-z.

Gómez, A. And Mendez, M. 2007. Marine Protected Areas in South America: spatial assessment of cetacean distribution coverage. Latin American Journal of Aquatic Mammals 6: 203-207.

Gormley, A.M., Slooten, E., Dawson, S., Barker, R.J., Rayment, W., du Fresne, S., Bräger, S. 2012. First evidence that marine protected areas can work for marine mammals. Journal of Applied Ecology 49: 474-480.

Green, G.A., Cardwell, R., Brancato, M.S. 1997. Comment on Elevated accumulation of tributyltin and its breakdown products in bottlenose dolphins (*Tursiops truncatus*) found stranded along the U.S. Atlantic and Gulf coasts. Environmental Science and Technology 31: 3032-3034.

Hammond, P.S., Bearzi, G., Bjørge, A., Forney, K.A., Karkzmarski, L., Kasuya, T., Perrin, W.F., Scott, M.D., Wang, J.Y. , Wells, R.S., Wilson, B. 2012. *Tursiops truncatus*. *In*: IUCN 2012. IUCN Red List of Threatened Species. Version 2012.2, www.iucnredlist.org. Downloaded on 11 June 2013.

Hamner, R.M., Pichler, F.B., Heimeier, D., Constantine, R., Baker, C.S. 2012. Genetic differentiation and limited gene flow among fragmented populations of New Zealand endemic Hector's and Maui's dolphins. Conservation Genetics 13: 987-1002.

Hansson, L., 1991. Dispersal and connectivity in metapopulations. Biological Journal of the Linnean Society 42: 89-103.

Hoelzel, A.R. 1994. Genetics and ecology of whales and dolphins. Annual Review of Ecology and Systematics 25: 377-399.

Hoelzel, A.R. 1998. Genetic structure of cetacean populations in sympatry, parapatry, and mixed assemblages: implications for conservation policy. Journal of Heredity 89: 451-458.

Hoyt, E. 2005 Creating better marine protected areas for cetaceans: steps towards the design, establishment and management of protected areas for cetaceans. *In*: Hoyt E. (Ed.), Marine protected areas for whales, dolphins and porpoises. Earthscan, London, pp. 68–82.

Kannan, K., Senthilkumar, B.G., Loganathan, S., Takahasi, D.K., Odell, D., Tanabe, S. 1997. Elevated accumulation of tributyltin and its breakdown products in bottlenose dolphins (*Tursiops truncatus*) found stranded along the U.S. Atlantic and Gulf Coasts. Environmental Science and Technology 31: 296-301.

Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. Bulletin of the Entomological Society of America 15: 237-240.

Marcovecchio, J., Moreno, V., Bastida, R., Gerpe, M., Rodriguez, D. 1990. Tissue distribution of heavy metals in small cetaceans from the southwestern Atlantic Ocean. Marine Pollution Bulletin 21: 299-304.

Marcovecchio, J.E., Gerpe, M.S., Bastida, R.O., Rodriguez, D.H., Moron, S.G. 1994. Environmental contamination and marine mammals in coastal waters from Argentina: an overview. Science of the Total Environment 154: 141-151.

Möller, L.M. and Beheregaray, L.B. 2004. Genetic evidence for sex-biased dispersal in resident bottlenose dolphins (*Tursiops aduncus*). Molecular Ecology 13: 1607-1612.

Natoli, A., Peddemors, V.M., Hoelzel, R.A. 2004. Population structure and speciation in the genus *Tursiops* based on microsatellite and mitochondrial DNA analyses. Journal of evolutionary biology 17: 363-375.

Pfeiffer, C.J., Sharova, L.V., Gray, L. 2000. Functional and ultra-structural cell pathology induced by fuel oil in cultured dolphin renal cells. Ecotoxicology and Environmental Safety 47: 210-217.

Rodríguez, A. and Delibes, M. 2003. Population fragmentation and extinction in the Iberian lynx. Biological conservation 109: 321-331.

Rosel, P., Hansen, L., Hohn, A.A. 2009. Restricted dispersal in a continuously distributed marine species: common bottlenose dolphins *Tursiops truncatus* in coastal waters of the western North Atlantic. Molecular Ecology 18: 5030-5045.

Sutherland, W.J. 2000. The conservation handbook: Research, management and policy. Blackwell, Hoboken, NJ.

Venerus, L. 2006. Dinámica espacial del salmón de mar *Pseudopercis semifasciata* (Cuvier, 1829) (*Pinguipedidae*)—implicancias para el uso sustentable de los sistemas de arrecifes rocosos. Dissertation, Universidad de Buenos Aires, Buenos Aires, Argentina.

Wells, R.S. 1986. Population structure of bottlenose dolphins: Behavioral studies along the central west coast of Florida. Contract Report to National Marine Fisheries Service, Southeast Fisheries Center. Contract No.45-WCNF-5–00366, 58 pp.

Wells, R.S. and Scott, M.D. 1990. Estimating bottlenose dolphin population parameters from individual identification and capture–release techniques. Report to the International Whaling Commission Special Issue 12: 407-415.

Wells, R.S. 1991. The role of long-term study in understanding the social structure of a bottlenose dolphin community. *In:* Pryor, K. and Norris, K.S. (Eds.), Dolphin societies: Discoveries and puzzles. University of California Press, Berkeley, CA, pp. 199-225.

Würsig, B. and Würsig, M. 1977. The photographic determination of group size, composition and stability of coastal porpoises (*Tursiops truncatus*). Science 198: 755-756.

APPENDICES

1. GENETIC DIVERSITY

After

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ABSTRACT - Knowledge about the ecology of bottlenose dolphins in the Southwestern Atlantic Ocean is scarce. Increased by-catch rates over the last decade in coastal waters of Southern Brazil have raised concerns about the decline in abundance of local dolphin communities. Lack of relevant data, including information on population structure and connectivity, have hampered an assessment of the conservation status of bottlenose dolphin communities in this region. Here we combined analyses of 16 microsatellite loci and mitochondrial DNA (mtDNA) control region sequences to investigate genetic diversity, structure and connectivity in 124 biopsy samples collected over six communities of photographically identified coastal bottlenose dolphins in Southern Brazil, Uruguay and central Argentina. Levels of nuclear genetic diversity were remarkably low (mean values of allelic diversity and heterozygosity across all loci were 3.6 and 0.21, respectively), a result that possibly reflects the small size of local dolphin communities. On a broad geographical scale, strong and significant genetic differentiation was found between bottlenose dolphins from Southern Brazil-Uruguay (SB-U) and Bahía San Antonio (BSA), Argentina (AMOVA mtDNA $\Phi_{ST} = 0.43$; nuclear $F_{ST} = 0.46$), with negligible contemporary gene flow detected based on Bayesian estimates. On a finer scale, moderate but significant differentiation (AMOVA mtDNA $\Phi_{ST} = 0.29$; nuclear $F_{ST} = 0.13$) and asymmetric gene flow was detected between five neighbouring communities in SB-U. Based on the results we propose that BSA and SB-U represent two distinct Evolutionarily Significant Units (ESUs), and that communities from SB-U comprise five distinct Management Units (MUs). Under this scenario, conservation efforts should prioritise the areas in Southern Brazil where dolphins from three MUs overlap in their home ranges and where by-catch rates are reportedly higher.

KEYWORDS - cetacean, conservation, connectivity, population genetics, microsatellite, mitochondrial DNA

1.1. INTRODUCTION

Bottlenose dolphins (*Tursiops* sp.) are cetaceans able to explore, occupy and adapt to different marine environments, with the exception of polar regions. Many genetic studies of bottlenose dolphins around the globe have reported moderate genetic differentiation among regional populations, despite some reproductive exchange (Sellas et al., 2005; Rosel et al., 2009; Tezanos-Pinto et al., 2009; Urian et al., 2009; Mirimin et al., 2011). Over large spatial scales, genetic discontinuities appear to coincide with ecological and topographic breaks, such as distinct water masses, currents and depth contours (Hoelzel et al., 1998a; Natoli et al., 2004; Bilgmann et al., 2007). On the other hand, habitat selection (e.g., open coast vs. estuarine ecosystems) and local adaptation to prey resources are believed to shape population structure over small spatial scales (Möller et al., 2007; Wiszniewski et al., 2010). Therefore, a combination of environmental, geomorphological and evolutionary factors appears to influence the genetic structure of bottlenose dolphin populations, although some may represent cryptic species-level differences (e.g., Natoli et al., 2004; Rosel et al., 2009).

Despite being extensively studied in many regions of the world, limited information is available for bottlenose dolphins of the Southwestern Atlantic Ocean (SWA); particularly scarce are details of their genetic diversity and population structure. Understanding population sub-divisions and connectivity provides information critical to the identification of relevant biological units to be conserved. These include Evolutionary Significant Units (ESUs) – a group of historically isolated populations with unique genealogical and adaptive legacy – and Management Units (MUs) – demographically distinct populations that should be managed separately to ensure the viability of the larger metapopulation (see Funk et al., 2012 for definitions and a recent perspective on ESUs and MUs). This is especially important in cases where populations are restricted in distribution, have small population sizes and are subject to human induced mortality, which is the case for bottlenose dolphins of the SWA. It has been reported that in the SWA coastal bottlenose dolphins are mainly found between Santa Catarina State, in Southern Brazil, and Central Argentina – and particularly along a narrow coastal corridor between Southern Brazil and Uruguay (SB-U) (Laporta et al., in press). In this region, bottlenose dolphins occur in bays and estuaries, and between the surf zone and 2km from the coastline when in the open-coast, with occasional records between 2 – 4 km (Laporta, 2009; Di Tullio, 2009). The distribution of coastal and offshore bottlenose dolphins apparently does not overlap and their feeding ecology is distinct, at least in part of the SWA (e.g., Botta et al., 2012). Concerns about the conservation of coastal bottlenose dolphins in SWA has recently emerged due to their relatively small population sizes (Laporta, 2009; Fruet et al., 2011; Daura-Jorge et al., 2013), vulnerability to by-catch (Fruet et al., 2012) and substantial coastal development, particularly in Southern Brazil (Tagliani et al., 2007). A long-term study of dolphin strandings has revealed high levels of mortality along Brazil's southernmost coastline, mainly in areas adjacent to the Patos Lagoon Estuary where by-catch seems to be the main cause of death (Fruet et al., 2012).

Systematic photo-identification studies have shown that coastal bottlenose dolphins of the SWA consist of small communities with high site fidelity to estuaries and river mouths (and each community not exceeding 90 individuals; Fruet et al., in press a). These are often bordered by other small bottlenose dolphin communities that show more extensive movements along the coast, in contrast to estuarine communities (Laporta et al., in press). Photo-identification efforts in the two main estuaries of Southern Brazil suggest that bottlenose dolphins exhibit long-term residency in these areas (Fruet et al., 2011; Daura-Jorge et al., 2013). Although there is distribution overlap of dolphins from these estuarine-associated and the adjacent coastal communities, no information is available on the levels of genetic connectivity among them. For example, social network analyses has revealed the existence of at least three distinct communities, which partially overlap in range near the Patos Lagoon Estuary, in Southern Brazil (Genoves, 2013). This includes the year-round resident community of the Patos Lagoon Estuary and two coastal communities: one that regularly moves from Uruguay to Southern Brazil during winter and spring (Laporta, 2009) and another which appears to inhabit the adjacent coastal waters of the Patos Lagoon Estuary year-round. Such range overlap suggests potential for interbreeding among individuals of these communities, which would have implications for MUs classification and conservation management efforts. Given the assumption of demographic independence between different MUs, their delineation requires a direct or indirect estimate of current dispersal rates (Palsbøll et al., 2007). However, dispersal rates can be difficult to estimate, particularly in the marine environment, which lacks marked physical barriers and where many organisms are not easily accessible for long-term field studies of identifiable or tagged individuals. In these cases, genetic methods generally offer a suitable alternative to assess dispersal rates and other indicators of demographic independence, as well as for estimating genetic diversity.

In this study we investigate the genetic diversity and population structure of bottlenose dolphins along the SWA coast using data from nuclear microsatellite markers and mtDNA control region sequences. We use this information to assess the strength and directionality of genetic connectivity over a range of spatial scales. Our sampling design allows comparisons among neighbouring coastal communities in Southern Brazil-Uruguay (SB-U), and between these and a community inhabiting Bahía San Antonio (BSA) in the Patagonian coast – the most southern resident bottlenose dolphin community known for the SWA and located in a different marine biogeographical region to Southern Brazil-Uruguay. We hypothesise that specialisation for, or association with particular habitat types such as estuaries and open coasts may promote genetic differentiation on small spatial scales, while the biogeographical disjunction may influence differentiation at broad scale. The adjacent dolphin communities sampled in SB-U include two estuarine and three open coast communities. If habitat type specialisation or, association with, drives genetic structure, we might expect to find lower genetic differentiation between communities inhabiting the contiguous open coast habitat than those living in sheltered estuarine environments, irrespective of geographical distances. We also expect that greater differentiation would characterise communities from different biogeographical regions. By delineating conservation units for coastal bottlenose dolphins in the SWA we expect to provide scientific support to guide strategies for population monitoring efforts, conservation status assessment and short-term management goals.

1.2. MATERIALS AND METHODS

1.2.1 Sampling scheme

The study area covers approximately 2,112 km of linear distance along the coast. It extends from Florianópolis, in Southern Brazil, to Bahía San Antonio, in the Patagonian Argentina. Along this region we surveyed six locations between 2004 and 2012 and collected 135 samples (Figure 26). Samples consisted primarily of skin tissue obtained from free-ranging coastal bottlenose dolphins (common bottlenose dolphins, *Tursiops truncatus* – see Wang et al. (1999) for Southern Brazil bottlenose dolphins molecular taxonomic identification) belonging to communities inhabiting a variety of habitat types: Florianópolis (FLN, coastal, *n* = 9), Laguna (LGN, estuarine, *n* = 11), north of Patos Lagoon (NPL, coastal, *n* = 21), Patos Lagoon Estuary (PLE, estuarine, *n* = 71), south of Patos Lagoon/Uruguay (SPL/URU, coastal, *n* = 14) and Bahía San Antonio, Argentina (BSA, coastal bay, *n* = 12) (Table 16). Samples were collected using a crossbow with 150 lb (68 KG) draw weight and darts and tips especially designed for sampling small cetaceans (Ceta-Dart, Copenhagen, Denmark). We attempted to individually identify sampled dolphins through simultaneous photo-identification (see Fruet et al., in press b for details). Samples were grouped according to the sampled location. For those collected in the adjacent coastal areas of Patos Lagoon Estuary, where three distinct communities live in close proximity and overlap in their range, identified individuals were grouped according to the social unit to which they were previously assigned based on social network analysis (Genoves, 2013). Our dataset also included four samples from freshly stranded carcasses, two collected in La Coronilla, Uruguay, and two in Southern Brazil from animals known to belong to the NPL community as photo-identified based on their natural marks prior to their death. Samples were preserved in 20% dimethyl sulphoxide (DMSO) saturated with sodium chloride (Amos and Hoelzel, 1991) or 98% ethanol.

1.2.2 Genetic methods

Genomic DNA was extracted from all samples following a salting-out protocol (Sunnucks and Hales, 1996). Sex of each biopsy sample was determined by the amplification of fragments of the *SRY* and *ZFX* genes through the polymerase chain reaction (PCR) (Gilson et al., 1998), with PCR conditions described in Möller et al. (2001). Samples were genotyped at 16 microsatellite loci (Online Resource 1) and a fragment of approximately 550 bp of the control region was sequenced using primers Dlp-1.5 and Dlp-5 (Baker et al., 1993) on an ABI 3730 (Applied Biosystems) with GenScan 500 LIZ 3130 internal size standard. Procedures for microsatellite PCR and genotyping are found in Möller and Beheregaray (2004), and for mtDNA PCR and sequencing in Möller and Beheregaray (2001). For microsatellites, bins for each locus were determined and genotypes scored in GENEMAPPER 4.0 (Applied Biosystems). Rare alleles (i.e., frequency < 0.05) or alleles that fell in between two bins were re-genotyped. Micro-Checker 2.2.3 (Van Oosterhout et al., 2004) was used to check for potential scoring errors, the presence of null alleles, stuttering and large allelic drop out. Genotyping error rates were estimated by re-genotyping 30 randomly selected samples, representing 22% of the total sample size used in this study. We used GENALEX 6.5 (Peakall and Smouse, 2012) to find potential matches between genotypes and to estimate the probability of identity as an indicator of the power of the 16 markers to distinguish between two sampled individuals. Samples matching at all genotypes or those mismatching at only a few alleles (1-2) were double-checked for potential scoring errors. Sequences of the mtDNA were edited using SEQUENCHER 3.0 (Gene Codes Corporation, Ann Arbor, MI) and aligned using the ClustalW algorithm in MEGA 5.05 (Tamura et al., 2011). Haplotypes were defined using DNASP 5.0 (Librado and Rozas, 2009). After careful examination, samples sharing identical genotypes at all loci, same mtDNA haplotype and sex were considered as re-sampled individuals and one of each pair was removed. Re-sampled individuals identified by photo-identification (n = 7) were also confirmed through genetic methods.

1.2.3 Data analysis

Population structure

We used 10,000 permutations in SPAGEDI to test for the relative importance of a stepwise mutation model as a contributor to genetic diversity and structure (Hardy and Vekemans, 2002). This provides a way to assess whether F_{ST} or R_{ST} potentially provides a more appropriate statistic to estimate genetic structure since R_{ST} accounts for divergence times between microsatellite alleles and is thus expected to better reflect older divergences (Hardy et al., 2003). Allele size permutation test in SPAGEDI were non-significant for all loci. This suggests that F_{ST} is likely the most appropriate estimator, and only F_{ST} values are therefore reported hereafter. ARLEQUIN 3.5.1.2 was used for an analysis of molecular variance (AMOVA) to evaluate differentiation between SB-U and BSA dolphins, and among SB-U communities, for both nuclear and mtDNA datasets. Degree of genetic differentiation among locations was also assessed using ARLEQUIN to calculate F_{ST} (Weir and Cockerham, 1984) for microsatellites, and both F_{ST} and Φ_{ST} measures for mtDNA. For each of these measures we used the Tamura and Nei (1993) model with a gamma correction of 0.5. Significance was tested based on 10,000 permutations. We also estimated the statistical power to detect nuclear differentiation using POWSIM (Ryman and Palm, 2006) by simulating six populations with samples sizes of each sampled community (8, 10, 19, 63, 12, 12) with F_{ST} of 0.05 (combining generation, time t = 25 with effective population size, N_e = 500), which approximates the lowest empirical fixation index found based on 15 loci (see Results). The α (Type I) error was assessed running the same simulated scenario, but sampling directly from the base population (i.e., setting drift time t = 0). A thousand replicates were run and the significance of the tests was assessed with Fisher's exact tests and chi-square tests.

The Bayesian clustering method implemented in STRUCTURE 2.3.3 (Pritchard et al., 2000) was also used for inferring population structure based on the microsatellite data. We assumed correlated allele frequencies and an admixture model using sampling location as prior information (LOCPRIOR function) (Hubisz et al., 2009). Simulations were performed using a 200,000 step burn-in period and 10^6 repetitions of the Markov Chain Monte Carlo (MCMC) search, assuming number of clusters (K) varying between 1 and 6. We performed 20 independent runs to limit the influence of stochasticity, to increase the precision of the parameter estimates, and to provide an estimate of experimental reproducibility (Gilbert et al., 2012). The most likely K was explicitly determined by examining ΔK (Evanno et al., 2005) in STRUCTURE HARVESTER (Earl and vonHoldt, 2012). Following the recommendations of Evanno et al. (2005), we ran an iterative process where, for each most likely K detected by STRUCTURE, we independently re-analysed the data to test for further sub-division. This process was repeated until the most likely K was 1.

Isolation by distance (IBD) was assessed by conducting Mantel tests (Mantel, 1967) between matrices of F_{ST} genetic distances and geographical distances measured as the shortest marine coastal distance between two locations. Given the large geographical distance between the southernmost sampling site (BSA) and others, we excluded BSA from the IBD analysis. We also used partial Mantel tests to test for an association between habitat type (estuarine versus coastal) and genetic distance, while controlling for the effect of geographical distance. Both tests were run with 1,000 random permutations in GENODIVE 2.0.

Gene flow

Magnitude and direction of contemporary gene flow among the six sampled communities was estimated using BAYESASS 3.0 (Wilson and Rannala, 2003). The software uses a MCMC algorithm to estimate the posterior probability distribution of the proportion of migrants from one population to another. This was conducted with ten independent MCMC runs of 10^7 steps, with the first 10^6 repetitions discarded as burn-in. To reach the recommended acceptance rates of total iterations between 20% and 40% we adjusted the values of continuous parameters such as migration rates (Δ_M), allele frequencies (Δ_A) and inbreeding coefficient (Δ_F) to 0.9, 0.6 and 0.8, respectively. Samples were collected every 200 iterations to infer the posterior probability distributions of parameters. Trace files were monitored for convergence and runs with potential problems were discarded. Additionally, convergence was checked by comparing the migration rate profile between the runs according to their average total likelihood and associated credible confidence interval (CI).

Genetic diversity

For microsatellites, genetic diversity, expressed as number of alleles (NA), expected (H_E) and observed (H_O) heterozygosity, as well as the inbreeding coefficient (F_{IS}) were estimated for each community in GENODIVE 2.0 (Meirmans and Van Tienderen, 2004). Departures from Hardy–Weinberg equilibrium and linkage disequilibrium were tested using the Fisher's exact test and a Markov chain method with 1,000 iterations in GENEPOP 4.2 (Rousset, 2008). Allelic richness (AR) was estimated in FSTAT 2.9.3.2 (Goudet, 1995). All statistical tests followed sequential Bonferroni correction to address type I errors associated with multiple comparisons (Rice, 1989). For the mtDNA sequences, we used ARLEQUIN 3.5.1.2 (Excoffier and Lischer, 2010) to estimate haplotypic and nucleotide diversities. A median-joining network from the mtDNA haplotypes was constructed using NETWORK 4.6.1.1 (Bandelt et al., 1999).

1.3. RESULTS

1.3.1 Summary statistics

A total of 134 biopsy samples and four samples from stranded carcasses were used. All samples were successfully amplified at 16 microsatellite loci and sequenced for approximately 550bp of the mtDNA control region. Only eight out of 450 repeated genotypes (1.7%) did not match but were resolved by re-genotyping. The probability of two unrelated individuals or siblings sharing the same genotypes was very low for all communities (Table 16). Multiple lines of evidence (identical genotype, same mtDNA sequence and sex) suggested that 14 biopsied individuals were sampled twice, including seven individuals that were suspected re-samples based on photo-identification. All re-sampled animals were biopsied in the same location: eight in PLE, two in SPL/URU, two in NPL, one in LGN, and one in FLN. After removal of duplicates, 124 samples were included in the final dataset analysed. From these, 61 samples were males and 63 were females (Table 16).

The microsatellite locus Tur91 was monomorphic and therefore excluded from further analysis. We found no evidence for effects of large allelic dropout in any locus. Null alleles were detected for two loci but these were not consistent among sampled locations (locus TUR80 in PLE and Ttr04 in BSA), and therefore the loci were kept for all analyses. One locus pair (TUR105 and EV37) showed evidence of linkage disequilibrium. However, because similar results were obtained when analyses were run both with and without TUR105 this locus was kept in the dataset. Laguna was the only sample location that showed significant deviation from Hardy-Weinberg equilibrium when averaged across all loci, likely due to inbreeding (F_{IS} = 0.28) in this small community. Inbreeding coefficient was low and non-significant for all other communities (Table 16).

1.3.2 Genetic structure

The AMOVA results showed strong differentiation between SB-U and BSA for both microsatellites (F_{ST} = 0.46, $p < 0.001$) and mtDNA (Φ_{ST} = 0.43, $p < 0.0001$). On a smaller spatial scale, the AMOVA indicated moderate differentiation among SB-U communities, for both microsatellites (F_{ST} = 0.13, $p < 0.0001$) and mtDNA (Φ_{ST} = 0.29, $p < 0.0001$). Accordingly, significant differentiation was observed for all pairwise comparisons using microsatellites (Table 17), but over a wide range of F_{ST} values (0.066-0.617). Excluding BSA, which was by far the most differentiated (average F_{ST} of 0.51 for all comparisons with other communities), moderate but significant differentiation was found between all other pairwise comparisons, with the two geographically closest communities (PLE and NPL) having the lowest value of F_{ST} (F_{ST} = 0.06; $p < 0.001$). POWSIM simulations for 15 microsatellite loci and the sample sizes used in this study suggested a 100% probability of detecting differentiation above the lowest empirical F_{ST} level of differentiation, indicating satisfactory statistical power for our analyses. The estimated type I error varied from 0.041 with Fisher's exact tests to 0.083 with X^2 tests, which approximates the conventional 5% limit for significance testing.

Results of pairwise comparisons using mtDNA were generally congruent with results from the microsatellite analyses, albeit with higher levels of differentiation between communities. The exceptions were NPL and PLE (for both F_{ST} and Φ_{ST}), and NPL and FLN (for Φ_{ST} only), which showed no significant differentiation (Table 18). All three of these communities are dominated by the most common mtDNA haplotype (H08). Pairwise significant F_{ST} values ranged between 0.097 (NPL – FLN) to 1 (LGN – BSA), with BSA the most differentiated community across all comparisons.

Mantel tests revealed a positive and significant correlation between microsatellites and mtDNA fixation indices and geographical distances, suggesting a pattern of IBD (Figure 28). For the mtDNA data, the correlation was not as strong ($r^2 = 0.428$) as for the microsatellites ($r^2 = 0.934$), but still significant. Results of partial Mantel tests (details not shown) suggested that differentiation was more likely influenced by distance than by habitat type (estuarine versus coastal). When controlling for geographical distances, non-significant relationships between locations and clusters (cluster 1 and 2: estuarine and coastal communities, respectively) were found for both microsatellites ($r^2 = -0.437$; $p = 0.51$) and mtDNA ($r^2 = -0.525$; $p = 0.52$).

Bayesian posterior probabilities indicated that the dataset is best explained by the clustering of samples into two genetic populations (K = 2), with all individuals from BSA placed in one cluster and remaining individuals sampled in SB-U placed in a second cluster (Figure 29 a). Negligible admixture appears to exist between these two clusters, with assignment estimates of all individuals to their respective clusters above 0.99 and 0.98, respectively. Testing for further sub-division by running STRUCTURE for the set of northern communities led to the identification of additional partitioning within SB-U most consistent with five populations (Figure 29 b-d). No sub-division was detected within BSA (data not shown).

1.3.3 Gene flow

Estimates of contemporary gene flow inferred in BayesAss suggested very low gene flow from BSA to SB-U communities (2.2%) and negligible gene flow in the opposite direction (0.3%). Within the SB-U region, BayesAss revealed moderate and complex asymmetrical migration rates (Table 19; Figure 30) consistent with the inferred pattern of IBD. Generally, higher migration occurred between neighbouring communities than between those separated by greater geographic distances, with the exception of LGN, which seems to exchange more migrants with more distant communities than with its closest neighbouring community (FLN). Migration estimates between sampling locations at the extremities of the sampling distribution was low. Estimated migration rates from FLN to NPL and from SPL/URU to PLE were at least twice the rates between all other community pairs (Figure 30). For the estuarine communities, PLE seems to act as a sink with a considerable rate of migrants coming from LGN, NPL and SPL/URU, and negligible migration in the opposite direction. In contrast, LGN seems to be more closed to immigration while contributing genetic migrants to PLE and NPL.

1.3.4 Genetic diversity

Levels of genetic variation were remarkably low for all samples as measured by both allelic richness (AR) and expected heterozygosity (H_E) (Table 16; Table 20). Observed heterozygosity (H_O) ranged from 0.15 to 0.26, with a mean across all loci of 0.21. AR ranged from 1.5 to 2.0, being higher in PLE, NPL and URU, and lower in LGN and BSA. Number of alleles per locus ranged from two to seven (Table 20) with a mean across all loci of 3.6, while the mean number of alleles per community was two. Out of 17 'private' (unique) alleles identified, nine were found in PLE, five in SPL/URU, two in NPL and one in BSA (Table 16). The only private allele in BSA was found in high frequency in that community, while in all other communities unique alleles had low frequencies.

After sequence alignment and editing, 457bp of the mtDNA control region could be analysed for the same 124 individuals used for the microsatellite analysis. Thirteen polymorphic sites (all transitional mutations) revealed nine distinct haplotypes. The number of haplotypes detected in each sampled location varied from one to five, and haplotype diversity ranged from 0 to 0.75. Overall, nucleotide diversity among all individuals was low ($\pi = 0.009$), and haplotype diversity moderate ($h = 0.712$), although values varied among communities. FLN community displayed the highest level of haplotype diversity, while PLE had the highest nucleotide diversity (Table 16). The most common and widely dispersed haplotype (H8) was found in 49.6% of the individuals and across all locations, except in LGN and BSA where all dolphins shared the same haplotypes (H7 for LGN and H4 for BSA). Private haplotypes were found in four of the six communities (FLN, $n = 1$; NPL, $n = 1$; SPL/URU, $n = 2$; BSA, $n = 1$) (Figure 26).

The median-joining network showed two main groups of haplotypes separated by a minimum of five mutational steps (Figure 27). Individuals from PLE, NPL and SPL/URU communities were present in both groups while individuals from LGN, BSA and FLN were represented in only one of the groups. Bahía San Antonio retains a unique haplotype (H05), which is fixed for this location and differs from the most common haplotype (H08) by one mutational step.

1.4. DISCUSSION

This study comprises the first comprehensive assessment of population structure and genetic diversity of coastal bottlenose dolphins (*Tursiops truncatus*) along the Southwestern Atlantic Ocean (SWA). On a large spatial scale, we report on two genetic populations (SB-U and BSA) that are highly differentiated and show very low level of gene flow. On a smaller spatial scale, we detected low to moderate levels of asymmetric gene flow between communities within the SB-U population and an influence of geographic distance in shaping patterns of connectivity, perhaps with the exception of Laguna. Here we also show that coastal bottlenose dolphins in the SWA have very low levels of genetic diversity. This reduced gene flow and genetic diversity, combined with the small size and probable demographic independence of communities, limit the likelihood of replenishment if they undergo a genetic or demographic decline, highlighting the need to implement local-based monitoring and conservation plans.

1.4.1 Large-scale population structure in SWA bottlenose dolphins

On a broad geographical scale, our results indicate that bottlenose dolphins in coastal Argentinean Patagonia (BSA community) are highly differentiated from those sampled along the Southern Brazil – Uruguay (SB-U) coast, likely reflecting a combination of IBD and environmental differentiation. Several studies have argued that bottlenose dolphins are capable of specialisation for a variety of habitats and prey types, and that such specialisation could promote genetic divergence (Hoelzel et al., 1998a; Natoli et al., 2004; Möller et al., 2007; Tezanos-Pinto et al., 2009; Wiszniewski et al., 2010; Möller, 2012). Bahía San Antonio is located in the San Matías Gulf (Figure 26), which is part of the Northern Patagonian gulfs of Argentina. Geomorphological characteristics (bathymetry and coastal complexity), oceanographic processes (upwelling, nutrient input, sea surface temperature regimes and currents), and biological community structure biogeographically distinguishes the Patagonian region from the rest of the Atlantic coast (Balech and Ehrlich, 2008; Tonini, 2010). For example, archaeozoological evidence suggests that one of the main prey species of bottlenose dolphins in SB-U, the white croaker (*Micropogonias furnieri*) (Pinedo, 1982; Mehsen et al*.,* 2005), is currently absent from BSA (Scartascini and Volpedo 2013), which is the northernmost limit for many prey species confirmed to be part of the diet of bottlenose dolphins in Patagonia (e.g., pouched lamprey (*Geotria australis*), Patagonian octopus (*Octopus tehuelchus*), Argentine Hake (*Mercluccius hubbsi*) (Crespo et al., 2008), as it is located at the boundary between two biogeographic regions (Galván et al., 2009). Regional differences in prey distribution and abundance are thought to play a role on the genetic structuring of bottlenose dolphins elsewhere (e.g., Bilgmann et al., 2007). Therefore, BSA bottlenose dolphins may have different foraging adaptations compared to SB-U bottlenose dolphins. The high degree of differentiation at neutral markers and the results from the Bayesian analysis of migration rates imply negligible gene flow between bottlenose dolphin communities of these two regions. Future studies combining morphological, genetic, environmental, and ecological data are needed to better clarify the taxonomic status between BSA and SB-U coastal bottlenose dolphins.

1.4.2 Fine-scale population structure in SWA bottlenose dolphins

In spite of their high dispersal potential, several empirical studies have shown that coastal bottlenose dolphins often form discrete population units, even at very small geographical scales (e.g., Sellas et al., 2005; Möller et al., 2007; Rosel et al., 2009; Ansmann et al., 2012). Our results from both fixation indices and the Bayesian clustering analysis confirmed that the five studied communities within the SB-U population are genetically distinct, indicating higher genetic differentiation than expected over small geographical scales. Relatively lower degrees of nuclear genetic differentiation are commonly reported for bottlenose dolphins over comparable spatial scales with the exception of the high differentiation found among the neighbouring communities of *T. truncatus* in Irish coastal waters (Shannon Estuary and Connemara-Mayo communities $F_{ST} = 0.179$; Mirimin et al., 2011). For instance, lower differentiation was found between neighbouring communities of *T. truncatus* along the coast of the western North Atlantic (minimum and maximum reported F_{ST} values of 0.002 and 0.015, respectively; Rosel et al., 2009) and Bahamas (F_{ST} = 0.048; total distance between two sampling sites was 116km; Parsons et al., 2006).

For highly mobile, long-lived animals with low reproductive rates such as cetaceans, it is well accepted that a combination of mechanisms including habitat selection, specialised foraging behaviours, social structure and natal philopatry can drive population differentiation across small spatial scales (Hoelzel, 2009; Möller, 2012). For a closely related species, the Indo-Pacific bottlenose dolphins, restricted gene flow between some coastal and estuarine communities appears to have occurred after coastal dolphins colonised the embayment, as a consequence of high site fidelity and resource and behavioural specialisations (Möller et al., 2007). In our study, however, we actually found similar levels of genetic differentiation when comparing coastal and estuarine communities or among coastal communities of the common bottlenose dolphin in SWA. This pattern is contrary to what would be expected if habitat type was a main driver of bottlenose dolphin population structure in the region. Instead, for most communities, structure appeared to follow an isolation-by-distance model, where exchange of individuals seems to more likely occur between adjacent communities, irrespective of habitat type. The only exception was Laguna, which appeared as an outlier to the IBD model. In Laguna, a unique foraging tactic involving cooperative interactions between dolphins and beach-casting fishermen has evolved. It has been suggested that the propagation of such behaviour through social learning has a matrilineal origin, where the mother–calf relationship might create conditions suitable for behavioural information exchange (Daura-Jorge et al., 2012). In such special conditions, the costs to individuals of leaving a suitable habitat is likely greater than the risk of searching for more profitable locations. In contrast, some PLE dolphins frequently interact with animals from other communities in the coastal zone, and there is no evidence of particular feeding specialisations compared to LGN. Thus, it appears that feeding specialisations (LGN) and sociality (PLE), instead of habitat type *per se*, may play a role in shaping genetic structure of bottlenose dolphins in these regions.

The contemporary asymmetric gene flow found in our study system suggests moderate levels of connectivity among communities in SB-U ESU, which are consistent with a meta-population. Gene flow is particularly mediated by coastal communities, especially FLN and SPL/URU, although estuarine communities exchange genes as well. It seems that PLE potentially acts as a sink, receiving low to moderate number of migrants while not contributing substantially to other communities. In contrast, LGN showed much lower gene flow with adjacent communities, apparently constituting a more closed genetic unit. This pattern is also supported by mitochondrial data, which suggested high connectivity between PLE and the adjacent coastal community (NPL), but high maternal philopatry and restricted dispersal of LGN dolphins.

1.4.3 Remarkably low levels of genetic diversity in SWA bottlenose dolphins

Low genetic variation was detected with both mitochondrial and nuclear DNA markers across all communities. Levels of variation at the mtDNA control region were similar to those reported for *T. truncatus* in other parts of the world. In contrast, nuclear DNA variation for all communities was much lower than that reported for other local coastal communities elsewhere (see Online Resource 2 for comparisons with studies of Parsons et al., 2006; Rosel et al., 2009; Tezanos-Pinto et al., 2009; Mirimin et al., 2011; Caballero et al., 2012). This is supported by the low numbers of alleles, reduced allelic richness and reduced heterozygosity. For LGN and BSA communities in particular, the remarkably low variation at both marker types fall within the range observed for cetaceans with extremely small populations sizes (i.e., < 100 individuals), such as the subspecies of Hector's dolphins, *Cephalorhyncus hectori mauii* (Hamner et al., 2012), and the Black Sea subspecies of the harbour porpoise, *Phocoena phocoena relicta* (Rosel et al., 1995). These findings are consistent with the current abundance estimates of less than 90 individuals for the BSA, PLE, and LGN communities (Vermeulen and Cammareri, 2009; Fruet et al., 2011; Daura-Jorge et al., 2013) and may also reflect the potential small size of the other communities (such as FLN, NPL and SPL/URU) for which estimates of abundance are not currently available. Several authors have suggested that coastal populations bottlenose dolphin elsewhere might have originated via independent founder events from offshore populations, followed by local adaptation and natal philopatry (Hoelzel et al., 1998a; Natoli et al., 2004; Sellas et al., 2005; Möller et al., 2007; Tezanos-Pinto et al., 2009), leading to a reduction in genetic diversity.

1.4.4 Conservation implications

On a large geographical scale our results strongly support that SB-U and BSA dolphins constitute at least two distinct ESUs, and these warrant separate conservation and management strategies. The SB-U ESU comprises a set of communities (or sub-populations) distributed along a narrow strip of the coast between Florianopolis (27°21' S) in Southern Brazil, and the southern limit of the Uruguayan coast (34°55'S). The BSA ESU geographical range goes possibly from the northern border of the Province of Río Negro, at the Río Negro Estuary (41°01' S), to southern Golfo Nuevo (43°05' S), as suggested by sightings of bottlenose dolphins in Northern Patagonia (Vermeulen and Cammareri 2009; Coscarella et al., 2012). Our results indicate that these two ESUs are genetically isolated which has important implications for future conservation plans. It is fundamental that managers design appropriate conservation strategies for each ESU, taking into account their respective threats, genetic and ecological processes shaping structure, and geographical distribution in space and time, as their responses to future environmental changes may possibly differ. This is of particular relevance for BSA dolphins since they apparently constitute the only population within that ESU with reduced abundance and signs of historical decline (Bastida and Rodríguez, 2003; Coscarella et al., 2012).

The most serious and continuous threats for bottlenose dolphins along the SWA coast are found within the SB-U ESU, where they have experienced increased rates of human-related mortalities during the past decade (Fruet et al., 2012). These animals also face considerable coastal habitat degradation as a consequence of ongoing industrial and port development activities (Tagliani et al., 2007). Based on this study we suggest that these dolphin communities within SB-U are functionally independent, and therefore should be treated as separate MUs for conservation purposes. We advocate for managers to adopt the proposed MUs reported here (see Figure 26), while recognising that their boundaries may change as more information on dolphin home ranges and population genetic structure becomes available. Under this proposed management scenario, conservation programs should be directed towards the Patos Lagoon Estuary and adjacent coastal waters where dolphins from distinct communities (PLE, NPL and SPL/URU) show overlapping home ranges, and where by-catch rates are higher (Figure 26). Protecting dolphins in this region would reduce the risk of disrupting connectivity between MUs and increase the chances of long-term viability. Strategies should reduce the impact of by-catch and maximise the protection of 'corridors' in coastal areas for maintaining connectivity between adjacent dolphin communities.

The very low levels of genetic diversity in coastal bottlenose dolphins from SWA could be a source for concern. The importance of genetic variation relates to multiple aspects of population resilience and persistence, and is usually assumed to be critical for long-term fitness and adaptation (Franklin, 1980; Charlesworth and Willis, 2009), although some studies have shown that minimal genetic variation is not always a reliable predictor of extinction risk in wild populations (e.g., Schultz et al., 2009). We propose, however, the adoption of a precautionary approach for coastal bottlenose dolphins in SWA. Although there is no evidence of inbreeding depression for bottlenose dolphins in this region, the possibility of inbreeding in the small LGN community (Table 16) may, in the long-term, be detrimental to its viability since inbreeding can increase vulnerability to environmental stressors (O'Brien et al., 1985; Frankham 1995; Spielman et al., 2004; Hale and Briskie, 2007). Bottlenose dolphins from Laguna and their neighbouring community (FLN) are being affected by a chronic dermal infection, the fungal Lobomycosis, and Lobomycosis-like disease (LLD) (VanBressen et al., 2007, Daura-Jorge and Simões-Lopes, 2011), with evidence of an increase in the number of affected animals in recent years (Daura-Jorge and Simões-Lopes, 2011). While our results suggest restricted dispersal of LGN dolphins, which may limit the spread of the disease, the isolated nature of this community can potentially accelerate fungal transmission among resident dolphins.

1.4.5 Conclusions

Common bottlenose dolphins from coastal waters of the Southwestern Atlantic Ocean are characterised by unprecedentedly low mitochondrial and nuclear DNA diversity. Moderate to strong levels of population differentiation at both marker types were also disclosed and are likely associated with a combination of geographical, environmental and social factors. The pattern of genetic differentiation and the negligible migration rates detected suggest two distinct lineages, or Evolutionarily Significant Units, one in Argentina and the other in Southern Brazil-Uruguay. In addition, five distinct communities, or Management Units, characterised by low to moderate asymmetrical gene flow were identified in Southern Brazil-Uruguay – a region where human activities negatively impact upon common bottlenose dolphins. We propose that policies and practices relevant to conservation management of common bottlenose dolphins in coastal waters of the Southwestern Atlantic Ocean should recognise the existence of two lineages, as well as promote connectivity between the estuarine and open-coast populations in Southern Brazil and Uruguay to ensure their long-term persistence.

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1.5. Tables and Figures

Table 16 - Ecological information and summary of genetic diversity for the six communities and the two proposed Evolutionary Significant Units (ESUs) of coastal common bottlenose dolphins (*Tursiops truncatus*) based on mtDNA control region sequences and 15 microsatellite loci. N = total number of individuals (separated by sex); PA = number of private alleles; NA = mean number of alleles per locus; AR = mean allelic richness; HE = mean expected heterozygosity HO = mean observed heterozygosity; FIS = inbreeding coefficient; PIU, PISIBS: probabilities of identity for unbiased samples and samples of full-sibs, respectively

					mtDNA		Microsatellites							
		N (f:m)	Pop. Size (95% CI)	Habitat type	*h*	π	PA	NA	AR	H_E	H_O	F_{IS}	PI_U	PI_{SIBS}
Southern Brazil – Uruguay ESU	FLN	8 (6:2)	Unknown	Coastal	0.7500 (0.0965)	0.0045 (0.0032)	0	1.6	1.6	0.19	0.23	-0.22	1.5 x 10^{-3}	4.3 x 10^{-2}
	LGN	10 (2:8)	59 (49–72)[1]	Estuarine	0.0000 (0.0000)	0.0000 (0.0000)	0	1.6	1.5	0.21	0.15	0.28*	1.3 x 10^{-3}	3.6 x 10^{-2}
	NPL	19 (8:11)	Unknown	Coastal	0.5425 (0.1231)	0.0067 (0.0041)	2	2.3	1.9	0.20	0.19	0.06	7.5 x 10^{-4}	3.5 x 10^{-2}
	PLE	63 (38:25)	86 (78-95)[2]	Estuarine	0.4808 (0.0621)	0.0072 (0.0042)	9	3.0	2.0	0.26	0.26	-0.01	4.6 x 10^{-5}	9.7 x 10^{-3}
	SPL/URU	12 (5:7)	Unknown	Coastal	0.6484 (0.1163)	0.0067 (0.0041)	5	2.1	1.9	0.20	0.23	-0.02	3.5 x 10^{-4}	2.4 x 10^{-2}
	Total	112 (59:53)	-	-	0.6457 (0.0404)	0.0096 (0.0053)	16	3.7	2.2	0.22	0.22	0.02	-	-
BSA ESU	BSA	12 (2:10)	76 (70-97)[3]	Coastal Bays	0.0000 (0.0000)	0.0000 (0.0000)	1	1.76	1.76	0.19	0.18	0.08	2.6 x 10^{-3}	5.4 x 10^{-2}
	Total	124 (61:63)	-	-	0.7022 (0.0352)	0.0195 (0.0100)	-	3.6	-	0.28	0.23	0.194*	-	-

*Significant multi-locus p-value ($P < 0.001$). [1] Daura-Jorge et al., 2013; [2] Fruet et al., 2011; [3] Vermeulen and Cammareri, 2009

Table 17 - Estimates of microsatellite differentiation among six coastal communities of common bottlenose dolphins (*Tursiops truncatus*) sampled along the Southwestern Atlantic Ocean. Differentiation is expressed as FST based on 15 microsatellites loci. FLN = Florianópolis; LGN = Laguna; NPL = north Patos Lagoon; PLE = Patos Lagoon Estuary; SLP/URU = south Patos Lagoon/Uruguay; BSA = Bahía San Antonio

	FLN	LGN	NPL	PLE	SPL/URU	BSA
FLN	-					
LGN	0.131**	-				
NPL	0.147**	0.169**	-			
PLE	0.144**	0.101**	0.066**	-		
SPL/URU	0.289**	0.250**	0.156**	0.101**	-	
BSA	0.617**	0.502**	0.538**	0.423**	0.477**	-

*$P < 0.05$; **$P < 0.01$

Table 18 - Estimates of mitochondrial differentiation among six coastal communities of common bottlenose dolphins (*Tursiops truncatus*) sampled along the Southwestern Atlantic Ocean. Differentiation is expressed as ⍰ST (above diagonal) and FST (below diagonal) based on 457-bp of the mtDNA control region. FLN = Florianópolis; LGN = Laguna; NPL = north Patos Lagoon; PLE = Patos Lagoon Estuary; SLP/URU = south Patos Lagoon/Uruguay; BSA = Bahía San Antonio

	FLN	LGN	NPL	PLE	SPL/URU	BSA
FLN	-	0.659**	0.100*	0.209**	0.249**	0.687**
LGN	0.893**	-	0.622**	0.572**	0.666**	1.000**
NPL	0.040	0.744**	-	0.009	0.297**	0.679**
PLE	0.198*	0.489**	0.06	-	0.329**	0.638**
SPL/URU	0.531**	0.466**	0.392**	0.230**	-	0.689**
BSA	0.639**	1.000**	0.399**	0.340**	0.609**	-

*$p < 0.05$; **$p < 0.01$

Table 19 - Estimates of recent migration rates among six coastal communities of common bottlenose dolphins (*Tursiops truncatus*) sampled along the Southwestern Atlantic Ocean. Bold denotes the proportion of non-migrants in each dolphin community. 95% CI values are given in brackets. FLN = Florianópolis; LGN = Laguna; NPL = north Patos Lagoon; PLE = Patos Lagoon Estuary; SLP/URU = south Patos Lagoon/Uruguay; BSA = Bahía San Antonio

	TO						
FROM		FLN	LGN	NPL	PLE	SPL/URU	BSA
	FLN	**0.6915** **(0.646-0.736)**	0.0232 (0.019-0.066)	0.2152 (0.133-0.296)	0.0237 (0.019-0.067)	0.0232 (0.019-0.065)	0.0232 (0.019-0.063)
	LGN	0.0209 (0.017-0.058)	**0.6887** **(0.648-0.728)**	0.1289 (0.016-0.241)	0.1197 (0.007-0.232)	0.0209 (0.017-0.058)	0.0210 (0.017-0.059)
	NPL	0.0126 (0.011-0.036)	0.0127 (0.011-0.036)	**0.8454** **(0.738-0.952)**	0.1036 (0.001-0.208)	0.0127 (0.012-0.037)	0.0129 (0.010-0.036)
	PLE	0.0050 (0.004-0.015)	0.0054 (0.004-0.015)	0.0455 (0.003-0.094)	**0.9343** **(0.883-0.985)**	0.0049 (0.010-0.019)	0.0049 (0.004-0.014)
	SPL/URU	0.0181 (0.015-0.051)	0.0179 (0.016-0.052)	0.0237 (0.029-0.076)	0.2367 (0.141-0.331)	**0.6855** **(0.621-0.749)**	0.0180 (0.015-0.051)
	BSA	0.0182 (0.015-0.051)	0.0183 (0.015-0.051)	0.0182 (0.015-0.052)	0.0185 (0.015-0.052)	0.0183 (0.015-0.052)	**0.9084** **(0.841-0.975)**

Table 20 - Genetic diversity screened at 16 microsatellite loci in six coastal communities of common bottlenose dolphin sampled along the Southwestern Atlantic. NA, number of alleles; HO, observed heterozygosity; HE, expected heterozygosity; P, p-value of exact test using Markov chain; * Significant deviation from Hardy-Weinberg equilibrium (P < 0.05); NA, not available. [1]Nater et al. (2009); [2]Krützen et al. (2001); [3]Hoelzel et al. (1998b); [4]Valsecchi and Amos (1996); [5]Rooney et al. (1999); [6]Rosel et al. (2005)

	FLN (n = 8)				LGN (n = 10)				NPL (n = 19)				PLE (n = 63)				SPL/URU (n = 12)				BSA (n = 12)			
	NA	H_O	H_E	P	NA	H_O	H_E	P	NA	H_O	H_E	P	NA	H_O	H_E	P	NA	H_O	H_E	P	NA	H_O	H_E	P
Tur4_142[1]	1	0.00	0.00	NA	1	0.00	0.00	NA	1	0.00	0.00	NA	2	0.01	0.01	1.00	1	0.00	0.00	NA	1	0.00	0.00	NA
Tur4_91[1]	1	0.00	0.00	NA	1	0.00	0.00	NA	1	0.00	0.00	NA	1	0.00	0.00	NA	1	0.00	0.00	NA	1	0.00	0.00	NA
Tur4_141[1]	2	0.25	0.23	1.00	1	0.00	0.00	NA	1	0.00	0.00	NA	2	0.06	0.06	1.00	2	0.08	0.08	1.00	2	0.08	0.08	1.00
Tur4_F10[1]	1	0.00	0.00	NA	1	0.00	0.00	NA	1	0.00	0.00	NA	3	0.06	0.09	0.05	2	0.08	0.08	1.00	2	0.25	0.23	1.00
Tur4_E12[1]	3	0.75	0.66	0.77	3	0.30	0.59	0.02*	3	0.45	0.53	0.15	4	0.68	0.65	0.85	3	0.67	0.68	0.21	2	0.33	0.39	1.00
Tur4_105[1]	1	0.00	0.00	NA	1	0.00	0.00	NA	1	0.00	0.00	NA	4	0.04	0.04	1.00	1	0.00	0.00	NA	2	0.25	0.23	1.00
Tur4_80[1]	1	0.00	0.00	NA	2	0.10	0.10	1.00	2	0.05	0.05	1.00	5	0.03	0.08	0*	2	0.08	0.23	0.13	1	0.00	0.00	NA
Tur4_87[1]	1	0.00	0.00	NA	1	0.00	0.00	NA	1	0.00	0.00	NA	3	0.03	0.03	1.00	1	0.00	0.00	NA	1	0.00	0.00	NA
Mk6[2]	1	0.00	0.00	NA	1	0.00	0.00	NA	1	0.00	0.00	NA	1	0.00	0.00	NA	1	0.00	0.00	NA	2	0.58	0.52	1.00
Mk8[2]	3	0.62	0.62	0.73	2	0.60	0.53	1.00	5	0.50	0.45	0.13	4	0.43	0.46	0.03*	4	0.75	0.69	0.45	2	0.42	0.43	1.00
Kw2[3]	2	0.75	0.50	0.43	2	0.20	0.50	0.08	5	0.60	0.62	0.92	5	0.55	0.67	0.15	3	0.08	0.70	0.55	1	0.00	0.00	NA
Kw12a[3]	1	0.00	0.00	NA	2	0.30	0.39	0.48	2	0.15	0.14	1.00	2	0.46	0.39	0.20	1	0.00	0.00	NA	2	0.08	0.08	1.00
Ev37mn[4]	2	0.62	0.46	0.48	2	0.20	0.50	0.08	3	0.25	0.23	1.00	3	0.44	0.43	1.00	4	0.17	0.30	0.09	1	0.00	0.00	NA
TexVet5[5]	2	0.12	0.12	1.00	1	0.00	0.00	NA	2	0.05	0.05	1.00	1	0.00	0.00	NA	2	0.08	0.08	1.00	2	0.25	0.23	1.00
Ttr63[6]	2	0.12	0.12	1.00	1	0.00	0.00	NA	3	0.35	0.50	0.23	3	0.63	0.51	0.06	2	0.33	0.29	1.00	1	0.00	0.00	NA
Ttr04[6]	2	0.50	0.40	1.00	3	0.70	0.65	0.37	4	0.65	0.66	0.37	5	0.78	0.75	0.69	4	0.58	0.47	1.00	3	0.42	0.68	0.28

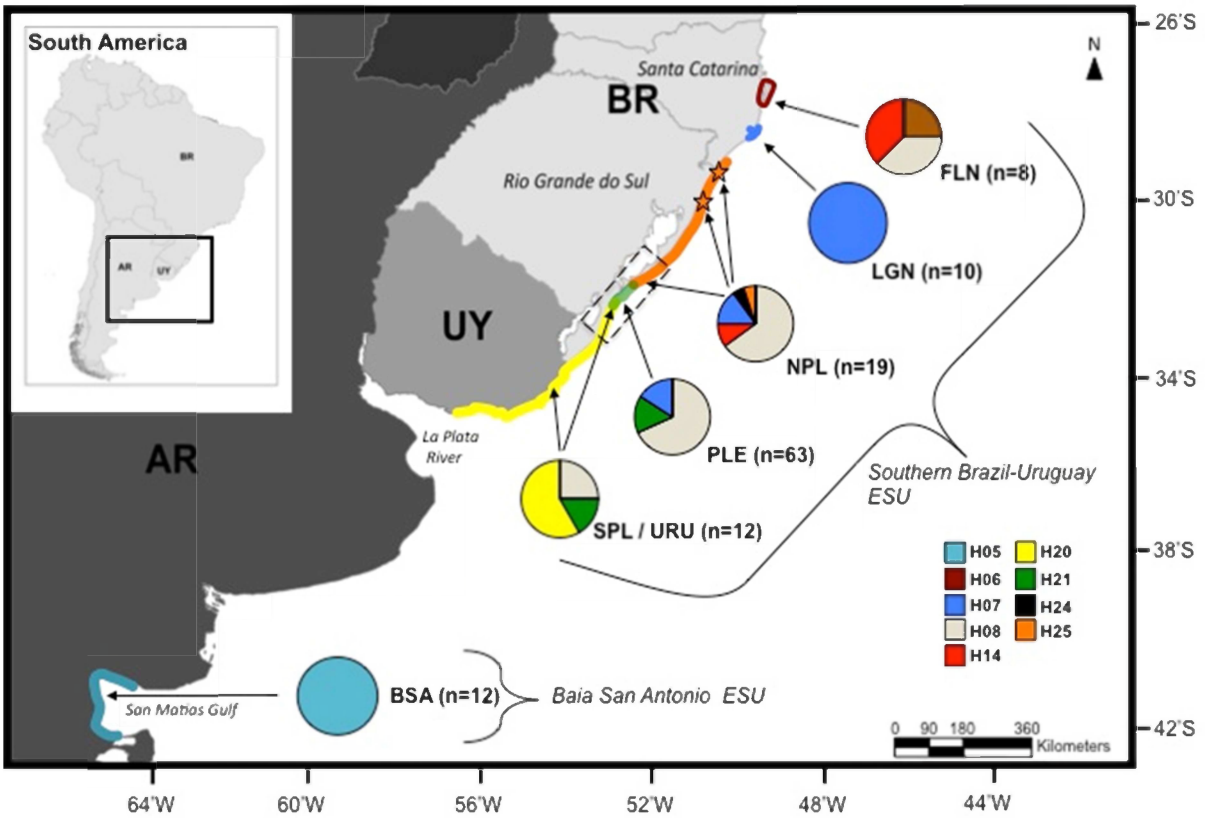


Figure 26 - Study area in the Southwestern Atlantic Ocean showing the proposed evolutionary significant units (ESUs) and management units (MUs) (colour counter lines) for coastal common bottlenose dolphins (*Tursiops truncatus*), and the respective frequencies of mitochondrial control region haplotypes (pie charts). Arrows indicate the main sampling locations for each dolphin community. Approximate geographic boundaries of management units were built combining the results of this study with current knowledge on residency, social structure and movement patterns of bottlenose dolphins along this region. Specifically for NPL, the genetic assignment of some individuals regularly sighted approximately 400km north of Patos Lagoon Estuary (represented by stars) to NPL community were used as a proxy to define the northern limit of the community range (Fruet et al., in prep). The dashed rectangle highlights the area of heightened conservation concern proposed by this study (see 'conservation implications' section for details). FLN = Florianópolis; LGN = Laguna; NPL = north Patos Lagoon; PLE = Patos Lagoon Estuary; SLP/URU = south Patos Lagoon/Uruguay; BSA = Bahía San Antonio

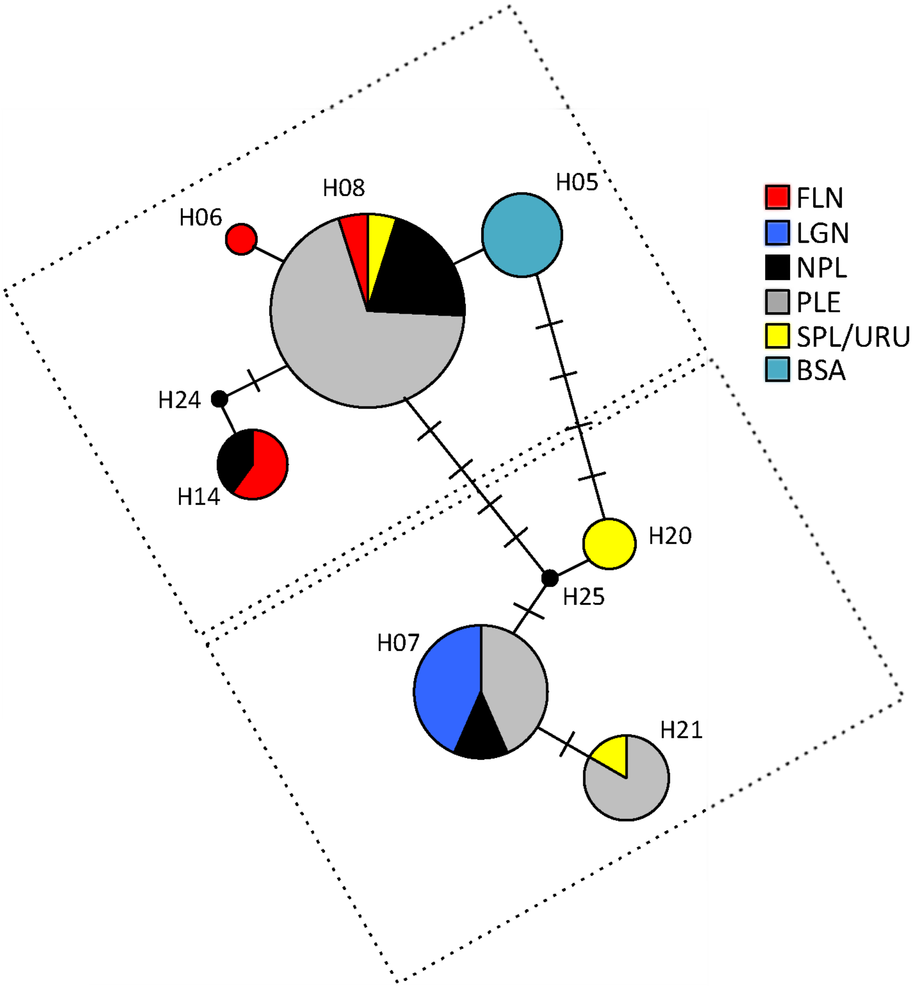


Figure 27 - Median-joining network of mtDNA control region haplotypes in coastal common bottlenose dolphins (*Tursiops truncatus*). The size of the circles is proportional to the total number of individuals bearing that haplotype. Dashed lines separate the two main groups of haplotypes. Different colours denote the different sampled communities: FLN = Florianópolis; LGN = Laguna; NPL = north Patos Lagoon; PLE = Patos Lagoon Estuary; SLP/URU = south Patos Lagoon/Uruguay; BSA = Bahía San Antonio. Dashes represent extinct or unsampled haplotypes

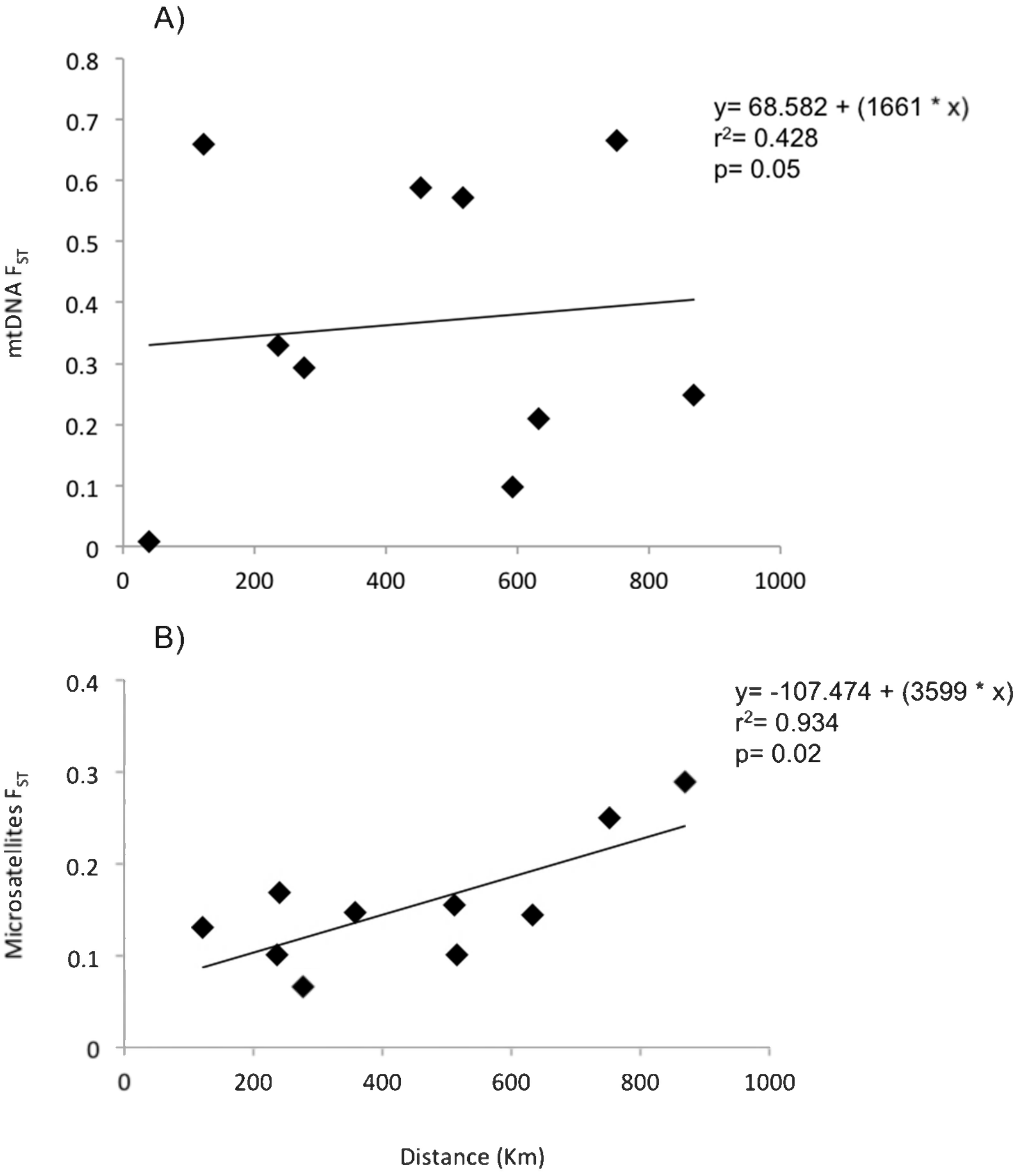


Figure 28 - Isolation by distance plots using Euclidean distance (km) and genetic distance (FST) among five coastal communities of common bottlenose dolphins (*Tursiops truncatus*) inhabiting Southern Brazil - Uruguay based on A) mtDNA control region and B) 15 microsatellite loci (lower box)

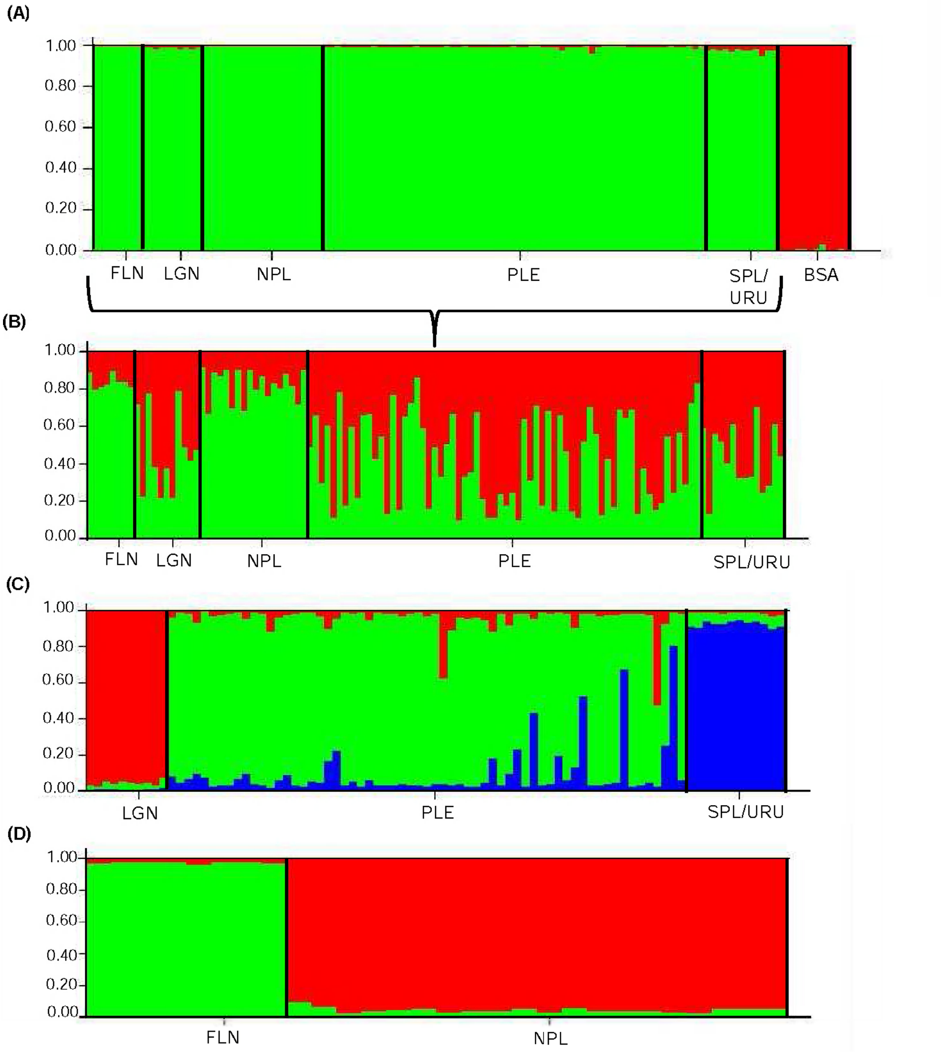


Figure 29 - STRUCTURE Bayesian assignment probabilities for common bottlenose dolphins (*Tursiops truncatus*) based on 15 microsatellite loci. Each vertical line represents one individual dolphin and vertical black lines separate the sampled communities. We run an iterative process where for each most likely K detected by STRUCTURE we independently re-analysed the data to test for further sub-division (Evanno et al., 2005; Pritchard et al., 2007). This process was repeated iteratively until the highest likelihood values resulted in K = 1. When all samples were analysed together, STRUCTURE clearly separated individuals sampled in BSA from all those sampled in Southern Brazil/Uruguay, resulting in K = 2 (A). The highest K for the next run within Southern Brazil/Uruguay populations was for K = 2, clustering LGN, PLE and SPL/URU, and FLN and NPL (B). When we run STRUCTURE independently for the above-mentioned clusters, the highest K resulted for K = 3 (C) and K = 2 (D), respectively. FLN, Florianópolis. LGN, Santo Antônio Lagoon. NPL, north Patos Lagoon. PLE, Patos Lagoon Estuary. SPL/URU, south Patos Lagoon/Uruguay. BSA, Bahía San Antonio

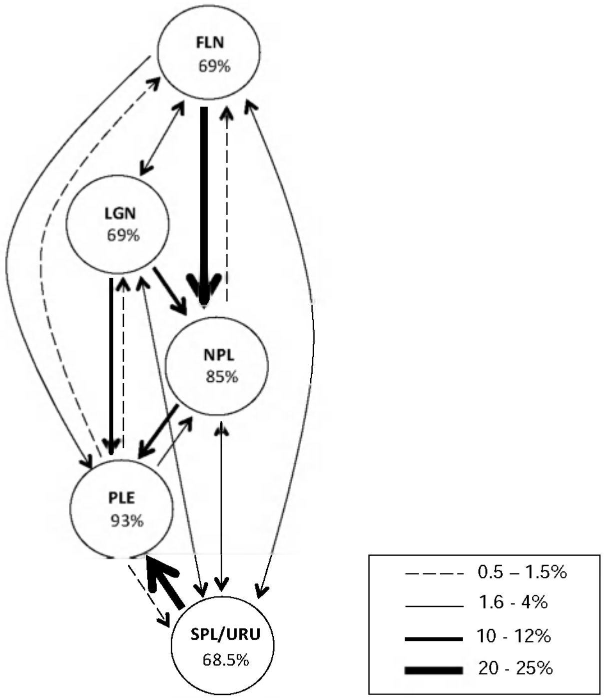


Figure 30 - Schematic diagram showing the recent asymmetric migration rates estimated between five coastal communities of common bottlenose dolphins (*Tursiops truncatus*) sampled along Southern Brazil and Uruguay. The width of the arrows corresponds to the rates of gene flow between putative populations

Online Resource 1 - Details of the 16 microsatellites screened in this study and their polymorphism in 124 common bottlenose dolphin samples. Colours depict co-loaded loci

	Locus	Isolated from	*Repeat motif*	Primer sequence 5' - 3	PCR Condition	Multiplex	Label	ASR (bp)	NA	H_O	H_E
1	*Tur4_142*[1]	*Tursiops aduncus*	$(GATA)_9$	F: GGCCCCCTTTTCCATCCTCA R: CCAGCCCCCAAAATCACGAGT	Wiszniewski et al. 2012	1	FAM	350-354	2	0.003	0.003
2	*Tur4_91*[1]	*Tursiops aduncus*	$(GATA)_{14}$	F:GTTGGCTCTCCAGCTCTCAGGT R: CAGTGGCTCCCATCTGTATTAGTCA	Wiszniewski et al. 2012	1	FAM	235	1	NA	NA
3	*Tur4_141*[1]	*Tursiops aduncus*	$(GATA)_9$	F: CACAAGCCTCAACCCTGGTGT R: CTAGTCTGCCAATCTGCCCTACAG	Wiszniewski et al. 2012	2	PET	234-258	3	0.080	0.078
4	*Tur4_F10*[1]	*Tursiops aduncus*	$(GATA)_9$	F: TCTTGATGGCTCAGAGGATGATTTTAC R: AGCCAAACTGAAGATGCAACTGACTAC	Wiszniewski et al. 2012	2	PET	406-414	3	0.066	0.068
5	*Tur4_E12*[1]	*Tursiops aduncus*	$(GATA)_9$	F: CTGGGCACTGTCCTCTGAACATC R: AGGAACGGCACATAAAGCACTGA	Wiszniewski et al. 2012	3	NED	284-292	4	0.530	0.587
6	*Tur4_105*[1]	*Tursiops aduncus*	$(GATA)_{11}$	F: CCCCGGCCTGCTTACCTCTG R: CCGCCCCCTCCCCAAGTC	Wiszniewski et al. 2012	3	NED	410-418	4	0.050	0.046
7	*Tur4_80*[1]	*Tursiops aduncus*	$(GATA)_{10}$	F: AGCCAATGTCAGGGTGCTGGAT R: GGGGCTTCTTGGCCTCTGTAA	Wiszniewski et al. 2012	4	VIC	326-342	5	0.044	0.078
8	*Tur4_87*[1]	*Tursiops aduncus*	$(GATA)_8$	F: CCCCATATGATGCCTTTGTAAGTCC R: AATTCCTTGTAACAAACCTCTTTATCT	Wiszniewski et al. 2012	4	VIC	192-220	3	0.005	0.005
9	*Mk6*[2]	*Tursiops aduncus*	$(GT)_{17}$	F: GTCCTCTTTCCAGGTGTAGCC R: GCCCACTAAGTATGTTGCAGC	Möller and Beheregaray (2004)	single	VIC	188-190	2	0.097	0.086
10	*Mk8*[2]	*Tursiops aduncus*	$(CA)_{23}$	F: TCCTGGAGCATCTTATAGTGGC R: CTCTTTGACATGCCCTCACC	Möller and Beheregaray (2004)	single	NED	113-123	7	0.553	0.528
11	*Kw2*[3]	*Orcinus orca*	-	F: GCTGTGAAAATTAAATGT R: CACTGTGGACAAATGTAA	Möller and Beheregaray (2004)	single	FAM	164-176	6	0.490	0.500
12	*Kw12a*[3]	*Orcinus orca*	-	F: CCATACAATCCAGCAGTC R: CACTGCAGAATGATGACC	Möller and Beheregaray (2004)	single	PET	192-194	2	0.166	0.170
13	*Ev37mn*[4]	*Megaptera novaeangliae*	$(AC)_{27}$	F:AGCTTGATTTGGAAGTCATGA R: TAGTAGAGCCGTGATAAAGTGC	Same conditions as KW2 and KW12	single	FAM	219-231	5	0.281	0.324
14	*TexVet5*[5]	*Tursiops truncatus*	$(CA)_{24}$	F: GATTGTGCAAATGGAGACA R: TTGAGATGACTCCTGTGGG	Same conditions as KW2 and KW12	single	VIC	219-223	3	0.085	0.080
15	*Ttr63*[6]	*Tursiops truncatus*	$(CA)_{34}$	F: CAGCTTACAGCCAAATGAGAG R: GTTTCTCCATGGCTGAGTCATCA	Wiszniewski et al. 2012	single	FAM	130-134	3	0.241	0.240
16	*Ttr04*[6]	*Tursiops truncatus*	$(CA)_{25}$	F: CTGACCAGGCACTTTCCAC R: GTTTGTTTCCCAGGATTTTAGTGC	Same conditions as KW2 and KW12	single	NED	132-140	5	0.605	0.604

[1]Nater et al. (2009); [2]Krützen et al. (2001); [3]Hoelzel et al. (1998a); [4]Valsecchi and Amos (1996); [5]Rooney et al. (1999); [6]Rosel et al.(2005)

Online Resource 2 - Summary of genetic variation for mtDNA control region sequences and nuclear microsatellite for coastal common bottlenose dolphins (*Tursiops truncatus*) worldwide, including findings from this study. N = total number of individuals; h = haplotypic diversity; π = nucleotide diversity; NA = mean number of alleles per locus; AR = mean allelic richness; H_O = mean observed heterozygosity; H_E = mean expected heterozygosity. Note: values can slightly differ from original source because they were adjusted to standardise decimal places

			mtDNA					*Microsatellite*									
Region	**Source**	**Sampling site**	**N**	***h***		**π**		**N**	**Loci**	**NA**		**AR**		**H_O**		**H_E**	
USA	Rosel et al. 2009	Virginia and North	100	0.761 (0.022)		0.013 (0.007)		87	18	8.3		7.4		0.66		0.68	
	Rosel et al. 2009	Southern North Carolina	51	0.756 (0.029)		0.003 (0.002)		50	18	7.3		7.0		0.62		0.64	
	Rosel et al. 2009	Charleston, SC and surrounding area	110	0.498 (0.053)		0.002 (0.001)		100	18	7.6		6.8		0.63		0.65	
	Rosel et al. 2009	Georgia	40	0.573 (0.067)		0.002 (0.002)		40	18	7.1		7.1		0.67		0.68	
	Rosel et al. 2009	Jacksonville	78	0.558 (0.039)		0.002 (0.002)		77	18	7.8		7		0.67		0.69	
	Rosel et al. 2009	Florida panhandle, Gulf of Mexico	72	0.754 (0.027)		0.009 (0.005)		77	18	7		6.4		0.62		0.65	
Ireland	Mirimin et al. 2011	Shannon Estuary	44	0.274 (0.076)		0.005 (0.003)		46	15	1.6		1.2		0.20		0.18	
	Mirimin et al. 2011	Connemara–Mayo	12	0.530 (0.136)		0.008 (0.005)		12	15	3.3		1		0.46		0.48	
New Zealand	Tezanos-Pinto et al. 2011	Northland	127	0.880 (0.01)		0.019 (0.010)		-	-	-		-		-		-	
	Tezanos-Pinto et al. 2011	Fiordland	24	0.760 (0.07)		0.015 (0.008)		-	-	-		-		-		-	
Caribean	Caballero et al. 2013	Bahamas, Cuba, Mexico, Puerto Rico, Virgin Islands	112	0.578 (0.049)		0.009 (0.005)		-	-	-		-		-		-	
Bahamas	Parsons et al. 2006	East and South Abbaco, White Sand Ridge	56	0.763 (0.046)		0.007 (0.004)		56	16	5.1		-		0.60		0.65	
Southern Brazil - Uruguay	This study	Florianópolis	8	0.750 (0.096)	0.646 (0.040)	0.004 (0.003)	0.019 (0.010)	8	15	1.6	3.7	1.6	2.2	0.23	0.22	0.19	0.22
	This study	Laguna	10	0.000 (0.000)		0.000 (0.000)		10	15	1.6		1.5		0.15		0.21	
	This study	North Patos Lagoon	19	0.542 (0.123)		0.007 (0.004)		19	15	2.3		1.9		0.19		0.20	
	This study	Patos Lagoon Estuary	63	0.481 (0.062)		0.007 (0.004)		63	15	3.0		2.0		0.26		0.26	
	This study	South Patos Lagoon/ Uruguay	12	0.648 (0.116)		0.007 (0.004)		12	15	2.1		1.9		0.23		0.20	
Argentina	This study	Bahía San Antonio	12	0.000 (0.000)		0.000 (0.000)		12	15	3.6		1.8		0.19		0.20	

1.6. REFERENCES

Anderson, O.R.J., Small, C.J., Croxall, J.P., Dunn, E.K., Sullivan, B.J., Yates, O., Black, A. 2011. Global seabird bycatch in longline fisheries. Endanger Species Research 14: 91-106.

Ansmann, I.C., Parra, G.J., Lanyon, J.M., Seddon, J.M. 2012. Fine-scale genetic population structure in a mobile marine mammal: inshore bottlenose dolphins in Moreton Bay, Australia. Molecular Ecology 21: 4472-4485.

Baker, C.S., Perry, A., Bannister, J.L., Weinrich, M.T., Abernethy, R.B., Calambokidis, J., Lien, J., Lambertensen, R.H., Urbán-Ramírez, J., Vasquez, O., Clapham, P.J., Alling, A., O'Brien, S.J., Palumbi, S.R. 1993. Abundant mitochondrial DNA variation and world-wide population structure in humpback whales. Proceedings of the National Academy of Sciences 90: 8239-8243.

Balech, E. and Ehrlich, M.D. 2008. Esquema biogeográfico del mar Argentino. Revista de Investigación y Desarrollo Pesquero 19: 45-75.

Bandelt, H.J., Forster, P., Röhl, A. 1999. Median-joining networks for inferring intraspecific phylogenies. Molecular Biology and Evolution 16: 37-48.

Bastida, R. and Rodríguez, D. 2003. Mamíferos Marinos Patagonia Antartida. Vázquez Mazzini Editors, Buenos Aires, Argentina, 206 pp.

Bilgmann, K., Möller, L.M., Harcourt, R.G., Gibbs, S.E., Beheregaray, L.B. 2007. Genetic differentiation in bottlenose dolphins from South Australia: association with local oceanography and coastal geography. Marine Ecology Progress Series 341: 265-276.

Botta, S., Hohn, A.A., Macko, S.A., Secchi, E.R. 2012. Isotopic variation in delphinids from the subtropical western South Atlantic. Journal of Marine Biological Association of the United Kingdom 92: 1689-1698.

Caballero, S., Islas-Villanueva, V., Tezanos-Pinto, G., Duchene, S., Delgado-Estrella, A., Sanchez-Okrucky, R., Mignucci-Giannoni, A.A. 2012. Phylogeography, genetic diversity and population structure of common bottlenose dolphins in the Wider Caribbean inferred from analyses of mitochondrial DNA control region sequences and microsatellite loci: conservation and management implications. Animal Conservation 15: 95-112.

Charlesworth, D. and Willis, J.H. 2009. The genetics of inbreeding depression. Nature Reviews Genetics 10: 783-796.

Coscarella, M., Dans, S.L., Degrati, M., Garaffo, G.V., Crespo, E.A. 2012. Bottlenose dolphins at the southern extreme of the southwestern Atlantic: local population decline? Journal of the Marine Biological Association of the United Kingdom 92: 1843-1849.

Crespo, E.A., García, N.A., Dans, S.L., Pedraza, S.N. 2008. Mamíferos marinos. *In*: Boltovskoy, D. (Ed.), Atlas de Sensibilidad Ambiental de la Costa y el Mar Argentino. Secretaría de Ambiente y Desarrollo Sustentable de la Nación, Argentina.

Daura-Jorge, F. and Simões-Lopes, P.C. 2011. Lobomycosis-like disease in wild bottlenose dolphins *Tursiops truncatus* of Laguna, southern Brazil: monitoring of a progressive case. Diseases of Aquatic Organisms 93: 163-170.

Daura-Jorge, F.G., Cantor, M., Ingram, S.N., Lusseau, D., Simões-Lopes, P.C. 2012. The structure of a bottlenose dolphin society is coupled to a unique foraging cooperation with artisanal fishermen. Biology Letters 8: 702-705.

Daura-Jorge, F., Ingram, S.N., Simões-Lopes, P.C. 2013. Seasonal abundance and adult survival of bottlenose dolphins (*Tursiops truncatus*) in a community that cooperatively forages with fishermen in southern Brazil. Marine Mammal Science 29: 293-311.

Davidson, A.D., Boyer, A.G., Kim, H., Pompa-Mansilla, S., Hamilton, M.J., Costa, D.P., Ceballos, G., Brown, J.H. 2012. Drivers and hotspots of extinction risk in marine mammals. Proceedings of the National Academy of Sciences 109: 3395-3400.

Earl, D.A. and vonHoldt, B.M. 2012. STRUCTURE HARVESTER: a website and program for visualizing STRUCTURE output and implementing the Evanno method. Conservation Genetics Resources 4: 359-361.

Evanno, G., Regnaut, S., Goudet, J. 2005. Detecting the number of clusters of individuals using the software STRUCTURE: a simulation study. Molecular Ecology 14: 2611-2620.

Excoffier, L. and Lischer, H.E.L. 2010. Arlequin suite ver 3.5: a new series of programs to perform population genetics analyses under Linux and Windows. Molecular Ecology Resources 10: 564-567.

Frankham, R. 1995. Inbreeding and extinction: a threshold effect. Conservation Biology 9: 792-799.

Franklin, I. 1980. Evolutionary changes in small populations. *In*: Soulé M, Wilcox B (Eds.), Conservation Biology: An evolutionary-ecological perspective. Sinauer Associates, Suderland, pp. 135-140.

Fruet, P.F., Flores, P.A.C., Laporta, P. in press a. Report of the working group on population parameters and demography of *Tursiops truncatus* in the Southwestern Atlantic Ocean. Latin American Journal of Aquatic Mammals.

Fruet, P.F., Dalla Rosa, L., Genoves, R.C., Valiati, V.H., Freitas, T.R.O., Möller, L.M. in press b. Biopsy darting of common bottlenose dolphins (*Tursiops truncatus*) in southern Brazil: evaluating effectiveness, short-term responses and wound healing. Latin American Journal of Aquatic Mammals.

Fruet, P.F., Secchi, E.R., Di Tullio, J.C., Kinas, P.G. 2011. Abundance of bottlenose dolphins, *Tursiops truncatus* (Cetacea: Delphinidae), inhabiting the Patos Lagoon estuary, southern Brazil: implications for conservation. Zoologia 28: 23-30.

Fruet, P.F., Kinas, P.G., Silva, K.G., Di Tullio, J.C., Monteiro, D.S., Dalla Rosa, L, Estima, S.C., Secchi, E.R. 2012. Temporal trends in mortality and effects of by-catch on common bottlenose dolphins, *Tursiops truncatus*, in southern Brazil. Journal of the Marine Biological Association of the United Kingdom 92: 1865-1876.

Funk, W.C., McKay, J.K., Hohenlohe, P.A., Allendorf, F.W. 2012. Harnessing genomics for delineating conservation units. Trends in Ecology and Evolution 27: 489-496.

Galván, D.E., Venerus, L.A., Irigoyen, A.J. 2009. The reef-fish fauna of the northern Patagonian gulfs, Argentina, southwestern Atlantic. Open Fish Science Journal 2: 90-98.

Genoves, R.C. 2013. Estrutura social do boto, *Tursiops truncatus* (Cetacea: Delphinidae) no estuário da Lagoa dos Patos e águas costeiras adjacentes, sul do Brasil. Dissertation, Universidade Federal do Rio Grande, Rio Grande, Brazil

Gilbert, K.J., Andrew, R.L., Bock, D.G. et al. 2012. Recommendations for utilizing and reporting population genetic analyses: the reproducibility of genetic clustering using the program structure. Molecular Ecology 21: 4925-4930.

Gilson, A., Syvanen, M., Levine, K.F., Banks, J.D. 1998. Deer gender determination by polymerase chain reaction: validation study and application to tissues, bloodstains, and hair forensic samples from California. California Fish and Game 84: 159-169.

Goudet, J. 1995. FSTAT (Version 1.2): A Computer Program to Calculate F-Statistics. Journal of Heredity 86: 485-486.

Hale, K.A. and Briskie, J.V. 2007. Decreased immunocompetence in a severely bottlenecked population of an endemic New Zealand bird. Animal Conservation 10: 2-10.

Halpern, B.S., Walbridge, S., Selkoe, K.A. et al. 2008. A global map of human impact on marine ecosystems. Science 319: 948-952.

Hamner, R.M., Pichler, F.B., Heimeier, D., Constantine, R., Baker, C.S. 2012. Genetic differentiation and limited gene flow among fragmented populations of New Zealand endemic Hector’s and Maui’s dolphins. Conservation Genetics 13: 987-1002.

Hardy, O. and Vekemans, X. 2002. Spagedi: a versatile computer program to analyse spatial genetic structure at the individual or population levels. Molecular Ecolology Notes 2: 618-620.

Hardy, J.O., Charbonnel, N., Fréville, H., Heuertz, M. 2003. Microsatellite allele sizes: A simple test to assess their significance on genetic differentiation. Genetics 163: 1467-1482.

Hoelzel, A.R. 2009. Evolution of population genetic structure in marine mammal species. *In*: Bertorelle, G., Bruford, M., Hauffe, H. (Eds.), Population genetics for animal conservation. Cambridge University Press, Cambridge, pp. 294-318.

Hoelzel, A.R., Potter, C.W., Best, P.B. 1998a. Genetic differentiation between parapatric ‘nearshore’ and ‘offshore’ populations of the bottlenose dolphin. Proceedings of the Royal Society of London. Series B: Biological Sciences 265: 1177-1183.

Hoelzel, A.R., Dahlheim, M., Stern, S.J. 1998b. Low genetic variation among killer whales (*Orcinus orca*) in the eastern north Pacific and genetic differentiation between foraging specialists. Journal of Heredity 89: 121-128.

Hubisz, M.J., Falush, D., Stephens, M., Pritchard, J.K. 2009. Inferring weak population structure with the assistance of sample group information. Molecular Ecological Resources 9: 1322-1332.

Jackson, J.B.C., Kirby, M.X., Berger, W.H. et al. 2001. Historical overfishing and the recent collapse of coastal ecosystems. Science 293: 629-637.

Krützen, M., Valsecchi, E., Connor, R.C., Sherwin, W.B. 2001. Characterization of microsatellite loci in *Tursiops aduncus*. Molecular Ecology Notes 1: 170-172.

Laporta, P. 2009. Abundância, distribuição e uso do habitat do boto (*Tursiops truncatus*) em Cabo Polonio e La Coronilla (Rocha, Uruguai). Dissertation, Universidade Federal do Rio Grande, Rio Grande, Brazil.

Laporta, P., Di Tullio, J.C., Vermeulen, E., Domit, C., Albuquerque, C., Lodi, L. in press. Report of the working group on habitat use of *Tursiops truncatus* in the Southwestern Atlantic Ocean. Latin American Journal of Aquatic Mammals.

Librado, P. and Rozas, J. 2009. DnaSP v5: a software for comprehensive analysis of DNA polymorphism data. Bioinformatics 25: 1451-1452.

Mantel, N. 1967. The detection of disease clustering and a generalized regression approach. Cancer Research 27: 209-220.

Mehsen, M., Secchi, E.R., Fruet, P., Di Tullio, J. 2005. Feeding habits of bottlenose dolphins, *Tursiops truncatus*, in southern Brazil. Paper SC/58/SM8 presented during the International Whaling Commission Meeting. Ulsan, South Korea. Available online at http://www.botosdalagoa.com.br/arquivos/docB.pdf.

Meirmans, P.G. and Van Tienderen, P.H. 2004. Genotype and Genodive: two programs for the analysis of genetic diversity of asexual organisms. Molecular Ecology Notes 4: 792-794.

Menni, R.C. 1983. Los peces en el medio marino. Estudio Sigma. Buenos Aires, Argentina.

Mirimin, L., Miller, R., Dillane, E., Berrow, S.D., Ingram, S., Cross, T.F., Rogan, E. 2011. Fine-scale population genetic structuring of bottlenose dolphins in Irish coastal waters. Animal Conservation 14: 342-353.

Möller, L.M. 2012. Sociogenetic structure, kin associations and bonding in delphinids. Molecular Ecology 21: 745-764.

Möller, L.M. and Beheregaray, L.B. 2001. Coastal bottlenose dolphins from southeastern Australia are *Tursiops aduncus* according to sequences of the mitochondrial DNA control region. Marine Mammal Science 17: 249-263.

Möller, L.M. and Beheregaray, L.B. 2004. Genetic evidence for sex-biased dispersal in resident bottlenose dolphins (*Tursiops aduncus*). Molecular Ecology 13: 1607-1612.

Möller, L.M., Beheregaray, L.B., Harcourt, R.G., Krützen, M. 2001. Alliance membership and kinship in wild male bottlenose dolphins (*Tursiops aduncus*) of southeastern Australia. Proceedings of the Royal Society of London. Series B: Biological Sciences 268: 1941-1947.

Möller, L.M., Wiszniewski, J., Allen, S.J., Beheregaray, L.B. 2007. Habitat type promotes rapid and extremely localised genetic differentiation in dolphins. Marine and Freshwater Research 58: 640-648.

Morin, P.A. and Dizon, A. 2009. Genetics for management. *In*: Perrin, W., Würsig, B., Thewissen, J. (Eds.), Encyclopedia of Marine Mammals, 2nd edn. Elsevier, San Diego, pp. 477-483.

Moritz, C. 1994. Defining ' Evolutionarily Significant Units'. Trends in Ecology and Evolution 9: 373-375.

Myers, R.A. and Worm, B. 2003. Rapid worldwide depletion of predatory fish communities. Nature 423: 280-283.

Nater, A., Kopps, A.M., Krützen, M. 2009. New polymorphic tetranucleotide microsatellites improve scoring accuracy in the bottlenose dolphin *Tursiops aduncus*. Molecular Ecological Resources 9: 531-534.

Natoli, A., Peddemors, V.M., Hoelzel, A.R. 2004. Population structure and speciation in the genus *Tursiops* based on microsatellite and mitochondrial DNA analyses. Journal of Evolutionary Biology 17: 363-375.

Natoli, A., Peddemors, V.M., Hoelzel, A.R. 2008. Population structure of bottlenose dolphins (*Tursiops aduncus*) impacted by bycatch along the east coast of South Africa. Conservation Genetics 9: 627-636.

O'Brien, S.J., Roelke, M.E., Marker, L., Newman, A., Winkler, C.A., Meltzer, D., Colly, L., Evermann, J.F., Bush, M., Wildt, D.E. 1985. Genetic basis for species vulnerability in the Cheet. Science 227: 1428-1434.

Palsbøll, P.J., Bérubé, M., Allendorf, F.W. 2007. Identification of management units using population genetic data. Trends in Ecology and Evolution 22: 11-16.

Peakall, R., Smouse, P.E. 2012. GenAlEx 6.5: genetic analysis in Excel. Population genetic software for teaching and research: an update. Bioinformatics 28: 2537-2539.

Pinedo, M.C. 1982. Análise dos conteúdos estomacais de *Pontoporia blanvillei* (Gervais e D'Orbigny, 1844) e *Tursiops gephyreus*(Lahille, 1908)(*Cetácea, Platanistidae e Delphinidae*) na zona estuarial e costeira de Rio Grande, RS, Brasil. Dissertation, Universidade Federal do Rio Grande, Rio Grande, Brazil.

Pritchard, J., Stephens, M., Donnelly, P. 2000. Inference of population structure using multilocus genotype data. Genetics 155: 945-959.

Pritchard, J.K., Wen, X., Falush, D. 2007. Documentation for structure software: version 2.2. Available from http://pritch.bsd.uchicago. edu/software.

Rice, W. 1989. Analyzing tables of statistical tests. Evolution 43: 223-225.

Rooney, A.P., Merritt, D.B., Derr, J.N. 1999. Microsatellite diversity in captive bottlenose dolphins (*Tursiops truncatus*). Journal of Heredity 90: 228-231.

Rosel, P.E., Dizon, A.E., Haygood, M.G. 1995. Variability of the mitochondrial control region in populations of the harbour porpoise, *Phocoena*, on interoceanic and regional scales. Canadian Journal of Fisheries and Aquatic Sciences 52: 1210-1219.

Rosel, P.E., Forgetta, V., Dewar, K. 2005. Isolation and characterization of twelve polymorphic microsatellite markers in bottlenose dolphins (*Tursiops truncatus*). Molecular Ecology Notes 5: 830-833.

Rosel, P., Hansen, L., Hohn, A.A. 2009. Restricted dispersal in a continuously distributed marine species: common bottlenose dolphins *Tursiops truncatus* in coastal waters of the western North Atlantic. Molecular Ecology 18: 5030-5045.

Rousset, F. 2008. Genepop'007: a complete re-implementation of the genepop software for Windows and Linux. Molecular Ecology Resources 8: 103-106.

Ryman, N. and Palm, S. 2006. POWSIM: a computer program for assessing statistical power when testing for genetic differentiation. Molecular Ecology 6: 600-602.

Scartascini, F.L. and Volpedo, A.V. 2013. White croaker (*Micropogonias furnieri*) paleodistribution in the southwestern Atlantic ocean: an archaeological perspective. Journal of Archaeological Science 40: 1059-1066.

Schultz, J., Baker, J.D., Toonen, R.J., Bowen, B. 2009. Extremely low genetic diversity in the endangered Hawaiian Monk Seal (*Monachus schauinslandi*). Journal of Heredity 100: 25-33.

Schwartz, M.K., Luikart, G., Waples, R.S. 2007. Genetic monitoring as a promising tool for conservation and management. Trends in Ecology and Evolution 22: 25-33.

Sellas, A.B., Wells, R.S., Rosel, P.E. 2005. Mitochondrial and nuclear DNA analyses reveal fine scale geographic structure in bottlenose dolphins (*Tursiops truncatus*) in the Gulf of Mexico. Conservation Genetics 6: 715-728.

Smolker, R., Richards, A., Connor, R., Mann, J., Berggren, P. 1997. Sponge carrying by dolphins (Delphinidae, *Tursiops* sp.): A foraging specialization involving tool use? Ethology 103: 454-465.

Spielman, D., Brook, B.W., Briscoe, D.A., Frankham, R. 2004. Does inbreeding and loss of genetic diversity decrease disease resistance? Conservation Genetics 5: 439-448.

Sunnucks, P. and Hales, D.F. 1996. Numerous transposed sequences of mitochondrial cytochrome oxidase I-II in aphids of the genus *Sitobion* (*Hemiptera: Aphididae*). Molecular Biology and Evolution 13: 510-524.

Tagliani, P.R.A., Asmus, M.L., Tagliani, C.R.A., Polette, M., Costa, C.S.B., Salas, E. 2007. Integrated coastal zone management in the Patos Lagoon estuary (South Brazil): state of art. Wit Transactions on Ecology and the Environment 103: 679-686.

Tamura, K. and Nei, M. 1993. Estimation of the number of nucleotide substitutions in the control region of mitochondrial DNA in humans and chimpanzees. Molecular Biology and Evolution 10: 512-526.

Tamura, K., Peterson, D., Peterson, N., Stecher, G., Masatoshi, N., Kumar, S. 2011. MEGA5: molecular evolutionary genetics analysis using maximum likelihood, evolutionary distance, and maximum parsimony methods. Molecular Biology and Evolution 28: 2731-2739.

Tezanos-Pinto, G., Baker, C.S., Russell, K., Martien, K., Baird, R.W., Hutt, A., Stone, G., Mignucci-Giannoni, A.A., Caballero, S., Endo, T., Lavery, S., Oremus, M., Olavarría, C., Garrigue, C. 2009. A worldwide perspective on the population structure and genetic diversity of bottlenose dolphins (*Tursiops truncatus*) in New Zealand. Journal of Heredity 100: 11-24.

Tonini, M. 2010. Modelado numérico del ecosistema de los golfos norpatagónicos. 2010. Dissertation, Universidad Nacional del Sur, Bahía Blanca, Argentina.

Urian, K.W., Hofmann, S., Wells, R.S., Read, A.J. 2009. Fine-scale population structure of bottlenose dolphins (*Tursiops truncatus*) in Tampa Bay, Florida. Marine Mammal Science 25: 619-638.

Valsecchi, E., Amos, W. 1996. Microsatellite markers for the study of cetacean populations. Molecular Ecology 5: 151-156.

Van Bressen, M.F., Van Waerebeek, K., Reyes, J.C. et al. 2007. A preliminary overview of skin and skeletal diseases and traumata in small cetaceans from South American waters. Latin American Journal of Aquatic Mammals 6: 7-42.

Van Oosterhout, C., Hutchinson, W.F., Wills, D.P.M., Shipley, P. 2004. Micro-Checker: Software for identifying and correcting genotyping errors in microsatellite data. Molecular Ecology Notes 4: 535-538.

Vermeulen, E. and Cammareri, A. 2009. Residency patterns, abundance, and social composition of bottlenose dolphins (*Tursiops truncatus)* in Bahía San Antonio, Patagonia, Argentina. Aquatic Mammals 35: 379-386.

Wallace, B.P., Lewison, R.L., McDonald, S.L., McDonald, R.K., Kot, C.Y., Kelez, S., Bjorkland, R.K., Finkbeiner, E.M., Helmbrecht, S., Crowder, L.B. 2010. Global patterns of marine turtle bycatch. Conservation Letters 3: 131-142.

Wang, J.Y., Chou, L-S., White, B.N. 1999. Mitochondrial DNA analysis of sympatric morphotypes of bottlenose dolphins (genus: *Tursiops*) in Chinese waters. Molecular Ecology 8: 1603-1612.

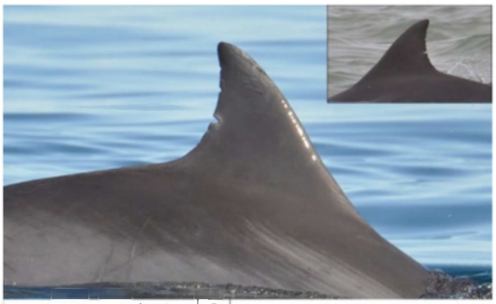
Weir, B.S. and Cockerham, C.C. 1984. Estimating F-Statistics for the analysis of population structure. Evolution 38: 1358-1370.

Wilson, G.A. and Rannala, B. 2003. Bayesian inference of recent migration rates using multilocus genotypes. Genetics 163: 1177-1191.

Wiszniewski, J., Beheregaray, L.B., Allen, S.J., Möller, L.M. 2010. Environmental and social influences on the genetic structure of bottlenose dolphins (*Tursiops aduncus*) in Southeastern Australia. Conservation Genetics 11: 1405-1419.

Wiszniewski, J., Corrigan, S., Beheregaray, L.B., Möller, L.M. 2012. Male reproductive success increases with alliance size in Indo-Pacific bottlenose dolphins (*Tursiops aduncus*). Journal of Animal Ecology 81: 423-431.

2. IDENTIFICATION CATALOGUE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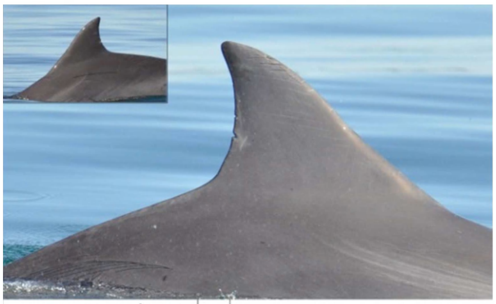
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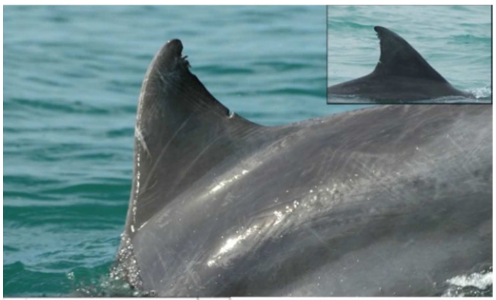
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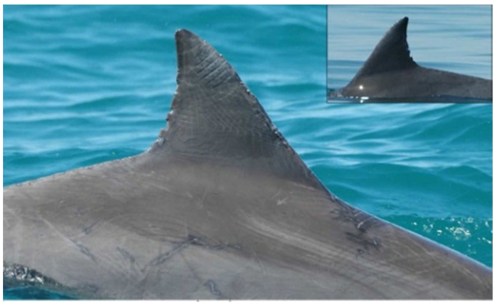
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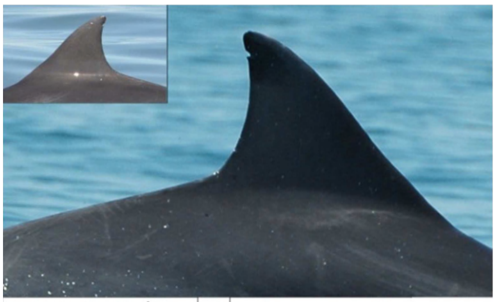
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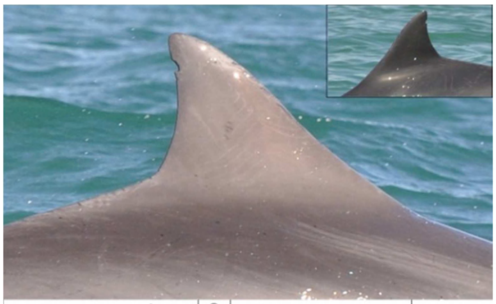

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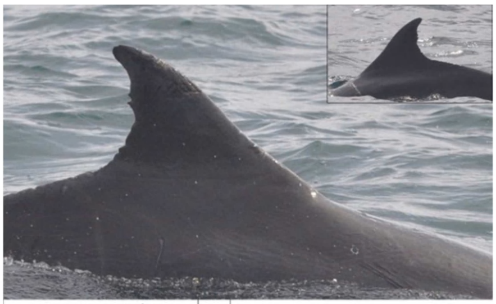

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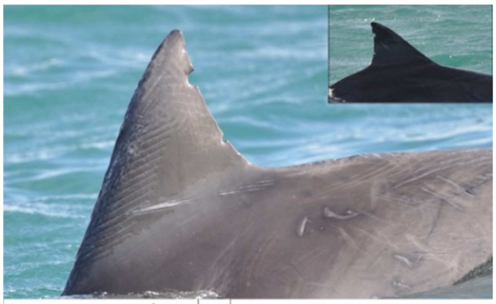
RN-BSA-12/06 ♂ Azul



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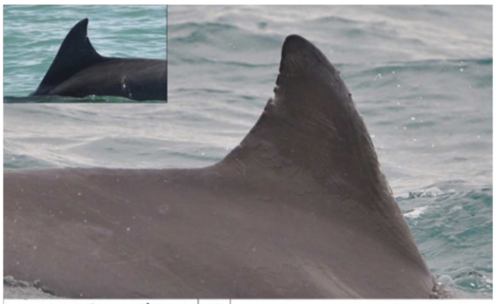

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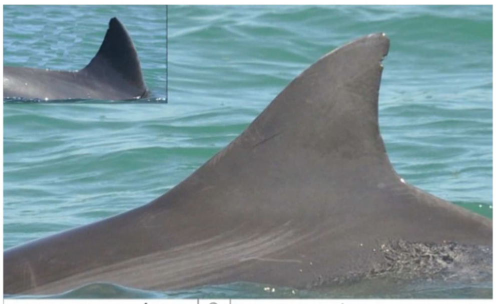

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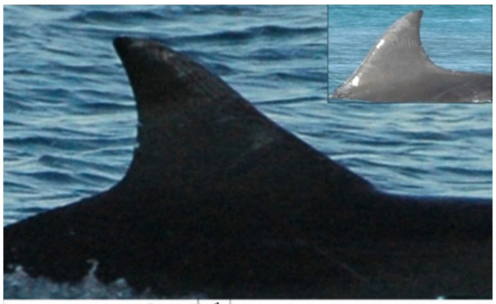

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RN-BSA-21/06 ♀

RN-BSA-22/07 ♂ Yaco

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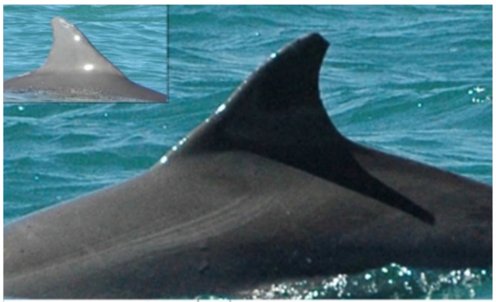
RN-BSA-26/07

RN-BSA-28/06 ♀ Estella †

RN-BSA-29/07 Mai



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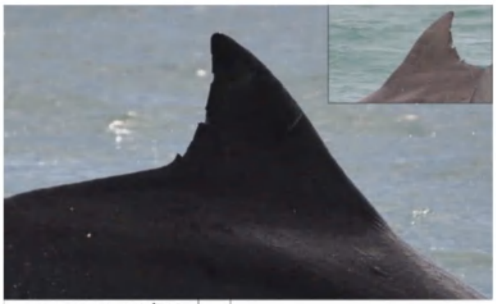

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RN-BSA-38/07 ♀ Eva

RN-BSA-39/07 ♂

RN-BSA-40/07 ♂

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RN-BSA-42/07

RN-BSA-43/07 ♀

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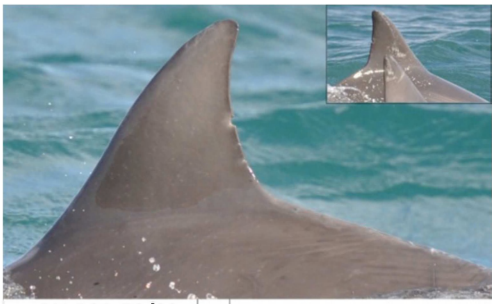

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RN-BSA-51/08 Juno

*2006
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RN-BSA-53/08

RN-BSA-55/08 ♂ Ale

RN-BSA-56/08 ♀ Grace

RN-BSA-56b/08

RN-BSA-57/08 ♂ Agus

RN-BSA-58/08

RN-BSA-59/08

RN-BSA-60/08 ♂ Fede

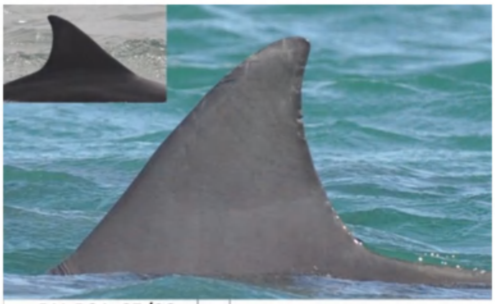
*2006
m: RN-BSA-16/06

RN-BSA-61/08

*2006
m: RN-BSA-9a/06

RN-BSA-62/08

RN-BSA-63/09

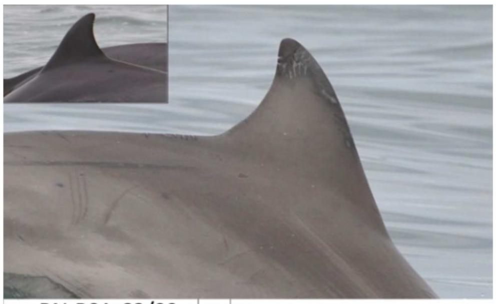


RN-BSA-65/08

RN-BSA-66/10 Gabi

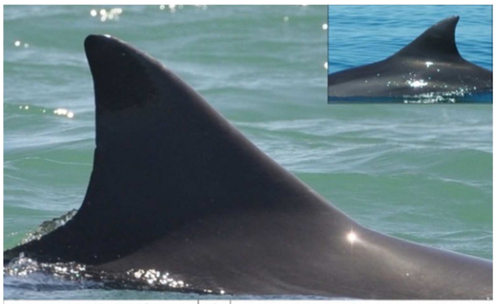
*2008
m: RN-BSA-38/07

RN-BSA-67/08



RN-BSA-68/09 Toni

RN-BSA-70/08 ♀



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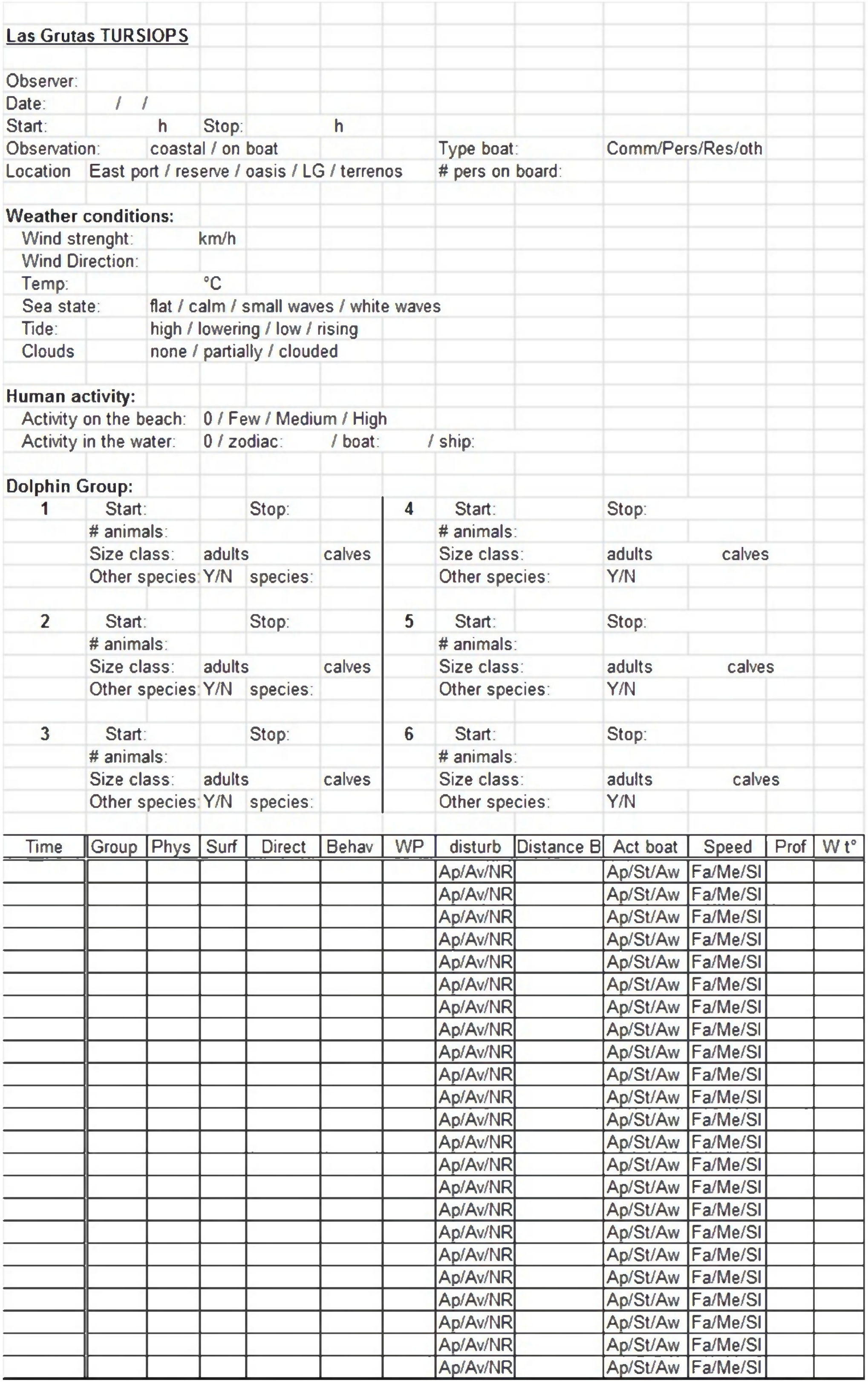
3. OBSERVATION SCHEME



Las Grutas TURSIOPS

Observer:
Date: / /
Start: h Stop: h
Observation: coastal / on boat Type boat: Comm/Pers/Res/oth
Location East port / reserve / oasis / LG / terrenos # pers on board:

Weather conditions:
Wind strenght: km/h
Wind Direction:
Temp: °C
Sea state: flat / calm / small waves / white waves
Tide: high / lowering / low / rising
Clouds none / partially / clouded

Human activity:
Activity on the beach: 0 / Few / Medium / High
Activity in the water: 0 / zodiac: / boat: / ship:

Dolphin Group:

1 Start: Stop:
\# animals:
Size class: adults calves
Other species: Y/N species:

2 Start: Stop:
\# animals:
Size class: adults calves
Other species: Y/N species:

3 Start: Stop:
\# animals:
Size class: adults calves
Other species: Y/N species:

4 Start: Stop:
\# animals:
Size class: adults calves
Other species: Y/N

5 Start: Stop:
\# animals:
Size class: adults calves
Other species: Y/N

6 Start: Stop:
\# animals:
Size class: adults calves
Other species: Y/N

Time	Group	Phys	Surf	Direct	Behav	WP	disturb	Distance B	Act boat	Speed	Prof	W t°
							Ap/Av/NR		Ap/St/Aw	Fa/Me/Sl		
							Ap/Av/NR		Ap/St/Aw	Fa/Me/Sl		
							Ap/Av/NR		Ap/St/Aw	Fa/Me/Sl		
							Ap/Av/NR		Ap/St/Aw	Fa/Me/Sl		
							Ap/Av/NR		Ap/St/Aw	Fa/Me/Sl		
							Ap/Av/NR		Ap/St/Aw	Fa/Me/Sl		
							Ap/Av/NR		Ap/St/Aw	Fa/Me/Sl		
							Ap/Av/NR		Ap/St/Aw	Fa/Me/Sl		
							Ap/Av/NR		Ap/St/Aw	Fa/Me/Sl		
							Ap/Av/NR		Ap/St/Aw	Fa/Me/Sl		
							Ap/Av/NR		Ap/St/Aw	Fa/Me/Sl		
							Ap/Av/NR		Ap/St/Aw	Fa/Me/Sl		
							Ap/Av/NR		Ap/St/Aw	Fa/Me/Sl		
							Ap/Av/NR		Ap/St/Aw	Fa/Me/Sl		
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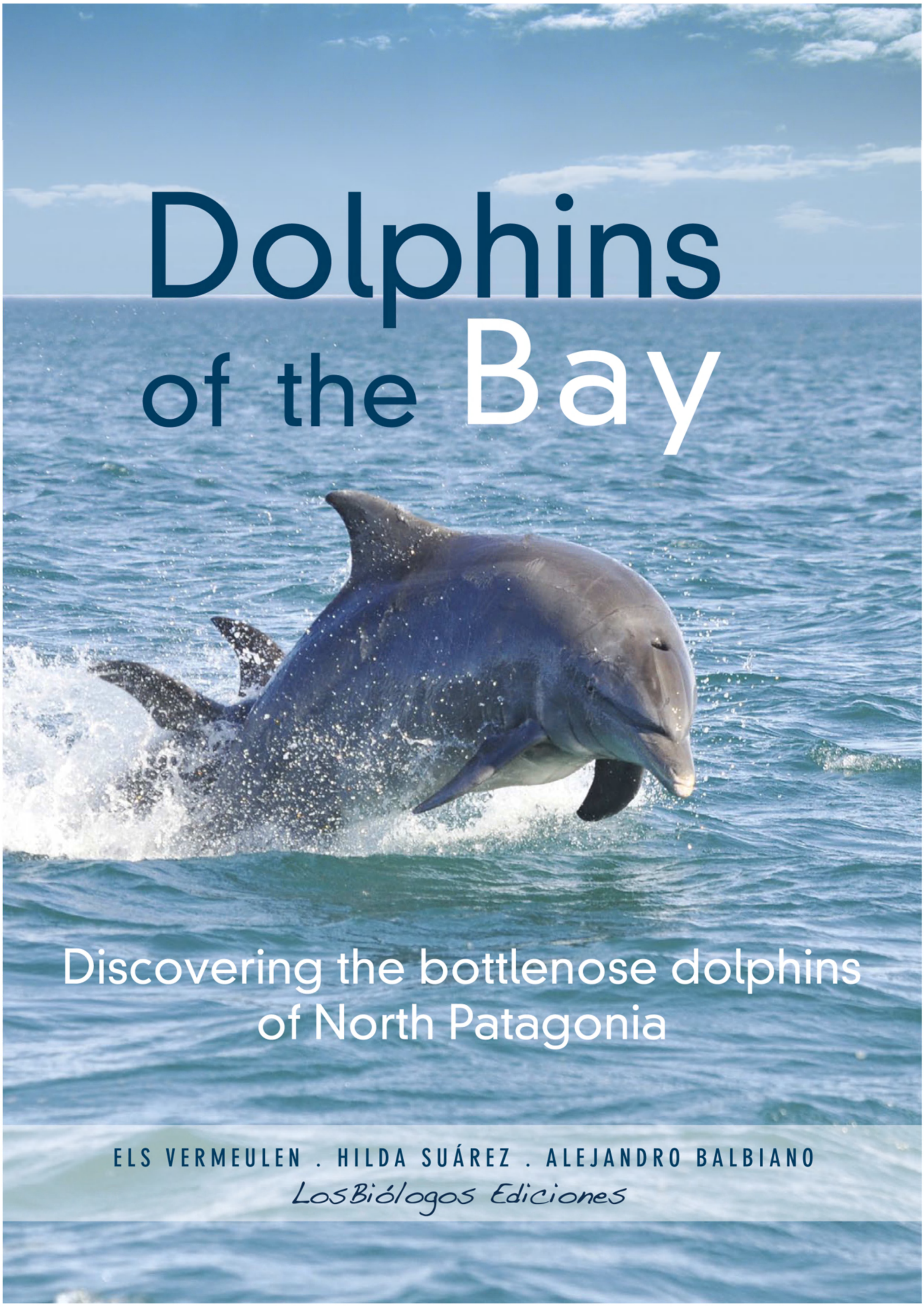
							Ap/Av/NR		Ap/St/Aw	Fa/Me/Sl		
							Ap/Av/NR		Ap/St/Aw	Fa/Me/Sl		
							Ap/Av/NR		Ap/St/Aw	Fa/Me/Sl		

4. EDUCATIONAL BOOK 'DOLPHINS OF THE BAY'

The most important research results of this study were gathered and converted into a children's book entitled "Toninas de la Bahía". The aim of this educational book was to share the obtained knowledge regarding this small and vulnerable population of dolphins and increase the awareness of the local communities.

In total, 3,000 copies of the book have been distributed locally in Northern Patagonia during an educational project conducted in November 2013. During this project, presentations were given to nearly 1,000 children and their teachers of all the schools in the area around Bahía San Antonio. Furthermore, this educational project exceeded its original idea and included eventually also university students, parents, local fishermen, tour operators and environmental agencies of the provincial government.
To maintain the observed interest, a Facebook page called 'Toninas de la Bahía' was created where the electronic version of the book is freely downloadable, as well as the given presentations, the complete identification catalogue, sound files and general information on bottlenose dolphins. Through the use of this social media, it is aimed to keep local inhabitants interested in the conservation of the species and possibly reach a wider public in the country.

As this book was aimed in the first place for distribution in Argentina, it was originally written in Spanish. However, due to the large international interest and to ensure its wider distribution, the book was translated into English and is now freely downloadable from various websites (e.g., https://www.facebook.com/groups/157084411154762/).



Dolphins of the Bay

Discovering the bottlenose dolphins of North Patagonia

ELS VERMEULEN . HILDA SUÁREZ . ALEJANDRO BALBIANO

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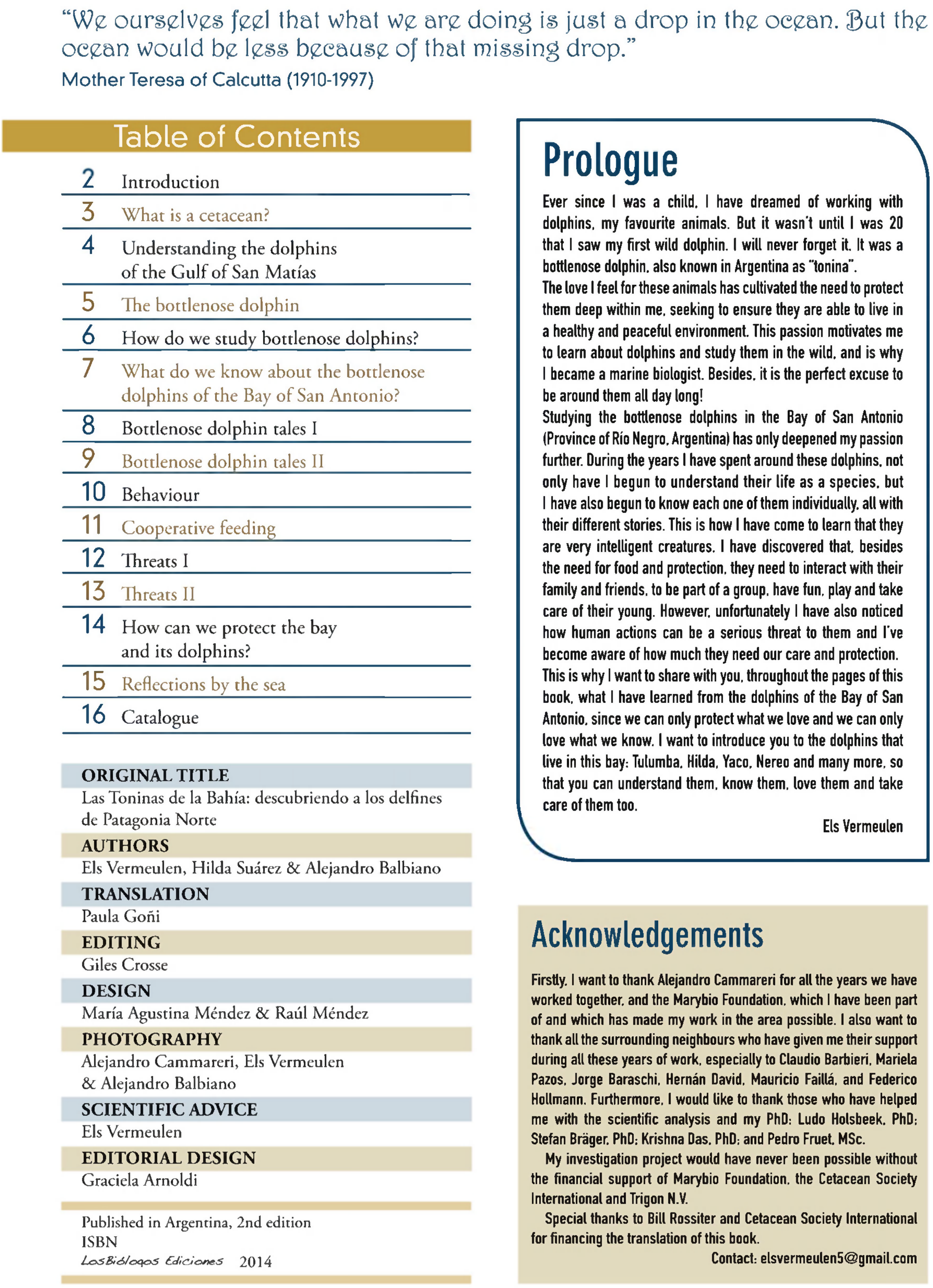

> “We ourselves feel that what we are doing is just a drop in the ocean. But the ocean would be less because of that missing drop.”
>
> Mother Teresa of Calcutta (1910-1997)

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Paula Goñi
EDITING
Giles Crosse
DESIGN
María Agustina Méndez & Raúl Méndez
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Prologue

Ever since I was a child, I have dreamed of working with dolphins, my favourite animals. But it wasn't until I was 20 that I saw my first wild dolphin. I will never forget it. It was a bottlenose dolphin, also known in Argentina as "tonina".

The love I feel for these animals has cultivated the need to protect them deep within me, seeking to ensure they are able to live in a healthy and peaceful environment. This passion motivates me to learn about dolphins and study them in the wild, and is why I became a marine biologist. Besides, it is the perfect excuse to be around them all day long!

Studying the bottlenose dolphins in the Bay of San Antonio (Province of Río Negro, Argentina) has only deepened my passion further. During the years I have spent around these dolphins, not only have I begun to understand their life as a species, but I have also begun to know each one of them individually, all with their different stories. This is how I have come to learn that they are very intelligent creatures. I have discovered that, besides the need for food and protection, they need to interact with their family and friends, to be part of a group, have fun, play and take care of their young. However, unfortunately I have also noticed how human actions can be a serious threat to them and I've become aware of how much they need our care and protection.

This is why I want to share with you, throughout the pages of this book, what I have learned from the dolphins of the Bay of San Antonio, since we can only protect what we love and we can only love what we know. I want to introduce you to the dolphins that live in this bay: Tulumba, Hilda, Yaco, Nereo and many more, so that you can understand them, know them, love them and take care of them too.

Els Vermeulen

Acknowledgements

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Dolphins of the Bay

Discovering the bottlenose dolphins of North Patagonia

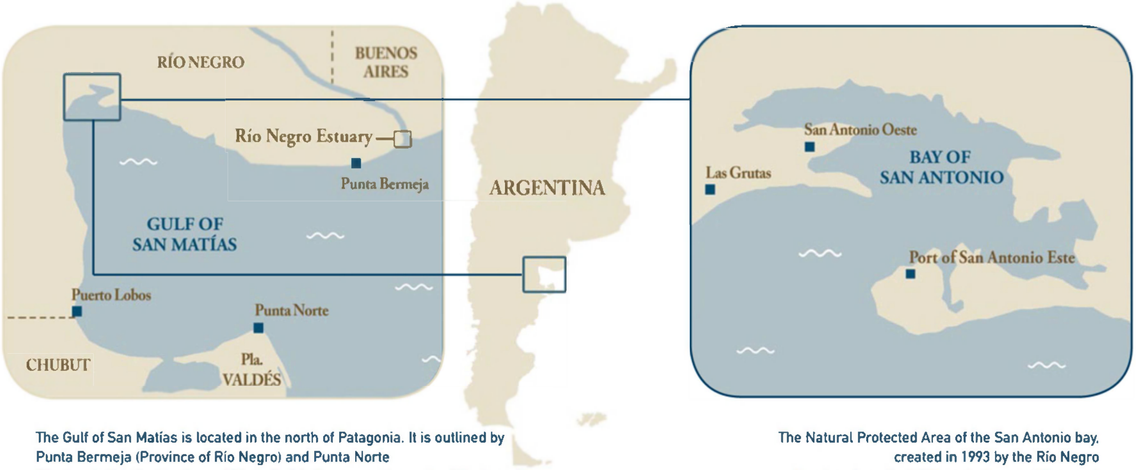
LosBiólogos Ediciones

Introduction

The Bay of San Antonio is privileged, as its protected coasts and shallow waters are inhabited by unique species. The southern right whale, migratory birds such as the red knot and several species of dolphins are just some of them. But why do they choose this area to spend part of their lives?

Located in the north-west of the Gulf of San Matías, in the Province of Río Negro, Argentina, the Bay of San Antonio is 20 km long, 10 km wide and no more than 30 metres deep. The region is not only famous because of its shallowness and lack of strong currents, it is also well known for having the warmest waters of the entire Argentine coastline, with maximum temperatures around 24° C in summer. In winter, temperatures drop considerably, with differences of more than 16° C between summer and winter. Another characteristic of the area is the large tidal range and the existence of large quantities of food, both in its clear waters and its sandy beaches and rocky coasts.

All of these unique characteristics make the Bay of San Antonio the ideal home for a group of bottlenose dolphins, many of which remain in the area the entire year. It is one of the best places to observe them within their natural habitat, which gives us an excellent opportunity to study their lives, habits and behaviour. And as if that were not enough, due to the enormous decrease in bottlenose dolphin sightings in other areas, the Bay of San Antonio may be one of the last remaining homes within Argentina for this species.



The Gulf of San Matías is located in the north of Patagonia. It is outlined by Punta Bermeja (Province of Río Negro) and Punta Norte (Peninsula Valdés, Province of Chubut). It is the second largest gulf in Argentina, with an area of approximately 18.000 km2. It has an average depth of 100 metres, with a maximum depth of around 200 metres.

The Natural Protected Area of the San Antonio bay, created in 1993 by the Río Negro Province Law No. 2670, protects one of the most important places for migratory birds in the south-west Atlantic.

Southern right whale.

Red knots.

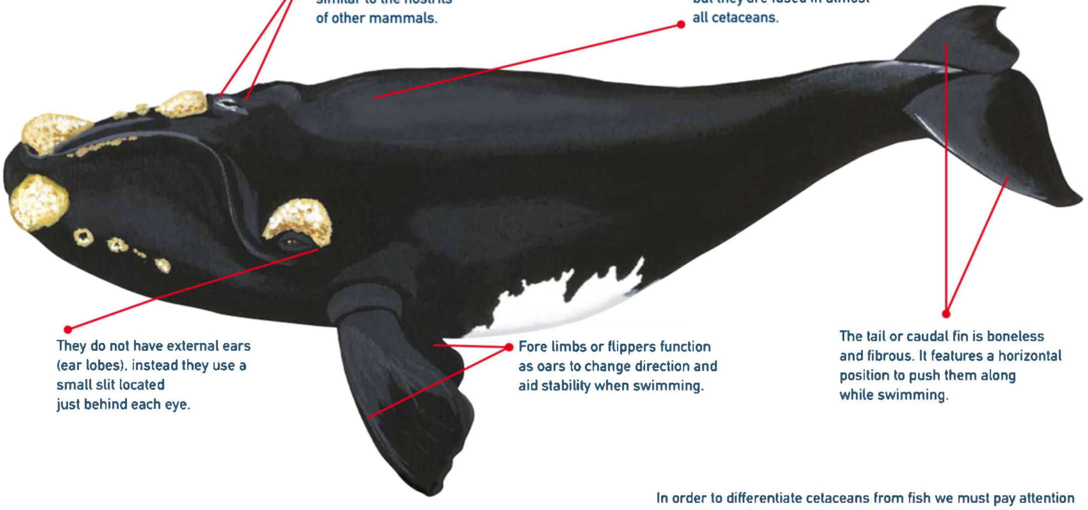
What is a cetacean?

Cetaceans are mammals, just like us, but are adapted completely to an aquatic life. The word "cetacean" has a dual origin, from the Latin cetus, meaning large sea creature, and the ancient Greek ketos, meaning sea monster.

Like all mammals, cetaceans are "warm-blooded" animals, which means they have mechanisms that allow them to maintain a constant body temperature, in spite of temperature variations in the environment. Furthermore, they have lungs through which they breathe atmospheric air and produce milk to feed their calves, which grow and develop inside the womb of their mother.

But, besides the characteristics shared with other mammals, cetaceans have some special features that enable them to live in water. These adaptations are related to both their anatomy and function. Let's look at some examples. Cetaceans' bodies feature a hydrodynamic shape which, together with their short and rigid necks, improves their movement in water and allows them to swim at great speed. Instead of arms, they have flippers, and they don't have hind limbs. Instead, they have a muscular tail which helps them swim powerfully and most of them have a fibrous dorsal fin, which helps them stabilise their bodies in the water. Because they have lungs, they must come to the surface to breathe and hold their breath while swimming underwater. They are excellent divers though, a very important ability when it comes to hunting fish! They also give birth and nurse their calves underwater, and they never have more than 1 calf at a time.

Although it may seem hard to believe, the ancestors of cetaceans were land mammals that walked on 4 legs. The first real cetaceans appeared on Earth around 55 or 60 million years ago and were called Archaeoceti. They were similar to the large cetaceans with teeth that live today, but they became extinct almost 30 million years ago.



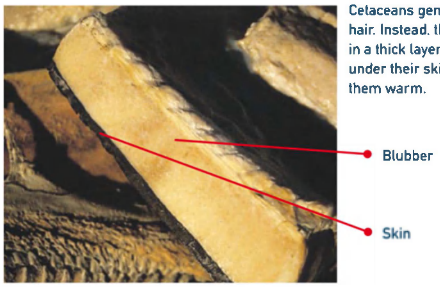
They breathe through their blowhole: 1 or 2 holes on the top of their head similar to the nostrils of other mammals.

Their neck bone is formed of 7 vertebrae, as in all mammals, but they are fused in almost all cetaceans.

They do not have external ears (ear lobes), instead they use a small slit located just behind each eye.

Fore limbs or flippers function as oars to change direction and aid stability when swimming.

The tail or caudal fin is boneless and fibrous. It features a horizontal position to push them along while swimming.



Cetaceans generally do not have hair. Instead, they are covered in a thick layer of blubber (fat) under their skin which keeps them warm.

In order to differentiate cetaceans from fish we must pay attention to 2 characteristics: the tail and their way of breathing. Cetaceans have a horizontal tail, which moves up and down, and blowholes on the top of their head. Fish have a vertical tail, which moves from side to side, and gills on both sides of their head.

Getting to know the dolphins of the Gulf of San Matías

Cetaceans include all the animals known as whales and dolphins. Although the term whale is usually associated with cetaceans of great size and the term dolphin with smaller ones, size is not the characteristic that distinguishes them. Scientists classify cetaceans into 2 groups: odontocetes or toothed whales and mysticetes or baleen whales. As well as teeth, odontocetes have a single blowhole. Among them are, for example, dolphins, sperm whales and beaked whales. The mysticetes, which do not have teeth and have 2 blowholes, include amongst others humpback whales and blue whales. Instead of teeth, mysticetes have a set of triangular plates called baleen, which grow down the upper jaw sieving prey from the water. Interestingly, the killer whale, which of course is a toothed whale, is the largest dolphin in the world!

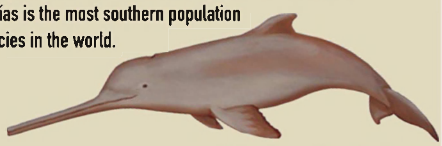
We can also find differences between dolphins. On the one hand, those which are part of the family of "real dolphins" live exclusively in the ocean, with beaks of different sizes, numerous conical teeth and a dorsal fin on the back of their body. On the other hand, "river or freshwater dolphins" live in some of the largest rivers in Asia and South America, except for the La Plata dolphin which actually lives in the estuaries and coastal marine environments of South America. A peculiar aspect of the dolphins of the second group is their neck mobility which, unlike other dolphins, has unfused cervical vertebrae. This page shows some of the dolphins which live in the Gulf of San Matías.

Communication

Distances in the ocean are enormous, but sound travels 5 times faster underwater than in the air. Cetaceans produce sounds to communicate with one another, some of which have been classified as the most complex sounds in nature and may be divided into dialects, in the case of killer whales, or songs, in the case of humpback whales. Some of the different sounds are very strange, such as the "signature whistles" of bottlenose dolphins, used not only to identify themselves, but also to recognice others. To dolphins, these are something like the individual names we use to talk to each other.

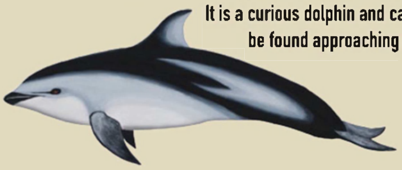
La Plata Dolphin or Franciscana

With a length of 1.3 to 1.7 metres, this is the smallest dolphin in the gulf and one of the smallest dolphins in the world. The body is greyish brown, similar to the robe of Franciscan monks, hence the name. The dorsal fin is rounded at the tips and it has an extremely long and narrow beak. The population of the Gulf of San Matías is the most southern population of this species in the world.



Dusky Dolphin

This dolphin reaches about 1.5 to 2 metres in length. It features a dark colour on its back and has a lighter belly. Its body is very compact and has 2 clear stripes which extend up to its flanks. It has a prominent dorsal fin and a short and thick beak. It is a curious dolphin and can commonly be found approaching ships at sea.



Common Dolphin

This dolphin can reach lengths of 1.7 to 2.5 metres. Colour patterns on the common dolphin are very characteristic: a dark back, light grey flanks behind the dorsal fin and yellowish-tan forward of the dorsal fin, and a white belly. The dorsal fin and beak are dark and prominent. This dolphin is very energetic and lives in large groups. It produces piercing sounds that are easily heard from outside the water.

Bottlenose Dolphin

This dolphin grows to be 2 to 4 metres long. Its colour varies considerably, but generally it is dark grey. It is a robust dolphin with a large and rounded head, and a short and stubby beak. It has a tall, triangular or falcate (sickle-shaped) dorsal fin. It is a sociable and active dolphin which lives in small groups.

Killer Whale or Orca

This dolphin can reach lengths of 5 to 10 metres, and is the largest of the dolphin family. Male killer whales are bigger and heavier than females and can weight around 9 tons. It has a distinctive black and white colour pattern, with white patches behind the eyes and behind and under its tall dorsal fin. Killer whales typically live in mixed family groups.

The bottlenose dolphin

It is common to name the same animal in different ways. For example the bottlenose dolphin, which is the most popular dolphin found in oceanariums, is also bottle-nosed dolphin in English or “tonina” in Spanish. In order to avoid confusion, researchers assign a scientific name to every species, in this case, Tursiops truncatus. Tursiops finds its origin in the Latin word tursio, which means “dolphin”, and the Greek suffix -ops, which means “to look like”; while truncatus in Latin means shortened or cut-off, referring to the bottlenose dolphins’ relatively short beak, in comparison to other dolphins’ beaks.

This dolphin lives in temperate and tropical coastline waters worldwide, but it may also be found offshore. In Argentina, it can be found from Bahía Samborombón, in the Province of Buenos Aires, to the Province of Chubut, but they have occasionally been seen in the Provinces of Santa Cruz and Tierra del Fuego. The previous page listed some of its general characteristics which distinguish the bottlenose dolphin from other dolphins. Now let’s look at some of the most characteristic features of the ones in the Bay of San Antonio.

Fully grown males are slightly larger than females, reaching lengths from 2.5 to 3.5 metres and their average weight is between 200 and 350 kg. Differences in colour, body shape and dorsal fins among individuals are related to the different geographical locations. Females live about 50 years, while males rarely live longer than 40 years.

Gestation lasts 12 months and newly born calves weight about 10 to 30 kg with a length of 0.85 to 1.40 metres. Calves nurse for as long as 18 months, a period which may be extended for a total of 8 years, although they start to eat solid food 4 months after birth. A female dolphin can potentially bear a single calf every 3 to 6 years. Like every cetacean, they give birth to only a few calves throughout their lives as the care and training of the calves, which males are not involved in, lasts several years.

Bottlenose dolphins usually live in groups or pods comprised of adult females and their daughters and granddaughters, which may stick together for more than 6 years or even their entire lives. In contrast, males remain with their mother for a while after nursing and then typically gather in groups with other juvenile males.

Their diet is based around fish, squid and crustaceans, such as shrimp, which they hunt while diving. Although bottlenose dolphins are not great divers, there are records of dives of more than 200 metres, with apneas, or suspension of external breathing, for more than 20 minutes.

Calves are mostly born in summer and spring, although births can take place at any time of the year.

Bottlenose dolphins are very sociable and usually gather in groups of 2 to 20 individuals, although groups of hundreds of dolphins have been registered offshore.

Echolocation

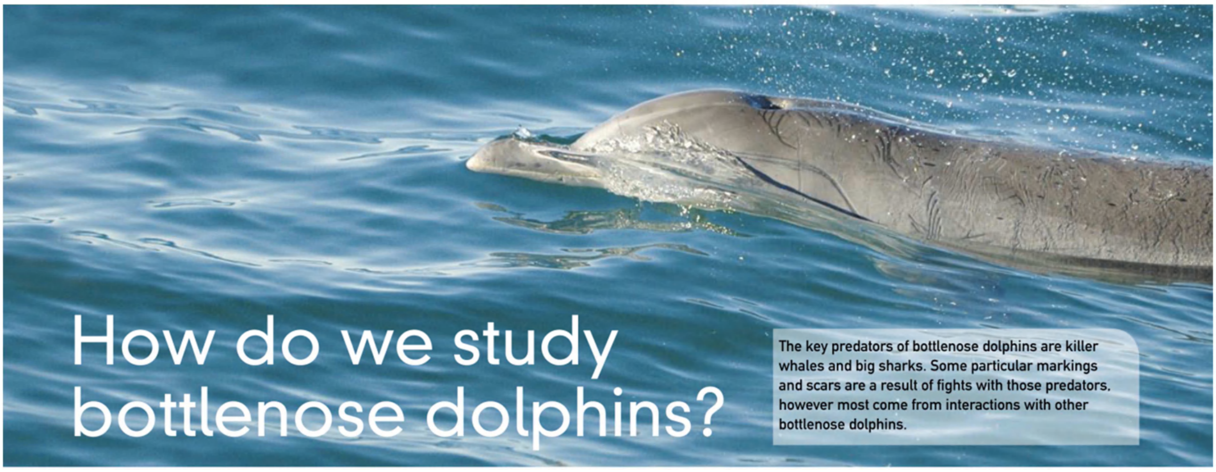
The dolphin’s echolocation system, also called bio sonar, is used to locate prey and gather information on the environment. How does it work?

Firstly, dolphins send out brief sound waves or “clicks”, which bounce back from objects creating echoes. Dolphins then listen to these echoes and form a mental “image” of the objects.

To understand this better we can compare the process to the images created with an ultrasound scan.

Sonar used by submarines and other vessels is also based on this system. Other toothed cetaceans, like sperm whales, also use echolocation, as well as certain bats.

The bio sonar is useful at sea, where vision is often limited by lack of light and murky water. Echolocation should not be confused with the sounds dolphins produce to communicate with each other.



How do we study bottlenose dolphins?

The key predators of bottlenose dolphins are killer whales and big sharks. Some particular markings and scars are a result of fights with those predators, however most come from interactions with other bottlenose dolphins.

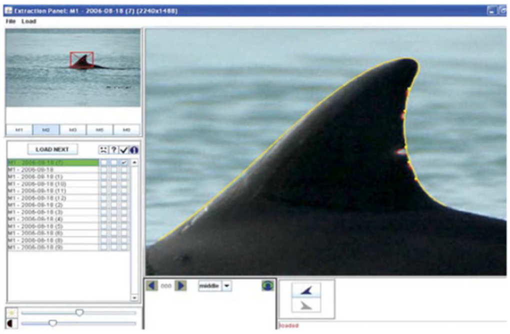
Observing dolphins in the wild is one of the most beautiful and intense experiences anyone can have. No one can remain indifferent in the face of such beauty and grace. However, there are not many places in the world to observe dolphins. The Bay of San Antonio is one of the few places in Argentina where bottlenose dolphins can be observed almost every day. This is why this location was chosen by researchers to study these dolphins.

A fundamental concept when observing animals in the wild is to avoid interrupting their activities and to be very patient. Surveys may be conducted from the coast, using a spotting scope with a strong zoom, or also from small vessels. These surveys enable researchers to find out, among other things, how often dolphins can be seen in the area and what their home range is, that is the area in which they forage (eat), rest and reproduce. And, perhaps most importantly, these surveys can tell us more about their population dynamics, that is whether there is an increase or decrease in the number of dolphins over time.

But you must wonder how is it possible to study all these aspects from an animal that spends most of its life underwater? One solution is to identify each individual and recognise them when they surface to breathe. But, how do we know which dolphin we are observing? We can identify each dolphin through the physical characteristics of their dorsal fin and other parts of their body, looking closely at the shape and markings such as cuts and important scars, all which are considered unique and permanent, making it possible to tell one animal from another. This is the reason why scientists try to get the best pictures while observing dolphins, as they try to capture these distinctive markings from all individuals. Each dolphin can then be assigned an identification code to help scientists recognise them when observed in a different area or at different times. Typically, it is an alphanumeric code. For example, RN-BSA-6/06 means that the dolphin has been observed in Río Negro, in the Bay of San Antonio, that it is individual number 6, identified in 2006. Every identified dolphin is then gathered into an identification catalogue. This method is known among scientists as "photo-identification" and is the fundamental basis for studying animal populations over time. As we will see in the following pages, these kinds of studies also help us understand the life stories and lifecycles of bottlenose dolphins.

Watching dolphins from the coast through a spotting scope with a long zoom.

Photographing dolphins from a small boat.



A software program compares each new picture of a dolphin with those already part of the catalogue. If there is a 75% or higher coincidence with the shape of the fin and the markings, it may have already been identified. If not, then it is almost certainly a new individual that has not yet been catalogued.

Calves are much smaller than adults and they are always spotted swimming near their mothers.

What do we know about bottlenose dolphins in the Bay of San Antonio?

The first wild bottlenose dolphin studies in Argentina can be traced back to the 1970s and 80s, when the first photo-identification catalogue of the species was created in the country. In those days, 53 individual dolphins had been identified in Peninsula Valdés (Province of Chubut) and 30 in the Province of Buenos Aires.

Since 2006, scientists have identified 67 individual bottlenose dolphins in the Bay of San Antonio. Thanks to this research, and bearing in mind that young dolphins cannot be identified due to the lack of scars, today it is estimated that the entire population comprises a total number of 80 to 100 dolphins. Researchers also try to understand the dolphins' social interactions, what their daily activities are, where they carry out most of these activities and whether or not they remain in the area the entire year. Here is some of the information we currently have about this population:

. Approximately 57% of the identified bottlenose dolphins are considered resident in the Bay of San Antonio, meaning that they were seen in the bay in all 4 seasons of the year. Research also showed that, although all these dolphins know each other, they generally associate with one another very randomly. Nevertheless, some individuals clearly prefer each other's company and form long term friendships or family bonds. Surveys clearly show that dolphins use the Bay of San Antonio mainly to rest, forage and nurse their young.

. Groups are usually made up of 4 individuals, although solitary animals or groups of up to 50 dolphins can also be found. Variation in the group size clearly depends on the activities they carry out and, in turn, these activities vary according to the time of year.

. During winter and spring, more dolphins can be seen in the bay, gathering in numerous groups related to cooperative feeding and social activities. During autumn, the amount of dolphins in the bay sharply decreases, possibly due to the lack of prey in the region. But, where do they go if they're not in the Bay of San Antonio? As we will see in the following pages, this is not the only place where they live.

Generally, coastal dolphins do not make huge migration trips, but they can easily range over 300 km.

The larger groups are formed during winter and spring to feed cooperatively and socialise.

Bottlenose dolphin tales I

All the dolphins identified in the Bay of San Antonio have been given an alphanumerical name, while some have also been given a common name. Why? As we have observed these dolphins over the years, we have got to know each one individually by looking at all the different aspects of their lives. For example Hilda and Tulumba have provided a better understanding of the social and family relations among dolphins.

Hilda

Bay of San Antonio. Up to that moment, it was nothing more than a nice picture of a dolphin. However, years later, when scientists spoke about the catalogue they were making, they compared the pictures and realised that the dolphin was specimen RN-BSA-16/06, a female that had been spotted in 2006 with a calf, and in 2010 with a second calf. Today she is the eldest photo-identified dolphin of the population and we all know her as Hilda.

Tulumba

Another very special dolphin is Tulumba (RN-BSA-31/07). When identified for the first time in 2007, she was already an adult female with a very sociable attitude, often approaching vessels. From that moment on to 2011, she has been seen 44 times throughout all 4 seasons of the year; hence she is a permanent resident of the bay. However, she has never been seen with a calf, which may indicate she is already old and cannot have calves anymore. Tulumba might be the 'Grandmother of the bay' and the eldest of her group, with an estimated age of 40. As she is always seen in the company of other females and calves, she shows that bottlenose dolphins may form strong social groups integrated by grandmothers, daughters and granddaughters that live together for a lifetime.

Bottlenose dolphin tales II

The Bay of San Antonio is not the only place in Argentina where bottlenose dolphins live. Photo-identification has made it possible to learn that some dolphins of this bay also frequent other areas. Researchers have described geographical variations of bottlenose dolphins and identified the areas where they live on the Argentine coastline. While those which live in the Province of Buenos Aires have triangular dorsal fins, those which live further south have falcate dorsal fins. These differences suggest that both populations are isolated from one another, which has conservation implications. This shows how the identification catalogue is an indispensable tool not only in learning about the species, but also in preserving it. But where do the dolphins go when they travel and how far do they travel?

Yaco

Yaco (RN-BSA-22/07) is a male adult dolphin with a very distinctive dorsal fin, which enables his identification even from land. He is considered a "scout" dolphin, since he approaches new or unknown elements like boats, to observe and investigate whether there is any sort of danger. He has allowed us to begin to understand the movements and seasonal shifts of dolphins and their home range.

There are around 20 dolphins, including 3 mothers with their calves, which have been photo-identified in the estuary of Río Negro, around 180 km east of the bay. It is believed that they enter the river to feed mostly in autumn, which may be a result of the lack of food in the bay during this season.

"The Falcates"

Among the dolphins living in the bay, there are 5 that look different from the others. Two of them are male adults (#55 and #57), and they are very big, active and curious. The other 3 comprise a female (#56) and her 2 calves. One of which (#56b) was with her when she was first identified in 2008 (see picture above) and a new one which was born in the summer of 2011, named Yagui (see picture below).

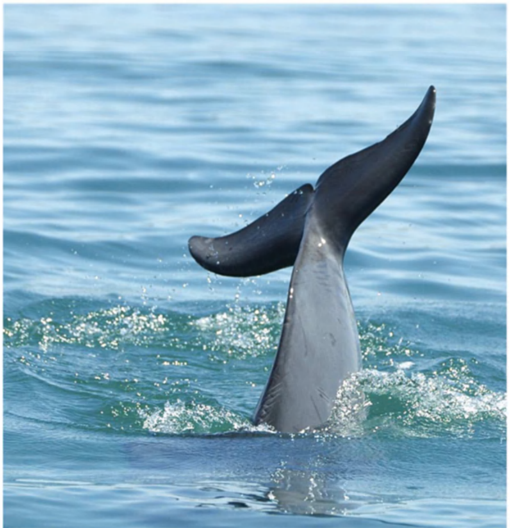
The group is known as "the falcates", due to their sickle-shaped dorsal fin. They are darker and larger than the rest of the bottlenose dolphins and their beak is notably shorter. These characteristics were also observed in the 53 dolphins studied in the Province of Chubut during the 70s and 80s. It would not be surprising if "the falcates" formed part of that original population. They are always seen together, something very unusual among the other dolphins in the Bay of San Antonio, but they have also been spotted regularly with the other dolphins. "The falcates" have also been observed in Puerto Lobos, 150 km to the south, strengthening the hypothesis that they originate from the population in Chubut. Recent studies have shown their differences are not only physical, but also genetic.

Behaviour

The bottlenose dolphin is a curious and smart species. Research reveals that in the Bay of San Antonio, bottlenose dolphins spend most of their time resting and feeding, depending on the time of year. In winter and spring they are more social and engage in cooperative feeding, while diving time increases in summer, probably related to the capture of demersal (living on or near the bottom of the sea) prey species.

Given that dolphins spend most of their life under water, it is often extremely difficult to interpret what behaviour their activities represent. The following images allow us to see some of their most distinctive behaviour.

JUMPING: They usually leap clear out of the water and then land with a great splash. They jump to swim faster (since air is less dense than water), to look around while swimming, to hunt and/or to communicate.



FLUKING: A dolphin will often lift its fluke above the water surface when about to dive. This kind of dive is not performed every time, but only when there is prey at the bottom of the sea they want to hunt. Therefore, tail raising in the air is generally a sign that the dolphin is diving in search of food.

SOCIAL INTERACTION: Dolphins are very sociable animals, but they are also strong and dominant. Their physical interactions strengthen their friendships and family bonds, but they may also show aggressive behaviour at times.

BOW-RIDING AND SURFING: Some dolphins love to ride on the waves near beaches or on the bow or stern waves of ships. However, not all of them approach vessels. Some dolphins are more curious while others are shyer and reserved.

SPYHOPPING: Although the bottlenose dolphins' world is mainly underwater and their senses relate to sound, they also have good vision outside the water. They poke their head above the surface to look around, perhaps to distinguish details onshore, ships and boats, or people approaching.

Cooperative feeding

In the Bay of San Antonio, bottlenose dolphins spend most of their time diving in small groups during summer. While diving, they hunt for demersal species like octopuses or flatfish which live near the sea bottom. However, during winter and spring, they feed from different species of schooling fish near the surface, like silverside, hake and whiting. When hunting, more than 40 dolphins gather together! They cooperate with each other to catch prey. How do they manage to do it? First of all, they group together around the prey to encircle it. This is how they herd the fish and bring them to the surface. Dolphins are experts in organising a hunt, communicating with each other through sounds and visual signs. They synchronise so perfectly and efficiently that no fish can escape from this "cooperative web". Fish group together as a defence, but near the surface this strategy becomes a trap since there is no way to escape. This is the moment to start eating, so now the dolphins start to capture them one by one.

During these "feeding fests", other species participate as well, benefiting from the dolphins' work herding the fish. Therefore, not only do colonies of penguins and sea lions make good use of dolphin hunting activities, but also seagulls, terns, petrels and albatrosses participate!

A dolphin jumps while chasing its prey, the sea lions jump in immediately after it, following which many seagulls dive into the water too. Everyone wants to take advantage of a dolphin-organised fishing trip.

Threats I

Overfishing and fishing discards are some of the main problems affecting productive seas and species worldwide.

A lot of dolphin and whale populations around the world are threatened. For example, in the waters of the South Atlantic Ocean, along the coast of South America, the La Plata dolphin is an endangered species due to entanglement in fishing nets. As a consequence, this species may disappear within the next 30 years if conditions do not change. Nowadays, at least the North Atlantic grey whale and the Yangtze River dolphin in China are believed to have become extinct due to human activities.

The bottlenose dolphin is not considered an endangered species and at the moment its future is stable due to their abundance and high adaptability to changing environments. However, we should bear in mind that in the 70s and 80s bottlenose dolphins were easily spotted along the entire Argentine coastline, but then the situation changed. Nowadays it is rare to see bottlenose dolphins in the Provinces of Buenos Aires and Chubut.

What caused this disappearance? Probably rising development and human activities brought about consequences such as pollution and overfishing. Accumulation of toxins in their body tissues and organs, such as heavy metals and pesticides, may kill bottlenose dolphins or make them more vulnerable to disease. Argentina is not without these problems, as evidenced by the high toxic concentrations recorded in some local populations. Samples from the Province of Buenos Aires, for example, have evidenced high concentrations of heavy metals and plastic material intake by several species of marine mammals.

Also, fishing activities have increased around the world. As a consequence, conflicts between humans and marine mammals have risen. One of them is the competition for food resources between fishing fleets and both whales and dolphins. Furthermore, as if this were not enough, accidental entanglements in fishing nets continue to increase the number of deaths.

There are even greater problems in countries like Peru, Japan and Denmark, where dolphins are caught to be sold to the captive industry or killed for human consumption with harpoons, rifles and nets. In certain areas of South America, their meat is also used as lobster and crab bait. They are sometimes killed as a way of falsely reporting the lack of fish, thus justifying today's excessive commercial and industrial fishing.

Previously, oceanariums enabled researchers to learn more about dolphins. However, nowadays they are only used for entertainment, as methods to study dolphins in the wild are widely available.

The increased traffic of commercial vessels affects marine environments around the world.

Threats II

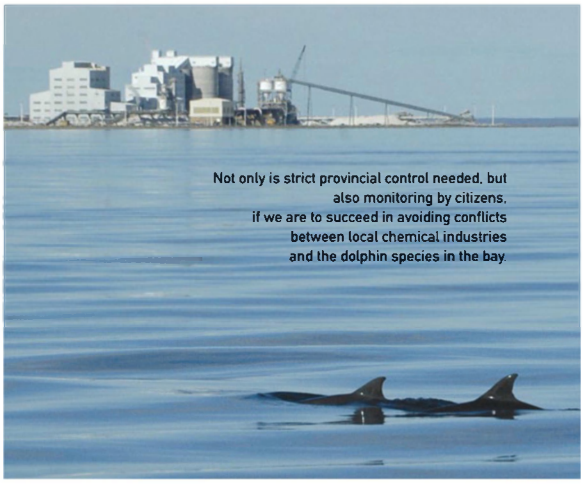
There are 3 urbanised areas along the coast of the Bay of San Antonio under full expansion and development: San Antonio Oeste, San Antonio Este and Las Grutas, one of the most popular tourism regions in Patagonia, which has grown enormously in the last few years. It is considered the most important and attractive resort in Patagonia, not only for its beaches and warm water, but also for its wide biodiversity. Big investment is taking place in the area, such as the building of hotels, resorts and restaurants. San Antonio Oeste is a city with antique railway houses, a traditional port and the most populated and developed urban centre of the bay. On the other hand, San Antonio Este has a deep-water seaport with the most import and export activity in Southern Argentina. More than 80% of the fruit and vegetable production of the valleys of the Provinces of Río Negro and Neuquén departs from its quays, as well as other Patagonian products, such as wool and minerals.

Human development has contributed to the contamination of the bay. Untreated sewage, toxic chemical products, heavy metals, industrial waste, pesticides and oil are a result of the urbanisation, chemical industries and mining activities in the area. Another threat to be taken into account is the overfishing of certain species from which dolphins feed. One of them is Argentine hake, which was once abundant in the area, but has now decreased in the north of the Gulf of San Matías. Furthermore, accidental captures in the fishing industry in Patagonia create victims, not only among birds, but also among marine mammals. And last but not least, a potential threat that cannot be disregarded is the destruction of their natural habitat, as a potential consequence of port dredging operations.

Bottlenose dolphins are an abundant species worldwide. However, some populations are seriously under threat, due to pollution of their environment and overfishing, among other things. Several activities are carried out in the bay, such as small-scale coastal and non-industrial fishing, tourism and shipping. Today, the bottlenose dolphins of the bay can be regarded as nationally threatened and recent studies have found that the population is decreasing. Therefore, we must protect them from both potential and real threats that affect the area.

Courtesy Federico Bernasconi

Fishing nets are a growing threat to bottlenose and La Plata dolphins.



Not only is strict provincial control needed, but also monitoring by citizens, if we are to succeed in avoiding conflicts between local chemical industries and the dolphin species in the bay.

Ports help economic development
but can create conflicts with local species.
A way to solve these dilemmas must be found.

How can we protect the Bay and its dolphins?

The dolphins of the Bay of San Antonio are isolated from Uruguayan and Brazilian dolphins because of the La Plata River. If this population continues to decrease, it may become extremely difficult for them to survive.

The Bay of San Antonio is a very important area for thousands of migratory coastal and sea birds as a resting and foraging site. The northern and eastern area has islets which are frequented by several species of non-migratory coastal birds to reproduce and rest. And as we have seen, its waters are the most important habitat of one of the most charismatic species of the Patagonian Sea: the bottlenose dolphin. These reasons are more than enough to justify why we should be careful; the cities surrounding the Bay of San Antonio are growing quickly, and besides generating progress and development, this causes a negative impact on the surrounding environment.

Dolphins have chosen this region for its protected waters; to rest and nurse their calves, and as a foraging site due to its great quantity of food. We now know that it is a resident population, perhaps the last one in Argentina. To protect the Bay of San Antonio and its dolphins, it is essential to continue scientific research, and to spread the knowledge acquired through educational projects.

One activity that could contribute to the protection of these dolphins is dolphin watching. If this activity is controlled and executed in a responsible and sensible way, it may be educational, sustainable and financially viable. Furthermore, it may encourage and promote the interest of local inhabitants, operators, fishermen, shellfish farmers and of course tourists, in the conservation and care of the marine environment. Coastal observation is another alternative that has no negative impact on dolphins. According to researchers, a dolphin may be spotted in the bay every 4 hours. This proves it is a very valuable place to look for wild dolphins in Argentina. If you visit the places mentioned in this book, you will not be disappointed when looking for dolphins. Indeed, you will never want to see dolphins in captivity again.

However, the information available about the Bay of San Antonio and its species will not be enough if laws protecting marine mammals are not enacted. This is the only way Río Negro may be turned into a province that truly protects its marine and coastal species. We can all be a part of this, urging municipal and provincial authorities to exercise real control in this unique natural habitat.

Whale watching contributes to awareness and the development of action for the protection and conservation of the southern right whale in Argentina. Something similar could be done with the bottlenose dolphins in the Bay of San Antonio.

General view of Las Grutas, which features the most important and attractive beaches in Patagonia.

Reflections by the sea

We have learned about the life stories of Hilda, Tulumba and Yaco. But there are many more! Manuel (#6), Yaco's best friend, and his friends Azul (#12) and Nereo (#25) also live in the bay. And Elsita (#11), an example of a mother who, after 8 years, is still accompanied by her daughter Juno (#51), and lives together with Hilda and Tulumba. They all need the bay as much as its human inhabitants do.

Although knowing and understanding these dolphins is important, it is not enough. They deserve our respect, not only because they are charismatic, but also because they are intelligent animals that live together in groups just like us. What is more, they should be respected because they transmit their culture from generation to generation, just like chimpanzees and killer whales. Although dolphins seem to be "smiling and happy" all the time, this is the result of our interpretation of their behaviour. Their "smile" is just an aspect of their anatomy and does not represent their mood.

Wherever humans and animals live together there is conflict. The Bay of San Antonio is no exception. We have become aware of the pollution and habitat destruction that accompanies ever increasing human activities, which makes it necessary to establish conservation measures to protect the resident coastal dolphins. Furthermore, implementation of these measures may contribute to the conservation of all species inhabiting these waters.

Today we know that the Bay of San Antonio is a safe haven for our friends and perhaps the last refuge remaining in Argentina for these dolphins. In the bay they can rest, feed, give birth and nurse their calves. In order to do that, they need clean and quiet waters, with an abundance of fish and squid. When we look after them, we take care of ourselves, as well as the sea and what it has to offer.

Although dolphins have a voice to communicate among themselves, they cannot speak with us to help us understand their problems and needs. However, they transmit their energy and joy when we see them! Therefore, we must act as the voice of these dolphins! Let the end of these pages be the beginning of a message that you can share with your family, friends and everybody you know:

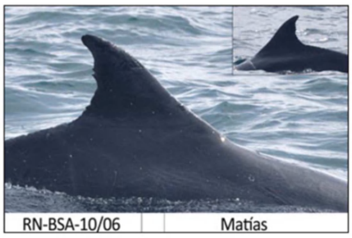
"Dolphins have been in the sea before humans inhabited this planet,
and they have managed to live in harmony with all other species.
We must learn to live in harmony with them too".

Catalogue

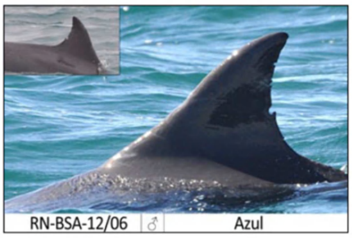
The following are some of the bottlenose dolphins photo-identified in the Bay of San Antonio. Researchers assign an alphanumerical name to each one of them, but they also receive a common name. As dolphins acquire more marks and scars over time, it is important this "identification catalogue" is updated regularly. Therefore these pictures have been updated since the previous publication.


RN-BSA-1/06 ♀ Sofi

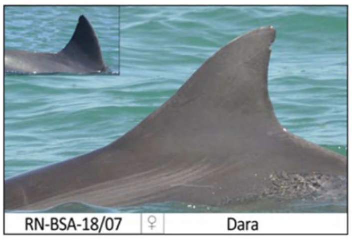

RN-BSA-6/06 ♂ Manuel


RN-BSA-10/06 Matías


RN-BSA-11/06 ♀ Elsita

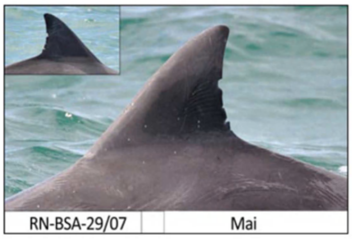

RN-BSA-12/06 ♂ Azul


RN-BSA-16/06 ♀ Hilda


RN-BSA-18/07 ♀ Dara


RN-BSA-22/07 ♂ Yaco


RN-BSA-25/07 ♂ Nereo


RN-BSA-29/07 Mai


RN-BSA-31/07 ♀ Tulumba

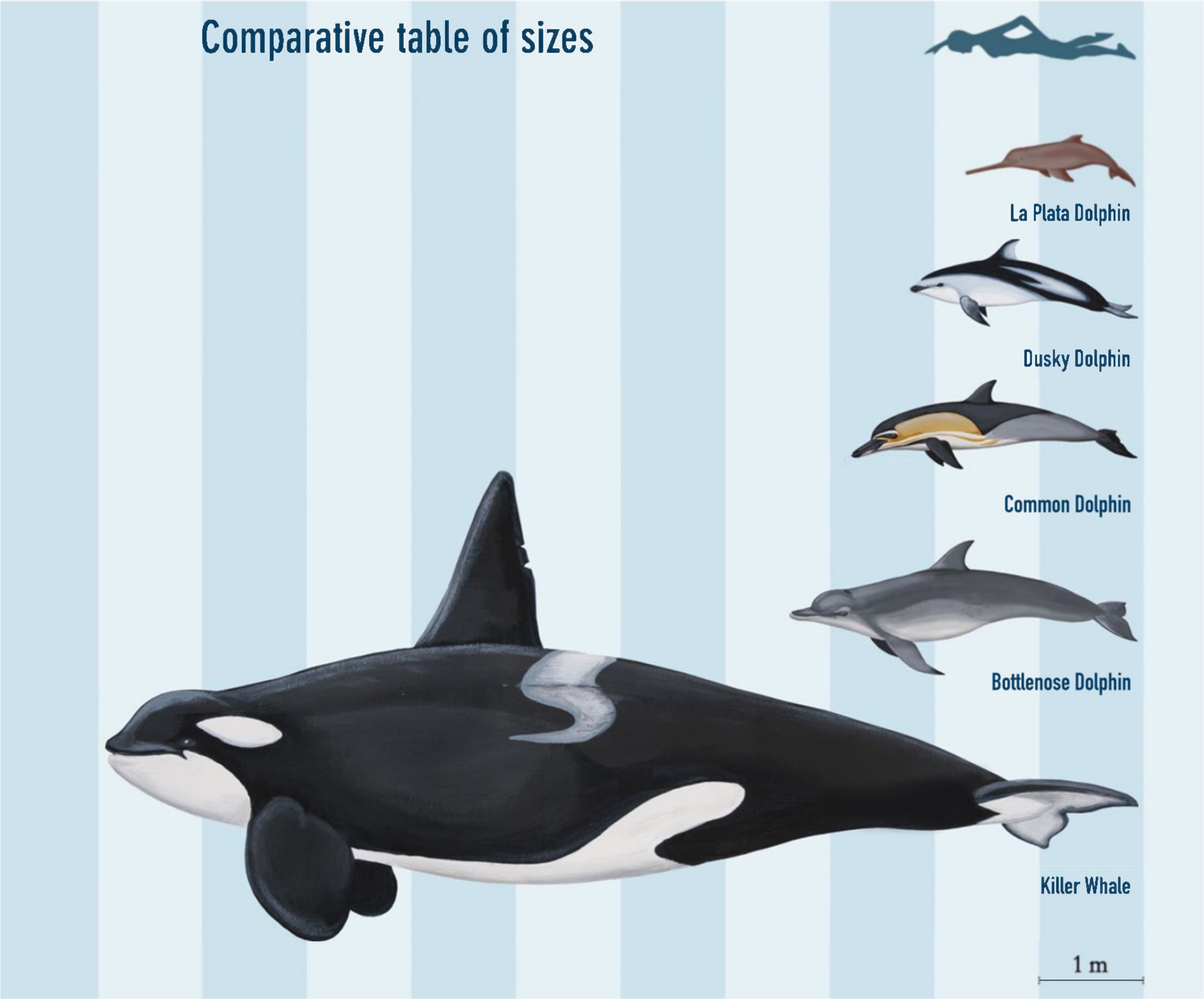

RN-BSA-51/08 Juno *2006 m: RN-BSA-11/06


RN-BSA-55/08 ♂ Ale


RN-BSA-56/08 ♀ Grace


RN-BSA-57/08 ♂ Agus

> “You are not a drop in the ocean.
> You are the entire ocean in a drop.”
> Rumi (Sufi Poet, 1207-1273)


Comparative table of sizes

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The bottlenose dolphins of the Bay of San Antonio tell us a story never before told, whose secrets have only been known by scientists but are now whispered in your ears. "Dolphins of the Bay" immerses us in an unknown, mysterious and amazing world and has been written by specialists in marine mammal biology and environmental education, who are devoted to the conservation of these animals. It is the result of scientific work carried out between 2006 and 2012 in the Bay of San Antonio and other locations in North Patagonia.

The purpose of this book is to share the results of these investigations, offering knowledge about this population of bottlenose dolphins to contribute to their preservation and care. The more we learn about these animals, the better equipped we are to protect and care for our marine neighbour, the bottlenose dolphin. Come and submerge yourself in their world...

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