**UNIVERSIDADE ESTADUAL DE SANTA CRUZ**

**PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA E CONSERVAÇÃO DA BIODIVERSIDADE – PPGECB**

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**USO DE HABITAT, COMPORTAMENTO E EMISSÕES ACÚSTICAS DAS BALEIAS-JUBARTE (*Megaptera novaeangliae*) NA REGIÃO DE SERRA GRANDE – BAHIA**

**ILHÉUS – BAHIA**

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Tese apresentada à Universidade Estadual de Santa Cruz como parte das exigências para obtenção do título de Doutor em Ecologia e Conservação da Biodiversidade.

Área de concentração: Ecologia e Conservação de Populações

Orientador: Prof. Júlio Ernesto Baumgarten

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Ilhéus, 31 de março de 2017.

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Dedico este trabalho aos meus pais, Maria José e António, por todos os ensinamentos e por todos os caminhos que eles sempre me ajudaram a percorrer.

E às baleias-jubarte, por toda a graciosidade e grandiosidade!

# AGRADECIMENTOS

*"Mar, metade da minha alma é feita de maresia*
*Pois é pela mesma inquietação e nostalgia,*
*Que há no vasto clamor da maré cheia,*
*Que nunca nenhum bem me satisfez.*
*E é porque as tuas ondas desfeitas pela areia*
*Mais fortes se levantam outra vez,*
*Que após cada queda caminho para a vida,*
*Por uma nova ilusão entontecida.*

*E se vou dizendo aos astros o meu mal*
*É porque também tu revoltado e teatral*
*Fazes soar a tua dor pelas alturas.*
*E se antes de tudo odeio e fujo*
*O que é impuro, profano e sujo,*
*É só porque as tuas ondas são puras."*

(Sophia de Mello Breyner Andresen)

# USO DE HABITAT, COMPORTAMENTO E EMISSÕES ACÚSTICAS DAS BALEIAS-JUBARTE (*Megaptera novaeangliae*) NA REGIÃO DE SERRA GRANDE - BAHIA

## RESUMO

As baleias-jubarte (*Megaptera novaeangliae*) com os seus padrões migratórios entre áreas de baixa e alta latitudes, usam a costa brasileira para se reproduzir e ter os seus filhotes entre julho e novembro. O número de indivíduos migrando para as águas brasileiras tem aumentado nos últimos anos, e tem se observado uma expansão da área usada ao longo de toda a costa, havendo uma falta de conhecimento detalhado sobre como ocorre esta reocupação. Desse modo, os objetivos deste estudo foram: 1) caracterizar o padrão de abundância relativa e uso de habitat dos indivíduos de baleia-jubarte na região de Serra Grande (Bahia, Brasil) ao longo da temporada; 2) descrever os padrões de movimento dos grupos nesta área e averiguar a influência das características espaço-temporais do ambiente e do comportamento nas trajetórias dos grupos; 3) revisar o estado da arte do conhecimento sobre os comportamentos percussivos em cetáceos; 4) caracterizar a estrutura do canto das baleias-jubarte e quantificar a mudança desta estrutura entre os anos. Entre julho e outubro de 2014 e 2015, foi realizado o monitoramento visual durante 67 dias através de ponto fixo usando uma estação total para rastrear os grupos que usam a área, e o monitoramento acústico passivo, usando até três unidades autônomas de gravação – *Oceanpods*. Os grupos mais observados foram duplas (32.23%), animais solitários (26.71%), e grupos de mãe com filhote (21.23% do total). Houve um aumento do número de indivíduos observados por hora de 2014 para 2015 e aproximação dos grupos à costa ao longo da temporada. A presença e o número de escortes nos grupos de mãe com filhote influenciam a sua distribuição espacial, o seu estado comportamental e as suas velocidades. Foi verificado um aumento da velocidade dos grupos com o aumento da distância à costa. As trajetórias dos grupos de baleias-jubarte foram mais erráticas no início da temporada, e aqueles grupos que se deslocavam para sul apresentaram rotas mais lineares, tendo sido predominantes ao longo do estudo. O canto dos machos apresentou um índice de similaridade de Distância de *Levenshtein* de 0,50 entre os dois anos. Houve variação no número de frases repetidas dentro de alguns temas. Apesar disso, a sequência dos temas dentro do ciclo de canto foi sempre a mesma. Este trabalho apoia a ideia da população de baleia-jubarte estar expandindo ao longo da costa. Os grupos de mãe com filhote permaneceram em descanso perto da costa, o que revela que a área é usada para os primeiros estágios de vida dos filhotes, podendo propiciar maior exposição a perturbações causadas por atividades antropogênicas. A presença de machos cantores também demonstra a ocorrência do comportamento associado à corte e acasalamento da espécie na região. Informações detalhadas sobre os padrões de uso de habitat e de comportamento da espécie na região podem auxiliar futuras medidas de proteção e gestão na região.

Palavras-chaves: Canto. Comunicação. Grupo de mãe com filhote. Ocorrência. Trajetórias.

# HABITAT USE, BEHAVIOUR AND ACOUSTIC EMISSIONS OF HUMPBACK WHALES (*Megaptera novaeangliae*) IN SERRA GRANDE REGION - BAHIA

## ABSTRACT

Humpback whales (*Megaptera novaeangliae*) present migratory patterns between low and high latitude areas and use the Brazilian coast to breed and calve between July and November. The number of individuals migrating to Brazilian waters has increased in recent years, and the area they use along the entire coast is in expansion, with a lack of detailed knowledge about this reoccupation. Thus, the objectives of this study were: 1) characterize relative abundance and habitat use patterns of the humpback whales in the Serra Grande region (Bahia, Brazil) throughout the season; 2) describe the movement patterns of the groups and to investigate the influence of spatial-temporal and behavioural features in group trajectories; 3) review the state of the art of percussive behaviours in cetaceans; 4) describe the structure of humpback whales song and quantify the change of the structure between the years. Between July and October of 2014 and 2015, visual monitoring was performed during 67 days from a land-based point using a total station to track groups using the area, and passive acoustic monitoring using up to three autonomous recording units - Oceanpods. Dyads (32.23%) and solitary animals (26.71%) were the most frequently observed groups, and mother and calf represented 21.23% of the sightings. The number of individuals observed per hour increased from 2014 to 2015 and the groups approached the coast during the season. The presence and number of escorts in mother and calf groups influenced their spatial distribution, behavioural status, and speeds. Group speed increased with the distance to the coast. The trajectories performed by groups of humpback whales were more erratic at the beginning of the season, and the groups moving south presented more linear routes, predominating throughout the study. Males song presented a Levenshtein distance similarity index of 0.50 between the two years. A variation in the number of repeated phrases within some themes was registered. Nevertheless, themes sequence within the song cycle was always the same. This work supports the fact that the humpback whale population is in expansion along the coast. Mother and calf groups were frequently observed resting near to the coast in the Serra Grande region, revealing how the area is essential for the first stages of life of the calves, where they could stay more exposed to disturbances caused by anthropogenic activities. Presence of male singers also demonstrates the occurrence of behaviour associated with courtship and mate of the species in the region. Detailed information on patterns of habitat use and species behaviour in the region can support future protection and management measures in the region.

Keywords: Communication. Mother and calf group. Occurrence. Song. Trajectories.

# SUMÁRIO

# 1 INTRODUÇÃO GERAL

As baleias-jubarte (*Megaptera novaeangliae* Borowski 1781), como a maioria dos misticetos possuem um ciclo anual envolvendo padrões migratórios, e apresentam uma distribuição mundial (CLAPHAM, 2000). Elas permanecem em altas latitudes durante o verão aproveitando a grande produtividade para se alimentarem, e durante o inverno migram para águas quentes em baixas latitudes para se reproduzirem e terem os seus filhotes (DAWBIN, 1966; CLAPHAM, 2000). As águas mais quentes, menos profundas e protegidas perto da costa ou de ilhas (DAWBIN, 1966; CLAPHAM, 2009) parecem diminuir o risco da presença de predadores (CORKERON; CONNOR, 1999), apresentando condições mais favoráveis para o nascimento e os primeiros períodos de vida dos filhotes (WHITEHEAD; MOORE, 1982). Vários estudos demonstraram que grupos de fêmeas com filhotes permanecem mais perto da costa em águas rasas para tentarem se manter afastados dos machos em busca de acasalamentos (SMULTEA, 1994; ERSTS; ROSENBAUM, 2003).

A espécie é conhecida por seus comportamentos exibicionistas como saltos (WHITEHEAD, 1985), batidas de caudal (WEINRICH, SCHILLING; BELT, 1992) e batidas de peitoral (BAKER; HERMAN, 1984). Apesar das várias incertezas da função desse tipo de comportamentos em cetáceos, vários trabalhos sugerem que eles podem participar na comunicação entre os indivíduos, como por exemplo em casos de agressão (BAKER; HERMAN, 1984; SILBER, 1986) ou para chamar a atenção (WHITEHEAD, 1985; DUNLOP, CATO; NOAD, 2010).

Um dos outros comportamentos mais conhecidos e estudados da espécie é a emissão do canto pelos machos (PAYNE; MCVAY, 1971), que se acredita estar relacionada com a seleção sexual (SMITH et al., 2008). Apesar de apresentar padrões repetitivos, o canto apresenta variações dentro do canto emitido por um mesmo indivíduo como entre diferentes indivíduos (PAYNE; MCVAY, 1971; ARRAUT; VIELLIARD, 2004). Estudos sobre a descrição do canto revelam como a sua análise pode ser subjetiva (CHOLEWIAK, SOUSA-LIMA; CERCHIO, 2013) mas estudos se fazem necessários para entender a sua função na comunicação das baleias-jubarte, como para tentar perceber como ocorre a sua evolução ao longo do tempo dentro da mesma população (ERIKSEN et al., 2005) como entre populações diferentes (DARLING; SOUSA-LIMA, 2005; GARLAND et al., 2011). Esse entendimento pode ajudar a esclarecer cada vez mais como o canto é transmitido e aprendido entre os indivíduos.

O Hemisfério Sul apresenta sete populações distintas (IWC, 2001), e a população que migra até à costa brasileira entre julho e novembro (MARTINS et al., 2001) pertence ao estoque reprodutivo A (IWC, 2005). As áreas de alimentação conhecidas para esta população são as Ilhas Geórgia do Sul e Sanduíche do Sul (ZERBINI et al., 2006; ENGEL; MARTIN, 2009; ZERBINI et al., 2011), separadas por aproximadamente 4000 km das áreas de reprodução (STEVICK et al., 2006). A rota de migração utilizada pelos indivíduos desta população saindo da costa brasileira é de 170º rumo às áreas de alimentação (HORTON et al., 2011; ZERBINI et al., 2011). No entanto, informações sobre os padrões de movimento em pequena escala das baleias-jubarte desta população durante o período reprodutivo são poucas.

No Brasil, a principal área de reprodução das baleias-jubarte é o Banco dos Abrolhos (ANDRIOLO et al., 2010; MARTINS et al., 2013). O número de baleias-jubarte que tem migrado para a costa brasileira tem aumentado nos últimos anos (ANDRIOLO et al., 2010; BORTOLOTTO et al., 2016; PAVANATO et al., 2017). Como este aumento tem sido observado ao longo de toda a costa brasileira (ZERBINI et al., 2004), Rossi-Santos et al. (2008) também o verificou ao norte do estado da Bahia (ROSSI-SANTOS et al., 2008) sugerindo que a espécie está ocupando áreas de reprodução usadas antes serem afetadas pela caça (MORAIS et al., 2016). Bortolotto et al. (2016) estimaram que em 2008, a população de baleias-jubarte representava pelo menos 60% da sua abundância relativamente à pré-exploração moderna entre 1602 até 1920 (MORAIS et al., 2016). Apesar desse aumento e expansão da sua ocupação pela costa, não existem muitos estudos (ROSSI-SANTOS et al., 2008) que caracterizem o uso de habitat detalhado da espécie para além da região do Banco dos Abrolhos (MARTINS et al., 2001; MORETE, BISI; ROSSO, 2007; MORETE et al., 2008) e da Praia do Forte (LUNARDI, ENGEL; MACEDO, 2008; ROSSI-SANTOS et al., 2008).

A IUCN (*International Union for the Conservation of Nature*) modificou o status da espécie de "Vulnerável" para "Menos preocupante" (REILLY et al., 2008) devido ao aumento populacional verificado para a maioria das populações. Apesar dessa recuperação após a exploração da indústria baleeira, as baleias-jubarte estão mais expostas às atividades antropogênicas devido à sua distribuição costeira durante o período reprodutivo. Ameaças como emalhamento em redes de pesca (MOURA et al., 2013), colisão com embarcações (BEZAMAT, WEDEKIN; SIMÕES-LOPES, 2014), mascaramento acústico devido a atividades da indústria petrolífera (ROSSI-SANTOS, 2015) e alteração do comportamento devido a atividades de *whale watching* (SOUSA-LIMA et al., 2002; SOUSA-LIMA; CLARK, 2008; 2009) são exemplos que podem ser mais recorrentes devido à sobreposição da ocupação

das regiões costeiras pelo ser humano e pela população de baleias-jubarte, que está aumentando (ANDRIOLO et al., 2010).

Esse parece ser o caso da região de Serra Grande no Sul do estado da Bahia, que apesar de estar integrada na Área de Proteção Ambiental – APA Costa de Itacaré/Serra Grande, ela está inserida numa extensa área de exploração e produção de gás natural e petróleo (RAMOS, SICILIANO; RIBEIRO, 2010), aproximadamente a 10 km da área onde está prevista a construção do complexo Porto Sul (BAMIN, 2011). O desenvolvimento deste tipo de atividades antrópicas pode causar impactos negativos mencionados anteriormente para as baleias-jubarte que utilizam a região, resultando no possível abandono de áreas tradicionais de ocorrência (JONES; SWARTZ, 2009). Medidas de conservação, como a criação e a expansão das áreas marinhas protegidas, podem garantir que a população de baleias-jubarte em recuperação continue saudável (MARTINS et al., 2013; CASTRO et al., 2014).

Nas últimas décadas tem se verificado o aumento da presença das baleias-jubarte na região de Serra Grande, não havendo informações detalhadas sobre os padrões de uso de habitat e de comportamento apresentados pelas mesmas a norte da região dos Abrolhos. A área de estudo apresenta características singulares de se encontrar na região onde a plataforma continental é mais curta na costa brasileira (IBGE, 2011; PRATES, GONÇALVES; ROSA, 2012), dando oportunidade de aproximação das baleias-jubarte à costa (ROSSI-SANTOS, 2012), associada à presença de um ponto alto perto da linha da costa que permite a sua observação sem a interferência no seu comportamento (WÜRSIG, CIPRIANO; WÜRSIG, 1991). Outras vantagens deste tipo de estudo é que são não invasivos, são relativamente baratos, e a sua logística é simples (MORETE, ABRAS; MARTINS, 2017). Apesar disso, estes estudos podem ocorrer em áreas isoladas como foi o caso deste trabalho, sendo necessário ter cuidados especiais com a segurança, e quando as condições meteorológicas se tornam adversas, é conveniente ter uma infraestrutura no local para guardar o equipamento e as pessoas ficarem protegidas (MORETE, ABRAS; MARTINS, 2017). Este tipo de metodologia apresenta algumas limitações: a cobertura geográfica é limitada, ou seja, a área amostrada pode representar uma pequena parte da distribuição da espécie; devido à distância não é possível identificar individualmente as baleias, o que pode causar problemas de falta de independência dos dados; e a detecção dos animais pode diminuir com o aumento da distância à costa onde os indivíduos se encontram (MORETE, ABRAS; MARTINS, 2017).

Outra metodologia aplicada durante este estudo na região foi o monitoramento acústico passivo (MAP). O MAP tem como vantagens: o extenso alcance de detecção, os animais são mais facilmente detectados acusticamente do que visualmente, o monitoramento

pode ser realizado durante a noite e em condições de má visibilidade durante longos períodos, e a coleta de dados pode ser automatizada (GORDON et al., 2004; NIEUKIRK et al., 2004; MELLINGER et al., 2007; SOUSA-LIMA; CLARK, 2009; SOUSA-LIMA et al., 2013). Permite ainda a caracterização detalhada da paisagem acústica de uma determinada área a um custo relativamente baixo, e é eficaz em áreas de difícil acesso (SOUSA-LIMA et al., 2013). O MAP tem como desvantagens que os equipamentos têm que ser recolhidos, não permitindo o monitoramento a tempo real, e as limitações de associação do número de sons gravados com o número de animais presentes, como a necessidade de mais de um equipamento para localizar o lugar de onde os sons estão sendo emitidos (SOUSA-LIMA et al., 2013). Quando possível, o monitoramento acústico e o visual devem ser complementares, pois para o uso do MAP é necessário que os animais estejam vocalizando (GORDON et al., 2004).

Desse modo, o objetivo geral deste estudo foi descrever o padrão de uso de habitat e o comportamento dos indivíduos de baleia-jubarte na região de Serra Grande (Bahia, Brasil). Os objetivos específicos foram:

1. Caracterizar o padrão de abundância e uso de habitat das baleias-jubarte ao longo da temporada na região de Serra Grande (capítulo 1).

Os padrões de uso de habitat dos indivíduos de baleia-jubarte na região são similares aos observados em Abrolhos, ou as diferentes características geomorfológicas e geográficas das regiões afetam esses padrões? Espera-se que os grupos de mãe com filhote permaneçam mais perto da costa como observado em outras áreas, mas que o número de baleias observado seja menor do que o observado na região do Banco dos Abrolhos, sendo a região uma área de menor densidade.

2. Descrever os padrões de movimento dos grupos de baleias-jubarte e investigar a influência das características espaço-temporal e do comportamento nas trajetórias dos grupos na região de Serra Grande (capítulo 2).

A região é utilizada pelas baleias-jubarte como área de passagem ou as baleias permanecem na região para, por exemplo, cuidar dos seus filhotes? Os padrões de movimento mudam ao longo da temporada? Espera-se que devido a ser uma região de mar aberto e menos protegida, que as baleias utilizem a região como uma área de trânsito, e que se observem mais grupos indo para Norte no início da temporada, e se deslocando mais para Sul perto do final da temporada.

3. Revisar o estado de arte sobre os comportamentos percussivos em cetáceos (capítulo 3).

Os comportamentos percussivos são utilizados para a comunicação entre os indivíduos? Sendo a comunicação acústica essencial para os cetáceos, espera-se que sim pois estes comportamentos resultam em produção de sons bem intensos.

4. Caracterizar a estrutura do canto das baleias-jubarte e quantificar a sua alteração entre os anos de 2014 e 2015 na região, e verificar variações intra e interanuais no número de frases dentro dos temas (capítulo 4).

Que alterações ocorrem na estrutura do canto de um ano para o outro? E que tipo variações encontramos? Espera-se encontrar alterações desde inserção e exclusão de unidades dentro das frases e de temas completos, como modificações de unidades dentro das frases. Como descrito na literatura, é possível se verificar variações do canto do mesmo indivíduo como entre indivíduos.

## 1.1 Referências

ANDRIOLO, A. et al. Humpback whales within the Brazilian breeding ground: distribution and population size estimate. **Endangered Species Research,** v. 11, p. 233–243, 2010.

ARRAUT, E. M.; VIELLIARD, J. M. E. The song of the Brazilian population of Humpback Whale *Megaptera novaeangliae*, in the year 2000: individual song variations and possible implications. **Annals of the Brazilian Academy of Science,** v. 76, n. 2, p. 373-380, 2004.

BAKER, C. S.; HERMAN, L. M. Aggressive behavior between humpback whales (*Megaptera novaeangliae*) wintering in Hawaiian waters. **Canadian Journal of Zoology,** v. 62, p. 1922-1937, 1984.

BAMIN. **Relatório de Impacto Ambiental Porto Sul**. Bahia Mineração Ltda., p.118. 2011

BEZAMAT, C.; WEDEKIN, L. L.; SIMÕES-LOPES, P. C. Potential ship strikes and density of humpback whales in the Abrolhos Bank breeding ground, Brazil. **Aquatic Conservation: Marine and Freshwater Ecosystems,** v. 25, n. 5, p. 712–725, 2014.

BORTOLOTTO, G. A. et al. Whale, Whale, Everywhere: Increasing Abundance of Western South Atlantic Humpback Whales (*Megaptera novaeangliae*) in Their Wintering Grounds. **PLoS ONE,** v. 11, n. 10, p. e0164596, 2016.

CASTRO, F. R. et al. Are marine protected areas and priority areas for conservation representative of humpback whale breeding habitats in the western South Atlantic? **Biological Conservation,** v. 179, p. 106-114, 2014.

CHOLEWIAK, D. M.; SOUSA-LIMA, R. S.; CERCHIO, S. Humpback whale song hierarchical structure: Historical context and discussion of current classification issues. **Marine Mammal Science,** v. 29, n. 3, p. E312–E332, 2013.

CLAPHAM, P. J. The Humpback Whale: Seasonal Feeding and Breeding in a Baleen Whale. In: MANN, J. et al. (Ed.). **Cetacean Societies: Field Studies of Dolphins and Whales**. Chicago: The University of Chicago Press, 2000. p. 173-196.

_____. Humpback Whale. In: PERRIN, W. F.; WÜRSIG, B.; THEWISSEN, J. G. M. (Ed.). **Encyclopedia of Marine Mammals**. 2nd. San Diego: Academic Press, 2009. p. 582-585.

CORKERON, P. J.; CONNOR, R. C. Why do baleen whales migrate? **Marine Mammal Science,** v. 15, n. 4, p. 1228-1245, 1999.

DARLING, J. D.; SOUSA-LIMA, R. S. Songs indicate interaction between humpback whales (*Megaptera novaeangliae*) populations in the Western and Eastern South Atlantic Ocean **Marine Mammal Science,** v. 21, n. 3, p. 557–566, 2005.

DAWBIN, W. H. The seasonal migratory cycle of humpback whales. In: NORRIS, K. S. (Ed.). **Whales, dolphins, and porpoises**. Berkeley: University of California Press, 1966. p. 145-170.

DUNLOP, R. A.; CATO, D. H.; NOAD, M. J. Your attention please: increasing ambient noise levels elicits a change in communication behaviour in humpback whales (*Megaptera novaeangliae*). **Proceedings of the Royal Society B,** v. 277, p. 2521–2529, 2010.

ENGEL, M. H.; MARTIN, A. R. Feeding grounds of the western South Atlantic humpback whale population. **Marine Mammal Science,** v. 25, p. 964-969, 2009.

ERIKSEN, N. et al. Cultural change in the songs of humpback whales (*Megaptera novaeangliae*) from Tonga. **Behaviour,** v. 142, p. 305-328, 2005.

ERSTS, P. J.; ROSENBAUM, H. C. Habitat preference reflects social organization of humpback whales (*Megaptera novaeangliae*) on a wintering ground. **Journal of Zoology,** v. 260, p. 337–345, 2003.

GARLAND, E. C. et al. Dynamic Horizontal Cultural Transmission of Humpback Whale Song at the Ocean Basin Scale. **Current Biology,** v. 21, p. 687-691, 2011.

GORDON, J. et al. A Review of the Effects of Seismic Surveys on Marine Mammals. **Marine Technology Society Journal,** v. 37, n. 4, p. 16-34, 2004.

HORTON, T. W. et al. Straight as an arrow: humpback whales swim constant course tracks during long-distance migration. **Biology Letters,** v. 7, p. 674–679, 2011.

IBGE. **Atlas geográfico das zonas costeiras e oceânicas do Brasil**. Rio de Janeiro: 2011. ISBN 978-85-240-4219-5.

IWC. Report of the sub-committee on the comprehensive assessment of whale stocks – in-depth assessments. **Journal of Cetacean Research and Management,** v. 3, n. Suppl., p. 177-208, 2001.

_____. Report of the Scientific Committee. Annex H - Report of the sub-committee on other southern hemisphere whale stocks. **Journal of Cetacean Research and Management,** v. 7, n. Suppl., p. 235-246, 2005.

JONES, M. L.; SWARTZ, S. L. Gray Whale *Eschrichtius robustus*. In: PERRIN, W. F.; WURSIG, B.; THEWISSEN, J. G. M. (Ed.). **Encyclopedia of Marine Mammals**. Amsterdam: Elsevier, 2009. p. 503-511.

LUNARDI, D. G.; ENGEL, M. H.; MACEDO, R. H. F. Behavior of humpback whales, *Megaptera novaeangliae* (Cetacea: Balaenopteridae): comparisons between two coastal areas of Brazil. **Revista Brasileira de Zoologia,** v. 25, n. 2, p. 159–164, 2008.

MARTINS, C. C. A. et al. Identifying priority areas for humpback whale conservation at Eastern Brazilian Coast. **Ocean & Coastal Management,** v. 75, p. 63-71, 2013.

_____. Aspects of habitat use patterns of humpback whales in the Abrolhos Bank, Brazil, breeding ground. **Memoirs of the Queensland Museum,** v. 27, n. 2, p. 563-570, 2001.

MELLINGER, D. K. et al. An Overview of Fixed Passive Acoustic Observation Methods for Cetaceans. **Oceanography,** v. 20, n. 4, p. 36-45, 2007.

MORAIS, I. O. B. et al. From the southern right whale hunting decline to the humpback whaling expansion: a review of whale catch records in the tropical western South Atlantic Ocean. **Mammal Review**, p. 1-13, 2016.

MORETE, M. E.; ABRAS, D.; MARTINS, C. C. A. Land-Based Studies of Aquatic Mammals in Latin America: Understanding Behavior for Conservation. In: ROSSI-SANTOS, M. R.; FINKL, C. W. (Ed.). **Advances in Marine Vertebrate Research in Latin America. Technological Innovation and Conservation**: SPRINGER, v.22, 2017. (Coastal Research Library). ISBN 978-3-319-56984-0.

MORETE, M. E. et al. Fluctuating abundance of humpback whales (*Megaptera novaeangliae*) in a calving ground off coastal Brazil. **Journal of the Marine Biological Association of the United Kingdom,** v. 88, p. 1229-1235, 2008.

MORETE, M. E.; BISI, T. L.; ROSSO, S. Temporal pattern of humpback whale (*Megaptera novaeangliae*) group structure around Abrolhos Archipelago breeding region, Bahia, Brazil. **Journal of the Marine Biological Association of the United Kingdom,** v. 87, p. 87-92, 2007.

MOURA, J. F. et al. Humpback whales washed ashore in southeastern Brazil from 1981 to 2011: stranding patterns and microbial pathogens survey. **Biologia,** v. 68, n. 5, p. 992—999, 2013.

NIEUKIRK, S. L. et al. Low-frequency whale and seismic airgun sounds recorded in the mid-Atlantic Ocean. **Journal of the Acoustical Society of America,** v. 115, n. 4, p. 1832–1843, 2004.

PAVANATO, H. J. et al. Estimating humpback whale abundance using hierarchical distance sampling. **Ecological Modelling,** v. 358, p. 10-18, 2017.

PAYNE, R. S.; MCVAY, S. Songs of humpback whales. **Science,** v. 173, p. 585–597, 1971.

PRATES, A. P. L.; GONÇALVES, M. A.; ROSA, M. R. **Panorama da Conservação dos Ecossistemas Costeiros e Marinhos no Brasil**. Brasília: MMA, 2012.

RAMOS, R.; SICILIANO, S.; RIBEIRO, R. **Monitoramento da Biota Marinha em Navios de Sísmica: seis anos de pesquisa (2001-2007)**. Vitoria: Everest Tecnologia em Serviços, 2010.

REILLY, S. B. et al. *Megaptera novaeangliae*. 10 de fevereiro de 2017. 2008

ROSSI-SANTOS, M. R. **Comportamento e ecologia acústica da baleia-jubarte (*Megaptera novaeangliae*) na região Nordeste do Brasil**. 2012. 173 f. Tese (Doutorado). Centro de Biociências, Universidade Federal do Rio Grande do Norte, Natal, 2012.

_____. Oil Industry and Noise Pollution in the Humpback whale (*Megaptera novaeangliae*) Soundscape Ecology of the Southwestern Atlantic Breeding Ground. **Journal of Coastal Research,** v. 31, n. 1, p. 184–195, 2015.

ROSSI-SANTOS, M. R. et al. Occurrence and distribution of humpback whales (*Megaptera novaeangliae*) on the north coast of the State of Bahia, Brazil, 2000–2006. **ICES Journal of Marine Science,** v. 65, p. 667–673, 2008.

SILBER, G. K. The relationship of social vocalizations to surface behavior and aggression in the Hawaiian humpback whale (*Megaptera novaeangliae*). **Canadian Journal of Zoology,** v. 64, p. 2075–2080, 1986.

SMITH, J. N. et al. Songs of male humpback whales, *Megaptera novaeangliae*, are involved in intersexual interactions. **Animal Behaviour,** v. 76, p. 467-477, 2008.

SMULTEA, M. A. Segregation by humpback whale (*Megaptera novaeangliae*) cows with a calf in coastal habitat near the island of Hawaii. **Canadian Journal of Zoology,** v. 72, p. 805-8 11, 1994.

SOUSA-LIMA, R. S.; CLARK, C. W. Modeling the Effect of Boat Traffic on the Fluctuation of Humpback Whale Sing Activity in The Abrolhos National Marine Park, Brazil. **Canadian Acoustics,** v. 36, n. 174-181, 2008.

_____. Whale sound recording technology as a tool for assessing the effects of boat noise in a Brazilian marine park. **Park Science,** v. 26, n. 1, p. 59-63, 2009.

SOUSA-LIMA, R. S. et al. Impact of boats on the vocal behavior of humpback whales off Brazil. **Journal of the Acoustic Society of America,** v. 112, n. 5, p. 2430-2431, 2002.

_____. A Review and Inventory of Fixed Autonomous Recorders for Passive Acoustic Monitoring of Marine Mammals. **Aquatic Mammals,** v. 39, n. 1, p. 23-53, 2013.

STEVICK, P. T. et al. A note on the movement of a humpback whale from Abrolhos Bank, Brazil to South Georgia. **Journal Cetacean Research Manager,** v. 8, n. 3, p. 297–300, 2006.

WEINRICH, M. T.; SCHILLING, M. R.; BELT, C. R. Evidence for acquisition of a novel feeding behaviour: lobtail feeding in humpback whales, *Megaptera novaeangliae*. **Animal Behaviour,** v. 44, p. 1059-1072, 1992.

WHITEHEAD, H. Humpback Whale Breaching. **Investigations of Cetacea,** v. 17, p. 117-155, 1985.

WHITEHEAD, H.; MOORE, M. J. Distribution and movements of West Indian humpback whales in winter. **Canadian Journal of Zoology,** v. 60, p. 2203-2211, 1982.

WÜRSIG, B.; CIPRIANO, F.; WÜRSIG, M. Dolphin Movement Patterns: Information from Radio and Theodolite Tracking Studies. In: PRYOR, K.;NORRIS, K. S. (Ed.). **Dolphin Societies - Discoveries and Puzzles**. Berkeley: University of California Press, 1991. p. 79-111.

ZERBINI, A. N.  et al. Winter distribution and abundance of humpback whales (*Megaptera novaeangliae*) off Northeastern Brazil. **Journal of Cetacean Research Manager,** v. 6, n. 1, p. 101–107, 2004.

_____. Migration and summer destinations of humpback whales (*Megaptera novaeangliae*) in the western South Atlantic Ocean. **Journal of Cetacean Research Manager,** v. 3, n. Special Issue, p. 113–118, 2011.

_____. Satellite-monitored movements of humpback whales *Megaptera novaeangliae* in the Southwest Atlantic Ocean. **Marine Ecology Progress Series,** v. 313, p. 295–304, 2006.

# CAPÍTULO 1:

# LOW LATITUDE HABITAT USE PATTERNS OF A RECOVERING POPULATION OF HUMPBACK WHALES

# PADRÕES DE USO DE HABITAT DE BAIXA LATITUDE DE UMA POPULAÇÃO DE BALEIAS-JUBARTE EM RECUPERAÇÃO

## RESUMO

A costa do Brasil é uma importante área de berçário para a baleia-jubarte (*Megaptera-novaeangliae*) em baixas latitudes. O número de baleias-jubarte na região tem aumentado nos últimos anos e a sua população tem reocupado áreas que foram devastadas na época de caça à baleia. O objetivo deste estudo foi realizar o monitoramento visual através de ponto fixo em 2014 e 2015 para caracterizar padrões de uso de habitat e abundância das baleias-jubarte que migram para uma dessas áreas de reocupação: Serra Grande, estado da Bahia. O tamanho médio de grupo observado foi de 2,12 ± 0,96 indivíduos e não variou ao longo da temporada nem entre os anos. As duplas (32,23%) e os animais solitários (26,71%) foram os grupos mais observados, e os grupos de mãe com filhote representaram 21,23% das avistagens. O número médio de baleias aumentou de 2014 para 2015. O uso de habitat variou ao longo da temporada. As baleias foram permanecendo em águas mais rasas perto da costa ao longo da temporada. A distribuição espacial dos grupos com filhotes foi dependente da presença e número de escortes. A segregação espacial dos grupos com filhotes mais perto da costa foi um fator chave para perceber a distribuição das baleias na área, sugerindo que as estratégias sociais são afetadas por fatores ambientais como observado em outras áreas de reprodução. Estudos em pequena escala a partir de ponto fixo, em áreas onde falta informação sobre a ocorrência da espécie, são economicamente viáveis. Eles dão informações sobre padrões comportamentais e espaciais gerais da distribuição da espécie, enquanto a ocorrência de atividades antrópicas ainda é baixa, permitindo uma melhor proteção do habitat e tomada de decisões de gestão, quando a implementação de atividades humanas é planejada.

Palavras-chave: Baleia-jubarte. Distribuição. Ocorrência. Ponto fixo. Profundidade. Uso de habitat.

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Running head: Habitat use patterns of humpback whales

**Low latitude habitat use patterns of a recovering population of humpback whales**

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**Abstract**

The coast of Brazil is an important low latitude nursery ground for humpback whales (*Megaptera novaeangliae*). The number of humpback whales in this region has increased and its population is reoccupying areas where it has been depleted during the whaling period. The goal of this study was to conduct land-based observations in 2014 and 2015 to characterize patterns of habitat use and abundance of humpback whales that migrate to one of these reoccupation areas: Serra Grande, Bahia state. The observed mean group size was 2.12 ± 0.96 individuals and did not vary along the reproductive season nor between years. Dyads (32.23%) and singletons (26.71%) were more frequently observed and groups with calves represented 21.23% of the sightings. The mean number of whales increased from 2014 to 2015. Habitat use varied along the season; whales used shallower waters closer to shore as the season progressed. The spatial distribution of groups with calves was dependent on the presence and number of escorts. Spatial segregation of groups with calves closer to shore is a key factor in understanding the overall distribution of whales in the area, suggesting that social strategies are affected by environmental factors as seen in other wintering grounds. Small-scale studies from land-based station, in areas where there´s no previous knowledge about the species, such as this are cost effective. It provides information about the overall behavioural and spatial patterns while the anthropogenic activity is still low, allowing habitat protection and management decisions before implementation and increase of human activities.

**Keywords:** humpback whale, land-based observation station, habitat use, distribution, depth, occurrence

INTRODUCTION

Humpback whales (*Megaptera novaeangliae*, Borowski 1781) have characteristic temporal and spatial migratory patterns that enable the species to take advantage of the great productivity of high latitude waters feeding during the austral summer, and breeding and calving in low latitudes during the winter months. Low latitude warmer and more protected waters (Clapham, 2000) with low predation risk (Corkeron & Connor, 1999) are thought to enhance the chances of survival of humpback whale new-born calves.

The population that migrates to the Brazilian coast between July and November (Martins *et al.*, 2001) is part of the breeding stock A (IWC, 2005). This population feeds off South Georgia and Sandwich Islands (Zerbini *et al.*, 2006; Engel & Martin, 2009; Zerbini *et al.*, 2011) which are approximately 4000 km apart from the breeding areas (Stevick *et al.*, 2006).

The number of humpbacks that migrate to Brazil is increasing (Freitas *et al.*, 2004; Andriolo *et al.*, 2010; Bortolotto *et al.*, 2016). For years, all research efforts were focused in the Abrolhos region (Martins *et al.*, 2001; Morete *et al.*, 2003), which continues to be the major concentration area (Andriolo *et al.*, 2006; Andriolo *et al.*, 2010). However, the species occurs along the entire north-eastern coast of Brazil (Zerbini *et al.*, 2004; Lunardi *et al.*, 2008) and the population shows a significant expansion northern of Abrolhos, reoccupying breeding areas (Rossi-Santos *et al.*, 2008; Andriolo *et al.*, 2010) used before the whaling period (Morais *et al.*, 2016). Surveys carried out between 2002 and 2005 showed a gradual increase in the Brazilian population reaching 6404 individuals in 2005 (Andriolo *et al.*, 2010). Bortolotto *et al.* (2016) had estimated 19429 humpback whales in 2012, while Pavanato *et al.* (2017) had estimated 12123 individuals in 2015 using different methodologies in a larger study area. The IUCN (International Union for the Conservation of Nature) has changed the species status from 'vulnerable' to 'least concern' (IUCN, 2013) due to the increase in size of most humpback whale populations worldwide.

Zerbini *et al.* (2004) surveyed the northeast of Brazil and found most humpback whale sightings to occur within 50 m of depth, which normally is associated with proximity to the coastline. Winter coastal distribution (Dawbin, 1956; Clapham, 2000) associated with islands and reef systems (Clapham, 2009) is common in many humpback whale populations. Females with calves occur even closer to shore in shallower and more protected waters (Whitehead & Moore, 1982; Smultea, 1994; Ersts & Rosenbaum, 2003).

In Brazilian coast, previous study mainly occurred on two regions: the Abrolhos Bank and Praia do Forte northern Bahia state. There´s a gap of knowledge about the species between

these two regions, where our study site is located, in the middle between Itacaré and Ilhéus, and where few anthropogenic activities currently occur. The region is unexplored except for a few boat-based surveys that reached the area (Rossi-Santos *et al.*, 2008; Baracho-Neto *et al.*, 2012). The presence of whales close to shore and the shore line features, with an elevated point, allowed observations from land-based station (Würsig *et al.*, 1991). This research methodology has been applied to study humpback whale for two decades in Abrolhos Archipelago (Morete *et al.*, 2003; Morete *et al.*, 2008), which is a unique environment when compared to other regions along the coast.

Between 2002 and 2005, during aerial surveys aiming humpback whale population estimates along Brazilian Coast, the Itacaré/Ilhéus region has indicated densities between 0.010 and 0.026 individuals per km$^2$ while Abrolhos Bank presented 0.028 and 0.091 individuals per km$^2$ (Andriolo *et al*., 2010). Is Itacaré/Ilhéus region as important as Abrolhos Bank for humpback whale breeding activities? Would the habitat use of these two areas with distinct geographically and geomorphological characteristics be different? Our aim in this study was to characterize patterns of relative abundance and habitat use throughout the season in Itacaré/Ilhéus region from a land-based station located at Serra Grande. Social strategies used during the reproductive season and other unknown aspects of humpback whales' distribution in this region will provide information to support better habitat protection and other management decisions.


## MATERIALS AND METHODS


**Study Site**

Data were collected from the highest point of Serra Grande (14°28'30" S; 39°01'50" W), approximately 34 km North from the city of Ilhéus, southern Bahia state, north-eastern Brazil (Figure 1). The land-based station is located 315 m from the coastline and elevated 93 m from the mean sea level. We considered a radius of 14 km from the observation point to define the study area between 70 and 184° degrees (True) covering 195.63 km$^2$. The orientation of the coastline, and the existence of vegetation and rocks block the monitoring of the northeast of the area.
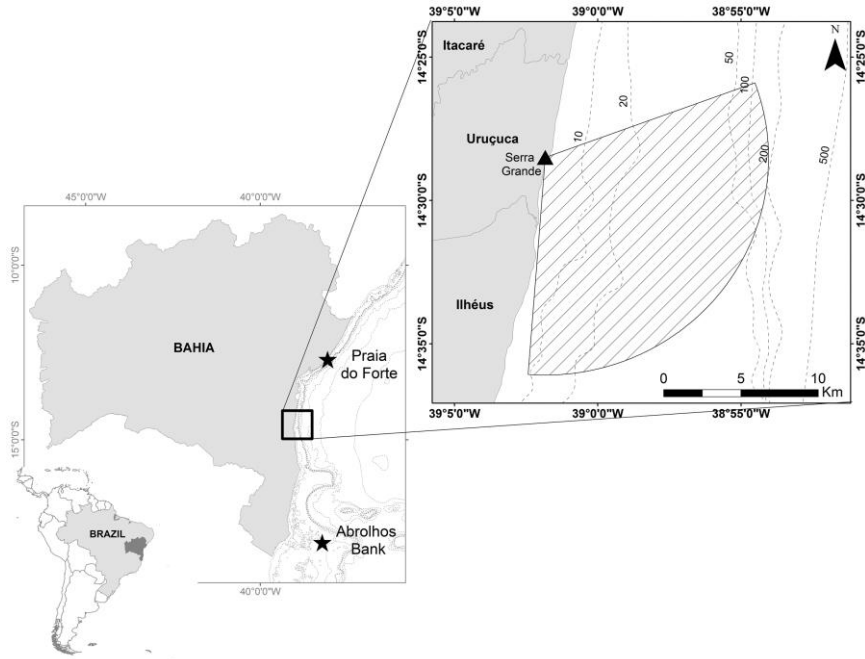
**Fig. 1**. Serra Grande study site located in north-eastern Brazil where a land-based observation station elevated 93 m was used to conduct visual surveys that covered an area of 195.63 km$^2$ (striped area).

The region's ocean floor is predominantly made of rocks and sand (Freire & Dominguez, 2006). Mean water temperature varies along the year between 24 and 29ºC (NOAA, 2016).

**Visual Surveys**

Observations were made between July and October in 2014 and 2015. Data collection was conducted during the daytime between 07:20 am and 04:05 pm following survey method (Mann, 1999) of one hour duration (Morete *et al.*, 2007; Morete *et al.*, 2008). Morning and afternoon surveys were done when weather conditions allowed satisfactory visibility and when sea state was below or equal Beaufort 4. The mean interval between surveys was 3.22 h (s.d.=0.68) allowing that the observed groups were not present in the area by the time of the second survey leading to sample independence (Frankel & Clark, 2002).

Each survey was conducted by 2 or 3 dedicated observers and active search done with naked eye and binoculars 7x50. Whales were located based on presence cues such as blows, water splash from aerial behaviours, or exposure of a body part (Morete *et al.*, 2008). When a group of whales was sighted, the main observer (same person throughout the study) tracked and monitored the group using a total station TOPCON ES105 with 5' of precision and 30-power monocular magnification until the location angle, size, composition, and behaviour of the

group was identified (Morete *et al.*, 2008). Meanwhile, the other observers kept monitoring the area searching for other whale groups.

In order to avoid counting groups twice, if there was any doubt about the discrimination of sighted groups during a survey, the effort was interrupted and the ongoing survey would be cancelled and another one started (Morete *et al.*, 2008). At the start and end of each survey and any time conditions changed, wind direction, cloud cover and Beaufort Sea state were registered by the main observer.


**Definitions**

A group was defined as a single or several individuals moving in coordination towards the same general direction and no more than 100 m apart from each other (Whitehead, 1983; Morete *et al.*, 2008).

Group composition categories were defined as a) mother with calf (MOC), b) mother and its calf accompanied by an escort (MOCE), c) mother and its calf accompanied by two or more escorts (MOCE/+), and in the absence of a calf, group definitions were based on the number of individual whales d) solitary (1AD), when a lone adult was observed, e) two adults (dyad) or f) more than two adults (multiple) (Morete *et al.*, 2007; Dunlop *et al.*, 2008). When it was not possible to determine the composition, the group was identified as "undetermined". The distance to the sightings did not allow the discrimination of juveniles, therefore we considered only two age classes: adults and calves, the later identified as such when its length was up to 50% that of an adult (Chittleborough, 1953).


**Spatial Analyses**

The total station TOPCON ES105 allows measurement of horizontal angles between two points, a known reference point and the target object, and also the vertical angle between the target object and the observer (Gailey & Ortega-Ortiz, 2002; Bailey & Lusseau, 2004). Total station and reference point UTM (Universal Transverse Mercator) coordinates were determined by GNSS (Global Navigation Satellite System) positioning, with millimetric precision. Orthometric altitudes of these points were determined using Geoidal MAPGEO 2010 model (Monico, 2008). These point locations added to the height of the installed total station and tidal variation allowed calculations of UTM (E, N) coordinates of all points measured using trigonometric equations (Santos, 2010). Errors due to Earth curvature (Vanicek & Krakiwsky, 1996) were corrected by transforming the horizontal distances to spherical distances.

Depth at the locations where groups where sighted were obtained using ARCGIS 9.3 Extraction tool of the Spatial Analyst using bathymetric information constructed from vectorization of nautical charts 1200 and 2105 from the Brazilian Navy (CHM, 2011-2015) followed by interpolation of depth values using ordinary kriging geostatistical analyses (Childs, 2004). Distance to coastline was calculated through the distances between the meridians of the position of the sighted group and the coast using Google Earth in order to acquire more precise values given the high resolution mapping and detailed images of the coast.

**Statistical Analyses**

GROUPS

In order to verify how group size varied in the area throughout the season, we considered only the data from groups which size and composition were determined with confidence. A generalized linear model (GLM) was used to fit the group size data into a Poisson distribution. Year and Julian day were used as predictors of group size.

ABUNDANCE

Because of the fluctuation of relative whale abundance between seasons (Morete *et al.*, 2008), the peak of each season was calculated using a segmented regression (Muggeo, 2008) of the whale counts per survey. The seasons were divided into three periods (initial, middle, and final) and the peak of the season was the centre of the middle period. Due to the lack of normality of the distribution, we used a Mann-Whitney U test to verify if hourly whale counts changed between the sampled years (2014 and 2015). A GLM was used to fit the number of whales sighted per hour (number of adults and calves separately) into a Poisson distribution and test if it changed as the season progressed. The model to explain adult relative abundance included year and lunar phase (4 categories considered by NOAA) as categorical predictors and, Julian days and sea state (Beaufort 1 to 4) as continuous predictor variables, as well as the interaction between the variables: year and Julian days. The model to explain calf abundance also included number of adults as a predictor variable. The number of individuals considered in undetermined groups was the maximum number of sighted animals to avoid underestimation of the total number of whales in such cases. The residuals and the residual variation were verified to ensure that the models were adequate with respect to the premises.

HABITAT USE

An ANOVA followed by a Tukey honest significant difference (HSD) test was used to verify if whale group´s mean distance to coast and depth were different among periods of the season.

Spatial distribution of groups in the sampled area along the season was mapped as Kernel densities using Hawth's Tools developed as an extension of ArcGIS (Beyer, 2004). We used default values for the parameters within this tool and the band (h) was defined as 1.0 km to smooth over 100x100 m surface cell size using the normal bivariate method. For comparison of the maps among the different periods, the values were normalized to a common scale (0 - 1). Statistical transformation was applied on a logarithmic function that rescaled the values maintaining the original form of distribution. We used t Tests to verify if distance to coast and depth were different between groups with and without calves. Within groups with calves, such differences were tested between MOC, MOCE and MOCE/+ using ANOVA. Mother and calf groups (MOC) was defined as the baseline to verify differences with MOCE and MOCE/+. All statistical analyses were run in R 3.0.2 (R, Development Core Team).

RESULTS

Ninety-three hours of surveys (Table 1) were carried out during 67 days in the field (37 days in 2014 and 30 in 2015). The identification of the number of individuals and age class (adult or calf) in the groups was possible for 146 (67.59%) out of the 216 groups sighted. Adult individuals were the majority (n=278) compared to calves (n=31).

**Table 1.** Number of surveys performed by period of the season from a land-based observation station in 2014 and 2015 in Serra Grande, Bahia state, Brazil.

|      | **Initial** | **Middle** | **Final** |
|------|-------------|------------|-----------|
| 2014 | 18          | 14         | 20        |
| 2015 | 9           | 19         | 13        |

**Groups**

The most common group composition was dyad 32.88% (n=48), followed by solitary individuals 26.71% (n=39) and groups with calves 21.23% (n=31). Groups with 3 or more adults were the least common in the area totalizing 19.18% (n=28) of sightings. Groups with calf were comprised mostly by MOC 61.29% (n=19), MOCE 22.58% (n=7), and 16.13% (n=5) of MOCE/+.

Group size varied from a single individual to 5 whales. Mean group size was 2.12 (s.d.=0.96). Year and day of the season did not affect group sizes (Table 2).

**Table 2.** Generalized Linear Model (Poisson distribution) parameter estimates and p-values for year and Julian day that explained group sizes of humpback whales observed from a land-based observation station in 2014 and 2015 in Serra Grande, Bahia state, Brazil.

|  | **Estimate** | **p-value** |
|---|---|---|
| Intercept | 142.828946 | 0.538 |
| Year | -0.070815 | 0.539 |
| Julian day | 0.002376 | 0.327 |

**Abundance**

Abundance in both 2014 and 2015 seasons was characterized by a segmented distribution with the break point between the end of August and beginning of September (Figure 2). The peak for 2014 was August 23rd and for 2015, September 04th. The segmented regression model was significant ($p<0.001$) and the regression coefficient was positive for the first half and negative for the second half. Adult hourly abundance pooled for both years varied from 0 to 14 and calves from 0 to 4 individuals. The maximum hourly abundance (17 individuals) was observed in the beginning of September 2015.
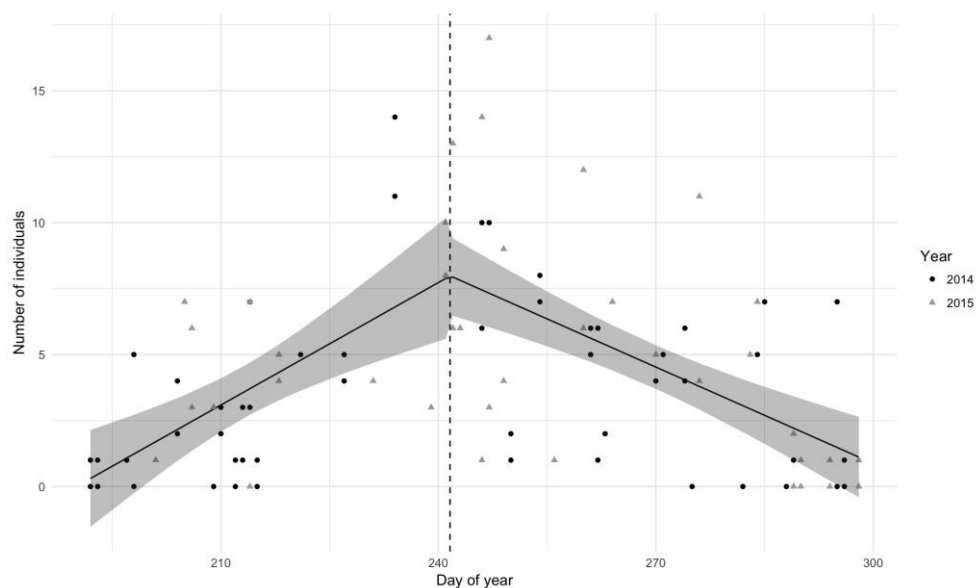


**Fig. 2.** Hourly number of humpback whales observed in Serra Grande (Bahia state, Brazil) along the Julian days in 2014 (dots) and 2015 (triangles) with the segmented regression 95% confidence interval model showed in grey.

In 2015, the mean number of individuals per hour (n=5.12, s.d.=4.18) was significantly greater (W=809, $p<0.05$) than in 2014 (n=3.44, s.d.=3.35). This difference was due to the higher number of adults observed per hour (W=813, $p<0.05$) in 2015 (n=4.68, s.d.=3.74)

when compared to adult numbers in 2014 (n=3.19, s.d.=3.13). The number of calves did not change significantly from 2014 to 2015 (W=949, p=0.24) although the absolute counts were higher in 2015 (n=0.44, s.d.=0.8; n=0.25, s.d.=0.52 in 2014).

Based on GLM, adult number was affected by the year (p<0.05) and lunar phase. The full moon was considered as the baseline lunar phase in the model and there were significantly fewer adults in the area during the new moon (p<0.001) and last quarter (p<0.01) but no significant difference was verified during the first quarter (p=0.33). The interaction between Julian day and year also influenced the adult numbers (p<0.05); different peaks in adult abundance occurred between the years and a sharper decrease in the adult numbers beginning in the end of September was observed for 2015 when compared to 2014. Sea state did not affect adult humpback whale abundance (Table 3).

**Table 3.** Parameter and p-values estimated using a Generalized Linear Model with Poisson distribution that explained adult relative abundance observed from a land-based observation station in 2014 and 2015 in Serra Grande (Bahia state, Brazil). Predictor variables were: year, Julian day, sea state (Beaufort), lunar phase and the interaction between Julian day and year.

| | **Estimate** | **p-value** |
|---|---|---|
| Intercept | 0. 762771 | 0. 21979 |
| Year2015[1] | 2. 245929 | 0. 01161 * |
| Julian day | 0. 001787 | 0. 45461 |
| Sea state | 0. 108550 | 0. 09855 |
| First quarter[2] | -4.430749 | 0. 00268 ** |
| Last quarter[2] | -0. 141395 | 0. 33329 |
| New moon[2] | -0. 700321 | 0.00002 *** |
| Year2015[1]*Julian day | -0. 007732 | 0. 03253 * |

Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 ' ' 1

[1]Difference from 2014

[2]Difference from Full moon

Number of calves was positively affected by the Julian day (p<0.01) and by the number of adults (p<0.001). Year, lunar phase and sea state did not affect the number of calves (Table 4).

**Table 4.** Parameter and p-values estimated using a Generalized Linear Model with Poisson distribution that explained calf relative abundance observed from a land-based observation station in 2014 and 2015 in Serra Grande. Predictor variables were: year, Julian day, sea state (Beaufort), lunar phase, number of adults and the interaction between Julian day and year.

|  | Estimate | P-value |
|---|---|---|
| Intercept | -11.21738 | 0.00368 ** |
| Year2015[1] | 3.93766 | 0.37122 |
| Julian day | 0.03663 | 0.00644 ** |
| Sea state | -0.43180 | 0.07253 |
| First quarter[2] | 0.52168 | 0.35213 |
| Last quarter[2] | 0.16947 | 0.76678 |
| New moon[2] | -0.15624 | 0.83201 |
| Adults | 0.24152 | 0.00001 *** |
| Year2015[1]*Julian day | -0.01379 | 0.40563 |

Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 ' ' 1

[1]Difference from 2014

[2]Difference from Full moon

**Habitat Use**

Depth increases as a function of distance from the coast and after 11 km this effect is higher (Figure 3). The majority of humpback whale groups (90.27%) were sighted in waters with less than 50 m of depth and 67.57% up to 10 km away from the coast. Mean values of distance to coast gradually decreased along the season (F=22.22, d.f.=139, p<0.001; Table 5, Figure 4) and were significantly different between initial and middle periods (p<0.01) and between initial and final periods (p<0.001), but not significant between middle and final periods (p=0.07). Similarly, mean depth values varied among periods (F=23.08, d.f.=139, p<0.001; Table 5), decreasing as the season progressed, being significantly different between the initial and middle periods (p<0.001) and between initial and final periods (p<0.001). No significant differences in mean depth of humpback whale sightings were observed between middle and final periods of the season (p=0.23).
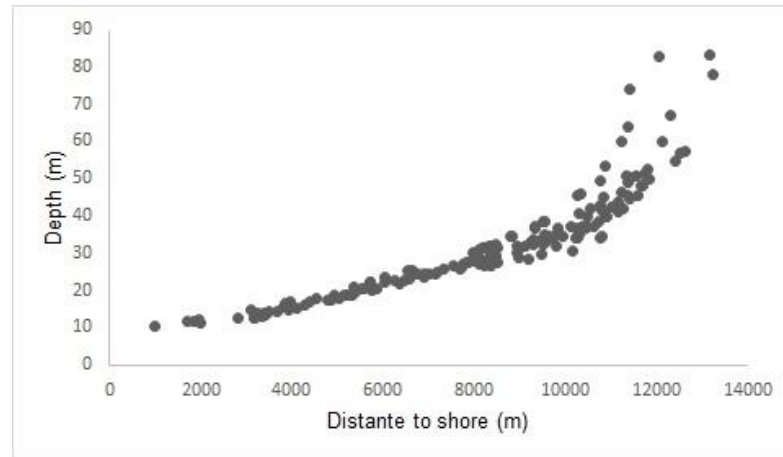
**Fig. 3.** Relationship between distance to coast and depth of humpback whale groups sighted from a land-based observation station in 2014 and 2015 in Serra Grande, Bahia state, Brazil.

**Table 5.** Descriptive statistics (mean ± standard deviation) for distance to coast and depth values of humpback whale groups sighted from a land-based observation station in Serra Grande (Bahia state, Brazil) per periods of the season (initial, middle, final) in the years 2014 and 2015.

|  | **Initial** | **Middle** | **Final** |
|---|---|---|---|
| Distance to coast (km) | 10.10 ± 2.12 | 7.98 ± 2.70 | 6.76 ± 2.97 |
| Depth (m) | 41.55 ± 13.93 | 29.79 ± 11.58 | 25.74 ± 11.87 |
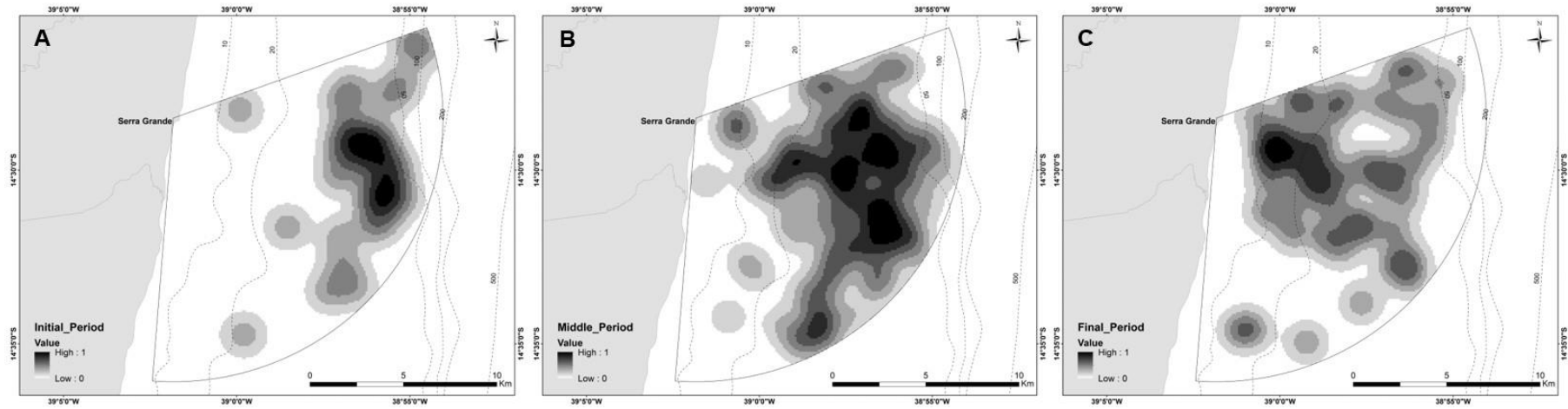
**Fig. 4.** Kernel density maps of all groups of humpback whales sighted in 2014 and 2015 from a land-based observation station at Serra Grande (Bahia state, Brazil) divided by periods of the season: (A) initial; (B) middle; (C) final.

Mean values for distance to coast were significantly greater (t=5.2019, d.f=39.588, p<0.001) for groups without calves (8.78 ± 2.33 km) than for groups with calves (5.58 ± 3.19 km). Within groups with calves, the distances where each group type were sighted were significantly different (F=7.161, d.f=29, p<0.05). Groups of MOC were sighted significantly closer to the coast than MOCE/+ (p<0.05) but no significant differences between MOC and MOCE (p=0.08) were found (Table 6).

**Table 6.** Mean and standard deviation of distance from coast and depth of the humpback whale groups with calves observed in 2014 and 2015 in Serra Grande, Brazil (MOC = mother and calf, MOCE = mother and calf and one escort, MOCE/+ = mother and calf and two or more escorts).

| | Distance to coast (km) | Depth (m) |
|---|---|---|
| MOC | 4.47 ± 2.71 | 17.72 ± 7.85 |
| MOCE | 6.76 ± 3.41 | 28.80 ± 18.44 |
| MOCE/+ | 8.15 ± 3.04 | 31.12 ± 12.06 |

We found significant differences in mean depth of groups with and without calves (t=4.3084, d.f=47.079, p<0.001). Groups with calves were in shallower waters (22.38 ± 12.67 m) than groups without calves (33.41 ± 12.28 m). Also, there were significant difference in the mean depth of sightings of the different types of groups with calves (F=8.265, d.f=29, p<0.05): MOC were sighted in shallower waters than MOCE (p<0.05) and MOCE/+ (p<0.05) (Table 6).

DISCUSSION

This is a pioneer study describing the habitat use patterns of humpback whales in Serra Grande coastal low latitude habitat. Description of baseline habitat use patterns in coastal areas while there´s low level of human disturbance are essential to humpback whale conservation, in particular where overlap with human activities may occur in the future, as the construction of a new port in the region (BAMIN, 2011).

**Group characteristics**

Mean humpback whale group size in Serra Grande was similar to those observed in other calving areas such as Abrolhos in Brazil (Martins *et al.*, 2001), the West coast of South Africa (Barendse *et al.*, 2010), Ecuador (Scheidat *et al.*, 2000; Félix & Haase, 2001) and East coast of Australia (Franklin *et al.*, 2011). We did not observe variation in group sizes along the season nor between the two sampled years as also occurred in Abrolhos (Morete *et al.*, 2007). Nonetheless, in Hawai'i (Baker & Herman, 1984) and in Ecuador (Félix & Haase, 2001), group sizes tend to increase as the season progresses due to an increase in mature male densities searching for receptive females in competitive groups. Each population might have different social strategies depending on site-specific contexts or even on culture.

The proportions of group composition observed are identical to the areas surveyed North of Serra Grande (Lunardi *et al.*, 2008; Rossi-Santos *et al.*, 2008). The proportion of groups with calves is much smaller in Serra Grande (21%) than around the Abrolhos Archipelago (48%) (Morete *et al.*, 2007), which is inserted in the main calving ground for the population that migrates to Brazil. Also the proportion of mother-calf pairs escorted by a single adult (MOCE) was much higher in Abrolhos (Morete *et al.*, 2007), and may be related to the geomorphological characteristics as further discussed.

**Abundance patterns**

It is not surprising that the number of whales sighted has increased from 2014 to 2015 since the population stock A has raised in the last years (Andriolo *et al.*, 2010; Bortolotto *et al.*, 2016).

The peak of the season varied between years; in 2015, it was 12 days later than 2014, nevertheless there was a drastic decrease in abundance in late September in 2015. These temporal fluctuations in relative abundance have been observed in other humpback whale reproductive areas (Baker & Herman, 1981; Corkeron *et al.*, 1994; Mattila *et al.*, 1994; Frankel & Clark, 2002; Morete *et al.*, 2008) and may be related to migratory triggers in low and high latitudes. Dawbin (1966) suggests that photoperiod plays a role in migratory timing in high latitudes. Sea surface temperature (Nishiwaki, 1959) and food resource availability in the previous summer (Craig *et al.*, 2003) are thought to be the most important factors that trigger humpback whale migration to the feeding grounds (Abras, 2014). The fat layer accumulated from summer feeding prior to migration to low latitudes would limit the permanence of individuals in their reproductive areas (Craig *et al.*, 2003). In Brazilian waters, the "*El Niño*" phenomenon caused an increase in the sea surface temperature in 2015 (NOAA,

2016). The temperature rise started in August 2015 and could have anticipated the return of humpback whales to Antarctica, explaining the sharp decrease in abundance after the peak of the 2015 season.

Highest and peak adult abundances coincided with full and last quarter lunar phases. Lunar phase affects when males are more likely to sing along the day in Abrolhos (Sousa-Lima & Clark, 2008). In Angola, lunar phase affects the relative abundance of singers (Cerchio *et al.*, 2014), where the authors detected fewer singers in full moon than in new moon. Humpback whale singers are often characterized by slow moving individuals (Tyack & Whitehead, 1983; Spitz *et al.*, 2002; Noad & Cato, 2007) and thus less likely to be detected by visual surveys (Noad & Cato, 2007) when compared to passive acoustic monitoring (Frankel *et al.*, 1995; Noad & Cato, 2007). One of the possible reasons for differences in number of whales counted by us during the new moon could be that the behaviour of singing males makes them harder to be detected from a land-based observation station, and we might have underestimated the number of adults by missing singers during the new moon. Alternatively, maybe the song keeps other acoustic competitors further away, consequently leading to the presence of a smaller number of individuals, or the low densities lead to males singing more to attract females. Studies on the abundance of singers in the area may elucidate these facts.

The number of calves rise throughout the season, the same pattern observed in Abrolhos, where the number of calves varied with the number of adults and the Julian day (Morete *et al.*, 2003). Surprisingly, the number of calves did not increase from 2014 to 2015, different from what was observed for adults. Morete *et al.* (2008) surveyed the Abrolhos Archipelago for seven years, and noted an increase in the number of adults but the number of calves remained the same, and only increased significantly in the last year sampled. During the same years, Morete *et al.* (2007) did not find evidence that the number of adults in the groups observed in Abrolhos increased along the years, concluding that females with calves could be using different areas or that the number of calves would be the result of falling birth rates. Clapham (1996) suggests that reproductive rates may be affected by food availability, as also proposed by Seyboth *et al* (2016) for reproductive success of the southern right whales. Therefore, the constant number of calves observed between 2014 and 2015 could be a result of lower food availability in 2014/2015 summer feeding ground or a change in preferred calving area by females in 2015.

Bad weather conditions that result in high sea state levels (Beaufort scale) may reduce whale detection probability (Corkeron *et al.*, 1994). Nonetheless, when observations were restricted to sea state up to Beaufort level 4, the number of adults and the number of calves sighted in

Serra Grande were not affected. Smultea (1994) had a limit for data collection of up to Beaufort 3 and also did not verify any effect in detection due to sea state. Frankel & Clark (2002) verified that the sighting rate was negatively affected by the sea state when working up to Beaufort 6, and noted this effect was particularly salient in offshore areas. There is a trade-off between the amount of data collected (considering higher sea state levels) and quality and reliability of sightings (missed detections).

**Social organization and habitat use**

Distribution of whales varied throughout the season, with groups using waters closer to the coast as the season progresses as also observed in Western Australia by Jenner *et al.* (2001), who suggested that the migratory route from the feeding areas to that calving ground would be further away from the coast and the path back to the feeding ground would be closer to the coast. The same pattern may be occurring off Serra Grande. Also, another reason that could explain this approximation is the spatial segregation of groups with and without calves that was identified in Serra Grande. The increase in the number of calves after the peak of the season affected the groups to stay closer to the coast as the season progressed.

Coastal areas, such as Serra Grande, where the shelf break is relatively closer to shore and depth changes abruptly lead to more concentration of mother and calf groups than areas where depth varies gradually, such as off islands and archipelagos. In Serra Grande, the difference in mean depth between the sightings of groups with and without calves is around 10 m, and in Abrolhos is smaller than 5 m (Martins *et al.*, 2001), where mean depth is 30 m, perhaps allowing escorts to have easier access to mothers and calves. Different habitat conditions along the distribution of humpback whales in Brazil may lead to differences in habitat use and social organization as observed in other populations (Félix & Botero-Acosta, 2011).

Groups with calves occupying shallower waters closer to shore is considered a social strategy (Ersts & Rosenbaum, 2003). Mothers could be protecting their calves against harassment from males trying to mate with them (Smultea, 1994), which may cause injury to the newly born calves (Baker & Herman, 1984) and higher energy costs for both mother and calves (Cartwright & Sullivan, 2009; Craig *et al.*, 2014). Parental care could also explain why mothers remain closer to shore in shallow waters where there are fewer predators (Smultea, 1994), less turbulence (Whitehead & Moore, 1982) and depth would limit the approach and manoeuvre of males (Ersts & Rosenbaum, 2003; Bruce *et al.*, 2014). However, females with calves may allow the presence of an escort during transit in areas where they would be exposed to deeper less protected waters (Ersts & Rosenbaum, 2003). An escort may offer

protection to the mother-calf pair (Herman & Antinoja, 1977), which was evidenced by the observations of escorts defending calves from predator attacks (Pitman *et al.*, 2015), acting as bodyguards (Mesnick, 1996; Wilson & Mesnick, 1997; Cartwright & Sullivan, 2009), or even protection from other males attempting to mate.

Groups with calves escorted by adults occur in deeper waters (Betancourt *et al.*, 2014; MacKay *et al.*, 2016) and in Serra Grande, as the number of escorts goes up, distances from shore increase. Craig *et al.* (2014) and Félix & Botero-Acosta (2011) observed similar results and suggest that water depth not only limits the association of escorts to mother-calf pairs but would also limit the movement of courting males. Bigger groups with calves would be comprised of inexperienced mothers that are unable to avoid being joined by multiple escorts (Elwen & Best, 2004). Distance to coast and water depth are environmental factors that explain the distribution of humpback whale groups, thus our results support the interaction between environmental constraints and social organization proposed for the species (Félix & Botero-Acosta, 2011).

**Conclusion**

Serra Grande has a lower percentage of groups with calves compared to Abrolhos but this percentage is comparable to other reproductive grounds (Ersts & Rosenbaum, 2003; Rasmussen *et al.*, 2011). Habitat use patterns also support the notion that this is a calving area because of the characteristic increase in the abundance of calves as the season progresses. As populations recover, the presence of humpback whale in other low latitude areas tend to expand. The importance of Serra Grande as a calving area will probably increase given the uniqueness of this site in having the shortest distance to the shelf break in Brazil (Prates *et al.*, 2012), allowing humpback whales to concentrate very near to the coast. It is noteworthy that despite being a small-scale study, we observed the same pattern verified in larger scale studies (Zerbini *et al.*, 2004) and reinforces this general pattern for humpback whales off Brazil. Land-based platforms in high altitude stations are cost effective and representative of habitat use patterns. These local efforts throughout the area of occurrence may reveal which environmental factors better explain humpback whale distribution and abundance on a larger scale. Inasmuch, decision making about the creation of protected areas (Andriolo *et al.*, 2010) and the implementation of human activities at sea will be supported by robust knowledge of site-specific abundance patterns avoiding potential problems such as collisions with vessels (Redfern *et al.*, 2013) and site abandonment (Jones & Swartz, 2009). Additionally, the general public can profit from touristic activities by experiencing land- or boat-based whale watching.

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## REFERENCES

**Abras D.R.** (2014) *Efeito de parâmetros ambientais na migração de baleias-jubarte (Megaptera novaeangliae) entre Mar de Scotia e Banco dos Abrolhos*. MSc Thesis. Universidade de São Paulo, São Paulo, Brazil.

**Andriolo A., Kinas P.G., Engel M.H., Martins C.C.A. and Rufino A.M.** (2010) Humpback whales within the Brazilian breeding ground: distribution and population size estimate. *Endangered Species Research* 11, 233–243.

**Andriolo A., et al.** (2006) The first aerial survey to estimate abundance of humpback whale (*Megaptera novaeangliae*) in the breeding ground off Brazil (Breeding Stock A). *Journal of Cetacean Research and Management* 8, 307-311.

**Bailey H. and Lusseau D.** (2004) Increasing the precision of theodolite tracking: modified technique to calculate the altitude of land-based observations sites. *Marine Mammal Science* 20, 880–885.

**Baker C.S. and Herman L.M.** (1981) Migration and local movement of humpback whales (*Megaptera novaeangliae*) through Hawaiian waters. *Canadian Journal of Zoology* 59, 460-469.

**Baker C.S. and Herman L.M.** (1984) Aggressive behavior between humpback whales (*Megaptera novaeangliae*) wintering in Hawaiian waters. *Canadian Journal of Zoology* 62, 1922-1937.

**BAMIN** (2011) Relatório de Impacto Ambiental Porto Sul. *Bahia Mineração Ltda.*, 118 pp.

**Baracho-Neto C.G., et al.** (2012) Site fidelity and residence times of humpback whales (*Megaptera novaeangliae*) on the Brazilian coast. *Journal of the Marine Biological Association of the United Kingdom* 92, 1783-1791.

**Barendse J., Best P.B., Thornton M., Pomilla C., Carvalho I. and Rosenbaum H.C.** (2010) Migration redefined? Seasonality, movements and group composition of humpback whales *Megaptera novaeangliae* off the west coast of South Africa. *African Journal of Marine Science* 32, 1–22.

**Betancourt L., Herrera-Moreno A. and Beddall K.** (2014) Spatial distribution of humpback whales (*Megaptera novaeangliae*) in Samaná Bay, Dominican Republic. *Journal Cetacean Research Manager* SC/64/O12, 1-10.

**Beyer H.L.** (2004) Hawth's Analysis Tools for ArcGIS. Available in: http://www.spatialecology.com/htools. Acesso em: 02/07/2010.

**Bortolotto G.A., Danilewicz D., Andriolo A., Secchi E.R. and Zerbini A.N.** (2016) Whale, Whale, Everywhere: Increasing Abundance of Western South Atlantic Humpback Whales (*Megaptera novaeangliae*) in Their Wintering Grounds. *PLoS ONE* 11, e0164596.

**Bruce E., Albright L., Sheehan S. and Blewitt M.** (2014) Distribution patterns of migrating humpback whales (*Megaptera novaeangliae*) in Jervis Bay, Australia: A spatial analysis using geographical citizen science data. *Applied Geography* 54, 83-95.

**Cartwright R. and Sullivan M.** (2009) Associations with multiple male groups increase the energy expenditure of humpback whale (*Megaptera novaeangliae*) female and calf pairs on the breeding grounds. *Behaviour* 146, 1573-1600.

**Cerchio S., Strindberg S., Collins T., Bennett C. and Rosenbaum H.** (2014) Seismic Surveys Negatively Affect Humpback Whale Singing Activity off Northern Angola. *PLoS ONE* 9, e86464.

**Childs C.** (2004) Interpolating Surfaces in ArcGIS Spatial Analyst. *ESRI Education Services*.

**Chittleborough R.G.** (1953) Aerial observations on the Humpback whale, *Megaptera nodosa* (Bonnaterre), with notes on other species. *Australian Journal of Marine and Freshwater Research* 4, 219-227.

**CHM** (2011-2015) Catálogo de cartas e publicações In 12001/2105001, Niterói: Diretoria de Hidrografia e Navegação, Centro de Hidrografia da Marinha.

**Clapham P.J.** (1996) The social and reproductive biology of Humpback Whales: an ecological perspective. *Mammal Review* 26, 27-49.

**Clapham P.J.** (2000) The Humpback Whale: Seasonal Feeding and Breeding in a Baleen Whale. In Mann J., Connor R.C., Tyack P.L. and Whitehead H. (eds) *Cetacean Societies: Field Studies of Dolphins and Whales.* Chicago: The University of Chicago Press, pp. 173-196.

**Clapham P.J.** (2009) Humpback Whale. In Perrin W.F., Würsig B. and Thewissen J.G.M. (eds) *Encyclopedia of Marine Mammals.* San Diego: Academic Press, pp. 582-585.

**Corkeron P.J., Brown M., Slade R.W. and Bryden M.M.** (1994) Humpback Whales, *Megaptera novaeangliae* (Cetacea : Balaenopteridae), in Hervey Bay, Queensland. *Wildlife Research* 21, 293-305.

**Corkeron P.J. and Connor R.C.** (1999) Why do baleen whales migrate? *Marine Mammal Science* 15, 1228-1245.

**Craig A.S., Herman L.M., Gabriele C.M. and Pack A.A.** (2003) Migratory timing of humpback whales (*Megaptera novaeangliae*) in the Central North Pacific varies with age, sex and reproductive status. *Behaviour* 140, 981-1001.

**Craig A.S., Herman L.M., Pack A.A. and Waterman J.O.** (2014) Habitat segregation by female humpback whales in Hawaiian waters: avoidance of males? *Behaviour* 151, 613–631.

**Dawbin W.H.** (1956) The Migrations of Humpback Whales which Pass The New Zealand Coast. *Transactions. of the Royal Society of New Zealand* 84, 147-196.

**Dawbin W.H.** (1966) The seasonal migratory cycle of humpback whales. In Norris K.S. (ed) *Whales, dolphins, and porpoises.* Berkeley: University of California Press, pp. 145-170.

**Dunlop R.A., Cato D.H. and Noad M.J.** (2008) Non-song acoustic communication in migrating humpback whales (*Megaptera novaeangliae*). *Marine Mammal Science* 24, 613–629.

**Elwen S.H. and Best P.B.** (2004) Environmental factors influencing the distribution of southern right whales (*Eubalaena australis*) on the south coast of South Africa 1: broad scale patterns. *Marine Mammal Science* 20, 567-582.

**Engel M.H. and Martin A.R.** (2009) Feeding grounds of the western South Atlantic humpback whale population. *Marine Mammal Science* 25, 964-969.

**Ersts P.J. and Rosenbaum H.C.** (2003) Habitat preference reflects social organization of humpback whales (*Megaptera novaeangliae*) on a wintering ground. *Journal of Zoology* 260, 337–345.

**Félix F. and Botero-Acosta N.** (2011) Distribution and behaviour of humpback whale mother–calf pairs during the breeding season off Ecuador. *Marine Ecology Progress Series* 426, 277–287.

**Félix F. and Haase B.** (2001) The humpback whale off The Coast of Ecuador, population parameters and behavior. *Revista de Biología Marina y Oceanografía* 36, 61 – 74.

**Frankel A., Clark C.W., Herman L.M. and Gabriele C.M.** (1995) Spatial distribution, habitat utilization, and social interactions of humpback whales, *Megaptera novaeangliae*, off Hawai's, determined using acoustic and visual techniques. *Canadian Journal of Zoology* 73, 1134-1146.

**Frankel A.S. and Clark C.W.** (2002) ATOC and other factors affecting the distribution and abundance of humpback whales (*Megaptera Novaeangliae*) off the North shore of Kauai. *Marine Mammal Science* 18, 644-662.

**Franklin T., Franklin W., Brooks L., Harrison P., Baverstock P. and Clapham P.J.** (2011) Seasonal changes in pod characteristics of eastern Australian humpback whales (*Megaptera novaeangliae*), Hervey Bay 1992–2005. *Marine Mammal Science* 27, 134–152.

**Freire A.F.M. and Dominguez J.M.L.** (2006) The holocene sequence of the central continental shelf of the State of Bahia, Brazil. *Boletim Geociências Petrobras* 14, 247-267.

**Freitas A.C., Kinas P.G., Martins C.C.A. and Engel M.H.** (2004) Abundance of humpback whales on the Abrolhos Bank wintering ground, Brazil. *Journal of Cetacean Research and Management* 6, 225-230.

**Gailey G. and Ortega-Ortiz J.G.** (2002) A note on a computer-based system for theodolite tracking of cetaceans. *Journal of Cetacean Research and Management* 4, 213–218.

**Herman L.M. and Antinoja R.C.** (1977) Humpback Whales in the Hawaiian Breeding Waters: Population and Pod Characteristics. *Scientific Reports of the Whales Research Institute,* no. 29, 59-85 pp.

**IUCN** (2013) The IUCN Red List of Threatened Species. *Version 2013.1.* vol. 2013.

**IWC** (2005) Report of the Scientific Committee. Annex H - Report of the sub-committee on other southern hemisphere whale stocks. *Journal of Cetacean Research and Management* 7, 235-246.

**Jenner K.C.S., Jenner M.-N.M. and McCabe K.A.** (2001) Geographical and temporal movements of humpback whales in Western Australian waters. *APPEA Journal*, 749-765.

**Lunardi D.G., Engel M.H. and Macedo R.H.F.** (2008) Behavior of humpback whales, *Megaptera novaeangliae* (Cetacea: Balaenopteridae): comparisons between two coastal areas of Brazil. *Revista Brasileira de Zoologia* 25, 159–164.

**MacKay M.M., Würsig B., Bacon C.E. and Selwyn J.D.** (2016) Humpback whale (*Megaptera novaeangliae*) hotspots defined by bathymetric features off Western Puerto Rico. *Canadian Journal of Zoology* 94, 517-527.

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

**Martins C.C.A., Morete M.E., Engel M.H., Freitas A.C., Secchi E.R. and Kinas P.G.** (2001) Aspects of habitat use patterns of humpback whales in the Abrolhos Bank, Brazil, breeding ground. *Memoirs of the Queensland Museum* 27, 563-570.

**Mattila D.K., Clapham P.J., Vásquez O. and Bowman R.S.** (1994) Occurrence, population composition, and habitat use of humpback whales in Samana Bay, Dominican Republic. *Canadian Journal of Zoology* 72, 1898-1907.

**Mesnick S.L.** (1996) *Sexual selection and biological diversification: Patterns and processes*. PhD Thesis. University of Arizona, Tucson, USA.

**Monico J.F.G.** (2008) *Posicionamento pelo GNSS – descrição, fundamentos e aplicações*. São Paulo: UNESP.

**Morais I.O.B., Danilewicz D., Zerbini A.N., Edmundson W., Hart I.B. and Bortolotto G.A.** (2016) From the southern right whale hunting decline to the humpback whaling expansion: a review of whale catch records in the tropical western South Atlantic Ocean. *Mammal Review*, 1-13.

**Morete M.E., Bisi T.L., Pace R.M. and Rosso S.** (2008) Fluctuating abundance of humpback whales (*Megaptera novaeangliae*) in a calving ground off coastal Brazil. *Journal of the Marine Biological Association of the United Kingdom* 88, 1229-1235.

**Morete M.E., Bisi T.L. and Rosso S.** (2007) Temporal pattern of humpback whale (*Megaptera novaeangliae*) group structure around Abrolhos Archipelago breeding region, Bahia, Brazil. *Journal of the Marine Biological Association of the United Kingdom* 87, 87-92.

**Morete M.E., Pace R.M., Martins C.C.A., Freitas A.C. and Engel M.H.** (2003) Indexing seasonal abundance oh humpback whales around Abrolhos Archipelago, Bahia, Brazil. *Latin American Journal of Aquatic Mammals* 2, 21-28.

**Muggeo V.M.R.** (2008) segmented: An R Package to Fit Regression Models with Broken-Line Relationships. *R news* 8, 20-25.

**Nishiwaki M.** (1959) Humpback whales in Ryukyuan water. *Scientific Reports of the Whales Research Institute,* no. 14, 49-87 pp.

**NOAA** (2016) Ocean Products. vol. 2016: Office of satellite and product operations.

**Noad M.J. and Cato D.H.** (2007) Swimming speeds of singing and non-singing humpback whales during migration. *Marine Mammal Science* 23, 481–495.

**Pavanato H.J., Wedekin L.L., Guilherme-Silveira F.R., Engel M.H. and Kinas P.G.** (2017) Estimating humpback whale abundance using hierarchical distance sampling. *Ecological Modelling* 358, 10-18.

**Pitman R.L., Totterdell J.A., Fearnbach H., Ballance L.T., Durban J.W. and Kemps H.** (2015) Whale killers: Prevalence and ecological implications of killer whale predation on humpback whale calves off Western Australia. *Marine Mammal Science* 31, 629–657.

**Prates A.P.L., Gonçalves M.A. and Rosa M.R.** (2012) *Panorama da Conservação dos Ecossistemas Costeiros e Marinhos no Brasil.* Brasília: MMA.

**Rasmussen K., Calambokidis J. and Steiger G.H.** (2011) Distribution and migratory destinations of humpback whales off the Pacific coast of Central America during the boreal winters of 1996–2003. *Marine Mammal Science* 28, 267–279.

**Redfern J.V., et al.** (2013) Assessing the Risk of Ships Striking Large Whales in Marine Spatial Planning. *Conservation Biology* 27, 292–302.

**Rossi-Santos M.R., Neto E.S., Baracho C.G., Cipolotti S.R., Marcovaldi E. and Engel M.H.** (2008) Occurrence and distribution of humpback whales (*Megaptera novaeangliae*) on the north coast of the State of Bahia, Brazil, 2000–2006. *ICES Journal of Marine Science* 65, 667–673.

**Santos M.S.** (2010) *Sazonalidade e interação com embarcação do boto-cinza, Sotalia guianensis, (Cetacea: Delphinidae) no Porto do Malhado, Ilhéus, Bahia-Brasil.* MSc Thesis. Universidade Estadual de Santa Cruz, Ilhéus, Brazil.

**Scheidat M., Castro C., Denkinger J., González J. and Adelung D.** (2000) A breeding area for humpback whales (*Megaptera novaeangliae*) off Ecuador. *Journal Cetacean Research Manager* 2, 165–171.

**Seyboth E., Groch K.R., Dalla Rosa L., Reid K., Flores P.A.C. and Secchi E.R.** (2016) Southern Right Whale (*Eubalaena australis*) Reproductive Success is Inflenced by Krill (*Euphausia superba*) Density and Climate. *Scientific Reports* 6, 28205.

**Smultea M.A.** (1994) Segregation by humpback whale (*Megaptera novaeangliae*) cows with a calf in coastal habitat near the island of Hawaii. *Canadian Journal of Zoology* 72, 805-808 811.

**Sousa-Lima R.S. and Clark C.W.** (2008) Modeling the Effect of Boat Traffic on the Fluctuation of Humpback Whale Sing Activity in The Abrolhos National Marine Park, Brazil. *Canadian Acoustics* 36.

**Spitz S.S., Herman L.M., Pack A.A. and Deakos M.H.** (2002) The relation of body size of male humpback whales to their social roles on the Hawaiian winter grounds. *Canadian Journal of Zoology* 80, 1938–1947.

**Stevick P.T., Godoy L.P., McOsker M., Engel M.H. and Allen J.** (2006) A note on the movement of a humpback whale from Abrolhos Bank, Brazil to South Georgia. *Journal of Cetacean Research and Management* 8, 297–300.

**Tyack P.L. and Whitehead H.** (1983) Male competition in large groups of wintering humpback whales. *Behaviour* 83, 132-154.

**Vanicek P. and Krakiwsky E.J.** (1996) Geodesy: The Concepts. *North - Holland Publishing Company*.

**Whitehead H.** (1983) Structure and stability of humpback whale groups off Newfoundland. *Canadian Journal of Zoology* 61, 1391-1391.

**Whitehead H. and Moore M.J.** (1982) Distribution and movements of West Indian humpback whales in winter. *Canadian Journal of Zoology* 60, 2203-2211.

**Wilson M. and Mesnick S.L.** (1997) An Empirical Test of the Bodyguard Hypothesis. In Gowaty P.A. (ed) *Feminism and Evolutionary Biology: Boundaries, Intersections and Frontiers.* Champman & Hall, pp. 505-511.

**Würsig B., Cipriano F. and Würsig M.** (1991) Dolphin Movement Patterns: Information from Radio and Theodolite Tracking Studies. In Pryor K. and Norris K.S. (eds) *Dolphin Societies - Discoveries and Puzzles.* Berkeley: University of California Press, pp. 79-111.

**Zerbini A.N., et al.** (2004) Winter distribution and abundance of humpback whales (*Megaptera novaeangliae*) off Northeastern Brazil. *Journal of Cetacean Research Management* 6, 101–107.

**Zerbini A.N., et al.** (2011) Migration and summer destinations of humpback whales (*Megaptera novaeangliae*) in the western South Atlantic Ocean. *Journal of Cetacean Research Management* 3, 113–118.

**Zerbini A.N., et al.** (2006) Satellite-monitored movements of humpback whales *Megaptera novaeangliae* in the Southwest Atlantic Ocean. *Marine Ecology Progress Series* 313, 295–304.

**CAPÍTULO 2:**

**FINE-SCALE MOVEMENT PATTERNS OF HUMPBACK WHALES (*Megaptera novaeangliae*) IN A BRAZILIAN WINTERING GROUND**

# PADRÕES DE MOVIMENTO EM FINA ESCALA DAS BALEIAS-JUBARTE (*Megaptera-novaeangliae*) EM UMA ÁREA BRASILEIRA NO INVERNO

## RESUMO

As baleias-jubarte migram entre áreas de alimentação e reprodução, e a orientação da linha da costa parece ser um fator chave que influencia a direção do seu movimento. Pouco se sabe sobre as rotas usadas pelas baleias-jubarte que se movem a norte da maior área de reprodução do Brasil, o Banco dos Abrolhos. O objetivo deste estudo foi conduzir observações através de ponto fixo para descrever os movimentos de baleias-jubarte em uma área de berçário de Serra Grande (estado da Bahia, Brasil), e verificar possíveis mudanças no padrão de movimento ao longo da temporada, entre os anos, devido a composição de grupos, estado comportamental, e distância à costa. A média da velocidade do passo dos grupos observados foi de 6,88 (±2,92) km/h e a média da velocidade líquida foi de 4,92 (±2,46) km/h. A velocidade do passo apresentou uma correlação positiva com a distância à costa. Houve um aumento da velocidade do passo e da distância à costa com o aumento do número de escortes nos grupos com filhotes. A linearidade média das trajetórias dos grupos foi de 0,81 (±0,19) e a taxa média de reorientação foi de 25,72 (±19,09) °/min. No início da temporada, os grupos apresentaram movimentos mais erráticos, e as rotas com rumo para Sul predominaram ao longo do estudo. Os grupos deslocando-se para Sul apresentaram trajetórias mais lineares que grupos se movendo para Norte ou para outras direções. Estratégias para poupar energia parecem afetar os padrões de movimento das baleias-jubarte em Serra Grande. Desse modo, uma atenção especial deve ser dada a atividades antropogênicas que podem perturbar ou aumentar os gastos de energia de baleias com filhotes e em reprodução que usam a região.

Palavras-chave: Berçário. Demandas energéticas. Distância à costa. Linearidade. Ponto fixo. Velocidade.

# Fine-scale movement patterns of humpback whales (*Megaptera novaeangliae*) in a Brazilian wintering ground

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Fine-scale movement patterns of humpback whales

**Abstract**

Humpback whales migrate between feeding and breeding areas, and the coastline orientation seems to be a key factor that influences the course of their movement. Little is known about the routes used by humpback whales that move north of the main calving area of Brazil, the Abrolhos Bank. The aim of this study was to conduct land-based surveys to describe the movements of humpback whales in the calving area of Serra Grande (Bahia state, Brazil), and to verify possible movement pattern changes along the season and between years, due to group composition, behavioural state, and distance to the coast. The mean leg speed of the groups sighted was 6.88 (±2.92) km/h and mean net speed was 4.92 (±2.46) km/h. Leg speed was positively correlated with distance to the coast. There was an increase in leg speed and distance to the coast with increasing number of escorts in the groups with calves. The mean linearity value for group trajectory was 0.81 (±0.19) and the mean reorientation rate was 25.72 (±19.09) °/min. Groups presented more erratic movements early in the season, and trajectories heading South were predominant throughout the study. Groups moving South showed more linear trajectories than groups moving North and to other directions. Strategies to save energy appear to affect the movement patterns of humpback whales in Serra Grande. Thereby, special attention should be given to anthropogenic activities disturbing or increasing energy expenditure of calving and reproducing whales that occur in the region.

**Introduction**

Humpback whales (*Megaptera novaeangliae* Borowski, 1781) have migratory patterns, reproducing in warmer waters of low latitudes during the winter and feeding in cooler waters during the summer (Clapham 2000; Dawbin 1966). In calving areas, humpback whales concentrate near the coast, islands and reef banks (Clapham 2009). Proximity to the coastline, islands and reefs ensures warmer water (Dawbin 1966) and protection from predation (Corkeron & Connor 1999) in shallower waters, which are thought to be ideal for whales to calve and nurse (Whitehead & Moore 1982).

Humpback whales are thought to have different movement patterns depending on their location and the phase of their lifecycle (breeding, migrating or feeding). Zerbini et al. (2006) noted that in feeding areas, humpback whales tend to move more erratically than in migratory corridors. Lagerquist et al. (2008) recorded lower speeds in breeding and feeding areas than in migratory corridors, which may be justified by search/encounter patterns when looking for mates or food. However, Dalla Rosa et al. (2008) suggested that variation in speed of humpback whales may occur due to individual behavioural patterns than to common patterns that differ among the areas or life stages. Coastline orientation also seems to be a key factor that influences the trajectories of migrating whales at least in some sites (Dawbin 1956; Findlay et al. 2011).

Humpback whales from the breeding stock A (BSA) (IWC 2005) migrate from their feeding area off South Georgia and South Sandwich Islands (Engel & Martin 2009; Zerbini et al. 2011) to breed along the Brazilian coast between June and November (Martins et al. 2001). The area of highest concentration of humpback whales in Brazil is the Abrolhos Bank (Andriolo et al. 2010). Nevertheless, the population is increasing (Bortolotto et al. 2016; Pavanato et al. 2017) and areas used before the whaling period are being reoccupied (Rossi-Santos et al. 2008).

Migration routes used by humpback whales leaving the Brazilian wintering ground are almost a straight course towards 170º (Horton et al. 2011; Zerbini et al. 2006, 2011), going to the feeding areas. Nevertheless, information on the small-scale movement patterns of humpbacks in the wintering grounds is still scarce. It is necessary to understand the influence of environmental and social context on the behaviour of humpback whales to explain their fine-scale movement variability (Kavanagh et al. 2016). In this sense, land-based observation surveys apply methods that allow the tracking of animals without interfering their behaviour (Sagnol & Reitsma 2014; Würsig et al. 1991), and have been used as an alternative to study habitat use (Danilewicz et al. 2016; Smultea 1994), the effect of whale watching (Schaffar et

al. 2009; Williams et al. 2002) and group movement patterns (Bailey & Thompson 2006; Best et al. 1995). It has been noted that movement parameters as speed and net course may be measured in land-based surveys with the same accuracy than from boat surveys (Godwin et al. 2016). Knowledge about location and speed from cetaceans is useful to investigate a number of ecological and behavioural questions (Bailey & Lusseau 2004). In special, it may show some light on questions related to individual/group small-scale movement decisions.

In this context, the aim of this study was to apply land-based surveys to characterize the movements of humpback whales in Serra Grande region, Northeastern Brazil, and investigate the influence of spatio-temporal and behavioural features on the movement patterns of the whales in this wintering ground

**Material and methods**

*Study area*

Data were collected from a land-based observation station in Serra Grande (14°28'30" S; 39°01'50" W), Bahia, Northeastern Brazil. The platform is 93 m high and is 315 m from the shoreline. The radius of observation of 15 km was considered from the land-based station between 70 and 184º (True) covering 224.5 km$^2$ (Figure 1). The orientation of the coastline, the presence of rocky coast and vegetation north of the land-based station reduced the monitoring of Northern areas.
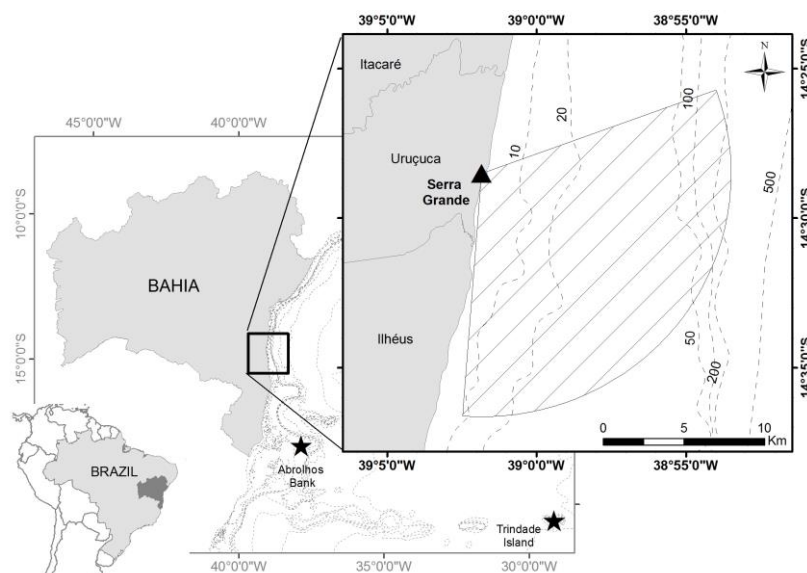


Figure 1. Serra Grande study area located in North-eastern Brazil where surveys occurred from a land-based observation station at a height of 93 m with 15 km radius, covering 224.5 km$^2$ (shaded area).

The study area is on the shortest continental shelf of the Brazilian coast (Prates et al. 2012), reaching 100 m at approximately 14 km from the coastline (Figure 1). The dominant southward Brazil Current occurs from October to March, and the northward North Brazil Undercurrent occurs from April to September. However, the northward currents are weak in April, August and September (Rezende et al. 2011).

*Visual surveys*

The visual monitoring of humpback whales occurred during the breeding season from July to October in the years 2014 and 2015. Data were collected during daytime between 07:22 am and 04:40 pm whenever weather conditions were favorable to ensure visibility and during sea state below or equal 4 on the Beaufort scale. The focal animal sampling methods was used when solitary individuals were sighted and a focal group approach was used when 2 or more individuals were sighted (Mann 1999). Focal follows lasted until the animals moved out of the study area or if visibility became an issue, which would affect the quality of observation (Morete et al. 2003). In the presence of more than one group in the area, the one which was easier to track was chose (Mann 1999); this choice was first made based on emerging and active behaviour of the individuals and then by the proximity of the groups to the coast. A total station TOPCON ES105 with 5' of precision and 30-power monocular magnification was used to track the groups. Group size and composition, time, angles and behavioural states were recorded. Each pair of angles was called fix and a set of fixes of a group was called track. Events of individuals joining or leaving groups were also recorded. On those cases, focal sampling continued with the easier group to track but considered a new group (Barendse et al. 2010; Best et al. 1995). In the presence of a group, the fix was taken from the individual which was in front of the group (directing the movement) or from the calf when present.

The land-based team was comprised of two or three observers: the principal observer (the same person throughout the study) who operated the total station; another observer who registered data; and a third one that followed the group with the aid of 7x50 binoculars, checking if any other group appeared in the area or approached the focal group.

Every 30 minutes or whenever weather conditions changed, wind speed and direction, cloud cover and sea state on the Beaufort scale were registered.

*Definitions*

A group was classified either as a single individual or an association of individuals based on a distance of up to 100 m from each other, and if all individuals were moving in the same general direction in a coordinated way (Morete et al. 2008; Whitehead 1983).

Group composition we considered as 1AD, when a solitary adult was observed; dyad, a group of two adults; multiple group, three or more adults, MOC, a group of mother and calf; MOCE, when mother and calf were escorted by another adult; and MOCE/+, a group of mother, calf and two or more escorts (Morete et al. 2007b). Due to the distance to the animals, we considered two age classes: adult and calf, being a calf an animal up to 50% of the size of an adult (Chittleborough 1953).

Behavioural states were classified as resting - when the whale(s) remained on the surface of the water, exposing the dorsal fin and with no apparent movement; swimming - when the whales(s) alternated from being submerged and on the surface; and; active - when aerial behaviours occurred (Morete et al. 2003; Morete 2007).

*Spatial analyses*

A total station provides horizontal and vertical angles to an object, wherein the first angle is between the object and a known reference point, and the second between the observer and the object (Bailey & Lusseau 2004). These angles allow calculation of the distance between the observer and the object (Gailey & Ortega-Ortiz 2002). Universal Transverse Mercator (UTM) coordinates from the total station and the reference point were measured with millimetric precision by Global Navigation Satellite System positioning. The orthometric altitudes of these points were determined by Geoidal MAPGEO 2010 model (Monico 2008). UTM coordinates (E, N) of all the measured points were calculated with the height of the total station and tidal variation through trigonometric equations (Santos 2010). The horizontal distances (calculated from data collected by the total station) were transformed for spherical distances considering the curvature of the earth (Vanicek & Krakiwsky 1996).

Distances between the group and coastline were calculated using the distances to the meridians considering the first fix sampled of the group using Google Earth to have more precise values due to higher resolution of the maps.

*Movement analyses*

We only considered tracks for those which four fixes were sampled for at least 10 min, and with group composition identified. The following parameters were calculated:

*Leg speed:* mean of speeds calculated between two consecutive fixes divided by the distance between two fixes and the time that took to travel between them (Barendse et al. 2010). Speeds above 30 km/h were not considered since the maximum speeds recorded for humpback whale vary from 18 km/h (Findlay & Best 1996) to 27 km/h (Zenkovich 1937 apud Winn & Reichley 1985).

*Net speed:* calculated by dividing the linear distance between the first and last fixes (net distance) and the total time of the track (Barendse et al. 2010; Findlay et al. 2011).

*Linearity*: index calculated by dividing the total distance between the first and last fixes (net distance) by the sum of the distances between each fix (cumulative distance) of the track (Barendse et al. 2010; Gailey et al. 2007; Williams et al. 2002). The values range from 0 to 1 with values closer to 0 representing more circular paths and values closer to 1 represent more direct trajectories (Burns 2010; Schaffar et al. 2009).

*Reorientation rate*: calculated as the sum of all absolute values of change of bearing between two consecutive fixes, dividing by the total time of the track (Gailey et al. 2007; Smultea & Würsig 1995). It represents the pattern of bearing that changes along a trackline, in which higher values of reorientation indicate more erratic paths (Burns 2010).

*Net course*: the true bearing in degrees considering the first and last fixes of the track (Barendse et al. 2010; Best et al. 1995; Findlay et al. 2011). We divided the net course into three classes: North (from 320 to 50º), South (from 140 to 230º) and other directions (between 50 and 140º and between 230 and 320º), considering the coastline orientation.

Martins (2012) equations were used to calculate all parameters cited above. When we observed more than one behavioural state during the same track, leg speed and reorientation rate were calculated for each behavioural state separately.

*Statistical analyses*

Active groups with more than one individual were excluded (n=16), except for analyses involving exclusively net course. The only exception to include active groups with more than one individual in the analyses was mother and calf groups when it was possible to follow the calf during the entire sighting. The reason to exclude the other groups was to avoid confusion in groups of several individuals performing aerial activities simultaneously. We checked whether assumptions of normality and equal variance were met before performing statistical tests. The distribution of variables in groups for t-Tests and errors in groups for Analyses of Variances (ANOVA) were visually inspected and moderate deviations were tolerated given the robustness of these tests. Differences in variances between groups were tested using Levene tests and the size of the ratio between the highest and the smallest variance.

*Groups:* To test whether the distances where groups were observed varied with the group composition and the period of the season an ANOVA followed a Tukey honest significant difference (HSD) test were used.

We considered three periods of the season (initial, middle and final, Table I) due to behavioural differences associated with each period (Morete et al. 2007a). As the number of

individuals varies throughout the season and the years, we calculated the day when the number of individuals would be higher for each season using a segmented regression model for the number of individuals observed throughout the season, and considered it as the center of the middle period (Gonçalves et al., first chapter).

Table I. Beginning and end dates of initial, middle and final periods considered for each year in the study in Serra Grande (Bahia state, Brazil). The middle period has 41 days.

| :ar | Initial p. | Middle p. | Final p. |
|---|---|---|---|
| 14 | 1 July–2 August | August–12 September | September–31 October |
| 15 | 0 July–14 August | August–24 September | September–25 October |

*Movement parameters:* To test whether there was a difference in parameter values between the two years we used t-Tests. To test whether the movement parameter values were influenced by group composition, the season period, behavioural state, and net course class, we used ANOVAs followed by Tukey honest significant difference (HSD) tests. For net course, we used a circular variance analysis, and to check if the movement of humpback whale groups presented circular uniformity throughout the study we used the Rayleigh's test (Zar 1974). Statistical analyses were run in R 3.0.2 (R Development Core Team) and in PAST 3.10 (Paleontological Statistics) with the critical value ($\alpha$) of 0.05.

**Results**

*Research effort*

We considered 125 tracks with a total of 2240 fixes during 67 days in the field. Minimum and maximum distances tracked were 0.21 km and 10.59 km respectively, with a mean tracked distance of 2.88±2.20 km per focal.

The total time of group tracking was 61.4 h, and varied throughout the season. Total tracking time was 10.3 h in the initial period, 25.7 h in the middle period and 25.4 h in the final period. Focal time ranged from 0.16 h to 1.93 h ($x$= 0.49±0.34 h). The focal time for each group composition was: 2.5 h for solitary animals, 6.2 h for dyads, 17.3 h for multiple groups, 21.5 h for MOCs, 5.7 h for MOCE, and 8.2 h for MOCE/+ groups (Table II).

Table II. Number of effort days and duration of the focal follows of groups along the periods of the season in the study area in Serra Grande (Bahia state, Brazil). Total duration of focal follows in hours and number in parentheses for each group type. 1AD = one adul, dyad = two adults, multiple = three or more adults, MOC = mother and calf, MOCE = mother and calf and one escort, MOCE/+ = mother and calf and two or more escorts.

| Year | | Period of the season | | | Total |
|------|------|---------|--------|-------|-------|
| | | Initial | Middle | Final | |
| | Field effort | 11 | 10 | 16 | 37 |
| | 1AD tracks | - | - | 0.6 (2) | 0.6 (2) |
| | Dyad tracks | 0.2 (1) | 0.9 (2) | 0.8 (2) | 1.9 (5) |
| 2014 | Multiple tracks | 2.7 (5) | 2.5 (2) | 2.1 (3) | 7.3 (10) |
| | MOC tracks | - | 1.6 (3) | 9.1 (15) | 10.7 (18) |
| | MOCE tracks | - | 0.7 (2) | 1.1 (3) | 1.8 (5) |
| | MOCE/+ tracks | 0.4 (1) | 0.4 (1) | 1.1 (3) | 1.9 (5) |
| | Field effort | 7 | 13 | 10 | 30 |
| | 1AD tracks | 0.9 (3) | 0.5 (2) | 0.5 (2) | 1.9 (7) |
| | Dyad tracks | 1.9 (4) | 1.8 (6) | 0.6 (1) | 4.3 (11) |
| 2015 | Multiple tracks | 1.9 (3) | 5.2 (7) | 2.9 (4) | 10.0 (14) |
| | MOC tracks | - | 6.1 (17) | 4.7 (11) | 10.8 (28) |
| | MOCE tracks | - | 3.4 (8) | 0.5 (1) | 3.9 (9) |
| | MOCE/+ tracks | 2.3 (3) | 2.6 (5) | 1.4 (3) | 6.3 (11) |

*Groups*

The most frequently tracked group types were those with calves (60.80%), followed by multiple groups (19.20%), dyads (12.80%) and solitary individuals (7.20%). Within groups with calf, MOC represents 60.52%, MOCE 22.37% and MOCE/+ 17.11%. A single group of 2 adults and 2 calves was observed but not considered for the analyses because it was not possible to distinguish which calf would be used to sample.

Mean distance from coast of groups without calf was significantly greater than for groups with calf ($t=-6.4417$, $df=114.07$, $P<0.001$, Table III). Within groups with calf, the number of escorts influenced the distance from coast of the groups sighted ($F=11.32$, $df=73$, $P<0.001$). Mean distance from coast of MOC was significantly lower than MOCE ($P<0.05$) and MOCE/+ ($P<0.001$) groups, and no significant difference in distance from coast was found

between MOCE and MOCE/+ (*P*=0.17, Table III). The period of the season influenced where groups were observed in relation to distance from coast (F=21.25, df=122, *P*<0.001) and distance values decreased along the season (Table III). There was a significant difference in group sighting distances from coast between initial and middle periods of the season (*P*<0.001) and between initial and final periods of the season (*P*<0.001) but no significant differences were found in distance of groups from the coast between middle and final periods of the season (*P*=0.35).

Table III. Mean values and standard deviation of distances to coast (km) where groups of humpback whales were initially observed from a land-based observation station in Serra Grande (Bahia state, Brazil) during 2014 and 2015: groups with calves and all groups between periods of the season. MOC = mother and calf, MOCE = mother and calf and one escort, MOCE/+ = mother and calf and two or more escorts.

|  | Mean (±SD) |
| --- | --- |
| Without calf | 8.38 (±2.95) |
| With calf | 5.21 (±2.50) |
|  |  |
| MOC | 4.14 (±2.53) |
| MOCE | 6.07 (±3.30) |
| MOCE/+ | 7.84 (±1.75) |
|  |  |
| Initial period | 10.05 (±1.16) |
| Middle period | 6.12 (±3.14) |
| Final period | 5.37 (±2.76) |

MOC groups spent more time resting (46.22%) and MOCE and MOCE/+ swimming (66.46% and 80.29% respectively). Time spent resting decreases with increasing numbers of escorts. Time spent swimming increases with increasing number of escorts (Figure 2).
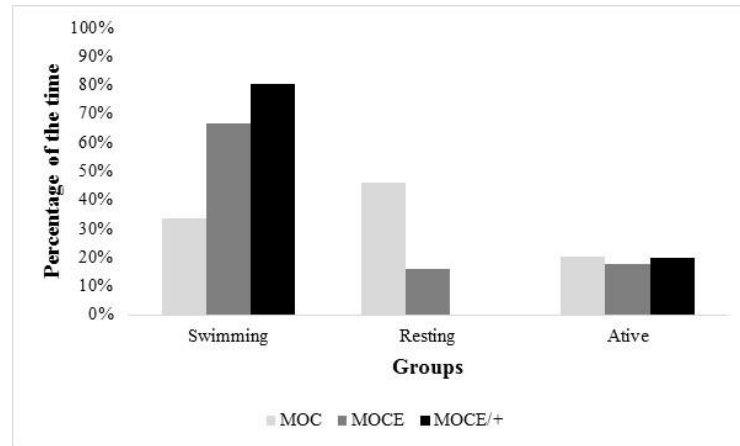
Figure 2. Percentage of time spent in the different behavioral states by humpback whale groups with a calf observed from a land-based observation station in Serra Grande (Bahia, Brazil) in 2014 and 2015. MOC = mother and calf, MOCE = mother and calf and one escort, MOCE/+ = mother and calf and two or more escorts.

*Movement parameters*

*Leg and net speed*: Mean leg speed of groups sighted in Serra Grande was 6.88 km/h and mean net speed was 4.92 km/h (Table IV). Net and leg speed showed a positive correlation (r=0.72; *P* < 0.001). Therefore, for the remaining analyses we used the leg speed only considering the full path travelled by the group, in order to avoid underestimating the speed values (Lagerquist et al. 2008; Noad & Cato 2007). Leg speed and distance from coast showed a positive correlation (r=0.51; *P* < 0.001), with an increase in leg speed with increasing distance from coast. No difference in leg speed was found between years 2014 and 2015 (t=-0.79263, df=68.834, *P*=0.4307).

Table IV. Descriptive statistics (mean, standard deviation, minimum, and maximum values) of movement parameters of humpback whale groups tracked from a land-based observation station in Serra Grande (Bahia state, Brazil) during 2014 and 2015.

|  | Mean | SD | Minimum | Maximum |
|---|---|---|---|---|
| Net speed (km/h) | 4.92 | ±2.46 | 0.20 | 11.34 |
| Leg speed (km/h) | 6.88 | ±2.92 | 0.70 | 15.73 |
| Linearity | 0.81 | ±0.19 | 0.19 | 1.00 |
| Reorientation rate (°/min) | 25.72 | ±19.09 | 0.45 | 93.09 |
| Net course (°) | 178.22 | 65.34 | 2.48 | 359.59 |

We found significant differences in mean values of leg speed between group compositions (F=8.764, df=104, $P<0.001$): between MOC and MOCE/+ ($P<0.001$), MOCE and MOCE/+ ($P<0.05$), and MOC and multiple groups ($P<0.001$). Leg speed of groups with calf increases with increasing number of escorts (Figure 3a). The decrease of leg speed along the periods of the season did not imply significant differences between them (F=2.438, df=107, $P=0.092$) or between net course classes (F=0.8447, df =107, $P=0.4326$). Mean values of leg speed varied between behavioural states (F=10.16, df=89, $P<0.001$) with significantly lower values in resting groups than active ($P<0.05$) and swimming groups ($P<0.001$, Figure 3b). Within groups with calf which were swimming, there was a significant difference in leg speed (F=9.357, df=42, $P<0.001$): MOCE/+ moved significantly faster than MOC ($P<0.001$) and than MOCE ($P<0.05$). When resting, no difference was found in mean values of leg speed between MOC and MOCE groups (F=0.557, df=22, $P=0.463$).
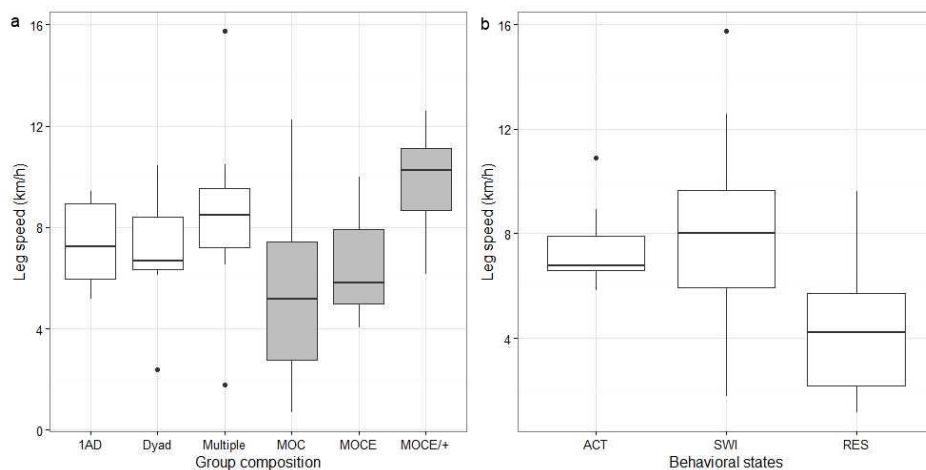


Figure 3. Box plot of leg speed between group composition (a) and between behavioural states (b) of humpback whale groups sighted from a land-based observation station in Serra Grande (Bahia, Brazil) in 2014 and 2015. 1AD = solitary individual, Dyad = two adults, Multiple = three or more adults, MOC = mother and calf, MOCE = mother and calf and one adult, MOCE/+ = mother and calf and two or more adults. ACT = active groups, SWI = swimming groups, RES = resting groups.

*Linearity*: Linearity mean value of groups tracked was 0.81 (Table IV) and 69.09% of humpback whale tracks showed values above 0.80. No significant difference was found between years (t=0.3466, df = 78.581, $P=0.7298$) nor between group composition (F=0.6478. df=104, $P=0.6638$). Linearity values varied (F=6.44, df=107, $P<0.05$) and increased along periods of season (Figure 4a): being significantly lower in the initial period than in final period ($P<0.05$). There was a greater linearity variation in the initial and middle periods than

in the final (Figure 4a). No significant difference was found between behavioural states (F=1.031, df=89, *P*=0.3608). Linearity values showed a significant difference depending on net course classes (F=14.87, df=107, *P*<0.001) between South and North (*P*<0.05) and between South and other directions (*P*<0.001). Groups moving South presented more linear trajectories (x=0.87±0.13) than groups moving to North (*x*=0.73±0.25) and towards another direction (*x*=0.62±0.21, Figure 5).
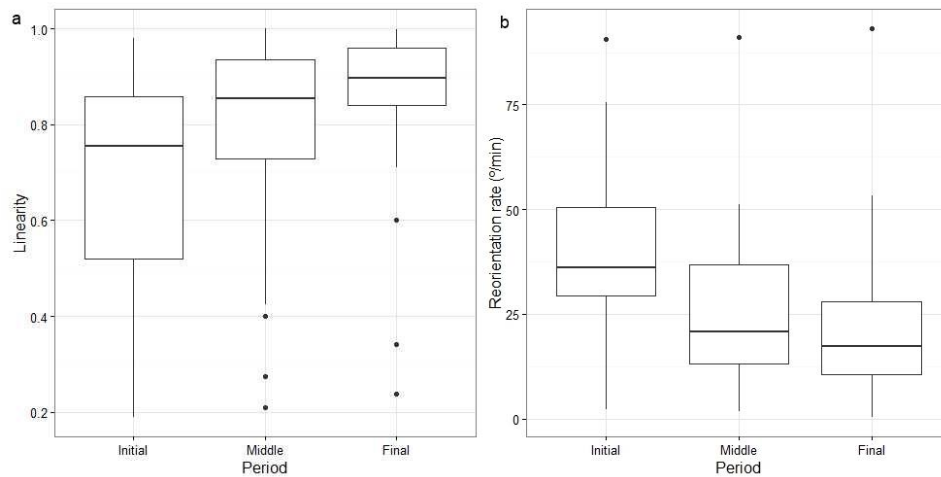


Figure 4. Boxplot of linearity (a) and of reorientation rate (b) of humpback whale groups observed from a land-based observation station in Serra Grande (Bahia state, Brazil) in 2014 and 2015 between periods of the season.
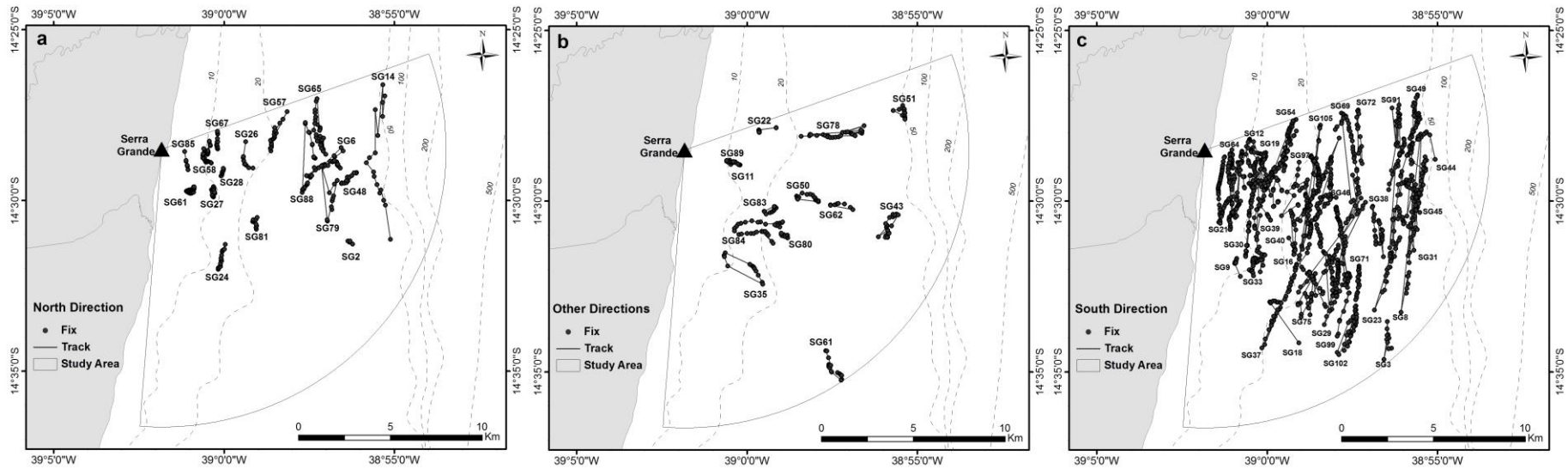
Figure 5. Tracks of humpback whale groups sighted from a land-based observation station in Serra Grande (Bahia state, Brazil) in 2014 and 2015 by the different classes of net course. North = from 320 to 50º (a), Other directions = between 50 and 140 and between 230 and 320º (b), South = from 140 to 230º (c).

*Reorientation rate*: The mean reorientation rate was 25.72 °/min (Table IV). There was no significant difference between reorientation rates between 2014 and 2015 (t=-0.4145, df=81.524, *P*=0.6796) or among group composition (F=0.641, df=104, *P*=0.0669). Reorientation rate varied significantly between periods of the season (F=6.71, df=107, *P*<0.05), being higher in the initial period of the season than in the final period (*P*<0.05, Figure 4b). Reorientation rate did not change with behavioural state (F=0.1443, df=89, *P*=0.8658) nor within classes of net course (F=2.682, df=107, *P*=0.073).

*Net course*: The mean value of net course of observed groups in Serra Grande was 178.22° (Table IV). The null hypothesis for uniformity of movement of the groups was rejected (Rayleigh's R=65.277, Rayleigh's Z = 34.054, r=0.522, *P*<0.001) with South direction predominating (Figure 6) throughout the season (Figure 7). We did not found significant difference of mean values of net course between the years (F=0.065, df=1, *P*=0.799), among group compositions (F=0.7204, df=5, *P*=0.7204), behavioural states (F=1.6782, df=2, *P*=0.5101) or season periods (F=0.9558, df=2, *P*=0.3873).
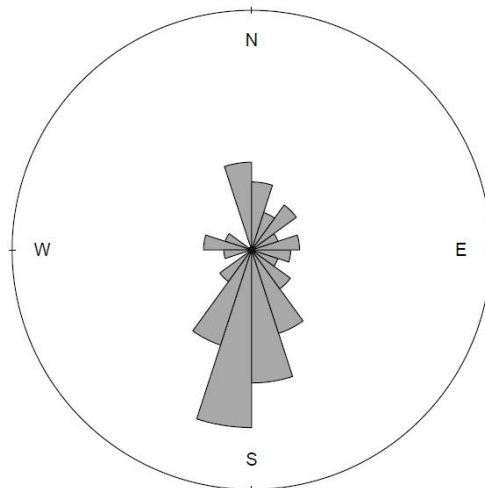


Figure 6. Frequencies of net course followed by humpback whale groups sighted from a land-based observation station in Serra Grande (Bahia, Brazil) in 2014 and 2015.
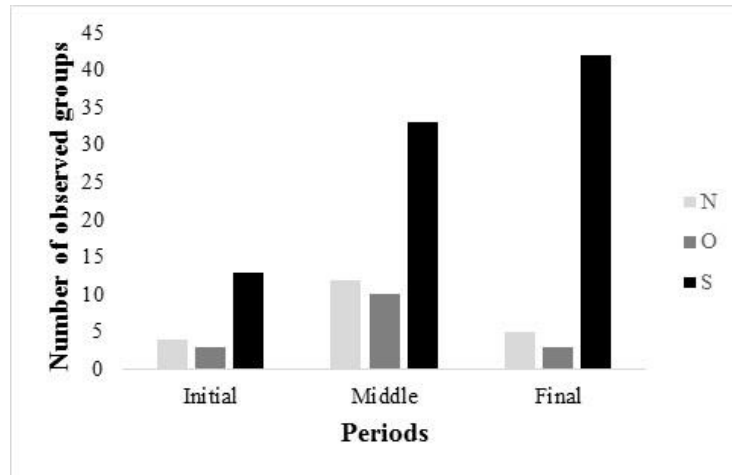
Figure 7. Frequencies of number of humpback whale groups observed from a land-based observation station in Serra Grande (Bahia, Brazil) among the periods of the season (initial, middle and final) by the different classes of net course. N = from 320 to 50º, O = between 50 and 140 and between 230 and 320º, S = from 140 to 230º.

## Discussion

Movement patterns of humpback whales in breeding areas are little known (Zerbini et al. 2006). This study showed that the movement of the groups from BSA that were observed in Serra Grande are influenced by the orientation of the coast which guides most trajectories parallel to it.

Most groups were sighted heading South, and we observed a shortening of the distance to coast as the season progressed. This may be interpreted as a result of temporal variation in habitat use in this area, while whales moving North may use more offshore waters and were not registered during our effort. Northward movement of groups observed further away from the coastline has also been observed in Australia (Jenner et al. 2001). Humpback whales sightings in July and August off Trindade Island (approximately 1100 km away from the coast) (Siciliano et al. 2012) support this hypothesized offshore movement of groups heading North early in the season. Whales moving South follow the coastline more closely until they get to the Abrolhos Bank, where part of the population migrates back to the feeding areas heading 170º (Zerbini et al. 2006, 2011).

Humpback whales may use the South Equatorial Current Bifurcation which reaches approximately 17ºS in July (Rodrigues et al. 2007) to get closer to the Brazilian coast. Whales might be taking advantage of the predominant current in the region to save energy. The North Brazil Undercurrent flows North until July and is stronger further away from shore (Rezende et al. 2011). In October, the Brazilian Current predominates (Rezende et al. 2011) and it could

help the whales going South. The net course of whale groups in oceanic habitats in Madagascar are influenced by the prevailing currents (Trudelle et al. 2016). Conclusive evidence of the use of the prevalent currents by whales coming from Southern feeding grounds towards the Brazilian coast would help us understand which are their preffered routes.

Humpback whale preference for shallow waters as the season progresses on the breeding ground could be another way of saving energy. Groups could be moving North before July, but because the visual surveys were initiated only in July and the weather conditions were not always ideal, this might have affected the number of observed groups towards that direction. Lower number of individuals observed in the initial period of the season (Gonçalves et al., first chapter) also resulted in less hours of focal follows during that period and may have affected our results.

Segregation of groups with calves closer to shore in shallower waters in Serra Grande corroborates the findings from other breeding areas (Ersts & Rosenbaum 2003; Guidino et al. 2014; Smultea 1994). The increase in distance from the coast of the groups with calves with increasing number of escorts was also observed by Félix & Botero-Acosta (2011) in Ecuador and by Craig et al. (2014) in Hawaii using two different platform of observation, opportunistic boat sightings and from a land-based station, respectively. Concentration of mothers with calves in shallower waters may be a strategy to avoid male harassment, maternal care disturbance, and calf injury during male courting behaviour (Craig et al. 2014; Ersts & Rosenbaum 2003; Smultea 1994).

The number of escorts of a mother and calf group, besides increasing their distance from the coastline, also resulted in an increased movement speed. Faster movements can lead to an increase in energy expenditure (Craig et al. 2014) for both mother and calf and a decrease in the growth rate of the calf (Braithwaite et al. 2015). In fact, we found the same general pattern of increased speeds with greater distance from shore for all group compositions as observed in Madagascar (Trudelle et al. 2016). Cartwright & Sullivan (2009) found that, despite the increase of speed related to the number of escorts, there was no significant difference in movement patterns between MOC and MOCE groups, and the same pattern was observed in Serra Grande. Those authors suggested that females choose to have a single male escort close by, as proposed by the bodyguard hypothesis (Mesnick 1996). A single chosen escort may protect females with calves from harassment of other males when the pair mother-calf becomes more vulnerable in open waters and away from the coast (Cartwright & Sullivan 2009).

Two factors that contribute to energy expenditure in humpback whales are the mean movement speed and the time spent in resting versus swimming (Braithwaite et al. 2015). Our data suggests that time spent resting by MOCE comparing to MOC groups was reduced to less than half, and resting was not observed in MOCE/+. The opposite was observed in time spent swimming, which doubles for mothers and calves that are escorted by one male and becomes the dominant activity of MOCE/+ groups. Additionally, resting is a strategy that benefits the pair mother-calf providing more time for nursing (Braithwaite et al. 2015). Thereby, groups of mother and calf seem to adjust their movement patterns with social factors, as the presence of escorts.

The mean leg speed of 6.88 km/h observed in Serra Grande was higher than found in similar studies conducted from a land-based platform. The mean leg speed off breeding areas in South Africa was 4.6 km/h (Barendse et al. 2010), and during Southern migration on the east coast of Australia was 4.7 km/h (Burns 2010). Differences in local current speeds could be one of the reasons to explain those differences. The mean net speed obtained in our study was close to that found from other breeding areas (Findlay et al. 2011; Frankel et al. 1995) but higher than the ones calculated for an area next to a bay, with possible quieter waters (Barendse et al. 2010) than Serra Grande, which is an open ocean area. Environmental variables may influence the behaviour of humpback whales (Kavanagh et al. 2016), and more protected waters could allow moving at lower speeds. During satellite-monitoring studies of humpback whales of BSA, Zerbini et al. (2011) found speeds of 3.34 km/h and 0.93 km/h for migrating and feeding areas, respectively. It is interesting that the expected lower speed in breeding areas was not observed in our study. Speed data may show variation depending on how they were obtained (Findlay et al. 2011), using land-based surveys or satellite telemetry, with more detail data obtained from land platforms. For example, Chittleborough (1953) reported a mean speed of 8.0 km/h during aerial surveys in Australia on short-term observations during migration.

As observed by Dalla Rosa et al. (2008), speed was affected by the behavioural state. However, no variation in the reorientation rate and linearity was observed among behavioral states: whales in swimming behaviour did not show more directional paths as initially expected. Traveling individuals could follow more direct paths than individuals resting or searching for mates but this was not observed. Nevertheless, reorientation rate and linearity were influenced by the period of the season. Groups at the beginning of the season had more erratic movements and as the season progressed they were gradually showing more linear movements, which may be related to the approaching migration to feeding areas. We found

that the groups going South showed higher linearity than other groups. Groups with less linear paths might be still searching for a mate or may be pregnant females are arriving to give birth at the calving grounds. However, despite the differences in linearity, no differences were found in the speed of groups moving to North or South as also observed by Noad & Cato (2007) in migratory corridors. Individuals may maintain a similar speed regardless of the direction they follow, since while they are in the breeding area, some individuals may be trying to mate and mothers take advantage of the time before the migratory period to feed the calves.

The mean linearity value obtained here suggests limited migration movement in the study area (Barendse et al. 2010), which highlights that the population of humpback whales using Serra Grande area uses it as a calving ground and is indeed reoccupying areas previously affected by whaling (Rossi-Santos et al. 2008). The linearity values were similar to those observed in other breeding areas (Schaffar et al. 2009), lower than in migratory areas (Burns 2010) but higher than observed in feeding areas (Stanistreet et al. 2013). Groups of humpback whales in Serra Grande showed erratic movements with great change of direction per minute and reorientation rates higher than other breeding areas such as at the calm waters of New Caledonia (Schaffar et al. 2009). There were no differences in the reorientation rate between group composition contrasting to what Noad & Cato (2007) have found for groups with calves in Australia that change their direction more often during migration. Linearity patterns of groups with calves in Serra Grande were similar to those observed in the Abrolhos Bank (Bisi 2006). However, the higher speed observed for groups with calves in Serra Grande could be due to less shallow and protected waters comparing to Abrolhos Bank.

Movement patterns of humpback whales can vary between breeding and feeding areas and migratory corridors (Lagerquist et al. 2008). These patterns can also vary within breeding areas, where humpback whales can adjust their behaviour depending on the characteristics of the area as energy demands. Serra Grande is an area that is used during the reproductive season by mothers with calves to rest, and despite being within a protected area (APA Costa de Itacaré/Serra Grande), anthropogenic activities may impact these animals due faulty reinforcement of protective measures. Resting areas are particularly sensitive to disturbance because the interruption of resting behaviour may lead to decreased lactation time and growth of calves (Braithwaite et al. 2015). Consequently, with the increase of the population (Bortolotto et al. 2016; Pavanato et al. 2017) special attention should be given to current and planned human activities in the region, such as the construction of a new offshore port approximately 10km from the study area (BAMIN 2011). Monitoring any changes in

movement patterns, such as increase in reorientation rate to avoid vessels and/or adoption of more linear paths and higher speeds to move away from the region would raise concerns for the humpback whales in Serra Grande.

**References**

Andriolo A, Kinas PG, Engel MH, Martins CCA, Rufino AM. 2010. Humpback whales within the Brazilian breeding ground: distribution and population size estimate. Endangered Species Research 11:233–243.

Bailey H, Lusseau D. 2004. Increasing the precision of theodolite tracking: modified technique to calculate the altitude of land-based observations sites. Marine Mammal Science 20:880–885.

Bailey H, Thompson P. 2006. Quantitative analysis of bottlenose dolphin movement patterns and their relationship with foraging. Journal of Animal Ecology 75:456–465.

BAMIN (2011) Relatório de Impacto Ambiental Porto Sul. Bahia Mineração Ltda.,

Barendse J, Best PB, Thornton M, Pomilla C, Carvalho I, Rosenbaum HC. 2010. Migration redefined? Seasonality, movements and group composition of humpback whales *Megaptera novaeangliae* off the west coast of South Africa. African Journal of Marine Science 32:1–22.

Best PB, Sekiguchi S, Findlay KP. 1995. A suspended migration of humpback whales *Megaptera novaeangliae* on the west coast of South Africa. Marine Ecology Progress Series 118:1-12.

Bisi TL. 2006. Comportamento de filhotes de baleia jubarte, *Megaptera novaeangliae*, na região ao redor do Arquipélago dos Abrolhos, Bahia. Master Thesis. Universidade de São Paulo, São Paulo: Instituto de Biociências. 90 pages.

Bortolotto GA, Danilewicz D, Andriolo A, Secchi ER, Zerbini AN. 2016. Whale, Whale, Everywhere: Increasing Abundance of Western South Atlantic Humpback Whales (*Megaptera novaeangliae*) in Their Wintering Grounds. PLoS ONE 11:e0164596. 17 pages.

Braithwaite JE, Meeuwig JJ, Hipsey MR. 2015. Optimal migration energetics of humpback whales and the implications of disturbance. Conservation Physiology 3:1-15.

Burns D. 2010. Population characteristics and migratory movements of humpback whales (*Megaptera novaeangliae*) identified on their southern migration past Ballina,

eastern Australia. Doctoral Thesis. Southern Cross University, Lismore: School of Environmental Science and Management. 248 pages.

Cartwright R, Sullivan M. 2009. Associations with multiple male groups increase the energy expenditure of humpback whale (*Megaptera novaeangliae*) female and calf pairs on the breeding grounds. Behaviour 146:1573-1600.

Chittleborough RG. 1953. Aerial observations on the Humpback whale, *Megaptera nodosa* (Bonnaterre), with notes on other species. Australian Journal of Marine and Freshwater Research 4:219-227.

Clapham PJ. 2000. The Humpback Whale: Seasonal Feeding and Breeding in a Baleen Whale. In: Mann J, Connor RC, Tyack PL, Whitehead H, editors. Cetacean Societies: Field Studies of Dolphins and Whales. Chicago: The University of Chicago Press, p 173-196.

Clapham PJ. 2009. Humpback Whale. In: Perrin WF, Würsig B, Thewissen JGM, editors. Encyclopedia of Marine Mammals. San Diego: Academic Press, p 582-585.

Corkeron PJ, Connor RC. 1999. Why do baleen whales migrate? Marine Mammal Science 15:1228-1245.

Craig AS, Herman LM, Pack AA, Waterman JO. 2014. Habitat segregation by female humpback whales in Hawaiian waters: avoidance of males? Behaviour 151:613–631.

Dalla Rosa L, Secchi ER, Maia YG, Zerbini AN, Heide-Jørgensen MP. 2008. Movements of satellite-monitored humpback whales on their feeding ground along the Antarctic Peninsula. Polar Biology 31:771-781.

Danilewicz D, Moreno IB, Tavares M, Sucunza F. 2016. Southern right whales (*Eubalaena australis*) off Torres, Brazil: group characteristics, movements, and insights into the role of the Brazilian-Uruguayan wintering ground. Mammalia.

Dawbin WH. 1956. The Migrations of Humpback Whales which Pass The New Zealand Coast. Transactions of the Royal Society of New Zealand 84:147-196.

Dawbin WH. 1966. The seasonal migratory cycle of humpback whales. In: Norris KS, editors. Whales, dolphins, and porpoises. Berkeley: University of California Press, p 145-170.

Engel MH, Martin AR. 2009. Feeding grounds of the western South Atlantic humpback whale population. Marine Mammal Science 25:964-969.

Ersts PJ, Rosenbaum HC. 2003. Habitat preference reflects social organization of humpback whales (*Megaptera novaeangliae*) on a wintering ground. Journal of Zoology 260:337–345.

Félix F, Botero-Acosta N. 2011. Distribution and behaviour of humpback whale mother–calf pairs during the breeding season off Ecuador. Marine Ecology Progress Series 426:277–287.

Findlay KP, Best PB. 1996. Estimates of the numbers of humpback whales observed migrating past Cape Vidal, South Africa, 1988-1991 Marine Mammal Science 12:354-370.

Findlay KP, Best PB, Meÿer MA. 2011. Migrations of humpback whales past Cape Vidal, South Africa, and an estimate of the population increase rate (1988–2002). African Journal of Marine Science 33:375–392.

Frankel AS, Clark CW, Herman LM, Gabriele CM. 1995. Spatial distribution, habitat utilization, and social interactions of humpback whales, *Megaptera novaeangliae*, off Hawai's, determined using acoustic and visual techniques. Canadian Journal of Zoology 73:1134-1146.

Gailey G, Ortega-Ortiz JG. 2002. A note on a computer-based system for theodolite tracking of cetaceans. Journal of Cetacean Research and Management 4:213–218.

Gailey G, Würsig B, McDonald TL. 2007. Abundance, behavior, and movement patterns of western gray whales in relation to a 3-D seismic survey, Northeast Sakhalin Island, Russia. Environmental Monitoring and Assessment 134:75–91.

Godwin EM, Noad MJ, Kniest E, Dunlop RA. 2016. Comparing multiple sampling platforms for measuring the behavior of humpback whales (*Megaptera novaeangliae*). Marine Mammal Science 32:268–286.

Guidino C, Llapapasca MA, Silva S, Alcorta B, Pacheco AS. 2014. Patterns of Spatial and Temporal Distribution of Humpback Whales at the Southern Limit of the Southeast Pacific Breeding Area. PLoS ONE 9:e112627. 13 pages.

Horton TW, Holdaway RN, Zerbini AN, Hauser N, Garrigue C, Andriolo A , et al. 2011. Straight as an arrow: humpback whales swim constant course tracks during long-distance migration. Biology Letters 7:674–679.

IWC. 2005. Report of the Scientific Committee. Annex H - Report of the sub-committee on other southern hemisphere whale stocks. Journal of Cetacean Research and Management 7:235-246.

Jenner KCS, Jenner M-NM, McCabe KA. 2001. Geographical and temporal movements of humpback whales in Western Australian waters. APPEA:749-765.

Kavanagh AS, Noad MJ, Blomberg SP, Goldizen AW, Kniest E, Cato DH , et al. 2016. Factors driving the variability in diving and movement behavior of migrating

humpback whales (*Megaptera novaeangliae*): Implications for anthropogenic disturbance studies. Marine Mammal Science.

Lagerquist BA, Mate BR, Ortega-Ortiz JG, Winsor M, Urbán-Ramirez J. 2008. Migratory movements and surfacing rates of humpback whales (*Megaptera novaeangliae*) satellite tagged at Socorro Island, Mexico. Marine Mammal Science 24:815–830.

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

Martins CCA, Morete ME, Engel MH, Freitas AC, Secchi ER, Kinas PG. 2001. Aspects of habitat use patterns of humpback whales in the Abrolhos Bank, Brazil, breeding ground. Memoirs of the Queensland Museum 27:563-570.

Martins CCA. 2012. Study of Baleen Whales' Ecology and Interaction with Maritime Traffic Activities to Support Management of a Complex Socio-Ecological System. Doctoral Thesis. Université de Montréal, Montréal: Département de Géographie. 236 pages.

Mesnick SL. 1996. Sexual selection and biological diversification: Patterns and processes. Doctoral Thesis. University of Arizona, Tucson: Department of Ecology and Evolutionary Biology. 293 pages.

Monico JFG 2008 Posicionamento pelo GNSS – descrição, fundamentos e aplicações. UNESP, São Paulo.

Morete ME, Freitas AC, Engel MH, Pace RM, Clapham PJ. 2003. A novel behavior observed in humpback whales on wintering grounds at Abrolhos Bank (Brazil). Marine Mammal Science 19:694-707.

Morete ME. 2007. Caracterização temporal da estrutura de grupos e do comportamento de baleias jubarte na área de reprodução da região do Arquipélago dos Abrolhos (Bahia, Brasil). Doctoral Thesis. Universidade de São Paulo, São Paulo: Instituto de Biociências. 142 pages.

Morete ME, Bisi TL, Rosso S. 2007a. Temporal pattern of humpback whale (*Megaptera novaeangliae*) group structure around Abrolhos Archipelago breeding region, Bahia, Brazil. Journal of the Marine Biological Association of the United Kingdom 87:87-92.

Morete ME, Bisi TL, Rosso S. 2007b. Mother and calf humpback whale responses to vessels around the Abrolhos Archipelago, Bahia, Brazil. Journal of Cetacean Research and Management 9:241–248.

Morete ME, Bisi TL, Pace RM, Rosso S. 2008. Fluctuating abundance of humpback whales (*Megaptera novaeangliae*) in a calving ground off coastal Brazil. Journal of the Marine Biological Association of the United Kingdom 88:1229-1235.

Noad MJ, Cato DH. 2007. Swimming speeds of singing and non-singing humpback whales during migration. Marine Mammal Science 23:481–495.

Pavanato HJ, Wedekin LL, Guilherme-Silveira FR, Engel MH, Kinas PG. 2017. Estimating humpback whale abundance using hierarchical distance sampling. Ecological Modelling 358:10-18.

Prates APL, Gonçalves MA, Rosa MR 2012 Panorama da Conservação dos Ecossistemas Costeiros e Marinhos no Brasil. MMA, Brasília.

Rezende LF, Silva PA, Cirano M, Peliz A, Dubert J. 2011. Mean Circulation, Seasonal Cycle, and Eddy Interactions in the Eastern Brazilian Margin, a Nested ROMS Model. Journal of Coastal Research 27:329–347.

Rodrigues RR, Rothstein LM, Wimbush M. 2007. Seasonal Variability of the South Equatorial Current Bifurcation in the Atlantic Ocean: A Numerical Study. Journal of Physical Oceanography 37:16-30.

Rossi-Santos MR, Neto ES, Baracho CG, Cipolotti SR, Marcovaldi E, Engel MH. 2008. Occurrence and distribution of humpback whales (*Megaptera novaeangliae*) on the north coast of the State of Bahia, Brazil, 2000–2006. ICES Journal of Marine Science 65:667–673.

Sagnol O, Reitsma F. 2014. Correcting Positional Errors in Shore-Based Theodolite Measurements of Animals at Sea. Journal of Marine Biology 2014:1-8.

Santos MS. 2010. Sazonalidade e interação com embarcação do boto-cinza, *Sotalia guianensis*, (Cetacea: Delphinidae) no Porto do Malhado, Ilhéus, Bahia-Brasil. Master Thesis. Universidade Estadual de Santa Cruz, Ilhéus. 70 pages.

Schaffar A, Madon B, Garrigue C, Constantine R (2009) Avoidance of whale watching boats by humpback whales in their main breeding ground in New Caledonia.

Siciliano S, Moura JF, Filgueiras HR, Rodrigues PP, Jeite Jr. NO. 2012. Sightings of humpback whales on the Vitória-Trindade Chain and around Trindade Island, Brazil. Brazilian Journal of Oceanography 60:455-459.

Smultea MA. 1994. Segregation by humpback whale (*Megaptera novaeangliae*) cows with a calf in coastal habitat near the island of Hawaii. Canadian Journal of Zoology 72:805-808 811.

Smultea MA, Würsig B. 1995. Behavioral reactions of bottlenose dolphins to the Mega Borg oil spill, Gulf of Mexico 1990. Aquatic Mammals 25:171–181.

Stanistreet JE, Risch D, Van Parijs SM. 2013. Passive Acoustic Tracking of Singing Humpback Whales (*Megaptera novaeangliae*) on a Northwest Atlantic Feeding Ground. PLoS ONE 8:e61263. 10 pages.

Trudelle L, Cerchio S, Zerbini AN, Geyer Y, Mayer F, Jung J , et al. 2016. Influence of environmental parameters on movements and habitat utilization of humpback whales (*Megaptera novaeangliae*) in the Madagascar breeding ground. Royal Society Open Science 3:160616.

Vanicek P, Krakiwsky EJ. 1996. Geodesy: The Concepts. North - Holland Publishing Company.

Whitehead H, Moore MJ. 1982. Distribution and movements of West Indian humpback whales in winter. Canadian Journal of Zoology 60:2203-2211.

Whitehead H. 1983. Structure and stability of humpback whale groups off Newfoundland. Canadian Journal of Zoology 61:1391-1391.

Williams R, Trites AW, Bain DE. 2002. Behavioural responses of killer whales (*Orcinus orca*) to whale-watching boats: opportunistic observations and experimental approaches. Journal of Zoology 256:255-270.

Winn HE, Reichley NE. 1985. Humpback whale *Megaptera novaeangliae* (Borowski, 1781). In: Ridgway SH, Harrison P, editors. Handbook of marine mammals. London: Academic Press, p 241-273.

Würsig B, Cipriano F, Würsig M. 1991. Dolphin Movement Patterns: Information from Radio and Theodolite Tracking Studies. In: Pryor K, Norris KS, editors. Dolphin Societies - Discoveries and Puzzles. Berkeley: University of California Press, p 79-111.

Zar. 1974. Probabilities of Rayleigh's test statistics for circular data. Behavior Research Methods & Instrumentation 6:450.

Zerbini AN, Andriolo A, Heide-Jørgensen MP, Pizzorno JL, Maia YG, VanBlaricom GR , et al. 2006. Satellite-monitored movements of humpback whales *Megaptera novaeangliae* in the Southwest Atlantic Ocean. Marine Ecology Progress Series 313:295–304.

Zerbini AN, Andriolo A, Heide-Jørgensen MP, Moreira SC, Pizzorno JL, Maia YG , et al. 2011. Migration and summer destinations of humpback whales (*Megaptera novaeangliae*) in the western South Atlantic Ocean. Journal of Cetacean Research Manager 3:113–118.

**CAPÍTULO 3:**

**A REVIEW OF PERCUSSIVE BEHAVIOURS AS COMMUNICATION SIGNALS IN CETACEANS**

# UMA REVISÃO DOS COMPORTAMENTOS PERCUSSIVOS COMO SINAIS DE COMUNICAÇÃO EM CETÁCEOS

## RESUMO

No ambiente aquático, a comunicação acústica assume um papel importante devido à eficiência da propagação do som a longas distâncias. Algumas espécies de baleias e golfinhos realizam comportamentos aéreos conhecidos como comportamentos ativos na superfície. Estes comportamentos resultam em médios e grandes movimentos de água e produção de som que se propaga acima e abaixo da superfície da água. As funções destes comportamentos têm sido amplamente discutidas, e acredita-se que incluem remoção de ectoparasitas, forrageio, brincadeira, e produção de sinais bimodais para comunicação. Estes sons não vocais podem expressar informação sobre o estado motivacional dos animais, como por exemplo estresse, agressão, aborrecimento e excitação, e também podem ser usados para transmitir informação sobre o movimento e coordenação do grupo. Funcionalmente eles podem atuar como sinais de ameaça, indicadores sexuais, de localização, alarme ou atenção. Nesta revisão, o atual estado de arte sobre a ocorrência e possíveis funções dos comportamentos percussivos em cetáceos é verificado.

Palavras-chave**:** Batida de caudal. Comportamento ativo na superfície. Comunicação. Salto. Som.

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**A review of percussive behaviours as communication signals in cetaceans**

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## Abstract

In the aquatic environments, acoustic communication signals play important roles due to propagation efficiency of sounds over long distances. Some species of whales and dolphins perform aerial behaviours, also called surface-active behaviours. These behaviours result in medium to large splashes on the water surface, and in the production of soundwaves that propagate above and below the surface. The functions of these behaviours have been discussed at length, and are believed to include: removal of ectoparasites, foraging, play, and production of bimodal communication signals (acoustic and visual). These non-vocal sounds are thought to encode information about the sender's motivational state (e.g., stress, aggression, annoyance, dominance, and arousal) and they may also facilitate information transfer related to group movement and coordination. Functionally, they may operate as threats, location indicators, alarm displays, attention callers or sexual signals. This is a review of the current state of knowledge on the occurrence and on the possible functions of percussive behaviours in cetaceans.

## Introduction

Communication is a process wherein the sender produces a specialized signal that changes the likelihood of the receiver's behaviour, and can be associated with the mediation of social interactions (Dudzinski et al. 2009) during foraging, reproduction, territorial defence and group cohesion (Tyack 2000). The study of animal communication includes identifying which information is encoded in the signals produced, and how that information is used by receivers. Of course, in order to have this information exchange, the signal must be successfully transmitted (Brumm 2013). A signal is a cue that has the function of being used to communicate, either because it simply evolved for that function or because it is intentionally communicative (Donath 2007). Signalling systems are dynamic, and senders and receivers continuously adjust the signal and response to an economic balance of costs and benefits (Donath 2007) and constraints posed by the propagation medium and the characteristics of the environments (Bradbury and Vehrencamp 2011; Walker 1998).

The specific adaptations of cetaceans to aquatic environments include changes related to locomotion, breathing, diving and also perception and communication. The sensory modalities for communication in cetaceans include chemical (taste and olfaction), tactile, visual, electrical and acoustic (Dudzinski et al. 2009; Tyack 2000). Olfaction and vision became less important because these modalities are less efficient in the water (Frankel 2009). Due to the characteristics of the marine environment, the acoustic channel became the most efficient for long distance communication - whales can communicate across hundreds of kilometres (Tyack and Janik 2013). Even at closer ranges, sound became the principal means of communication for cetaceans (Dudzinski et al. 2009; Frankel 2009).

Sound production in cetaceans can be either vocal and non-vocal (Clark 1990; Herzing 2006). In vocal communication, they have a basic pneumatic mechanism for producing sound using air from the lungs. As they vocalize, the air passes from the lungs through the sound production organs, and is collected in sacs in the upper respiratory pathway, and it can be recycled back for further vocalization during the dive (Tyack and Janik 2013). In mysticetes, it is believed that the sound production organ is the larynx, with vibrating tissue presenting a single U-shaped fold parallel to the air flow (Reidenberg and Laitman 2007). Odontocetes produce a great variety of sounds, e.g. clicks, barks and whistles, when air passes through bony nasal nares. In both cases, the air passing through the vibrating membrane creates pressure oscillations that produce sound waves (Tyack and Janik 2013).

On the other hand, non-vocal communication implicates the production of sound but not through the vocal pathway (Paulos 2004). Percussive behaviours produce sounds from the impact of any part of the body with a resonating object; in cetaceans, these can be the water surface or another part of the body. Cetacean percussive sounds are produced by aerial displays (also known as surface-active behaviours – SAB) or jaw claps. Acrobatic behaviours that generate sounds have been observed in several species. Leaps in bottlenose dolphins (*Tursiops truncatus*) (Würsig and Würsig 1979) and Atlantic white-sided dolphins (*Lagenorhynchus acutus*) (Weinrich et al. 2001); lobtailing in sperm whales (*Physeter macrocephalus*) (Weller et al. 1996), pectoral slapping in humpback whales (*Megaptera novaeangliae*) (Whitehead 1985a), and spins in spinner dolphins (*Stenella longirostris*) (Hester et al. 1963; Norris et al. 1994) are examples of such aerial behaviours which produce detectable sounds underwater (Whitehead 2003). Other kinds of non-vocal sounds that are not percussive but have been described in cetaceans result from the emission of bubbles from blowholes which produce broadband sounds as a consequence of cavitation (Fripp 2005; Pryor 1986; Silber 1986).

Percussive behaviours are thought to be important in cetacean communication(Caldwell 1973; Clapham 2000; Dunlop et al. 2008; Kavanagh et al. 2016; Pearson 2017; Simmonds 2006; Waters and Whitehead 1990; Watkins and Wartzok 1985; Würsig et al. 1989) but few studies were able to study and quantify SAB (Pacheco et al. 2013), or advance our understanding of their meaning (Félix and Botero-Acosta 2012). Determining how communication contributes to coordination between individuals in a group is also essential to understand their social behaviour (Dudzinski et al. 2002).

The objective of this work is to compile existing information on percussive behaviours performed by cetaceans, describing and discussing the known behavioural patterns and their hypothesised functions, to verify if there are enough studies that support the hypothesis of its use for communication.


**Percussive behaviours and their contexts**

Percussive behaviours have been described for dolphins and whales in different contexts and assumed to function: to express the animals' motivation (Pryor 1986), to remove ectoparasites (Fish et al. 2006; Silva-Jr and Sazima 2006), to stun or disorient prey (Simon et al. 2005; Weinrich et al. 1992), to reaffirm social bonds (Norris and Dohl 1980), to play (Izidoro and Le Pendu 2012), as an agonistic display (Baker and Herman 1984) or even as a sexual display (Slooten 1994). They might express arousal (Pryor 1986), annoyance (Clapham 2000), stress

(Dawson 1991) and provide cues for the sender's location (Frankel et al. 1995). However, we should consider that social contexts that lead to the performance of these behaviours in adults may not be the same for calves (Cartwright et al. 2016) because high levels of exercise during early life stages also promote the development of myoglobin stores in young mysticetes.

Percussive behaviours known in cetaceans (Table 1) will be reviewed, and the contexts in which they occur will be used to tentatively separate them into those most likely and less likely to function for social communication, i.e., to identify the behaviours that are involved in the processes of expression of motivation of the sender and/or of changing the behaviour of one or more receivers.


**Whale breaches and dolphin leaps**

A breach of a whale varies from a full jump clear out of the water to leisurely surges with more than half of the body emerging (Whitehead 1985b). Humpback whales breach at all angles up to 70 degrees from the surface of the sea. The breach of a sperm whale is often more perpendicular to the surface, which might result from deeper dives, or to anatomical differences (smaller flukes and a narrower head) (Waters and Whitehead 1990). Two breaches styles are suggested: the animals can fall back on the water (true breaches) or with the belly (belly flops). Lunge is another movement related to breaches. It's a thrust movement at the surface showing less than 40% of the body (Whitehead 1985a) and can be executed horizontally, vertically or at any angle between those extremes (Whitehead 1985b). Humpback whales also perform tail breaching which is a hurling of the tail and caudal peduncle sideways out of the water (Clapham 2000).

Whitehead (1985a) noted that the occurrence of all aerial displays in humpback whales was more frequent during the winter than in the summer, i.e., during breeding season, and during the occurrence of fusion and fission events in humpback and sperm whales (Félix and Botero-Acosta 2012; Waters and Whitehead 1990; Whitehead 1985a), suggesting complex social structures (Félix 2004). For sperm whales, almost all breaches were performed by females and immatures which are more sociable individuals than males (Waters and Whitehead 1990). Breaching is "contagious", and the probability of a whale that is breaching being related to another individual nearby which is also breaching is high (Whitehead 1985b).

Dunlop et al. (2008) found higher breaching rates during humpback whale migrations, in groups containing only one adult compared with other groups and suggested that the breach signal may be an inter-group rather than an intra-group signal. Frank et al. (1995) observed that males stopped singing when another whale breaches, suggesting that the sound produced

by the display may contain relevant information for other whales. It could be one of the reasons why lone singers perform less aerial displays than groups without singers (Whitehead 1985a). Sousa-Lima (2007) observed a group of humpback whales breaching over 107 times in a row while recording a singer, in contrast to what Frankel et al.(1995) observed.

The breach of the humpback whale can reach sound levels of up to 182dB re 1 µPa (McCauley et al. 2000). Studies on the angles of the breaching whale with the water surface, the percentage of the body out of the water and which part of the body falls into the water (Whitehead 1985a; Whitehead 2003) are important to assess differences in the intensity of the sound produced. High-speed photo analyses showed that breaching consists of two splashes: one created when the animal falls to the surface of the water and begins a crater under it, and another (secondary splash/slap sound) produced when the crater collapses, creating cavitation (Würsig and Whitehead 2009). The decrease in sound pressure levels with increasing distance between individuals may affect the detectability of the signal, and in that way, should be more efficient as a communication signal among nearby animals (Whitehead 1985b). In fact, breaches are more likely to occur when groups are at distances less than 10 km apart than in groups that are more distant (Whitehead 1985b). At any rate, there is presently no consensus about the function of humpback whale breaches.

Norris et al. (1977) suggested that in gray whales (*Eschrichtius robustus*) breaches represent sexual displays and are associated with the presence of males. These active displays are also observed in Southern right whale related to mating behaviour (*Eubalaena australis*) (Payne 1986).

A dolphin leap is characterized by the emergence of the entire body vertically or near vertically above the surface. If the animal re-enters the water smoothly with the head first, it is called a clean-entry leap (Lusseau 2006); if the animal falls back into the water onto its belly or side it is called a noisy leap (Würsig and Würsig 1979). In captivity, the leap of the bottlenose dolphin can produce an acoustic pressure up to 181 dB re 1 µPa (Nachtigall et al. 2000) or even 189 dB re 1 µPa with an estimated maximum detection range of 840 m (Finneran et al. 2000).

Spinner dolphins perform diverse leaps, such as the characteristic "spin", when the dolphin rotates around its longitudinal axis in the air (Silva-Jr et al. 2005). In the "tail-over-head-leap", the animal bursts from the water and slings its tail over the head in a wide arc and re-enters the water tail first (Norris et al. 1994). These leaps are observed during the day and also during the night, when vision is less useful, thus potentially promoting group cohesion through repeated short range omnidirectional sound signals (Norris and Dohl 1980; Silva-Jr et

al. 2005). Norris et al. (1994) highlight that the bubbles produced by the re-entry into the water may also be a temporary echolocation target used to define the precise location of the sender. The plume of bubbles produced by these kinds of behaviours in spinner dolphins typically extends 4 m of length for a considerable time before it dissipates. The volume occupied by the bubbles will vary with the type of leap, and its communicative potential will vary with the location and its propagation characteristics.

Norris and Dohl (1980) proposed that in dolphins, leaps act as a social facilitator that reaffirms social bonds, preparing the group for foraging. Another possibility is that it helps capturing prey, e.g. in dusky dolphins (Würsig and Würsig 1980). Coscarella et al. (2003) found that Commerson's dolphins (*Cephalorhynchus commersonii*) are more likely to leap during the interaction with boats for short periods of time, and then returning to their previous behaviour, suggesting some sign of temporary stress. Sloten (1994) suggests that leaps are used in the context of play by Hector's dolphins (*Cephalorhynchus hectori)*, as observed in studies of Guiana dolphins (Izidoro and Le Pendu 2012), and it can also express annoyance and general arousal (Pryor 1986; Würsig et al. 1989). Leaping was also observed in short-finned pilot whales (*Globicephala macrorhynchus*) in the context of aggression towards to sperm whales (Weller et al. 1996).

Certainly, breaching and leaping have high energetic costs for aquatic mammals (Kavanagh et al. 2016; Whitehead 2002). It is observed not only in very active species such as the dusky dolphin (*Lagenorhynchus obscurus*) (Würsig and Würsig 1980), spinner dolphin (Norris and Dohl 1980), or even the humpback whale (Félix 2004; Whitehead 1985b), but also in less conspicuous species such as the Guiana dolphin (*Sotalia guianensis*) (Souto et al. 2006), fin whale (*Balaenoptera physalus*) (Kot et al. 2013; Marini et al. 1996) and bowhead whale (*Balaena mysticetus*) (Würsig et al. 1989).

During a jumping sequence, there is a tendency of the next leap be lower than the previous one (Norris et al. 1977), indicated by the height of the leap or by the proportion of the body that is outside the water, which may result from fatigue (Whitehead 1985a; Würsig and Würsig 1980). Würsig et al. (1989) found that in bowhead whales, the intervals of occurrence of breaches, lobtaling and pectoral slaps increase respectively, which can be justified due to the amount of body mass that is necessary to move above the water surface. The energy consumed by a humpback whale during a breach might reach 1/100 of the daily minimum energy required, which could become a major expense considering that it is usually observed as a repetitive behaviour (Sousa-Lima 2007; Whitehead 1985a). The estimated speed that a humpback whale reaches before jumping is 27 km/h (Whitehead 1985a) and of a sperm whale

is 22 km/h (Whitehead 2003). Au and Weihs (1980) reported that for dolphins at high speed the repetitive leaps ("porpoising") are a way to save energy in fast and straight movement.

**Lobtail/ tail slap**

Lobtails or tail slaps are fluke thrashes on the surface of the water while the animal is nearly vertical at the surface (Waters and Whitehead 1990) either dorsal or ventral side up, generating a splash (Noren et al. 2009). It is observed in mysticetes and odontocetes. Typically, larger animals stay with the body at a vertical angle to the water surface, while smaller animals remain with the body parallel to the surface of the water (Würsig and Whitehead 2009).

Most observations of tail slaps are described as aggressive - defensive behaviour. Southern right whales and bowhead whales were observed performing lobtailing and pectoral slaps in the presence of killer whales (*Orcinus orca*) (Cummings et al. 1972; Payne 1986; Würsig et al. 1989). Baker and Herman (1984) suggest that lobtailing plays an important role in competitive groups of humpback whales, and Silber (1986) also interpret it as related to aggression. The tail slap is the most frequently observed aerial behaviour by Northern and Southern resident killer whales associated with the presence of vessels (Noren et al. 2009; Williams et al. 2002). During "marguerite formations", sperm whales were observed tail slapping apparently as defence displays in the presence of short finned pilot whales (Weller et al. 1996). Tail slaps have been reported in small cetaceans to expresses annoyance (Herzing 2006) and sometimes warning signals, functioning as alarm calls for the entire group (Pryor 1986). For Hector's dolphins it is an indication of motivation such as aggression (Slooten 1994). For bottlenose dolphins in the South Atlantic these displays were correlated to motor boat engine start-ups and group fusions (Würsig and Würsig 1979). They might also be used to call attention in dolphins (Herzing 2006) and sperm whales (Waters and Whitehead 1990) and were observed during surface feeding of humpback and killer whales (Allen et al. 2013; Laland and Janik 2006; Simon et al. 2005; Weinrich et al. 1992).

Humpback whales tail slap can reach up to 192 dB re 1 µPa (Thompson et al. 1986). In captivity bottlenose dolphin tail slap reach up to 175 dB re 1 µPa (Nachtigall et al. 2000) and 168 dB re 1 µPa with estimated detection range up to 180 m (Finneran et al. 2000).

This behaviour demands less energetic cost than a breach and tends to be performed by animals that move at lower speeds (Waters and Whitehead 1990; Whitehead 1985a). When the frequency of tail slapping is very high in dolphins, it has been called "motorboating"

(Würsig and Whitehead 2009; Würsig and Würsig 1980) because it results in sounds that resemble the noise of a slowly moving motorboat (Norris et al. 1994).

**Other aerial behaviours**

Flippering or pectoral slap is the movement of pectoral fin striking the surface of the water. Corkeron (1995) observed more pectoral slaps of humpback whales in the presence of vessels. In competitive groups, the principal male escort was observed to slap the pectoral fins while it was inverted on the surface (Baker and Herman 1984). Silber (1986) suggested that it represents an agonistic behaviour among males. Deakos (2002), on the other hand, noted that in competitive groups, female tends to flipper, which seems to encourage competition between males. Pectoral slaps were also observed in bowhead whales (Würsig et al. 1989) and Southern right whale (Payne 1986). Dunlop et al. (2008) did not observe the "slapping" (considered as lobtailing and flippering) in solitary animals, and it was more observed in dyads and in groups before splitting. Kavanagh et al. (2016) noted that the probability of occurrence of pectoral slapping decreased with increasing number of singers within 10 km. Humpback whale pectoral fin slap may produce acoustics pressures between 162 and 171 dB re 1 µPa (Thompson et al. 1986). In small cetaceans it appears to occur associated with sexual behaviour (Pryor 1986).

Another percussive behaviour is the head slap, the movement with a strike of the head on the water surface (Corkeron 1995) which seems to express annoyance or general arousal (Pryor 1986). It is also observed in spinner and Guiana dolphins (Izidoro and Le Pendu 2012; Norris and Dohl 1980), and in humpback whales as a proposed aggressive display (Silber 1986).

**Jaw claps**

Jaw claps are observed in odontocetes. Dolphin, while submerged, open the jaws, exposing the teeth, then suddenly close them producing a loud percussive sound. Jaw claps are usually associated with a peculiar body posture in which the animal arches its back while facing its opponent (Paulos 2004), representing dominance (McBride and Hebb 1948) or threat (Pryor 1986).

Jaw claps have been observed in Atlantic spotted dolphins (*Stenella frontalis*) and bottlenose dolphins, occasionally during agonistic or aggressive interspecific interactions (Herzing 1996; Herzing 2006) and also intraspecific interactions (Overstrom 1963). Jaw claps have been observed in river dolphins of the genus *Inia* during aggressive interspecific interactions (Sousa-Lima, unpublished data). The acoustic pressure of jaw claps in captive bottlenose

dolphins can reach up to 201 dB re 1 µPa, with estimated detection ranges up to 1040 m (Finneran et al. 2000). This behaviour is also observed in sperm whales but rarely occurs in aggressive contexts (Whitehead 2003).

**Table 1** Description summary of the percussive behaviours observed in cetaceans and their possible functions according with the most recent literature

| Percussive behaviours signals | Definition | Functions |
|---|---|---|
| Breaching | Varies from a full jump clear of the water to leisurely surges with more than half of the body of a whale emerging (Whitehead 1985b) | Aggressive (Tyack and Whitehead 1983) and sexual displays (Norris et al. 1977), call attention (Dunlop et al. 2010; Whitehead 1985a), social interactions (Waters and Whitehead 1990; Whitehead 1985a) |
| Leaping | Dolphin leaves the water vertically, its entire body clears out of the water, and then re-enters into the water (Lusseau 2006) | Location and deployment of school (Norris et al. 1994), social facilitator during feeding (Norris and Dohl 1980), motivation (Slooten 1994), annoyance (Pryor 1986; Würsig et al. 1989), arousal (Pryor 1986; Würsig et al. 1989), aggression (Weller et al. 1996), stress (Coscarella et al. 2003), play (Pryor 1986; Würsig et al. 1989) |
| Lobtailing | Thrashes of the flukes onto the water while the animal is nearly vertical in the water (Waters and Whitehead 1990) | Interspecific interactions (Cummings et al. 1972; Payne 1986), aggression (Silber 1986; Slooten 1994), defense (Weller et al. 1996), annoyance (Herzing 2006), warning (Pryor 1986) and attention signals (Herzing 2000; Waters and Whitehead 1990), feeding (Weinrich et al. 1992; Simon et al., 2005) |
| Flippering | Animal strikes the surface of the water with its pectoral fin (Corkeron 1995) | Agonistic (Silber 1986) and sexual displays (Deakos 2002; Pryor 1986) |
| Head slap | Animal strikes on the surface of the water with its head (Corkeron 1995) | Annoyance, agression (Silber 1986) and arousal (Pryor 1986) |
| Jaw claps | Open the jaw, exposing the teeth, then close producing a loud percussive sound (Paulos 2004) | Dominance (McBride and Hebb 1948), threat (Pryor 1986), aggressive displays (Herzing 1996; Herzing 2006) |

**Discussion**

Some sounds produced through percussive behaviours are described as loud, intense, and broadband (Dunlop et al. 2008; Thompson et al. 1986), and are clearly associated with communication (Dunlop et al. 2008; Kavanagh et al. 2016). However, to demonstrate the occurrence of communication, the sound emitted by an individual must modify the behaviour of another individual in a predictable way (Clark 1990). This requires that the behaviour and the sounds produced by each individual are followed and identified (Clark 1990), which is often very difficult in cetaceans. Besides, the visual-based definition of "group", as an aggregation of animals that are close enough with coordinated behaviour (Shane 1990; Whitehead 1983), seems inappropriate considering the potential of acoustic communication. Since distant individuals may hear each other over long distances, an animal that is in acoustic contact with another should not be considered alone (Payne and Webb 1971).

In gregarious animals, there is a need to communicate with individuals about what to do, which direction to follow, as in the case of spinner dolphins that can indicate which direction to take through leaps (Norris et al. 1994). The occurrence of aerial displays seems to be related to the social complexity of structure of the groups (Waters and Whitehead 1990; Whitehead 1985a). Surface-active behaviour involves percussive sounds production, which may be important to define hierarchies, establish alliances or guide the whales (Félix 2004). If intentional actions are reliable predictors of behavioural events, they can become signals through a process of ritualization (Hauser 1997), becoming part of the communication process. An example is the lobtail feeding perform by humpback whales in the Gulf of Maine which consists of bubble-feeding resulting of striking the water's surface one to four times with the ventral side of the fluke. This behaviour is transmitted horizontally between individuals of the populational though its true function is not understood (Allen et al. 2013).

Signal detection theory proposes that the evolution of exaggerated signals should result in increased detectability or discriminability of signals by the intended receivers (Zuk and Kolluru 1998), reducing the probability of confusion (Wiley and Richards 1982). However, an exaggeration of signals could increase the costs for the sender, including additional energy expenditure and higher risks of interception by undesirable receivers such as predators or rivals (Wiley 2013; Zuk and Kolluru 1998). Nevertheless, it is not the cost of the signal that is considered primarily for the evolution of signals but the effect on the receiver, with the cost as a secondary consideration (Wiley 2013). The strategy to improve signal detection during high levels of ambient noise is to modify the behaviour of acoustic communication (Dunlop et al.

2013). While wind speeds and background noise levels increase, whales gradually change vocal communication by sounds produced on the surface of the water, although the two types of signals are maintained in the repertoire (Dunlop et al. 2010; Dunlop et al. 2013). Maybe the sounds produced on the surface of the water are less likely to be confused with high noise because they have higher frequencies ranges, and can be used to call attention (Dunlop et al. 2010). As the peak levels of the sounds produced on the surface are about 6 dB higher compared to social vocalizations (Dunlop et al. 2013), the information reception by the receivers must compensate the energy expenditure related to the production of the percussive signals.

Although vocal communication in mysticetes can be transmitted to greater distances and contain more information than percussive signals, these can be used easily to locate individuals nearby. They can call attention (Dunlop et al. 2010) and make receivers more likely to pay attention or even to get closer to senders, and in that way, communication becomes more efficient. Other studies have indicated that animals improve the efficiency of long-range communication through the modulation of signal design and the facultative addition of an alert (Ord and Stamps 2008). Signals that can only be detected at short distances could also help to prevent eavesdropping by conspecifics (Dawson 1991) and can prevent unwanted detection by prey and predators (Lusseau 2006). As individuals remain next to each other, males can use these signals to show solidarity or even threat, depending on the nature of the relationship between the individuals of the group (Barrett and Würsig 2014).

From the studies carried out until today, the hypothesis that percussive signals could be involved in the communication process between cetaceans seems valid. These behaviours are used in several contexts and except when used to stun prey, possibly to remove ectoparasites, and to play, i.e., when it occurs with no other apparent purpose than pleasurable (Würsig 2009), all other contexts are associated with communication, when individuals express their motivation states such as stress, annoyance, aggression, arousal and dominance, and also act as indicators of location, sexual behaviours and attention signals for individuals around them. Tail slap is the behaviour that is most related to undesirable contexts such as stress, aggression and annoyance. However, as we observed, the large repertoire of behaviours that generate percussive sounds in cetaceans enable their use in a wide range of situations and in different contexts such the leap. These different contexts may hinder and limit the understanding of their function when their main objective is not the emission of signal. Studies to measure acoustic characteristics as frequency, source levels and distances to which sounds can spread could help the understanding of the functional role in the communication,

integrating the signals in behaviour and social context of the groups. With the increase of anthropogenic noise in the ocean, several studies are being performed to verify the change in the vocal communication of cetaceans to anthropogenic noise, and it is important to associate the component of the non-vocal acoustic signals for species that have an active repertoire of percussive behaviour.

## Acknowledgments

## References

Allen J, Weinrich M, Hoppitt W, Rendell L (2013) Network-Based Diffusion Analysis Reveals Cultural Transmission of Lobtail Feeding in Humpback Whales Science 340:485-488

Au D, Weihs D (1980) At high speeds dolphins save energy by leaping Nature 284:548-550

Baker CS, Herman LM (1984) Aggressive behavior between humpback whales (*Megaptera novaeangliae*) wintering in Hawaiian waters Canadian Journal of Zoology 62:1922-1937

Barrett L, Würsig B (2014) Why Dolphins are not Aquatic Apes Animal Behavior and Cognition 1:1-18 doi:DOI: 10.12966/abc.02.01.2014

Bradbury JW, Vehrencamp SL (2011) Principles of Animal Communication. 2nd edn. Sinauer Associates, Sunderland, MA

Brumm H (2013) Animal Communication and Noise vol 2. Springer, New York. doi:10.1007/978-3-642-41494-7

Caldwell DK (1973) Dolphin Communication Journal of the Acoustical Society of America 53

Cartwright R et al. (2016) Tracking the Development of Muscular Myoglobin Stores in Mysticete Calves PLoS ONE 11:e0145893

Clapham PJ (2000) The Humpback Whale: Seasonal Feeding and Breeding in a Baleen Whale. In: Mann J, Connor RC, Tyack PL, Whitehead H (eds) Cetacean Societies: Field Studies of Dolphins and Whales. The University of Chicago Press, Chicago, pp 173-196

Clark CW (1990) Acoustic behavior of mysticete whales. In: Thomas JA, Kastelein RA (eds) Sensory Abilities of Cetaceans. Springer Science+Business Media, New York, pp 571-584

Corkeron PJ (1995) Humpback whales (*Megaptera novaeangliae*) in Hervey Bay, Queensland: behaviour and responses to whale-watching vessels Canadian Journal of Zoology 73:1290- 1299

Coscarella MA, Dans SL, Crespo EA, Pedraza SN (2003) Potential impact of unregulated dolphin watching activities in Patagonia Journal Cetacean Research Manager 5:77–84

Cummings WC, Fish JF, Thompson PO (1972) Sound production and other behavior of southern right whales, *Eubalaena australis* Transactions of The San Diego Society of Natural History 17:1-13

Dawson SM (1991) Clicks and Communication: The Behavioural and Social Contexts of Hector's Dolphin Vocalizations Ethology 88:265-276

Deakos MH (2002) Humpback Whale (*Megaptera Novaeangliae*) Communication: The Context and Potential Functions of Pec-slapping Behavior on the Hawai'ian Wintering Grounds. University of Hawaii Library

Donath J (2007) Signals, cues and meaning. In: Signals, Truth and Design. MIT Press,

Dudzinski KM, Thomas JA, Douaze E (2002) Communication. In: Perrin WF, Würsig B, Thewissen JGM (eds) Encyclopedia of Marine Mammals. First edn. Academic Press, San Diego, pp 248-268

Dudzinski KM, Thomas JA, Gregg JD (2009) Communication in Marine Mammals. In: Perrin WF, Würsig B, Thewissen JGM (eds) Encyclopedia of Marine Mammals. Second edn. Academic Press, San Diego, pp 260-269

Dunlop RA, Cato DH, Noad MJ (2008) Non-song acoustic communication in migrating humpback whales (*Megaptera novaeangliae*) Marine Mammal Science 24:613–629

Dunlop RA, Cato DH, Noad MJ (2010) Your attention please: increasing ambient noise levels elicits a change in communication behaviour in humpback whales (*Megaptera novaeangliae*) Proceedings of the Royal Society B 277:2521–2529

Dunlop RA, Noad MJ, Cato DH Modification of humpback whale social sound repertoire and vocal source levels with increased noise. In: America ASo (ed) Proceedings of Meetings on Acoustics, Montreal, 2013. American Institute of Physics, pp 1-6. doi:10.1121/1.4799213

Félix F (2004) Assessment of the level of surface activity in humpback whales during the breeding season Latin America Journal of Aquatic Mammals 3:25-36

Félix F, Botero-Acosta N (2012) Evaluating Humpback Whale (*Megaptera novaeangliae*) Social Behaviour Through Sexing Active Individuals Aquatic Mammals 38:311-316

Finneran JJ, Oliver CW, Schaefer KM, Ridgway SH (2000) Source levels and estimated yellowfin tuna (*Thunnus albacares*) detection ranges for dolphin jaw pops, breaches, and tail slaps Journal of the Acoustic Society of America 107:649-656

Fish FE, Nicastro AJ, Weihs D (2006) Dynamics of the aerial maneuvers of spinner dolphins The Journal of Experimental Biology 209:590-598 doi:doi:10.1242/jeb.02034

Frankel AS (2009) Sound Production. In: Perrin WF, Würsig B, Thewissen JGM (eds) Encyclopedia of Marine Mammals. Academic Press, San Diego, pp 1056-1071

Frankel AS, Clark CW, Herman LM, Gabriele CM (1995) Spatial distribution, habitat utilization, and social interactions of humpback whales, *Megaptera novaeangliae*, off Hawai's, determined using acoustic and visual techniques Canadian Journal of Zoology 73:1134-1146

Fripp D (2005) Bubblesstream whistles are not representative of a bottlenose dolphin's vocal repertoire Marine Mammal Science 21:29-44

Hauser MD (1997) The Evolution of Communication. MIT Press, Massachusetts

Herzing DL (1996) Vocalizations and associated underwater behavior of free-ranging Atlantic spotted dolphins, *Stenella frontalis* and bottlenose dolphins, *Tursiops truncatus* Aquatic Mammals 22:61-79

Herzing DL (2000) Acoustics and social behaviour of wild dolphins: implications for a sound society. In: Au WL, Popper AN, Fay RR (eds) Hearing by Whales and Dolphins. Springer, New York, pp 225-272

Herzing DL (2006) The Currency of Cognition: Assessing Tools, Techniques, and Media for Complex Behavioral Analysis Aquatic Mammals 32:544-553 doi:10.1578/AM.32.4.2006.544

Hester FT, Hunter JR, Whitney RR (1963) Jumping and Spinning Behavior in the Spinner Porpoise Journal of Mammalogy 44:586-588

Izidoro FB, Le Pendu Y (2012) Estuarine dolphins (*Sotalia guianensis*, Cetacea, Delphinidae) play at Porto de Ilhéus harbor, Bahia, Brazil Pan-American Journal of Aquatic Sciences 7:27-36

Kavanagh AS et al. (2016) Evidence for the functions of surface-active behaviors in humpback whales (*Megaptera novaeangliae*) Marine Mammal Science doi:doi:10.1111/mms.12374

Kot BW, Zbinden D, Sears R (2013) Aerial behavior by the fin whale (*Balaenoptera physalus*) in the wake of a freighter and near other boats Marine and Freshwater Behaviour and Physiology 46:267-272 doi:DOI:10.1080/10236244.2013.803695

Laland KN, Janik VM (2006) The animal cultures debate TRENDS in Ecology and Evolution 21:542-547

Lusseau D (2006) Why do dolphins jump? Interpreting the behavioural repertoire of bottlenose dolphins (Tursiops sp.) in Doubtful Sound, New Zealand Behavioural Processes 73:257–265 doi:10.1016/j.beproc.2006.06.006

Marini L, Consiglio C, Catalano B, Valentini T, Villetti G (1996) Aerial behavior in fin whales (*Balaenoptera physalus*) in the Mediterranean Sea Marine Mammal Science 12:89-495

McBride AF, Hebb DO (1948) Behavior of the captive bottle-nose dolphin, *Tursiops truncatus* Journal of Comparative and Physiological Psychology 41:111-123

McCauley RD et al. (2000) Marine seismic surveys - A study of enviromental implications APPEA Journal:692-708

Nachtigall PE, Au WWL, Pawloski JL, Andrews K, Oliver CW (2000) Measurements of the low frequency components of active and passive sounds produced by dolphins Aquatic Mammals 26:167–174

Noren DP, Johnson AH, Rehder D, Larson A (2009) Close approaches by vessels elicit surface active behaviors by southern resident killer whales Endangered Species Research 8:179–192 doi:10.3354/esr00205

Norris KS, Dohl TP (1980) Behavior of the havaiian spinner dolphin, *Stenella longirostris* Fishery Bulletin 70:821-849

Norris KS, Goodman RM, Villa-Ramirez B, Hobbs L (1977) Behavior of california gray whale, *Eschrichtius robustus*, in Southern Baja California, Mexico Fishery Bulletin 75:159-172

Norris SK, Wursig B, Wells RS (1994) Aerial Behavior. In: Norris KS, Wursig B, Wells RS, Wursig M (eds) The Hawaiian Spinner Dolphin. University of California Press, Berkeley, pp 103-121

Ord TJ, Stamps JA (2008) Alert signals enhance animal communication in "noisy" environments PNAS 105:18830–18835

Overstrom NA (1963) Association Between Burst-Pulse Sounds and Aggressive Behavior in Captive Atlantic Bottlenosed Dolphins (*Tursiops truncatus*) Zoo Biology 2:93-103

Pacheco AS, Silva S, Alcorta B, Balducci N, Guidino C, Llapapasca MA, Sanchez-Salazar F (2013) Aerial behavior of humpback whales *Megaptera novaeangliae* at the southern limit of the southeast Pacific breeding area Revista de Biología Marina y Oceanografía 48:185-191

Paulos RD (2004) Non-vocal communication in the atlantic spotted dolphin (*Stenella frontalis*) and the indo-pacific bottlenose dolphin (*Tursiops aduncus*). University of Southern Mississippi

Payne RS (1986) Long Term Behavioral Studies of the Southern Right Whale (*Eubalaena australis*) Report International Whaling Commission (Special Issue) 10:161-167

Payne RS, Webb D (1971) Orientation by means of long range acoustic signaling in baleen whales Annals of the New York Academy of Sciences 188:110-141

Pearson HC (2017) Unravelling the function of dolphin leaps using the dusky dolphin (*Lagenorhynchus obscurus*) as a model species Behaviour 154:563–581 doi:doi:10.1163/1568539X-00003434

Pryor KW (1986) Non-acoustic communicative behavior of the great whales: Origins, comparisons, and implications for management Report International Whaling Commission (Special Issue) 8:89-96

Reidenberg JS, Laitman JT (2007) Discovery of a Low Frequency Sound Source in Mysticeti (Baleen Whales): Anatomical Establishment of a Vocal Fold Homolog The Anatomical Record 290:745-759 doi:doi:10.1002/ar.20544

Shane SH (1990) Behavior and ecology of the bottlenose dolphin at Sinabel Island, Florida. In: Leatherwood S, Reeves RR (eds) The bottlenose dolphin. Academic Press, San Francisco, pp 245-265

Silber GK (1986) The relationship of social vocalizations to surface behavior and aggression in the Hawaiian humpback whale (*Megaptera novaeangliae*) Canadian Journal of Zoology 64:2075–2080

Silva-Jr JM, Sazima I (2006) Whalesuckers on spinner dolphins: an underwater view Marine Biodiversity Records 1:1-5 doi:10.1017/S1755267206002016

Silva-Jr JM, Silva FJL, Sazima I (2005) Rest, nurture, sex, release, and play: diurnal underwater behaviour of the spinner dolphin at Fernando de Noronha Archipelago, SW Atlantic Journal of Ichthyology and Aquatic Biology 9:161-176

Simmonds MP (2006) Into the brains of whales Applied Animal Behaviour Science 100:103–116

Simon M, Wahlberg M, Ugarte F, Miller LA (2005) Acoustic characteristics of underwater tail slaps used by Norwegian and Icelandic killer whales (*Orcinus orca*) to debilitate herring (*Clupea harengus*) The Journal of Experimental Biology 208:2459-2466 doi:10.1242/jeb.01619

Slooten E (1994) Behavior of hector's dolphin: classifyng behavior by sequences analysis Journal of Mammalogy 75:956-964

Sousa-Lima RS (2007) Acoustic Ecology of Humpback Whales (*Megaptera novaeangliae*) in the Abrolhos National Marine Park, Brazil. Doctoral Theses, Cornell University

Souto A, Araújo JP, Geise L, Araújo ME (2006) The surface behavior of the estuarine dolphin in Baía dos Golfinhos, RN, Brazil: a field and comparative study Revista Brasileira de Zoociências 8:183-192

Thompson PO, Cummings WC, Ha SJ (1986) Sounds, source levels, and associated behavior of humpback whales, Southeast Alaska Journal of the Acoustical Society of America 80:735-740

Tyack PL (2000) Functional Aspects of Cetacean Communication In: Mann J, Connor RC, Tyack PL, Whitehead H (eds) Cetacean Societies: Field Studies of Dolphins and Whales. The University of Chicago Press, Chicago and London, pp 270-307

Tyack PL, Janik VM (2013) Effects of Noise on Acoustic Signal Production in Marine Mammals. In: Brumm H (ed) Animal Communication and Noise. Springer, New York, pp 251-271

Tyack PL, Whitehead H (1983) Male competition in large groups of wintering humpback whales Behaviour 83:132-154

Walker SF (1998) Animal Communication. In: Mey JL (ed) Concise Encyclopedia of Pragmatics. Elsevier, Amsterdam, pp 26-35

Waters S, Whitehead H (1990) Aerial behaviour in sperm whales Canadian Journal of Zoology 68:2076-2082

Watkins WA, Wartzok D (1985) Sensory Biophysics of Marine Mammals Marine Mammal Science 1:219-260

Weinrich MT, Belt CR, Morin D (2001) Behavior and ecology of the atlantic white-sided dolphins (*Lagenorhynchus acutus*) in coastal New England waters Marine Mammal Science 17:231-248

Weinrich MT, Schilling MR, Belt CR (1992) Evidence for acquisition of a novel feeding behaviour: lobtail feeding in humpback whales, *Megaptera novaeangliae* Animal Behaviour 44:1059-1072

Weller DW, Würsig B, Whitehead H, Norris JC, Lynn SK, Davis RW (1996) Observation of an interaction between sperm whales and short-finned pilot whales in the Gulf of Mexico Marine Mammal Science 12:588-594 doi:10.1111/j.1748-7692.1996.tb00071.x

Whitehead H (1983) Structure and stability of humpback whale groups off Newfoundland Canadian Journal of Zoology 61:1391-1391

Whitehead H (1985a) Humpback Whale Breaching Investigations of Cetacea 17:117-155

Whitehead H (1985b) Why Whales Leap Scientific America 252:84-93

Whitehead H (2002) Breaching. In: Perrin WF, Würsig B, Thewissen JGM (eds) Encyclopedia of Marine Mammals. Academic Press, San Diego, pp 162-164

Whitehead H (2003) Sperm Whales: Social evolution in the ocean. University of Chicago, Chicago

Wiley RH (2013) Signal Detection, Noise, and the Evolution of Communication. In: Brumm H (ed) Animal Communication and Noise, vol 2. Springer, New York, pp 7-32

Wiley RH, Richards DG (1982) Adaptations for acoustic communication in birds: sound transmission and signal detection. In: Kroodsma DH, Miller EH (eds) Acoustic communication in birds, vol 1. Academic Press, New York, pp 131–181

Williams R, Trites AW, Bain DE (2002) Behavioural responses of killer whales (*Orcinus orca*) to whale-watching boats: opportunistic observations and experimental approaches Journal of Zoology 256:255-270 doi:101017/S0952836902000298

Würsig B (2009) Playful Behavior. In: Perrin WF, Würsig B, Thewissen JGM (eds) Encyclopedia of Marine Mammals. Second edn. Academic Press, San Diego, pp 885-888

Würsig B, Dorsey EM, Richardson WJ, Wells RS (1989) Feeding, aerial and play behaviour of the bowhead whale, *Balaena mysticetus*, Summering in the Beaufort Sea Aquatic Mammals 15:27-37

Würsig B, Whitehead H (2009) Aerial Behavior. In: Perrin WF, Würsig B, Thewissen JGM (eds) Encyclopedia of Marine Mammals. Second edn. Academic Press, San Diego, pp 5-11

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

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

Zuk M, Kolluru GR (1998) Exploitation of sexual signals by predators and parasitoids The Quarterly Review of Biology 73:415–438

**CAPÍTULO 4:**

**MONITORING THEMES LINEAGES IN THE HUMPBACK WHALE SONGS OFF BRAZIL**

# MONITORAMENTO DAS LINHAGENS DOS TEMAS NO CANTO DAS BALEIAS-JUBARTE NO BRASIL

## RESUMO

As baleias-jubarte migram para a costa brasileira durante o inverno para se reproduzir e ter os seus filhotes. Os machos cantam complexos cantos com padrões repetitivos que são estruturados hierarquicamente em unidades, frases e temas. Cada população tem a tua própria versão do canto que muda gradualmente ao longo do tempo. Funções relacionadas à seleção sexual são descritas para a ocorrência do comportamento de canto. Os objetivos deste estudo são: 1) caracterizar a estrutura do canto em 2014 e 2015 em uma área de reprodução de Serra Grande (estado da Bahia, Brasil); 2) analisar a variação intra e interanual das frases dentro do ciclo do canto; e 3) quantificar a evolução do canto entre os anos usando o índice de similaridade da distância de *Levenshtein*. Foram descritos oito temas para ambos os anos, incluindo estáticos, progressivos, e sem padrão. Foram observadas alterações no canto entre os dois anos. Novas unidades apareceram, unidades já presentes sofreram alterações, e temas desapareceram e foram adicionados ao canto. Foi observada variação no número de frases repetidas dentro de cada tema, mas a sequência dos temas dentro do ciclo do canto não mudou na nossa amostra. O canto apresentou 50% de similaridade entre os anos. Métodos quantitativos e robustos devem continuar a ser aplicados no estudo da evolução do canto ao longo dos anos e entre áreas geográficas para melhor entender este comportamento complexo sem a subjetividade associada com as análises de canto qualitativas.

Palavras-chave: Comportamento de canto. Costa brasileira. Distância de *Levenshtein*. Evolução. Frases.

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**Monitoring themes lineages in the humpback whale song off Brazil**

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**Abstract**

Humpback whales migrate to the Brazilian coast during the austral winter to reproduce and calve. Males sing long complex songs with repetitive patterns which are structured hierarchically into units, phrases and themes. Each population has its own song version that gradually changes over time. Functions related to sexual selection are described for the occurrence of singing behaviour. The objectives of this study were manifold: 1) define the song structure in 2014 and 2015 in the reproductive area of Serra Grande (Bahia state, Brazil); 2) analyse intra and inter-annual variations of phrases within song cycles and 3) quantify the evolution of song between the years using the Levenshtein distance similarity index (LSI). Eight themes have been described for both years, including static, shifting, and unpatterned themes. Changes in song between the two years were observed. New units appeared, existing units have been modified, and themes have been subtracted and added to the song. Variation in the number of repeated phrases within each theme was observed but the sequence of themes within the song cycle has not changed in our sample. Song presented a similarity of 50% between the years according to the Levenshtein index. Quantitative and robust methods should continue to be applied to study the evolution of singing behaviour across years and geographical areas to better understand this complex behaviour without the subjectivity associated with qualitative song analyses.

Keywords: Brazilian coast, evolution, Levenshtein distance, phrases, singing behaviour

**Introduction**

Humpback whales (*Megaptera novaeangliae*) migrate to the Brazilian coast to breed and calve between July and November (Martins et al. 2001). Mainly during the breeding season, males (Baker and Herman 1984, Smith et al. 2008) sing complex songs (Payne and McVay 1971) but song also occurs along migratory corridors (Noad and Cato 2007) and in feeding areas (Stanistreet et al. 2013, Vu et al. 2012).

Unlike other vocalizations emitted by humpback whales of both sexes as social sounds (Dunlop et al. 2007, Silber 1986, Zoidis et al. 2008), the song has continuous and repetitive patterns (Payne and McVay 1971, Winn and Winn 1978). Song is structured hierarchically in units, phrases and themes: a sequence of combined units composes a phrase, the repetition of that phrase constitutes a theme and the cyclical repetition of themes is considered the song (Cholewiak et al. 2013, Payne and McVay 1971). Despite this repetitive pattern, variation in song occurs within and between individuals (Arraut and Vielliard 2004, Cerchio et al. 2001, Cholewiak et al. 2013, Payne and McVay 1971). However, all the singers in a population sing fundamentally the same version at the same time (Noad et al. 2000). Each population presents its own song version that gradually changes over time (Arraut and Vielliard 2004, Darling 2009, Darling and Sousa-Lima 2005, Winn and Winn 1978). Units may be excluded, included, and modified, leading to the disappearance or introduction of new themes (Arraut and Vielliard 2004, Cerchio 1993, Eriksen et al. 2005, Hatum 2015, Payne and McVay 1971). These modifications were thought to occur along the breeding season and during the feeding season, songs remained stable (Darling 2009). However, Garland et al. (2013) showed that song transmission could also occur in feeding grounds. The process by which changes occur is poorly understood but learning (Arraut and Vielliard 2004) and horizontal cultural transmission are suggested (Cerchio et al. 2001, Garland et al. 2011, Noad et al. 2000). Noad et al. (2000) found that the population of eastern Australia adopted the song of the population of western Australia after the migration of some individuals. Song similarities were already been verified between different populations separated by long distances, showing that some level of acoustic contact occurs (Darling and Sousa-Lima 2005).

Multiple functions associated with sexual selection are proposed for male singing (Smith et al. 2008, Tyack 1981). Song might function as a display to attract females (Medrano et al. 1994) as a spacing (Frankel et al. 1995, Winn and Winn 1978) and dominance (Darling and Bérubé 2001) mechanism among males, and to stimulate female receptivity (Baker and Herman 1984). The mating system proposed for humpback whales is the "floating lek": males exhibit

their attributes to attract females to try to mate but without rigid space territory (Clapham 1996). Herman (2016) suggested that collective singing could be a way to attract females to an arena instead of attracting females to a single singer. This author proposes that song evolved as a vector for recruiting colonists to new breeding grounds due to increased population pressures in the late Miocene–early Pliocene. Other proposed functions are that males sing as a sonar to locate other whales on the breeding ground (Frazer and Mercado 2000) or to help in orientation during migration (Clapham and Mattila 1990).

Studies have already been carried out to compare the structure of humpback whale song between different areas (Cerchio et al. 2001, Darling et al. 2014, Darling and Sousa-Lima 2005, Garland et al. 2015, Garland et al. 2013, Helweg et al. 1998, Winn et al. 1981) and of same population over time (Eriksen et al. 2005, Garland et al. 2015, Garland et al. 2013, Hatum 2015). Cholewiak et al. (2013) highlight the importance of creating lineages of phrases when similarity studies are carried out over time due to the subjectivity related to the describing and delineation of the phrases of a given song. Tracking the changes along phrase lineages provides a means to avoid confusion of the evolution of new phrases with the introduction of new song material. Quantitative metrics such as the Levenshein distance could be adopted as a more robust and objective way to verify such song changes (Garland et al. 2012, Tougaard and Eriksen 2005). It expresses the minimum of characters that have been deleted, inserted, or substituted to transform a string A into string B (Kohonen 1985), considering the sequences of themes in the song. This method is used to evaluate the changes occurring in humpback whale song at the sequence level of themes (Garland et al. 2012). Studies to investigate the change in the song structure at different levels are essential to understand the processes of cultural transmission of song and communication, as they allow to have a baseline to assess possible impacts of anthropic activities (Cerchio et al. 2014, Sousa-Lima and Clark 2008).

The objectives of this work are to describe the song structure of humpback whales in the years of 2014 and 2015 in the breeding area of Serra Grande (Bahia state, Brazil), to verify intra and inter-annual variation of the phrases within themes, and to quantify the changes in humpback song through the Levenshein distance.

**Materials and methods**

Study area

Serra Grande area (14°28'30" S; 39°01'50" W) is in the south of Bahia state in north-eastern Brazil (Figure 1), integrating the Environmental Protection Area APA Costa de Itacaré/Serra Grande. In this region of the Brazilian coast the continental shelf is short (Prates et al. 2012), and humpback whales concentrate near the coast (Gonçalves et al. first chapter). Average water temperature varies throughout the year between 24 and 29° C (NOAA 2016) and the oceanic bottom is predominantly constituted by rocks and sand (Freire and Dominguez 2006).
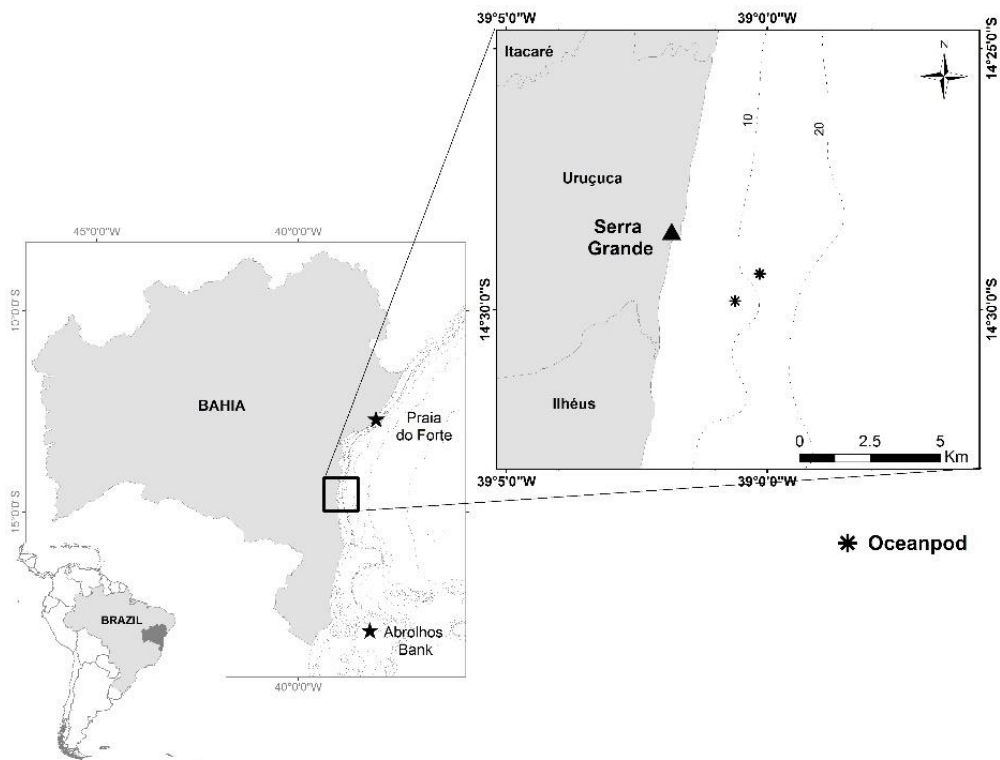


Figure 1. Serra Grande study site located in south of Bahia state, in north-eastern of Brazil, where passive acoustic monitoring was conducted through the deployment of Oceanpods (represented by asterisks).

Data collection

Passive acoustic monitoring was conducted between September and October of 2014 and 2015 using Oceanpods –autonomous underwater sound recorders developed by LADIM - São Paulo University (Caldas-Morgan et al. 2015, Sánchez-Gendriz and Padovese 2016). Recordings were performed at a sampling rate of 11.025 kHz through units deployed at depths

of 16 to 22 m, up to 2.7 km away from the coast (Figure 1). In 2014 two Oceanpods recorded between 07:00 am and 05:00 pm and in 2015 one Oceanpod recorded 24 hours per day.

Acoustic analyses

Aural and visual inspections were performed using the analyses software Raven Pro 1.5 (Cornell Lab of Ornithology) with a Hann window function of 1024-points and a 1024-point FFT size. Recordings were used when it was possible to distinguish between the singers present and when the signal-to-noise-ratio (SNR) was at least 10 dB (Cholewiak et al. 2013). Four days of recordings were analysed in 2014 (40 hours) and three days in 2015 (72 hours) allowing song characterization of multiple individuals to ensure an appropriate assessment of phrase structure as suggested by Cholewiak et al. (2013).

We considered the types of themes described by Payne and Payne (1985): static themes when the phrases within the theme are nearly identical; shifting themes when successive phrases progressively evolve from one to the other, being able to change the frequency and/or the form, duration, numbers, or are delivered at a slower or faster rate; or unpatterned themes which consist of themes with a variable number of units without a clear organization and not being subdivided into repeated phrases. Classification of each theme was performed qualitatively based on the phrase structure as suggested by Cholewiak et al. (2013) and maintained a nomenclature that simplifies the visualization of the evolution of the themes within the song between the two years. Themes were considered as the same if they maintained units with the same acoustic structure in the same positions in the sequence, presenting the same temporal and spectral characteristics, allowing variations in contours, frequencies and duration (Helweg et al. 1998).

Each type of phrase was counted only considering static themes to check the presence of a pattern phrase and variation of number of phrases per theme using chi-square test. Phrase lineages were created according to the first visualization of each unit type, where a capital letter indicates the position of the unit and the number of the year in which it was detected for the first time. When a new unit was detected in a phrase from the previous year, the unit was identified with a lowercase letter followed by the number of the year in which it was introduced (Arraut and Vielliard 2004, Hatum 2015).

*Levenshtein distance analyses*

We randomly considered song to begin in theme 1 to define the median song (Helweg et al. 1998). Levenshtein distances were calculated by comparing the median song of each year with the set of song sequences of the other year using the equation 1

$$LD (A, B) = \min (i+d+s) \tag{1}$$

where i, d and s represent respectively inserts, deletions and substitutions. The Mann-Whitney test was used to compare statistically LD values between the years (Tougaard and Eriksen 2005). Levenshtein distance similarity index (LSI) was calculated using the equation 2

$$LSI (A,B) = 1 - LD(A,B)/ \max(\text{len} (A), \text{len} (B)) \tag{2}$$

where len is the longer sequence observed (Helweg et al. 1998), and values close to zero indicate no similarity and values close to 1 indicate high similarity.

**Results**

Description and lineages of themes

In 2014 six themes were described (Figure 2), four of them were static themes (1, 2, 3 and 5A), one unpatterned theme (4), and one shifting theme (5B). Transitional phrases (Cholewiak et al. 2013) were found between themes 1/2 and 2/3. In 2015, theme 1 was changed into 1A, themes 2, 4 and 5A remained in song but from those, themes 2 and 5A became shifting themes. Theme 3 was deleted and a new static theme (6) was introduced (Figure 2). Transitional phrases occurred between themes 1A/2 in 2015.

| Year | 2014 | 2015 |
|---|---|---|
| Theme 1 | | |
| Theme 1A | | |
| Theme 2 | | |
| Theme 3 | | |
| Theme 4 | | |
| Theme 5A | | |
| Theme 5B | | |
| Theme 6 | | |

Figure 2. Song themes of humpback whales in Serra Grande region (Bahia state, Brazil) from 2014 and 2015. Each colour represents a theme and each lineage was represented by different shades of the same colour.

In 2014, theme 1 was represented by the pattern phrase A4B4 (99.19%, $\chi2$=1441.179, d.f.=3, p<0001) with A4 unit with the highest energy in the frequency of 50 Hz, starting with a noisy ascending component and finishing with a second descending component harmonic series, and a short B4 unit with harmonic inverted U shape with energy peak at the frequency of 150 Hz (Figure 3(a)). In 2015, theme 1 had changed, turning into theme 1A with the pattern phrase B5A5a5 (98.81%, $\chi2$=970.37, d.f.=2, p<0.0001). Units A and B reversed position, evolving to A5 and B5 and appearing a5. B5 unit developed a downsweep but maintained the same frequency. A5 unit lost the frequency modulation, presenting an initially pulsed sound and then becoming harmonic increasing the frequency peak to 150 Hz, and unit a5 was a downsweep with greater energy approximately in the 80 Hz (Figure 3(b)).
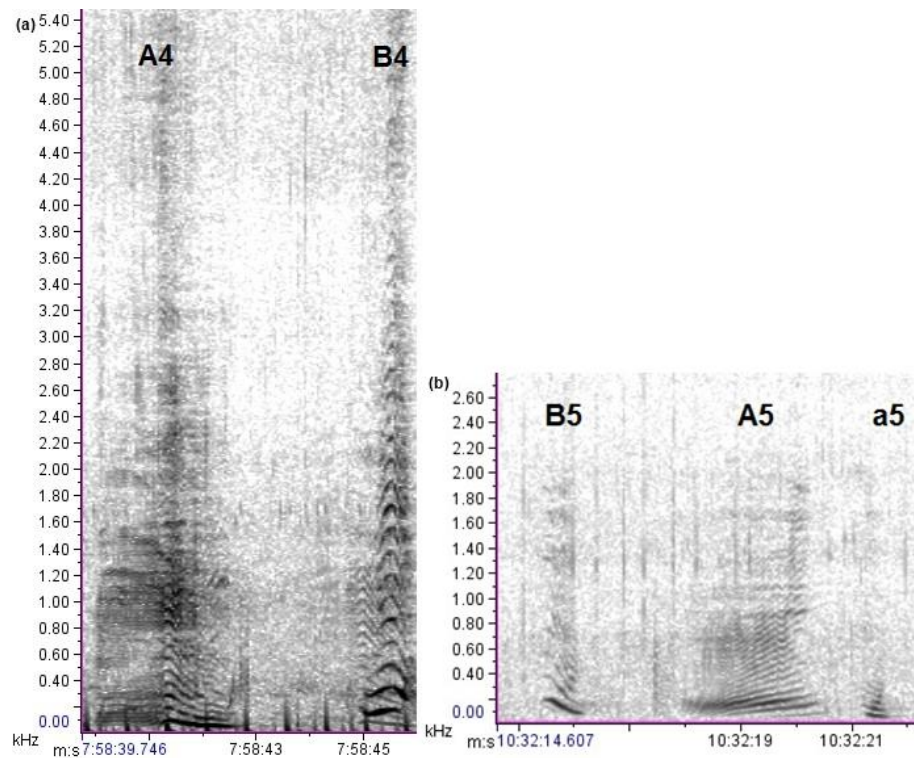


Figure 3. Spectrogram with the lineages of the pattern phrase of theme 1 of 2014 (a) and of theme 1A of 2015 (b) from humpback whale song recorded in Serra Grande region (Bahia state, Brazil).

In 2014, theme 2 exhibited the pattern phrase C4D4C4D4C4D4C4D4 (50.00%, $\chi2$=255.574, d.f.=7, p<0.0001) presenting a longer time interval between the first and second repetition of units C4D4. C4 was a pulsed sound with an energy peak approximately at the frequency of 21 Hz, and D4 was a ratchet with higher energy approximately at 300 Hz (Figure 4(a)). In 2015, theme 2 was characterized by one repetition of phrase C5D5 but over time the duration of

units decreased and the theme changed from static to shifting theme. Both units showed increase of peak energy frequencies (Figure 4(b)).



Figure 4. Spectrogram with the lineages of the pattern phrase of theme 2 of 2014 (a) and of phrase of the shifting theme 2 of 2015 (b) from humpback whale song recorded in Serra Grande region (Bahia state, Brazil).

Theme 3 was only present in 2014 with the pattern phrase E4F4E4F4E4F4E4F4E4F4E4F4 (84.62%, $\chi2$=421.404, d.f.=6, p<0.0001). E4 unit was a short pulsed sound with higher energy approximately at 60 Hz, and F4 exhibited an upward modulation with energy peak at approximately 200 Hz (Figure 5).



Figure 5. Spectrogram with the lineage of the pattern phrase of theme 3 of 2014 from humpback whale song recorded in Serra Grande region (Bahia state, Brazil).

Theme 4 was an unpatterned theme in both years (Figure 6), varying in its composition, and may present different number of units, which vary in duration but presenting harmonics with several inflection points.



Figure 6. Spectrogram of one example of theme 4 of 2014 (a) and of 2015 (b) from humpback whale song recorded in Serra Grande region (Bahia state, Brazil).

Theme 5A had the pattern phrase G4G4H4I4J4H4I4 (42.48%, $\chi2=638.569$, d.f.=21, p<0.0001) divided into two subphrases, the first was the repetition of G4 unit. Second subphrase was composed by H4I4J4H4J4, with H4 unit being short, I4 having harmonic characteristics with some inflection points, and J4 had similar characteristics with G4 but was shorter (Figure 7(a)). In 2015, theme 5A changed from static to shifting theme, and several times the first phrase of the theme was similar to the one presented in 2014 but not always (Figure 7(b)). Theme gradually changed until it became theme 6.
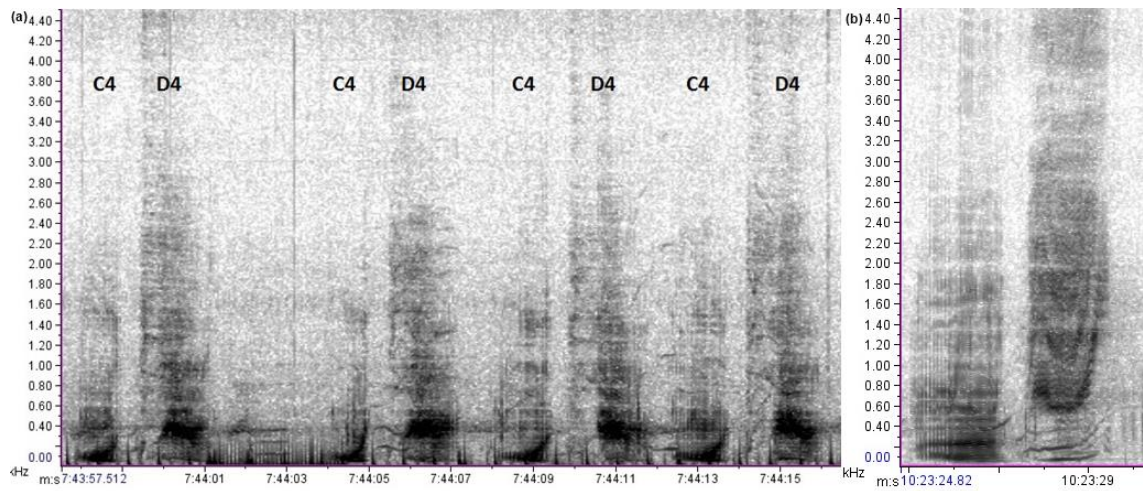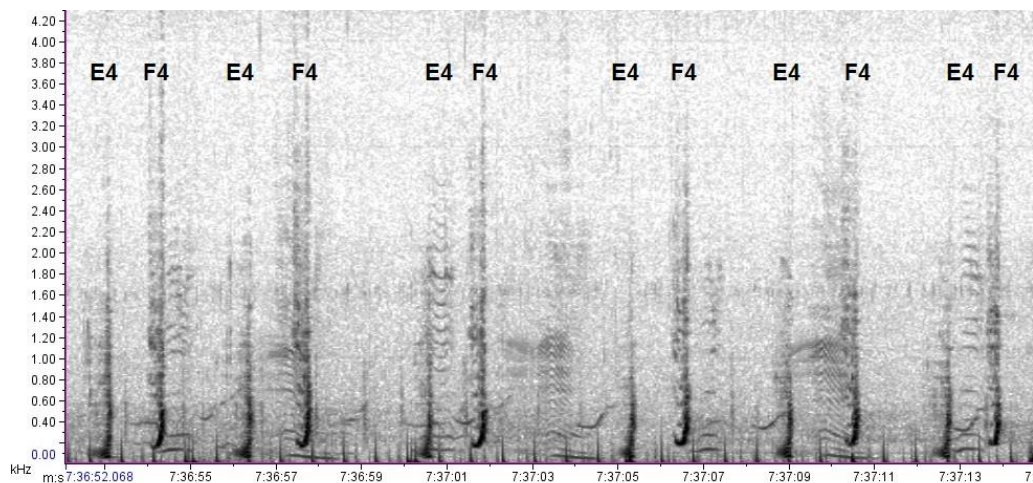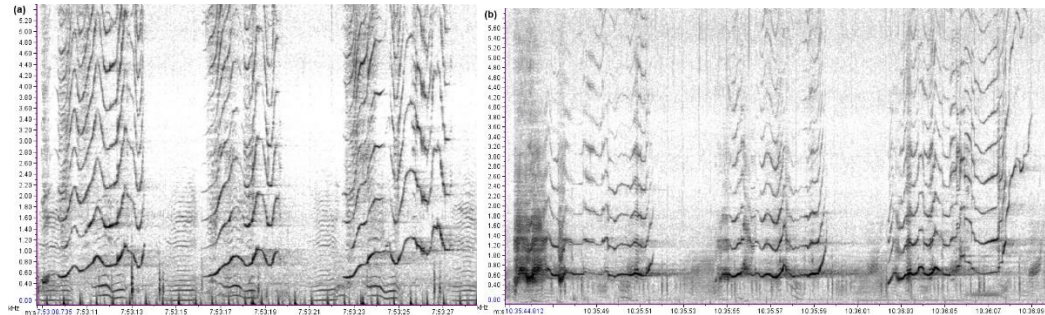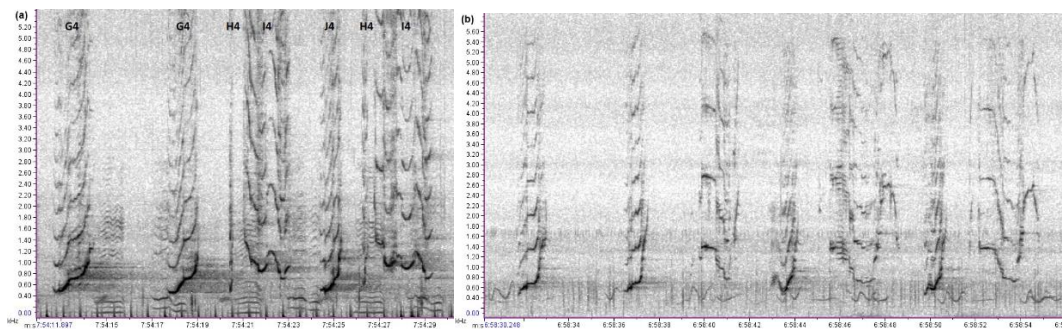


Figure 7. Spectrogram with the lineage of the pattern phrase of theme 5A of 2014 (a) and of the initial phrase of the shifting theme 5A of 2015 (b) from humpback whale song recorded in Serra Grande region (Bahia state, Brazil).

Theme 5B occurred in 2014 as a shifting theme (Figure 8). It was considered as a sub-division of theme 5 because although it does not interchange with theme 5A, it has the same first subphrase presented in theme 5A (G4G4), progressing until it becomes theme 1. In 2015 theme 5B was omitted.
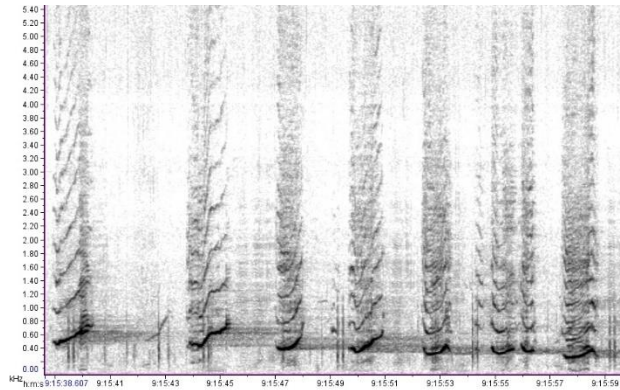
Figure 8. Spectrogram of the initial phrase of shifting theme 5B of 2014 from humpback whale song recorded in Serra Grande region (Bahia state, Brazil).

Theme 6 was inserted in the year 2015 with the pattern phrase K5L5M5 (87.91%, $\chi2$=808.22, d.f.=1, p<0.0001). K5 was a harmonic unit with several inflection points with higher energy in frequencies between 300 and 400 Hz in the first harmonic, L5 a harmonic series without frequency modulation with more energy at approximately 165 Hz, and M5 unit was a short downsweep with greater energy in the frequency of 117 Hz (Figure 9).
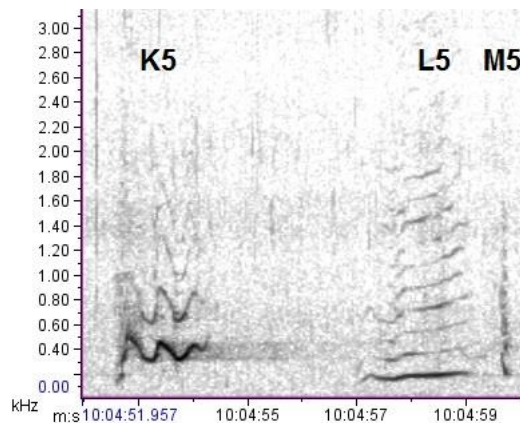


Figure 9. Spectrogram with the lineage of the pattern phrase of theme 6 of 2015 from humpback whale song recorded in Serra Grande region (Bahia state, Brazil).

Intra e inter-annual variation of song cycles

Only static themes were considered for the analysis of intra- and inter-annual variation of phrases. In 2014, theme 1 showed four different types of phrases but type AB was the predominant (n=487, Table 1). Theme 2 presented eight types of phrase variations, CDCDCDCD was the most common (n=61, Table 1) follow by CDCDCDCDCD (n=44, Table 1). Theme 3 presented seven variations of phrases, EFEFEFEFEFEFEF type was the dominant (n=88, Table 1). Theme 5A showed the greatest range of phrases, although

GGHIJHI was the most common (n=36, Table 1). Number of phrases in theme 1 ($\chi2$=77.273, d.f.=18, p<0.0001) and 2 ($\chi2$=38.032, d.f.=18, p=0.0038) varied significantly between the song cycles, and the opposite was observed in themes 3 ($\chi2$=6.55, d.f.=18, p=0.34) and 5A ($\chi2$=7.4348, d.f.=17, p=0.9772, Figure 10(a)).

Table 1. Number of repetitions of phrases of static themes per day of the analysed recordings of the humpback whale song in Serra Grande region in the year 2014. Units are represented by letters.

|  |  | 18/09 | 20/09 | 22/09 | 01/10 |
|---|---|---|---|---|---|
| **Theme 1** | AB | 119 | 76 | 185 | 107 |
|  | ABB | 1 | 0 | 0 | 1 |
|  | AAB | 0 | 0 | 1 | 0 |
|  | ABA | 0 | 0 | 1 | 0 |
| **Theme 2** | CDCCDCD | 0 | 0 | 1 | 0 |
|  | CDCDCD | 0 | 1 | 5 | 3 |
|  | CDCDCDCD | 6 | 8 | 32 | 15 |
|  | CDCDCDCDCD | 8 | 10 | 23 | 3 |
|  | CDCDCDCDCDCD | 3 | 0 | 1 | 0 |
|  | CDCDCDCDCDCDCD | 1 | 0 | 0 | 0 |
|  | CDCDCDCDD | 0 | 0 | 0 | 1 |
|  | CDCDCDCF | 1 | 0 | 0 | 0 |
| **Theme 3** | EFEF | 1 | 0 | 0 | 1 |
|  | EFEFEF | 0 | 0 | 0 | 1 |
|  | EFEFEFEF | 0 | 0 | 0 | 2 |
|  | EFEFEFEFEF | 2 | 1 | 2 | 1 |
|  | EFEFEFEFEFE | 0 | 1 | 0 | 0 |
|  | EFEFEFEFEFEF | 7 | 23 | 33 | 25 |
|  | EFEFEFEFEFEFEF | 0 | 0 | 2 | 2 |
| **Theme 5A** | GGGHIJHI | 0 | 0 | 0 | 1 |
|  | GGHI | 2 | 2 | 17 | 7 |
|  | GGHIHI | 2 | 1 | 9 | 1 |
|  | GGHIHIHI | 0 | 0 | 1 | 0 |
|  | GGHIJ | 0 | 0 | 1 | 0 |
|  | GGHIJHHI | 0 | 1 | 1 | 1 |
|  | GGHIJHI | 6 | 3 | 21 | 36 |
|  | GGHIJHIHI | 0 | 0 | 1 | 0 |
|  | GGHIJHIJH | 0 | 0 | 0 | 1 |
|  | GGHIJHIJHI | 3 | 0 | 4 | 4 |
|  | GGHIJI | 0 | 0 | 0 | 2 |
|  | GGHIJIJHI | 0 | 0 | 1 | 0 |
|  | GGHIJJHI | 0 | 0 | 1 | 1 |
|  | GGI | 0 | 0 | 1 | 0 |
|  | GGIH | 0 | 0 | 1 | 0 |
|  | GGIHI | 0 | 1 | 0 | 0 |
|  | GGIHJHIHI | 0 | 0 | 1 | 0 |
|  | GGIJHI | 0 | 0 | 1 | 1 |
|  | GGJHI | 0 | 0 | 11 | 2 |
|  | GGJHIJHI | 0 | 0 | 1 | 1 |
|  | GGJI | 0 | 0 | 0 | 1 |
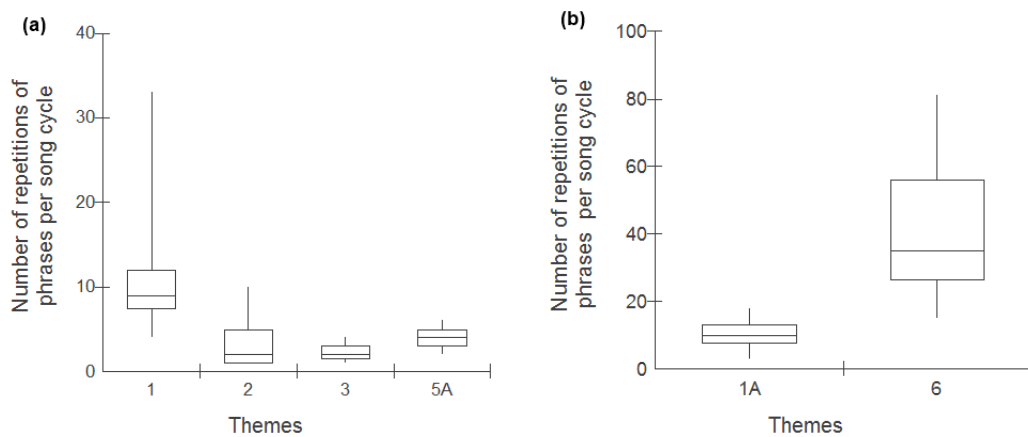
Figure 10. Boxplot of the number of repetitions of phrases of static themes per song cycle of humpback whales in Serra Grande region (Bahia state, Brazil) in 2014 (a) and in 2015 (b).

In 2015, fewer variations of phrases were observed. Theme 1A had three types and BAa was the predominant (n=497, Table 2), and theme 6 showed two types, dominating the pattern KLM (n=649, Table 2). Number of phrases of theme 1A did not vary significantly between the song cycles ($\chi 2$=34.714, d.f.=22, p=0.0415) contrasting theme 6 ($\chi 2$=253.124, d.f.= 26, p<0.0001, Figure 10(b)).

Table 2. Number of repetitions of phrases of static themes per day of the analysed recordings of the humpback whale song in Serra Grande region in the year 2015. Units are represented by letters.

|  |  | 20/09 | 03/10 | 25/10 |
|---|---|---|---|---|
| **Theme 1A** | Aa | 0 | 1 | 0 |
|  | BA | 0 | 5 | 0 |
|  | BAa | 144 | 262 | 91 |
| **Theme 6** | KL | 0 | 168 | 2 |
|  | KLM | 271 | 316 | 649 |

Theme sequences

No variation was observed in sequence of themes in any year. The sequence of themes in 20 song cycles analysed for 2014 was 1 2 3 4 5A 5B. Of the 28 song cycles analysed of 2015, all presented the theme sequence 1A 2 4 5A 6.

Levenshtein distance similarity index

As only one sequence of song cycle was observed in both years, it was considered the median song. Comparing the median song of each year with the set of sequences of the other year, a

significant difference was observed between the two years (p<0.0001). LSI between the two years was 0.50.

**Discussion**

In addition to Rossi-Santos (2012), our study extends the studies about the occurrence and/or description of humpback whale song from the breeding stock A (IWC 2005) in the North of the Abrolhos Bank region (Arraut and Vielliard 2004, Bittencourt et al. 2016, Sousa-Lima and Clark 2008), which is the main breeding area of the species in Brazil (Andriolo et al. 2010). Several changes in the singing behaviour between 2014 and 2015 were observed, which involved the appearance of new units, modification of units that resulted in the omission and the appearance of new themes. Changes in the types of themes from one year to the other were observed: in 2014, static themes with a pattern in the repetition of the phrases within the theme, evolved in the following year to shifting themes, in which phrases progressively change (Payne and McVay 1971) becoming unstable and transient (Payne and Payne 1985). These changes seem to be associated to the creation of new themes. It's essential to follow the song in the next years to verify the song evolution and if this really happens.

As observed by Arraut and Vielliard (2004) and Hatum (2015), variations in the number of phrases in some of the themes occurred within song session as among different song sessions, probably in the song of the same individual as between different individuals. Sousa-Lima et al. (2002) detected the decrease of number of phrases in themes in the presence of boat. In 2014, some themes presented a greater variation in the phrase pattern. Despite the variation at the phrase level, there was no variation at the level of the sequences of themes of song cycles in any year, with the same sequence always observed as the presence of all themes in all song cycles (Arraut and Vielliard 2004). As observed by Payne and Payne (1985), song presented a similar structure in phrases and themes, as in its sequences, but being unpredictable in the number of repetitions of each phrase in the themes. The differences of learning from each individual or the stability of the theme may be related to these variations.

Presence of bigrams (sequence of two units) (Green et al. 2011) was common in 2014. Green et al. (2011) suggests that these bigrams characterized by their relative acoustic features are resistant to the progressive changes of the song. This was not observed in our study because in 2015 only one of the bigrams was maintained (theme 2) and became a shifting theme.

Description of song as well as the study of its evolution over time or among different areas has an associated subjectivity. Cholewiak et al. (2013) suggested the creation of lineages that

allow tracking of how song changes. Nevertheless, quantitative measures should also be applied to improve and compare the evolution over time. In this study, the Levenshtein distance similarity index was applied for the first time in the analysis of the evolution of singing behaviour of the humpback whale population in the Brazilian coast. Brazil songs between 2014 and 2015 presented a similarity index of 50%, which represents a substantial change as already observed in other studies (Mercado et al. 2005). Eriksen et al (2005) found that the song presented LSI values between 0.375 and 0.857 in Tongan Islands from one year to the other, and that over time the song becomes increasingly different. We suggest that this method should be applied to long-term studies because it results in an accessible and sensible way (Garland et al. 2012) to measure cultural evolution. However, caution should be taken when defining the themes so that does not underestimate or overestimate similarity indices. Garland et al. (2013) suggest that further studies should be focused on matching themes based on the stereotyped sequence of units within a phrase. Comparative studies both at phrase and theme levels help to understand how the evolution of song occurs in humpback whales given that song is a fundamental marker of population identity (Garland et al. 2013).

**References**

Andriolo A, Kinas PG, Engel MH, Martins CCA, Rufino AM. 2010. Humpback whales within the Brazilian breeding ground: distribution and population size estimate. Endangered Species Research. 11:233–243

Arraut EM, Vielliard JME. 2004. The song of the Brazilian population of Humpback Whale *Megaptera novaeangliae*, in the year 2000: individual song variations and possible implications. Annals of the Brazilian Academy of Science. 76(2):373-380

Baker CS, Herman LM. 1984. Aggressive behavior between humpback whales (*Megaptera novaeangliae*) wintering in Hawaiian waters. Canadian Journal of Zoology. 62:1922-1937

Bittencourt L, Barbosa M, Secchi E, Lailson-Brito J, Azevedo A. 2016. Acoustic habitat of an oceanic archipelago in the Southwestern Atlantic. Deep-Sea Research. 1(115):103-111. doi:10.1016/j.dsr.2016.06.001.

Caldas-Morgan M, Alvarez-Rosario A, Padovese LR. 2015. An Autonomous Underwater Recorder Based on a Single Board Computer. PLoS ONE. 10(5):e0130297

Cerchio S. 1993. Geographic variation and cultural evolution in songs of humpback whales (*Megaptera novaeangliae*) in the eastern North Pacific [MSc Thesis]. San Jose: San Jose State University.

Cerchio S, Jacobsen JK, Norris TF. 2001. Temporal and geographical variation in songs of humpback whales, *Megaptera novaeangliae*: synchronous change in Hawaiian and Mexican breeding assemblages. Animal Behaviour. 62:313–329

Cerchio S, Strindberg S, Collins T, Bennett C, Rosenbaum H. 2014. Seismic Surveys Negatively Affect Humpback Whale Singing Activity off Northern Angola. PLoS ONE. 9(3):e86464. doi:10.1371/journal.pone.0086464.

Cholewiak DM, Sousa-Lima RS, Cerchio S. 2013. Humpback whale song hierarchical structure: Historical context and discussion of current classification issues. Marine Mammal Science. 29(3):E312–E332

Clapham PJ, Mattila DK. 1990. Humpback whale songs as indications of migration routes. Marine Mammal Science. 6(2):155-160

Clapham PJ. 1996. The social and reproductive biology of Humpback Whales: an ecological perspective. Mammal Review. 26(1):27-49

Darling J. 2009. Song. In: Encyclopedia of Marine Mammals. Second ed. San Diego: Academic Press. p. 1053-1056.

Darling JD, Bérubé M. 2001. Interactions of singing humpback whales with other males. Marine Mammal Science. 17(3):570-584

Darling JD, Sousa-Lima RS. 2005. Songs indicate interaction between humpback whales (*Megaptera novaeangliae*) populations in the Western and Eastern South Atlantic Ocean Marine Mammal Science. 21(3):557–566

Darling JD, Acebes JMV, Yamaguchi M. 2014. Similarity yet a range of differences between humpback whale songs recorded in the Philippines, Japan and Hawaii in 2006. Aquatic Biology. 21: 93–107

Dunlop RA, Noad MJ, Cato DH, Stokes D. 2007. The social vocalization repertoire of east Australian migrating humpback whales (*Megaptera novaeangliae*). Journal Of The Acoustical Society of America. 122(5):2893–2905

Eriksen N, Miller LA, Tougaard J, Helweg DA. 2005. Cultural change in the songs of humpback whales (*Megaptera novaeangliae*) from Tonga. Behaviour. 142:305-328

Frankel AS, Clark CW, Herman LM, Gabriele CM. 1995. Spatial distribution, habitat utilization, and social interactions of humpback whales, *Megaptera novaeangliae*, off

Hawai's, determined using acoustic and visual techniques. Canadian Journal of Zoology. 73:1134-1146

Frazer LN, Mercado E. 2000. A Sonar Model for Humpback Whale Song. IEEE Journal of Oceanic Engineering. 25(1):160-182. doi:10.1109/48.820748.

Freire AFM, Dominguez JML. 2006. The holocene sequence of the central continental shelf of the State of Bahia, Brazil. Boletim Geociências Petrobras. 14(2):247-267

Garland EC, Goldizen AW, Rekdahl ML, Constantine R, Garrigue C, Hauser ND, Poole MM, Robbins J, Noad MJ. 2011. Dynamic Horizontal Cultural Transmission of Humpback Whale Song at the Ocean Basin Scale. Current Biology. 21:687-691

Garland EC, Lilley MS, Goldizen AW, Rekdahl ML, Garrigue C, Noad MJ. 2012. Improved versions of the Levenshtein distance method for comparing sequence information in animals' vocalisations: tests using humpback whale song. Behaviour. 149:1413–1441

Garland EC, Gedamke J, Rekdahl ML, Noad MJ, Garrigue C. 2013. Humpback Whale Song on the Southern Ocean Feeding Grounds: Implications for Cultural Transmission. PLoS ONE. 8(11):e79422. doi:10.1371/journal.pone.0079422.

Garland EC, Noad MJ, Goldizen AW, Lilley MS, Rekdahl ML, Garrigue C, Constantine R, Hauser ND, Poole MM, Robbins J. 2013. Quantifying humpback whale song sequences to understand the dynamics of song exchange at the ocean basin scale. Journal of the Acoustical Society of America. 133(1):560–569

Garland EC, Goldizen AW, Lilley MS, Rekdahl ML, Garrigue C, Constantine R, Hauser ND, Poole MM, Robbins J, Noad MJ. 2015. Population structure of humpback whales in the western and central South Pacific Ocean as determined by vocal exchange among populations. Conservation Biology. doi:10.1111/cobi.12492.

Green SR, Mercado E, Pack AA, Herman LM. 2011. Recurring patterns in the songs of humpback whales (*Megaptera novaeangliae*). Behavioural Processes. 86:284-294

Hatum PS. 2015. The song of humpback whale and the potencial effects of whale-watching in the Abrolhos Bank, BA, Brazil [MSc Thesis]. Natal: Universidade Federal do Rio Grande do Norte.

Helweg DA, Cato DH, Jenkins PF, Garrigue C, McCauley RD. 1998. Geographic Variation in South Pacific Humpback Whale Songs. Behaviour. 135(1):1-27

Herman LM. 2016. The multiple functions of male song within the humpback whale (*Megaptera novaeangliae*) mating system: review, evaluation, and synthesis. Biological Reviews. doi:10.1111/brv.12309.

IWC. 2005. Report of the Scientific Committee. Annex H - Report of the sub-committee on other southern hemisphere whale stocks. Journal of Cetacean Research and Management. 7(Suppl.):235-246

Kohonen T. 1985. Median strings. Pattern Recognition. 3:309-313

Martins CCA, Morete ME, Engel MH, Freitas AC, Secchi ER, Kinas PG. 2001. Aspects of habitat use patterns of humpback whales in the Abrolhos Bank, Brazil, breeding ground. Memoirs of the Queensland Museum. 27(2):563-570

Medrano L, Salinas M, Salas I, Ladrón de Guevara P, Aguayo A, Jacobsen J, Baker CS. 1994. Sex identification of humpback whales, *Megaptera novaeangliae*, on the wintering grounds of the Mexican Pacific Ocean. Canadian Journal of Zoology. 72:1771-1774

Mercado E, Herman LM, Pack AA. 2005. Song copying by humpback whales: themes and variations. Animal Cognitation. 8:93-102. doi:10.1007/s10071-004-0238-7.

Ocean Products: Office of satellite and product operations

Noad MJ, Cato DH, Bryden MM, Jenner M, Jenner KCS. 2000. Cultural revolution in whale songs. Nature. 408:537

Noad MJ, Cato DH. 2007. Swimming speeds of singing and non-singing humpback whales during migration. Marine Mammal Science. 23(3):481–495. doi:10.1111/j.1748-7692.2007.02414.x.

Payne K, Payne R. 1985. Large Scale Changes over 19 Years in Song of Humpback Whales in Bermuda. Zeitschrift für Tierpsychologie. 68(89-114)

Payne RS, McVay S. 1971. Songs of humpback whales. Science. 173:585–597

Prates APL, Gonçalves MA, Rosa MR. 2012. Panorama da Conservação dos Ecossistemas Costeiros e Marinhos no Brasil. Brasília: MMA.

Rossi-Santos MR. 2012. Comportamento e ecologia acústica da baleia-jubarte (*Megaptera novaeangliae*) na região Nordeste do Brasil [Doctoral Thesis]. Natal: Universidade Federal do Rio Grande do Norte.

Sánchez-Gendriz I, Padovese LR. 2016. Underwater soundscape of marine protected areas in the south Brazilian coast. Marine Pollution Bulletin. 105:65-72

Silber GK. 1986. The relationship of social vocalizations to surface behavior and aggression in the Hawaiian humpback whale (*Megaptera novaeangliae*). Canadian Journal of Zoology. 64:2075–2080

Smith JN, Goldizen AW, Dunlop RA, Noad MJ. 2008. Songs of male humpback whales, *Megaptera novaeangliae*, are involved in intersexual interactions. Animal Behaviour. 76:467-477

Sousa-Lima RS, Morete ME, Fortes RC, Freitas AC, Engel MH. 2002. Impact of boats on the vocal behavior of humpback whales off Brazil. Journal of the Acoustic Society of America. 112(5):2430-2431. doi:10.1121/1.4779974.

Sousa-Lima RS, Clark CW. 2008. Modeling the Effect of Boat Traffic on the Fluctuation of Humpback Whale Sing Activity in The Abrolhos National Marine Park, Brazil. Canadian Acoustics. 36(174-181)

Stanistreet JE, Risch D, Van Parijs SM. 2013. Passive Acoustic Tracking of Singing Humpback Whales (*Megaptera novaeangliae*) on a Northwest Atlantic Feeding Ground. PLoS ONE. 8(4):e61263. doi:10.1371/journal.pone.0061263.

Tougaard J, Eriksen N. 2005. Analysing Differences among Animal Songs Quantitatively by Means of the Levenshtein Distance Measure. Behaviour. 143(2):239-252

Tyack P. 1981. Interactions between singing Hawaiian humpback whales and conspecifics nearby. Behavioral Ecology and Sociobiology. 8:105-116

Vu ET, Risch D, Clark CW, Gaylord S, Hatch LT, Thompson MA, Wiley DN, Van Parijs SM. 2012. Humpback whale song occurs extensively on feeding grounds in thewestern North Atlantic Ocean. Aquatic Biology. 14:175–183

Winn HE, Winn LK. 1978. The Song of the Humpback Whale *Megaptera novaeangliae* in the West Indies. Marine Biology. 47:97-114

Winn HE, Thompson TJ, Cummings WC, Hain J, Hudnall J, Hays H, Steiner WW. 1981. Song of the Humpback Whale - Population Comparisons. Behavioral Ecology and Sociobiology. 8:41-46

Zoidis AM, Smultea MA, Frankel AS, Hopkins JL, Day A, McFarland AS, Whitt AD, Ferti D. 2008. Vocalizations produced by humpback whale (*Megaptera novaeangliae*) calves recorded in Hawaii. Journal of the Acoustical Society of America. 123(3):1737–1746. doi:10.1121/1.2836750.

## 6 CONSIDERAÇÕES FINAIS

Este trabalho traz um cenário de referência para ocorrência, movimento, comportamento e comunicação acústica das baleias-jubarte na região de Serra Grande, conciliando metodologias não invasivas e economicamente viáveis para o monitoramento da espécie.

Foi observado que o padrão de abundância da espécie na região é similar ao que ocorre no Banco dos Abrolhos. Contudo, diferenças na proporção dos grupos predominantes foram registradas. Apesar da presença de grupos com filhotes ser superior no Banco dos Abrolhos em relação a Serra Grande, o aumento do número de filhotes ao longo da temporada assim como o tempo passado em descanso por grupos com a presença de filhotes, indica a importância da área para a reprodução da espécie e recuperação da população no Brasil.

Fatores ambientais e sociais se mostraram importantes nas estratégias apresentadas pelos grupos de mães com filhotes relativamente ao padrão de uso da região. Foi observado que a presença e aumento do número de escortes nos grupos de mães com filhotes levou a um aumento da distância à costa e profundidade onde os grupos se encontravam, assim como o aumento da velocidade adotada pelos grupos. A estratégia mais utilizada pelos grupos de mães com filhotes foi permanecer mais perto da costa, sem a presença de machos, onde podem ficar mais tempo em repouso e em menores velocidades, dedicando mais tempo ao cuidado com o filhote recém-nascido. Dessa forma, ocorre uma poupança no gasto energético que pode ser dedicada à amamentação e proteção do filhote. No entanto, ter um macho acompanhando pode ser uma estratégia do grupo para quando é necessário se deslocar em águas mais afastadas, garantindo uma proteção.

Os valores de linearidade dos grupos observados relevam que a área não é apenas utilizada como uma área de trânsito ou de deslocamento, o que apoia a ideia de a espécie está expandindo as suas áreas reprodutivas ao longo da costa brasileira. Os valores de linearidade também mostram como as estratégias de movimentação vão se alterando ao longo da temporada. Os grupos passam de movimentos mais erráticos no início da temporada para trajetórias mais lineares com a proximidade do início da migração para as áreas de alimentação. Surgem evidências que na costa brasileira, o movimento dos grupos indo para Norte parece ocorrer em águas mais afastadas do que o movimento para Sul, pois sempre foram observados mais grupos indo para Sul, mesmo no início da temporada.

Por último, a análise do canto revelou a presença de cantores na região, e como grandes alterações na estrutura do canto podem ocorrer de um ano para o outro, e que a

implementação de análises quantitativas e menos subjetivas são essenciais para o melhor entendimento do contexto deste comportamento entre os indivíduos e populações.

Dessa forma, a região de Serra Grande se revela importante para a ocorrência da baleia-jubarte a Norte do Banco dos Abrolhos. A presença de filhotes tão perto da costa chama a atenção para o cuidado que deve ser tomado para a futura implementação de atividades antropogênicas na região, como a construção do novo porto na região, para evitar o abandono de áreas tradicionais de ocorrência já observados em outros estudos. A colisão com embarcações e o mascaramento acústico, em espécies que usam o som como principal meio de comunicação, são ameaças graves e iminentes que podem ocorrer. As características ideias da área, com um ponto alto de observação e plataforma continental curta, fazem de Serra Grande um importante sítio de estudo para a condução de estudos de longo prazo por facilitar a identificação de padrões comportamentais, permitindo a associação de monitoramento visual e acústico em uma área reprodutiva com pouca influência de atividades antropogênicas.

**ANEXO A – Monitoramento visual a partir de ponto fixo através do uso de uma estação total em Serra Grande (Bahia, Brasil)**

Uma estação total ou um teodolito são instrumentos topográficos/geodésicos que permitem o rastreamento de animais pois medem ângulos horizontais entre um ponto arbitrário, selecionado como referência, e o objeto alvo, e o ângulo vertical entre o observador e o objeto alvo (WÜRSIG, CIPRIANO; WÜRSIG, 1991; GAILEY; ORTEGA-ORTIZ, 2002; BAILEY; LUSSEAU, 2004). Quando a altura acima da superfície do mar da estação total e as coordenadas da estação total e do ponto de referência são medidas com precisão juntamente com as alturas da maré para cada medição de ângulos, os dados dos ângulos até ao objeto podem ser traduzidas em coordenadas UTM (WÜRSIG, CIPRIANO; WÜRSIG, 1991) através de equações trigonométricas (SANTOS, 2010).

As coordenadas UTM da estação total (P1) e do ponto de referência (P2) foram determinadas através de um par de Receptores GNSS Geodésico de alta precisão, com 4 horas de rastreio utilizando a constelação dos satélites GPS (EUA) e GLONASS (Rússia). As alturas ortométricas de ambos os pontos foram determinadas usando o modelo Geoidal MAPGEO 2010 (MONICO, 2008). Para rastrear as baleias-jubarte (*Megaptera novaeangliae)* na região de Serra Grande (Bahia, Brasil) foi utilizada uma estação total TOPCON ES105 com 5 segundos de precisão angular e poder de ampliação de 30 vezes.

A partir da altitude da estação total e da baleia, combinada com o azimute a partir do Norte geográfico, sempre no sentido horário, e o ângulo horizontal ($\alpha$) referente ao alinhamento P2-P1 e P1-baleia, se calculou, através de equações trigonométricas, a distância entre a baleia e o ponto de observação P1 (figura 1) – equações de 1 a 4. Usando a distância ($D_{P1\text{-baleia}}$) e o alinhamento P1-baleia ($AZ_{P1\text{-baleia}}$) e as coordenadas de P1, pode se calcular as coordenadas UTM (E, N) da baleia na superfície da água (equações 5 a 9).

$$\beta = 180 - Z \tag{1}$$

$$H = h + Al \tag{2}$$

$$\text{tg } \beta = \text{tg } (180 - Z) = (D_{P1\text{-baleia}})/H \tag{3}$$

$$D_{P1\text{-baleia}} = \text{tg } (180 - Z) \, . \, H \tag{4}$$

$$AZ_{P1\text{-baleia}} = AZ_{P1\text{-P2}} + \alpha \tag{5}$$

$$\Delta E = \text{sen } AZ_{P1\text{-baleia}} \, . \, D_{P1\text{-baleia}} \tag{6}$$

$$\Delta N = \cos AZ_{P1\text{-baleia}} \, . \, D_{P1\text{-baleia}} \tag{7}$$

$$N_{baleia} = N_{P1} + \Delta N \tag{8}$$

$E_{baleia} = E_{P1} + \Delta E$ (9)

Onde:

H = altura total (estação total + ponto fixo)

h = altura do ponto fixo

AI = altura da instalação da estação total

Z = distância zenital

$N_{baleia}$ = coordenada norte da baleia

$E_{baleia}$ = coordenada leste da baleia

$\Delta E$ = projeção parcial da coordenada leste (E)

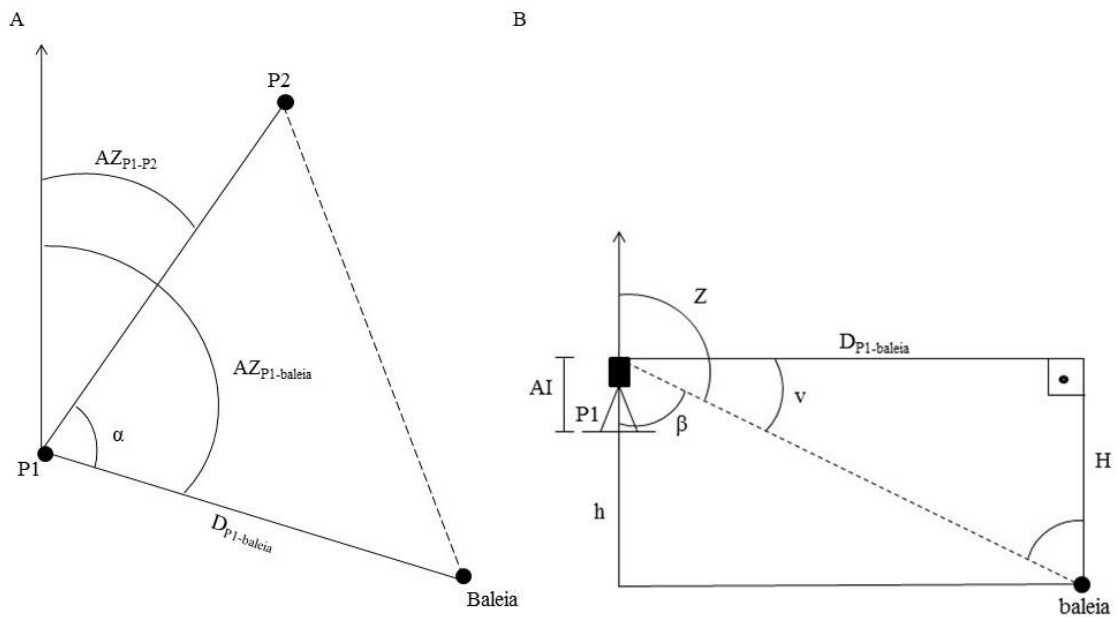$\Delta N$ = projeção parcial da coordenada norte (N)

$\alpha$ = ângulo horizontal

v = ângulo vertical

Coordenada UTM P1: 496680,197 m E 8399723,483 m N

Coordenada UTM P2: 496708,667 m E 8399754,111 m N

Figura 1 – Medidas entre o observador na estação total e os grupos de baleia-jubarte; vista de topo (A) e vista lateral (B) (adaptado de Santos (2010))

Devido à curvatura da Terra (VANICEK; KRAKIWSKY, 1996), um fator de correção foi utilizado transformando as distâncias horizontais (calculadas através dos dados medidos pela estação total) para distâncias esféricas utilizando as equações de 10 a 12. Para os cálculos considerou-se uma altitude de 92,88 m (altitude de P1). Chegou-se ao valor de correção de 0,0146049 m para cada 1000 m.

$$\text{Re } d = - (H/R_o + H) \cdot 10^6 \text{ ppm} \tag{10}$$

$$R_o = b / (1 - e^2 \text{ sen}^2 \varphi) \tag{11}$$

$$D_{\text{esférica}} = D_{\text{P1-baleia}} - (D_{\text{P1-baleia}} \cdot \text{Re } d) / 1000 \tag{12}$$

Onde:

Re d = fator de correção

H = altitude

$R_o$ = raio médio da Terra

b = 6356752,3141 m

$e^e$ = 0,00669438002290

$\varphi$ = latitude

Este tipo de monitoramento não perturba ou interfere o comportamento dos animais (SAGNOL; REITSMA, 2014) já que é realizado a partir de terra, mas é limitado a áreas com um grande relevo perto da linha da costa, onde os animais se aproximem da mesma (WÜRSIG, CIPRIANO; WÜRSIG, 1991).

**Referências**

BAILEY, H.; LUSSEAU, D. Increasing the precision of theodolite tracking: modified technique to calculate the altitude of land-based observations sites. **Marine Mammal Science,** v. 20, n. 4, p. 880–885, 2004.

GAILEY, G.; ORTEGA-ORTIZ, J. G. A note on a computer-based system for theodolite tracking of cetaceans. **Journal of Cetacean Research and Management,** v. 4, n. 2, p. 213–218, 2002.

MONICO, J. F. G. **Posicionamento pelo GNSS – descrição, fundamentos e aplicações**. São Paulo: UNESP, 2008.

SAGNOL, O.; REITSMA, F. Correcting Positional Errors in Shore-Based Theodolite Measurements of Animals at Sea. **Journal of Marine Biology,** v. 2014, p. 1-8, 2014.

SANTOS, M. S. **Sazonalidade e interação com embarcação do boto-cinza,** *Sotalia guianensis***, (Cetacea: Delphinidae) no Porto do Malhado, Ilhéus, Bahia-Brasil**. 2010. 70 f. Dissertação (Mestrado). Universidade Estadual de Santa Cruz, Ilhéus, Brazil, 2010.

VANICEK, P.; KRAKIWSKY, E. J. Geodesy: The Concepts. **North - Holland Publishing Company**, 1996.

WÜRSIG, B.; CIPRIANO, F.; WÜRSIG, M. Dolphin Movement Patterns: Information from Radio and Theodolite Tracking Studies. In: PRYOR, K. e NORRIS, K. S. (Ed.). **Dolphin Societies - Discoveries and Puzzles**. Berkeley: University of California Press, 1991.  p. 79-111.