Noise exposure and vocal behaviour of baleen whales off the Azores

Tese de Doutoramento

Miriam Romagosa Vergés

Doutoramento em

CIÊNCIAS DO MAR

SICUT AURORA SCIENTIA LUCET
UNIVERSIDADE DOS AÇORES

Horta
2021

Noise exposure and vocal behaviour of baleen whales off the Azores

Tese de Doutoramento

Miriam Romagosa Vergés

Orientadores

Doutora Mónica Cordeiro de Almeida e Silva, Okeanos- Instituto de Investigação em Ciências do Mar, Universidade dos Açores

Doutor Tiago André Lamas Oliveira Marques, Universidade de Lisboa

Professora Doutora Maria Manuela Fraga Juliano, Universidade dos Açores

Tese especialmente elaborada para obtenção do grau de Doutor em Ciências do Mar

This thesis was supported by the doctoral grant M3.1.a/F/028/2015 from the Fundo Regional da Ciência e Tecnologia (FRCT). The research stay was funded by the grant FC/FLAD/FMF/CND1/2017/002 of the "Programa Fundo de Mobilidade FLAD-UAc - Crossing the Atlantic".

And co-funded by the following research projects and institutions:

TRACE (PTDC/MAR/74071/2006)
MAPCET (M2.1.2/F/012/2011)
AWARENESS (PTDC/BIA-BMA/30514/2017)
MOVE-ON (IF/00943/2013/CP1199/CT0001)

Host Institutions:

Institute of Marine Research, Azores (IMAR)

Okeanos – Instituto de Investigação em Ciências do Mar, Universidade dos Açores

Acknowledgments

The completion of this thesis was only possible with the collaboration of many people and institutions.

Thanks to the Fundo Regional para a Ciência e a Tecnologia (FRCT) for my doctoral grant and to the University of the Azores, Okeanos – Instituto de Investigação em Ciências do Mar and IMAR for providing the right settings for this project. Thanks to the Fundação Luso Americana para o desenvolvimento (FLAD) for my grant under the Programa Fundo de Mobilidade FLAD-UAc - Crossing the Atlantic.

This thesis is the culmination of a lifetime child dream. As a kid, I played being a scientist deciphering humpback whale songs from a CD called “Music and whales”. Reality is always different from dreams and this 4-year journey has not been free of drama and difficult moments. Despite many personal and intellectual challenges though, I can say I have truly enjoyed every single moment of this adventure, and it wouldn´t have been like this without the essential support and help from many people.

I am deeply grateful to my supervisor, Mónica Silva, for being such a source of inspiration and an excellent scientist. She was always encouraging, motivating, and persuasive to get the very best of me. She provided the right environment and conditions for me to successfully complete this thesis. Her great sense of responsibility made her always available when I needed advice, corrections or meetings. She was also caring and helpful in my difficult moments, and I thank her for that too.

My gratitude also goes to my co-supervisor, Tiago Marques, for his smart comments and questions that make me improve my critical thinking. I also thank him for his teachings in statistics and for being such an empathic person that sees and values the “person” beyond work. I would also like to thank Ricardo Santos for his supervision during the first 3 years of this thesis and Manuela Juliano, for supervising my last year and carefully revising this document.

I would also like to thank Marc Lammers, for his technical advice and for providing the EARs, and Mark Baumgartner, for instructing me in using his automatic detector during my stay at Woods Hole Oceanographic Institution. Thanks to all co-authors of the published work resulting from this thesis. At the end of each published chapter, I included specific acknowledgements.

Special thanks goes to a friend and a work colleague, Irma Cascão, for deploying EARs and collecting the acoustic dataset used in this thesis and for teaching me how to set up hydrophones. A big thank you goes to another friend and work colleague, Sergi Pérez-Jorge, for his great willingness to help and collaborate and for his constant emotional support during endless manuscript revisions. I am also grateful to Rui Prieto for his help in many technical issues and for always being ready to give a hand. Thanks to Marta Tobeña and Cláudia Oliveira for your team work, to Sergio Gomes for his help with electronics and to skippers, Renato, Bruno and Paulinho for helping with EAR deployments and recoveries. I also thank my friend, Maria Rakka for helping me with the submission of this thesis and many other things.

Agradeço ao meu companheiro Pedro pela sua paciência e amor nos momentos difíceis, e a minha filha Júlia, que nasceu no percurso deste doutoramento, e é a alegria da minha vida. Obrigada também a todos os meus amigos do Faial pelo apoio incondicional i a les meves amigues de Sant Pol de Mar, en especial a la Cristina Bancells, per sempre estar a ben a prop tot i la distància.

En últim lloc vé l'agraiment més important. Aquesta tesi va tota dedicada als meus pares, Josep i Merçè, per haver donat suport als meus somnis des del principi, per estar sempre presents, pel seu amor incondicional e per la seva imesurable ajuda cuidant de la meva filla i de mi en moments dificils de salut. Sense ells no hauria pogut acabar aquesta tesi com ho he fet. Us estimo molt i espero passar moltes més aventures amb vosaltres.

Table of Contents

Abstract

Fin (*Balaenoptera physalus*), blue (*B. musculus*) and sei whales (*B. borealis*) produce very low frequency and high amplitude vocalisations that can be regularly repeated as songs or irregularly produced as single or grouped calls. While songs are produced by males, peak during the mating season and are believed to act as reproductive displays, calls may have multiple functions associated to feeding and social contexts. By using passive acoustic techniques, that allow long-term continuous monitoring of remote areas, the study of temporal and spatial patterns of vocalisations as well as their functions can elucidate important aspects of the biology and ecology of these highly mobile and elusive species that would otherwise be difficult or impossible to obtain. The main goal of this dissertation is to investigate the vocal behaviour of fin, blue and sei whales (with a special focus on the fin whale), to contribute to a better understanding of their ecology and behaviour during migration, the least known phase of their annual life cycle. This study also investigates shipping noise levels in relation to the vocal behaviour of these three species and discusses potential implications for their migratory behaviour.

Through the analysis of a large acoustic dataset collected over a period of five years in the Azores, this work studied the temporal occurrence of different vocalisations from three species of baleen whales, namely fin whale 20-Hz calls, blue whale AB and D calls and sei whale downsweeps. Fin and blue whales were acoustically present in the archipelago from autumn to spring and showed a seasonal shift in calling behaviours, from reproductive singing in winter to the production of foraging associated calls in spring. Sei whales showed a bi-seasonal calling pattern in spring and autumn, indicative of the migration timing of the species. Diel calling patterns showed higher diurnal fin whale singing activity, a lack of diel patterns for the two blue whale call types and increased sei whale calling during the day. Drivers of these patterns are discussed in relation to the ecology of each species and by comparing with other studies' findings.

The same dataset was used to study the function of two fin whale call types, the song forming 20-Hz call and the 40-Hz call, by examining their production in relation to season, year and zooplankton biomass, the main prey of this species. Results showed that production of 20-Hz

calls was strongly influenced by season, with a clear peak during the breeding months, and secondarily by year, likely due to changes in local whale abundance. These results support the reproductive function of the 20-Hz song used as an acoustic display. Conversely, season and year had no effect on variation in 40-Hz calling rates, but prey biomass did. This is the first study linking 40-Hz call activity to prey biomass, supporting the previously suggested food-associated function of this call

This work also investigated long-term changes in two fin whale song parameters (Internote intervals-INIs and peak frequencies) by compiling two decades of acoustic data from six different regions in the North Atlantic. First, this study documented a rapid replacement of INIs (from 19s to 12s) across a vast area of the central North Atlantic in just four winter seasons. During the transition period, both song types co-existed with hybrid songs (i.e., with intermediate INIs) and there was a clear south-westerly spatial gradient in the percentage of song types, that we attribute to a cultural revolution. Second, after the rapid song replacement, this work documented gradual changes in fin whale song characteristics (an increase in INIs and a decrease in the frequency of the high-frequency note of songs). These results are consistent with what has been documented in other ocean basins, as well as in blue whale songs, which may be the result of cultural evolution driven by different interacting selecting pressures.

Finally, this dissertation analysed low-frequency (<1 kHz) noise levels and shipping noise by using a 5-year acoustic dataset in three offshore areas of the Azores archipelago. Monthly average noise levels ranged from 90.3 dB re 1 µPa (Açores seamount) to 103.1 dB re 1 µPa (Condor seamount) and local ship noise was present up to 13% of the recording time in Condor. At this location, average contribution of local boat noise to background noise levels was almost 10 dB higher than wind contribution. Sound pressure levels measured in the Azores were lower than those reported for the Mediterranean basin and the Strait of Gibraltar. However, the currently unknown effects of baleen whale vocalization masking and the higher noise levels and shipping traffic reported in other areas of the archipelago underline the need for continuous monitoring to understand any long-term impacts on whales.

This work provides novel information on the vocal behaviour of fin, blue and sei whales during migration, contributes to the knowledge on the function of two fin whale call types, documents long-term fin whale song changes in the North Atlantic and reports the first underwater noise levels and shipping noise in the Azores region. Overall, outcomes from this work contribute to the knowledge on the ecology of three baleen whale species, and may ultimately assist in identifying functional habitats, predict negative impacts from human activities and support the implementation of conservation actions.

Resumo

As baleias comum (*Balaenoptera physalus*), azul (*B. musculus*) e sardinheira (*B. borealis*) produzem vocalizações de baixa frequência e grande amplitude que podem ser repetidas num padrão regular, formando canções, ou produzidas de forma irregular, como vocalizações individuais ou em grupo. As canções são produzidas por machos, sobretudo na época de acasalamento, e acredita-se serem usadas como exibições reprodutivas, enquanto as vocalizações irregulares podem ter varias funções associadas a contextos sociais e de alimentação. As técnicas de acústica passiva permitem monitorizar áreas remotas por longos períodos de tempo, possibilitando o estudo dos padrões temporais e espaciais das vocalizações, assim com as suas funções, e elucidando aspetos essenciais da biologia e ecologia destas espécies com elevada mobilidade e elusivas, que de outra maneira seria difícil ou impossível obter. O objetivo principal desta tese é investigar o comportamento vocal das baleias comum, azul e sardinheira (com um foco especial na baleia comum), para adquirir um melhor conhecimento da sua ecologia e comportamento durante a migração, a fase menos conhecida do seu ciclo de vida. Este estudo também investiga os níveis de ruído produzido pelo tráfego marinho em relação ao comportamento vocal destas três espécies, e discute as implicações potenciais para o seu comportamento migratório.

Através da análise de um extenso conjunto de dados acústicos recolhidos ao longo de cinco anos nos Açores, este trabalho investigou a ocorrência temporal de vocalizações de baleia comum, azul e sardinheira. As baleias comuns e azuis foram detetadas no arquipélago entre o outono e a primavera, demonstrando uma mudança sazonal no comportamento vocal, com a produção de canções reprodutivas no inverno e a produção de vocalizações associadas à alimentação na primavera. As baleias sardinheiras mostraram um padrão de detecções acústicas bi-sazonal, com picos evidentes na primavera e outono, coincidindo com o período conhecido da migração desta espécie pela área de estudo. Os padrões diários de vocalizações revelaram maior frequência de canções de baleia comum durante o dia, ausência de um padrão diário para ambos os tipos de vocalizações de baleia azul, e um incremento da taxa de vocalizações de baleias sardinheiras durante o período diurno. Os fatores que influenciam estes padrões são discutidos com base na ecologia de cada espécie e comparando com os resultados de outros estudos.

Os mesmos dados acústicos foram usados para estudar a função de dois tipos de vocalizações de baleia comum, a canção de 20-Hz e a vocalização dos 40-Hz, examinando a produção de cada tipo de vocalização em função do ano, estação do ano e biomassa de zooplâncton, a principal presa desta espécie. Os resultados revelaram que a taxa de produção da vocalização de 20-Hz é influenciada principalmente pela estação, com um pico claro durante os meses de reprodução, e secundariamente pelo ano, provavelmente devido a alterações na abundância local da espécie. Estes resultados suportam a função reprodutiva da canção de 20-Hz usada como exibição acústica. Por outro lado, estação e ano, não apresentaram nenhum efeito na variação da taxa de produção da vocalização de 40-Hz, e a única variável estatisticamente significativa foi a biomassa das presas. Estes resultados constituem a primeira evidência direta de uma função desta vocalização associada à alimentação.

Este trabalho também investigou mudanças a longo termo no comportamento vocal da baleia comum, através da análise de dois parâmetros acústicos (intervalos entre notas - INIs, e frequências pico), usando para isso duas décadas de registos acústicos recolhidos em seis regiões diferentes do Atlântico Norte. Os resultados documentam uma substituição rápida dos INIs (de 19s a 12s) em apenas quatro invernos numa vasta área do centro Atlântico. Durante o período de transição, canções com os dois tipos de INIs coexistiram com canções híbridas (i.e., com INIs intermédios), e posteriormente, observou-se um evidente gradiente espacial na percentagem de cada tipo de canção, consistente com uma revolução cultural na canção. Paralelamente, ocorreram mudanças graduais nas características das canções (aumento dos INIs e diminuição da frequência da nota de alta frequência), também documentadas em outros oceanos e nas canções da baleia azul, o que sugere uma evolução cultural, resultante da interação de diferentes pressões seletivas.

Finalmente, esta tese quantificou os níveis de ruído de baixa frequência (<1 kHz) e o ruído produzido pelo tráfego marítimo local usando cinco anos de registos acústicos em três áreas de mar aberto do arquipélago dos Açores. Os níveis médios de ruído variaram entre os 90.3 dB re 1 µPa (monte submarino Açores) e os 103.1 dB re 1 µPa (monte submarino Condor). A percentagem máxima de tempo com presença de ruído de barcos foi de 13% e ocorreu no Condor. Neste local, a contribuição média do ruído dos barcos para os níveis de ruído foi 10 dB mais elevada do que a contribuição do ruído do vento. Os níveis de pressão sonora medidos nos Açores foram geralmente inferiores aos reportados para o Mediterrâneo ou o

Estreito de Gibraltar. No entanto, desconhece-se se os níveis de ruído observado nos Açores poderão, ainda assim, mascarar as vocalizações das baleias de barbas. Por outro lado, sabe-se que os níveis de ruído do tráfego marítimo são consideravelmente mais elevados noutras áreas do arquipélago. Em conjunto, estes resultados sublinham a necessidade de uma monitorização contínua dos níveis de ruído subaquático para avaliar os possíveis impactos a longo prazo sobre as baleias de barbas.

Este trabalho contribui novas informações sobre o comportamento vocal das baleias comuns, azuis e sardinheiras durante a migração, fornece novas pistas sobre a função de dois tipos de vocalizações de baleia comum, revela as alterações ocorridas nas canções das baleias comuns no Atlântico Norte ao longo de duas décadas, e quantifica, pela primeira vez, os níveis de ruído subaquático e ruído do tráfego marítimo local na região dos Açores. No geral, os resultados deste trabalho contribuem para um melhor conhecimento da ecologia de três espécies de baleias de barbas, e poderão ser usados para a identificação futura de habitats funcionais, prever os impactos negativos das actividades humanas e apoiar o planeamento e implementação de acções de conservação deste grupo de cetáceos.

Chapter 1

Introduction

1.1 Baleen whale ecology

This dissertation focuses on three baleen whale (i.e., Mysticeti) species from the “rorqual” family (i.e., Balaenopteridae): the fin (*Balaenoptera physalus*), blue (*B. musculus*) and sei whale (*B. borealis*). Rorquals are characterised by their highly specialized filter-feeding apparatus, made up of baleen plates that hang from the upper jaw, and pleated throat grooves, that allow their mouths to expand when engulfing large amounts of water to filter prey. They have slender and streamline bodies that make them fast and efficient swimmers that facilitate long-distance migration (Geijer et al., 2016).

Blue whales are the largest member of the Balaenopteridae family, followed by fin and sei whales. These species can be found in all oceans, predominantly over deep waters or near the continental slopes of subtropical to subpolar waters (Aguilar, 2009; Prieto et al., 2012; Sears and Perrin, 2009). Most baleen whales undertake seasonal latitudinal migrations from feeding to wintering grounds (Mate et al., 1999; Mizroch et al., 2009; Prieto et al., 2014; Silva et al., 2013), although some fin and blue whales individuals remain year-round in temperate, tropical or high latitude areas (Bérubé et al., 1998, 2002; Moore et al., 2006; Širović et al., 2009). This year-round residency may be due to either a partial migration, where not all individuals of the population migrate, or a differential migration, where patterns differ between sexes, age or reproductive status (Dingle and Drake, 2007).

In the North Atlantic, blue whales appear to feed almost exclusively on krill (e.g. *Meganyctiphanes norvegica* and *Thysanoessa spp*) while fin whales also feed on other species of zooplankton and a variety of schooling fish (Gavrilchuk et al., 2014; Sigurjónsson and Víkingsson, 1997; Víkingsson et al., 2015). When they locate high concentrations of suitable prey, they feed by lunging, a process consisting of a rapid forward acceleration and subsequent mouth opening to engulf prey-laden water into an extensible buccal cavity. Then the mouth closes and water is expelled and prey filtered through baleen plates (Goldbogen et al., 2017). Sei whales primarily feed on calanoid species, especially on *Calanus finmarchicus*, and to a lesser extent on euphausiids (Sigurjónsson and Víkingsson, 1997). They are able to capture prey by lunging (i.e., engulfing), like fin and blue whales, or by skimming, which consists in capturing prey by filtering water while swimming slowly forward (Prieto et al., 2012; Watkins and Schevill, 1979).

Fin, blue and sei whales are usually found solitary or in small unstable groups (Aguilar, 2009; Horwood, 2009; Sears and Perrin, 2009) but temporary large aggregations may occur in highly productive areas (Baines et al., 2017; Baines and Reichelt, 2014; Víkingsson et al., 2015). Breeding activity (i.e., mating and calving) seems to take place mainly during the winter (Horwood, 2009; Kjeld, 1992; Lockyer, 1984; Mizroch et al., 1984; Ohsumi et al., 1958) but little is known about their reproduction strategies or the locations of specific breeding or calving grounds. The life expectancy of fin and blue whales is thought to be of at least 80–90 years but could be longer (Aguilar, 2009; Sears and Perrin, 2009). Predation pressure in these species is low and mainly due to killer whale attacks (Jefferson et al., 1991).

After the whaling period in the twentieth century, that largely depleted many species of baleen whale populations, other current human-caused threats are hindering the recovery of some of these populations (Clapham, 2016). These include ship strikes (Laist et al., 2001) and entanglement in fishing gear (Reeves et al., 2013), as well as threats for which population-level impacts are still unclear, like ocean noise (Nowacek et al., 2007) or climate change (Tulloch et al., 2019).

1.2 Baleen whale vocal behaviour

The vocal behaviour of terrestrial species (e.g. birds, frogs, insects, bats and primates) has been extensively studied for many years (Cheney and Seyfarth, 2018; Herzing, 1996; Kroodsma and Byers, 1991; Schwartz, 1994). Significant advances in knowledge about the behavioural context of the signal production of these taxa has been achieved by using methods such as playback experiments and signal modification, conditioning, cognitive experiments and decision-making choice tasks (Garcia and Favaro, 2017). For large marine pelagic and elusive species like baleen whales, these studies face obvious limitations and are often impossible; thus, knowledge about the vocal behaviour of this group lags behind that of terrestrial species. Yet, understanding baleen whale vocal behaviour and call function can be a powerful tool to infer into many aspects of their biology and ecology that would be otherwise impossible to acquire. Moreover, if these vocal behaviours are associated with the state of individuals or groups (e.g., reproductive status and success, social complexity), habitat quality (e.g., food resources) or animal density (e.g., call production rates) they may assist in identifying functional habitats, predict negative human impacts and support conservation planning (Teixeira et al., 2019).

Fin, blue and sei whales produce loud and low frequency vocalisations that are ideal for communication between individuals of such widely dispersed and nomadic species (Bannister, 2009). The most commonly reported fin whale vocalisation worldwide is the ~1-s downsweep centred at 20-Hz (20-Hz note) (Watkins et al., 1987) that, when repeated regularly as part of a song, is sometimes accompanied by a lower frequency (15-18Hz) “backbeat” and/or a higher frequency upsweep ranging from 99-130 Hz (Hatch and Clark, 2004; Širović et al., 2009). Fin whales also produce downsweeps from 75-40 Hz that are referred as “40-Hz calls” (Watkins, 1981). Vocalisations produced by blue whales are more varied than those of fin whales, and are often downswept tones (80-30Hz) of moderate duration (2-30s) (McDonald et al., 2006b; Miksis-Olds et al., 2018) regularly repeated as part of a song, or sporadically as singular calls or song fragments. Although several irregular infrasonic (<20 Hz) and higher frequency (30-200 Hz) blue whale calls have been described (Berchok et al., 2006), the best studied non-song call is the “D call”, a downsweep of about 1-s duration ranging from 60 to 45 Hz (McDonald et al., 2001; Mellinger and Clark, 2003; Thompson et al., 1996). Sei whale calls include a variety of frequency modulated up and downsweeps in the frequency band of 100-21 Hz (Fig. 1.1e) (Baumgartner et al., 2008b; Calderan et al., 2014; Español-Jiménez et al., 2019; Rankin and Barlow, 2007) and other higher frequency tonal sounds and sweeps (Gedamke and Robinson, 2010; Knowlton et al., 1991; McDonald et al., 2005; Thompson et al., 1979).

In the North Atlantic, songs produced by fin whales consist of regularly repeated 20-Hz notes (Watkins et al., 1987) that sometimes alternate with “backbeats” and are accompanied by a higher frequency “upsweep” (Hatch and Clark, 2004) (Fig. 1.1a). Songs can last up to tens of hours, with short interruptions to breathe (Watkins, 1981). Blue whale songs consist of long, patterned sequences of very-low-frequency sounds (15–20 Hz), hierarchically organized into two-part phrases repeated every 73s: a constant-frequency tonal ‘‘A’’ part lasting approximately 8s, followed by a frequency-modulated ‘‘B’’ part lasting approximately 11s (Mellinger and Clark, 2003) (Fig. 1.1c). Recent work suggests that sei whales may also produce songs because some patterning has been identified in the sequences of their vocalisations (Tremblay et al., 2019).

The behavioural and ecological context of call production can provide insights into call function. Fin and blue whale songs are believed to act as reproductive displays because all biopsied singing whales were males (Croll et al., 2002; McDonald et al., 2001; Oleson et al., 2007a) and peak during the breeding season of these species (Nieukirk et al., 2012; Watkins et al., 1987), which occurs in winter in the Northern Hemisphere (Mizroch et al., 1984; Ohsumi et al., 1958). In some areas, though, blue whales can sing year-round and singing activity peaks during the austral summer on their feeding grounds (Buchan et al., 2015; Širović et al., 2004; Stafford et al., 2001). The proximate function of songs is still not well understood but, as suggested for humpback whale (*Megaptera novaeangliae*) songs (Herman et al., 2013), they may serve to attract or court females, mediate male-male interactions or both (Croll et al., 2002; Oleson et al., 2007a; Watkins et al., 1987). Song characteristics can show an important geographic (Archer et al., 2020; Balcazar et al., 2015; Delarue et al., 2009; Hatch and Clark, 2004; McDonald et al., 2006b), seasonal (Morano et al., 2012; Oleson et al., 2014; Watkins et al., 1987) and inter-annual (Delarue et al., 2009; Širović et al., 2017; Weirathmueller et al., 2017) variation in both species. In fact, in the last decades, a decrease in blue and fin whale song frequencies and inter-unit intervals (i.e., time interval between calls) have been reported in different ocean basins (Gavrilov et al., 2012; Helble et al., 2020; Leroy et al., 2018; Malige et al., 2020; McDonald et al., 2009; Miksis-Olds et al., 2018; Weirathmueller et al., 2017).

Fin, blue and sei whales also produce calls irregularly, which have been generally associated with social interactions and feeding behaviours. Fin whale 40-Hz calls (Fig. 1.1b) (Širović et al., 2013; Watkins, 1981; Wiggins and Hildebrand, 2020), have been recorded from whales in groups engaged in foraging behaviours (Watkins, 1981) and as a relatively coordinated sequence by two tracked whales (Wiggins and Hildebrand, 2020). Irregular 20-Hz fin whale calls have been recorded in similar contexts to the 40-Hz call (Watkins, 1981) and also as counter-calls (McDonald et al., 1995). Blue whale downswept D calls (Fig. 1.1d) are produced by both sexes and have been recorded from single and aggregated whales (McDonald et al., 2001; Oleson et al., 2007a; Thode et al., 2000) engaged in foraging (Oleson et al., 2007a), in counter-calling (McDonald et al., 2001) and in male-male competitive interactions (Schall et al., 2020). Finally, in the North Atlantic, sei whales produce a downsweep call (84-Hz to 32-

Hz) (Fig. 1.1e), that may serve as individually distinctive contact calls since their end frequencies vary individually (Baumgartner et al., 2008b).

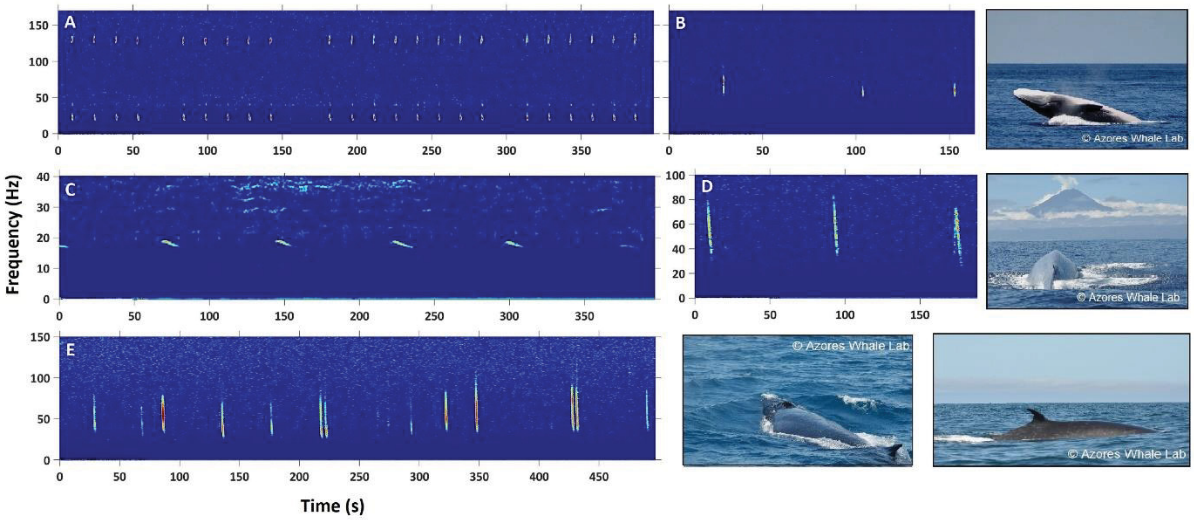


Figure 1.1. Spectrograms of vocalisations and photos of fin whales: (A) 20-Hz song and (B) 40-Hz call; blue whales: (C) A song and (D) D calls and sei whales: downsweep calls (E).

The temporal segregation in the activity of different call types has also provided further insights into the functions of fin and blue whale calls. The fin whale 40-Hz call and the blue whale D call were detected in late spring and summer in known feeding areas, suggesting a potential food-associated function for these calls, while songs were detected during the breeding season (Oleson et al., 2007b; Širović et al., 2013). Similarly, diel activity patterns, common among many organisms, are often associated with changes in acoustic behaviour (Baumann-Pickering et al., 2015; Bridges and Dorcas, 2000; Kamimura and Tatsuki, 1993). There is circumstantial evidence that calling activity in baleen whales is light-related, either directly or through the diel migrations of their prey, and that feeding and singing are not compatible (Baumgartner and Fratantoni, 2008; Oleson et al., 2007a; Simon et al., 2010; Širović et al., 2013; Stafford et al., 2005; Tripovich et al., 2015). Thus, spatial and seasonal variations in diel calling patterns can provide information on feeding ecology and prey preferences (Baumgartner and Fratantoni, 2008; Shabangu et al., 2019a). For example, in the Bering Sea and off Southern California, fin whale presumed food-associated 40-Hz calls showed higher diurnal activity when whales can feed more effectively, but the opposite pattern was found in the Gulf of California, possibly because fin whales may be feeding at night in that region (Širović et al., 2013). A recent study also found that diel patterns in blue whale singing activity differ between foraging and migrating behaviours at an individual and population level, which can be used as an acoustic signature for this behavioural transition (Oestreich et al., 2020).

Most relevant studies on the vocal behaviour of fin, blue and sei whales have been conducted in summer feeding areas like for example in waters off California (McDonald et al., 2001; Oleson et al., 2007a, 2007b; Širović et al., 2004, 2013), North-east USA (Baumgartner and Fratantoni, 2008; Delarue et al., 2009; Edds, 1988; Edds P. L., 1982; Watkins, 1981) and in subarctic and Antarctic regions (Escajeda et al., 2020; Širović et al., 2009; Stafford, 2003) but very few studies have focused on migratory habitats (Shabangu et al., 2019b).

1.3 Impacts of noise on baleen whales

Ocean noise (hereafter noise) is defined as the introduction of acoustic energy by human activities that can negatively affect the marine environment (Dekeling et al., 2014). Anthropogenic sources of noise are varied, including seismic surveys, installation of wind farms and offshore platforms, explosions, dredging, coastal constructions, military and civil sonars, echosounders, acoustic deterrents, shipping, and energy installations.

Noise can have diverse effects on baleen whales, a particularly vulnerable group that is highly dependent on sound for critical life history processes (Nowacek et al., 2007). In marine mammals, noise can induce acute effects, like injury, mortality and temporary or permanent shifts in hearing threshold (TTS, PTS) or moderate effects, like physiological stress, behavioural disturbance and acoustic interference (i.e. masking) (Nowacek et al., 2007; Richardson et al., 1995a; Southall et al., 2019). The type of effect depend on the intensity and characteristics of the received noise, as well as on the duration of the noise exposure and the animal's response, which may be influenced by the ecological and behavioural context during that exposure.

Balaenopterids emit sounds with fundamental frequencies below 1 kHz (Richardson et al., 1995b). Although audiograms are not available for this group, a general hearing sensitivity for the low-frequency group, that include all baleen whale species, has been estimated to range from ~30Hz to ~30kHz, based on a combination of available studies in audiometry, auditory anatomy, and sound production (Southall et al., 2007b, 2019). In this frequency band, shipping is the most important source of anthropogenic noise (Andrew et al., 2002;

Hildebrand, 2009; Klinck et al., 2012; McDonald et al., 2006a; Nieukirk et al., 2012; Wenz, 1962) and is responsible for the increased levels of ocean noise. In the North Atlantic, low frequency noise (at 50Hz) has increased by about 5.5 dB per decade from 1950 to 1970 (Ross, 2005) and about 2.8 dB from 1966 to 2013 (Širović et al., 2016). A similar trend has been found in the North Pacific with noise increasing at an average rate of 2.5–3 dB per decade at 30–50Hz since the 1960s (Andrew et al., 2002; Chapman and Price, 2011; McDonald et al., 2006a).

Shipping noise can cause behavioral disturbances and limit the range for successful detection of baleen whale signals, thus reducing their communication space (i.e., masking effect) (Fig. 1.2) (Erbe et al., 2015; Hatch et al., 2012; Ponce et al., 2012; Samaran et al., 2010). Most studies conducted to date focused on humpback whales and reported a variety of responses to shipping noise exposure. Humpback whales changed their vocal behaviour in the presence of high noise from vessels, by increasing the amplitude of their vocalisations, decreasing vocalisations rates (Pen et al., 2018) or even ceasing singing (Tsujii et al., 2018). While some studies noted changes in respiratory behaviour (Frankel and Clark, 2002), cessation of foraging (Blair et al., 2016) and decreased dive duration and travel speed (Dunlop, 2016), others did not find any response (Wensveen et al., 2017), which highlights the importance of context when considering noise effects. Studies on fin and blue whales also showed changes in vocal behavior associated with shipping noise. Fin whales decreased their 20-Hz note bandwidth, peak frequency, and center frequency under increased levels of background noise caused by large vessels (Castellote et al., 2012a). Blue whales increased source levels of D calls (<100 Hz) and the production of irregular B calls in the presence of commercial ships (McKenna, 2011) and also increased D calling activity when ships were nearby (Melcón et al., 2012). These changes in vocal behaviour are believed to arise from the acoustic interference and reduction in communication space (Cholewiak et al., 2018a; Clark et al., 2009; Putland et al., 2018).

In the long term, changes in vocal behavior caused by noise may increase the energetic costs of signalling (Bradbury and Vehrencamp, 1998) and compromise call function (Castellote et al., 2012a). Also, the potential avoidance of noisy areas that are important for foraging, breeding or resting (Castellote et al., 2012a), could reduce foraging or reproduction success and impact energy balance of individuals, potentially affecting population dynamics. However, determining a causal link between noise exposure, effects on individual vital rates and population consequences is extremely difficult, and further studies are needed to better understand these links (Pirotta et al., 2022).

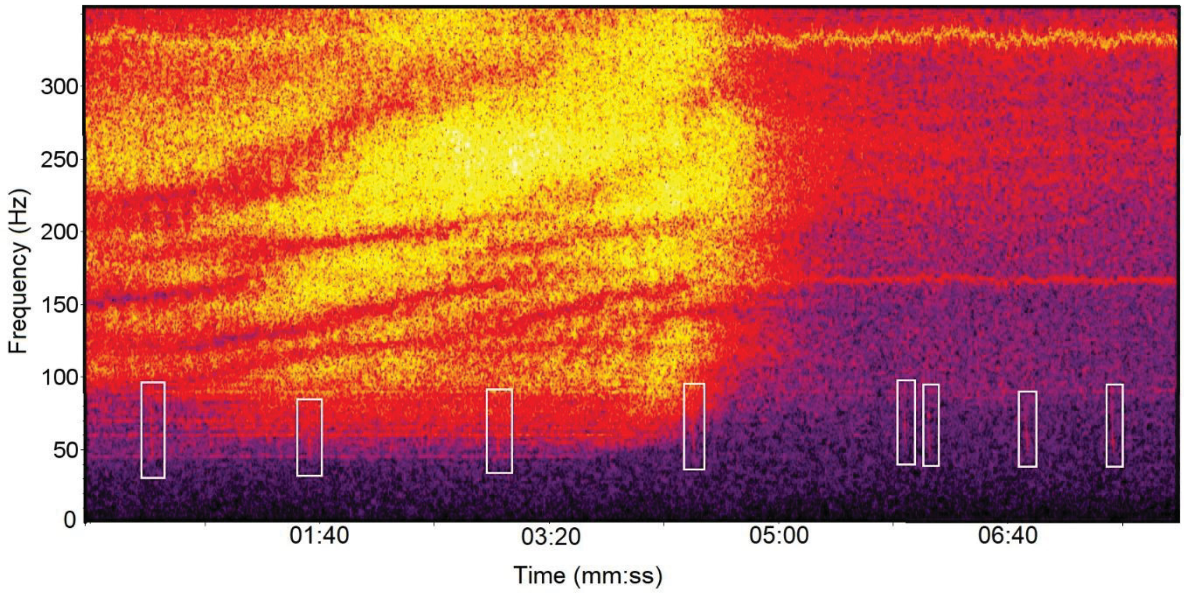


Figure 1.2. Spectrogram of shipping noise overlapping sei whale downsweep calls (white boxes).

1.4 Passive acoustic monitoring of baleen whales

Passive acoustic monitoring (PAM) is the use of sound recorders to survey and monitor wildlife and environments. PAM has become an increasingly important tool for studying cetaceans because firstly, they are a highly vocal taxonomic group and secondly, their visual detectability is limited by weather, light and behaviour. In addition, visual surveys of cetaceans can be highly expensive and their detection range is limited compared to that of acoustic surveys.

There are a wide variety of acoustic recorders available. The device that was mostly used in this study, known as the Ecological Acoustic Recorder (EAR) (Fig. 1.3) (Lammers et al., 2008), is a fixed microprocessor-based autonomous recorder that periodically acquires and stores acoustic data of up to 30 kHz into a hard drive. The EAR is bottom-moored underwater with weights, and linked to acoustic releases and buoys for the recovery of data and refurbishing.

These characteristics makes it cost efficient and suitable for monitoring remote open-ocean areas for 24 hours a day in all weather conditions.

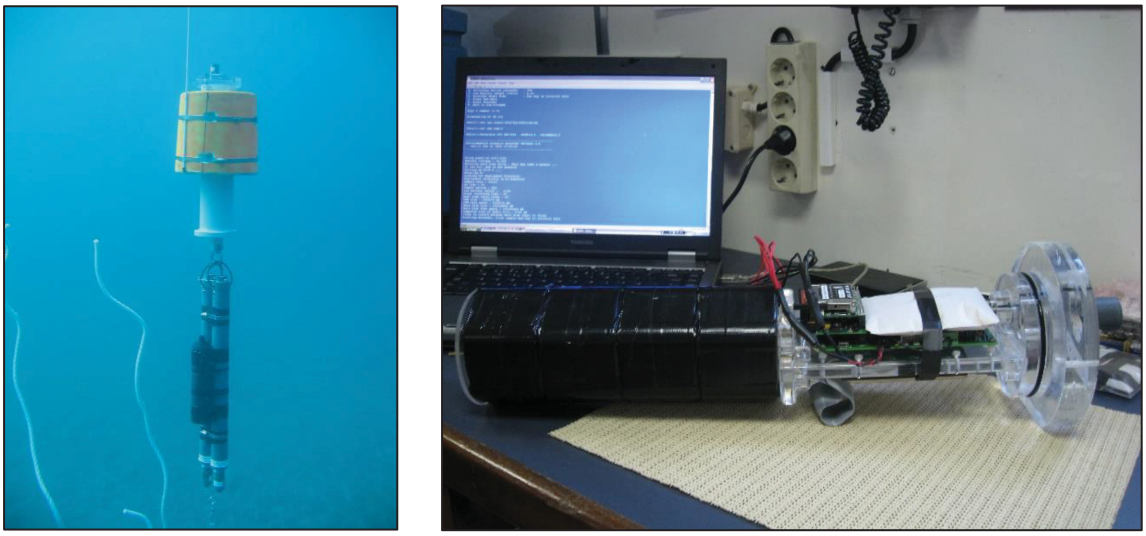


Figure 1.3. Bottom-moored EAR with acoustic releasers and float (left) and post-deployment EAR data downloading (right).

The use of multiple fixed autonomous recorders in arrays, can provide valuable large scale acoustic monitoring data and allow tracking of vocalising animals (Van Parijs et al., 2009). Similarly, Ocean Bottom Seismometers (OBS) used to measure earthquake activity, offer excellent opportunities to monitor and locate low frequency vocalisations of fin and blue whales (Pereira et al., 2020; Soule and Wilcock, 2013; Weirathmueller et al., 2013; Wilcock, 2012).

The repetitive and long-lasting nature of blue and fin whale songs makes them useful proxies of species presence during the singing season. Song recordings have revealed blue and fin whale presence in previously undocumented areas (Balcazar et al., 2015; Crance et al., 2015; Miksis-Olds et al., 2019) and seasons (Buchan et al., 2015; Simon et al., 2010; Stafford et al., 2007) and provided insights into migration patterns (Aulich et al., 2019; Leroy et al., 2016, 2021; Moore et al., 1998; Tripovich et al., 2015) and distributions (McCauley et al., 2018; Thomisch et al., 2016; Watkins et al., 2000). The correlation between song occurrence and environmental variables or prey proxies has also informed about drivers of blue and fin whale presence (Escajeda et al., 2020; Miksis-Olds et al., 2019; Shabangu et al., 2020; Wang et al., 2016) and habitat suitability (Burtenshaw et al., 2004; Širović and Hildebrand, 2011). Songs are also geographically distinct and these variations have been used to distinguish between populations and stocks (Archer et al., 2020; Balcazar et al., 2015; Delarue et al., 2009; Hatch and Clark, 2004; McDonald et al., 2006b). Long-term and large-scale acoustic presence and abundance estimates may even provide information on population trends and changing distributions caused by climate change (Davis et al., 2017; Širovic et al., 2015).

Like every methodology, PAM surveys also have limitations. One of them is that PAM relies on vocalising animals for detection and not all cetacean species produce sounds frequently (Mellinger et al., 2007). Baleen whales can be silent for long periods of time (Akamatsu et al., 2014; Baumgartner and Fratantoni, 2008) which could be equivocally attributed to the absence of whales. Use of reproductive songs to monitor species occurrence may produce unreliable results outside the breeding season, when animals may sing less or not even sing (Nieukirk et al., 2004; Watkins et al., 1987), and reflect only males' presence (Croll et al., 2002; Oleson et al., 2007a). By combining multiple calls (songs and irregular calls), we might reduce the bias caused by silent whales and sex-specific sounds, and obtain more accurate information on species' presence (Oleson et al., 2007b; Širović et al., 2013). Thus, an understanding of the acoustic repertoire, individual and group calling behaviour, and diel, seasonal, and regional variation in call production, is necessary to adequately interpret acoustic detections (Nowacek et al., 2016).

Another limitation is that PAM generates large amounts of acoustic data that are time-consuming to analyse and often require the use of automatic detectors (Hood et al., 2016; Kowarski and Moors-Murphy, 2020; Van Parijs et al., 2009; Roch et al., 2016). Nevertheless, with increasing knowledge of the vocal behaviour of cetaceans, the use of multiple calls and the advances in software and hardware technologies, these limitations will be reduced and some overcome. Overall, PAM technologies are invaluable because they provide large-scale spatial and temporal data that improves our understanding of the distribution and movements of highly mobile pelagic animals, like baleen whales, which has important conservation and management implications (Van Parijs et al., 2009; Redfern et al., 2006).

1.5 The use of model-based prey ecological models to study baleen whale vocal behaviour

The acoustic occurrence of baleen whales in relation to oceanographic or prey variables can provide valuable information on the drivers of whale presence and habitat use (Širović and

Hildebrand, 2011; Wang et al., 2016). However, obtaining long-term simultaneous acoustic, oceanographic and prey biomass data can be very expensive and difficult. An excellent alternative is the use of spatially and temporally explicit physical and biogeochemical models that can generate hindcast estimates of oceanographic and prey fields to use in combination with acoustic data. These models offer a very cost-effective alternative to prey sampling and enable avoiding complex time lagged associations between prey proxies (i.e., chlorophyll) and their predators (Grémillet et al., 2008).

The spatial ecosystem and population dynamics model SEAPODYM simulates spatial and temporal dynamics of production and biomass of different functional groups of migrant and non-migrant micronekton and mesozooplankton (i.e. both holo- and mero-zooplankton) (Lehodey et al., 2010, 2015). In the North Atlantic, fin, blue and sei whales feed mainly on zooplankton (Arregui et al., 2018; Sigurjónsson and Víkingsson, 1997; Silva et al., 2019). Thus, using simulated mesozooplankton biomass in relation to the acoustic activity of different call types offers an excellent opportunity to investigate their potential association to foraging. Additionally, acoustic detections of baleen whales in relation to prey biomass can provide a wide range of information on habitat use and function, movement patterns and behaviour. For example, SEAPODYM model has been successfully used for identifying sea turtle foraging grounds (Abecassis et al., 2013), describing large-scale movements of baleen whales (Pérez-Jorge et al., 2020), predicting cetacean habitat preferences (Lambert et al., 2014), simulating tuna population spatial dynamics (Senina et al., 2020; Sibert et al., 2012) and understanding the foraging behaviour of seals (Green et al., 2020).

1.6 The Azores: a North Atlantic migratory habitat for baleen whales

The study area of this dissertation is the North-east and Mid-North Atlantic Ocean with a focus on the Azores Archipelago (Fig. 1.4).

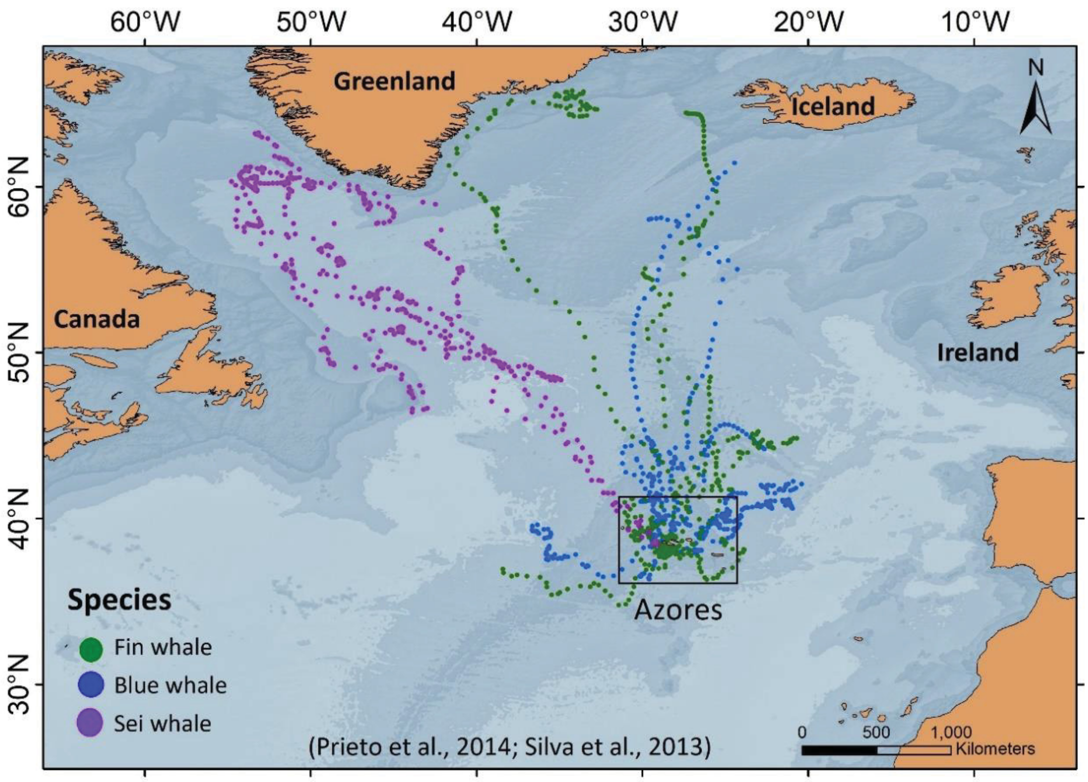


Figure 1.4. Satellite telemetry tracked fin, blue and sei whales tagged in the Azores Archipelago, in spring and summer of 2008-2012 (Prieto et al., 2014; Silva et al., 2013).

The Azores Archipelago is a group of 9 isolated volcanic islands located in the middle of the Atlantic and distancing about 1400 and 2000 km from continental Europe and north America, respectively. The archipelago is located on the Mid-Atlantic Ridge (MAR) and has a complex topography with steep submarine walls, ridges, submarine canyons and scattered seamounts (Morato et al., 2008a). The region suffers the influence of the north-eastward-flowing North Atlantic Current in the north of the Azores, and the eastward flowing Azores Current, in the south of the archipelago (Juliano and Alves, 2007). The Azores Current is related to a thermohaline front, the Azores Front/Current system, which includes an intense meander and meso-scale eddy generation capacity (Juliano and Alves, 2007) flowing through the southern part of the region (Caldeira and Reis, 2017; Santos et al., 1995).

The combination of this hydrodynamic systems with complex topographies makes the region around the Azores a hotspot for marine megafauna (Afonso et al., 2020; Morato et al., 2008b). In the Azores, 27 cetacean species can be sighted including fin, blue and sei whales that are seasonally present in the area (Silva et al., 2014). Blue and fin whales stop to feed in the archipelago on their way to northern latitudes (Silva et al., 2013), timing their arrival with the spring bloom in primary productivity (Visser et al., 2011). As spring advances and favourable habitat conditions move progressively further north, fin and blue whales resume their migration and abandon the Azores, generally leaving the area in summer, when habitat conditions are less suitable for them (Pérez-Jorge et al., 2020; Prieto et al., 2017). Sei whales transit quickly through the archipelago in spring, feeding only occasionally, while on their way to the Labrador Sea (Olsen et al., 2009; Prieto et al., 2014). Hence, the Azores is an excellent spot to investigate the vocal behaviour of these three species during migration.

In the Azores, the principal source of anthropogenic noise comes from shipping, mainly from fishing, recreational (whale watching, diving and sports fishing) and commercial (tankers and ferries) activities. The frequencies of shipping noise usually have higher energy overlap with the frequencies of fin, blue and sei whale vocalisations and for which these species should have high hearing sensitivities, and are therefore expected to have detrimental effects on these species. Thus, this thesis focuses on this source of noise in the Azores area.

1.7 Objectives and outline

This thesis uses large acoustic datasets from different regions to investigate the vocal behaviour of fin, blue and sei whales (with a special focus on the fin whale), to contribute to a better understanding of their ecology and behaviour during migration, the least known phase of their annual life cycle. This study also investigates shipping noise levels in relation to the vocal behaviour of these three species and discusses potential implications for their migratory behaviour.

The present dissertation consists of four research chapters, three of which have been published (Chapter 2, 3 and 5) in peer-reviewed international scientific journals and one is in preparation (Chapter 4). The thesis also includes a general Introduction (this Chapter) and a final Discussion (Chapter 6) that wraps up the main findings. Supplementary materials produced to complement each chapter are presented in the Appendices.

Chapter 1 (Introduction) reviews published information relevant to this thesis. It starts by describing the ecology and vocal behaviour of fin, blue and sei whales, followed by a brief review of the potential impacts of shipping noise on baleen whales and by an introduction to the methodologies used in this work (PAM and prey models). Chapter 1 finishes with a description of the study area.

Chapter 2 uses a 5-year acoustic dataset to investigate inter-annual, seasonal, and diel patterns in acoustic detections and behaviour of fin, blue and sei whales at a migratory habitat, the Azores Archipelago.

Chapter 3 explores variation in production rates of song-forming fin whale 20-Hz notes and 40-Hz calls in relation to year, season and simulated prey biomass, to infer the ecological context and potential functions of these calls.

Chapter 4 investigates long-term variations in fin whale song by using two decades of acoustic data collected across the North-east and central North Atlantic Ocean.

Chapter 5 describes the spatial and temporal variability of low-frequency underwater noise levels, determines the contribution of local ship and wind driven noise and discusses potential impacts to migratory baleen whales.

Chapter 6 summarizes and contextualizes the key findings of this thesis in light of available knowledge on baleen whale vocal behaviour and ecology, and on the impacts of anthropogenic noise.

Chapter 2

Baleen whale acoustic presence and behaviour at a Mid-Atlantic migratory habitat, the Azores Archipelago[1]

Abstract

The identification of important areas during the annual life cycle of migratory animals, such as baleen whales, is vital for their conservation. In boreal springtime, fin and blue whales feed in the Azores on their way to northern latitudes while sei whales migrate through the archipelago with only occasional feeding. Little is known about their autumn or winter presence or their acoustic behaviour in temperate migratory habitats. This study used a 5-year acoustic data set collected by autonomous recorders in the Azores that were processed and analysed using an automated call detection and classification system. Fin and blue whales were acoustically present in the archipelago from autumn to spring with marked seasonal differences in the use of different call types. Diel patterns of calling activity were only found for fin whales with more calls during the day than night. Sei whales showed a bimodal distribution of acoustic presence in spring and autumn, corresponding to their expected migration patterns. Diel differences in sei whale calling varied with season and location. This work highlights the importance of the Azores as a migratory and wintering habitat for three species of baleen whales and provides novel information on their acoustic behaviour in a mid-Atlantic region.

---

[1] Romagosa, M., Baumgartner, M., Cascão, I. Lammers, M. O., Marques, T. A., Santos, R. S. and Silva, M. A. (2020). Baleen whale acoustic presence and behaviour at a Mid-Atlantic migratory habitat, the Azores Archipelago. *Scientific Reports.* **10,** 4766. https://doi.org/10.1038/s41598-020-61849-8

2.1 Introduction

Fin, blue, and sei whales were intensively hunted during the past century, drastically reducing their populations throughout their range. Despite the cessation of the majority of commercial whaling, their populations have not yet recovered and are still well below pre-whaling numbers (Thomas et al., 2015). Protection measures for these species are urgently needed, especially as human impacts in the marine environment continue to increase (Lascelles et al., 2014). In the North Atlantic, fin, blue, and sei whales spend the summer at high-latitude feeding grounds and migrate to low latitudes during winter (Kellogg, 1929; Lesage et al., 2017; Prieto et al., 2014; Silva et al., 2013; Víkingsson, 1997a). Knowledge about the location of these wintering areas, as well as of their migratory pathways and timing is still scarce. Identifying the full range of habitats used throughout the annual cycle and annual variation in habitat use is a key step in understanding the habitat requirements of these migratory species and critical for the development of effective conservation strategies.

In the Azores Archipelago, located in the mid North Atlantic (Fig. 2.1), blue and fin whales stop to feed in spring while migrating to their high-latitude feeding areas (Silva et al., 2013). Habitat suitability modelling indicates that the presence of both species in the area follows the spring bloom primary productivity (Prieto et al., 2017). As spring advances and favourable habitat conditions move progressively further north, fin and blue whales abandon the Azores, generally leaving the area in summer (Prieto et al., 2017) when chlorophyll a concentrations are at an annual minimum (Santos et al., 2013). Sei whales seem to adopt a different strategy and transit through the archipelago quickly, feeding only occasionally, while on their way to the Labrador Sea (Olsen et al., 2009; Prieto et al., 2014). Information on the presence of these species in the archipelago comes mostly from sighting data and satellite telemetry studies conducted during spring and summer months (Silva et al., 2014, 2013). Occasional presence of fin, blue and sei whales in the Azores during autumn and winter is supported by a few sighting records (Silva et al., 2014) but long-term, continuous observations are scarce mainly due to the offshore habits of these species and bad weather conditions during winter.

Passive acoustics is an excellent tool that enables continuous, long term monitoring of cetacean presence during all weather conditions (Sousa-Lima, 2013). Many studies have used blue, fin, and sei whale low-frequency calls to study seasonal presence (Samaran et al., 2013;

Stafford et al., 2007), long-term temporal trends (Širovic et al., 2015), migration patterns (Simon et al., 2010), population structure (McDonald et al., 2006b; Morano et al., 2012), behaviour (Oleson et al., 2007a; Stimpert et al., 2015) , distribution (Thomisch et al., 2016), habitat use (Širović and Hildebrand, 2011; Wang et al., 2016) and abundance (Mcdonald, 1999) . Each baleen whale species produces several call types, which can be used for monitoring their occurrence in different behaviours and seasons. Blue and fin whales produce calls in a regular pattern as part of a song, or sporadically as singular units or song fragments (Cholewiak et al., 2018a; Clark et al., 2002; Edds P. L., 1982; Mellinger and Clark, 2003; Watkins et al., 1987). Songs are believed to act as reproductive displays because all biopsied singing whales were males (Croll et al., 2002; Oleson et al., 2007a) and peak during the breeding season (Nieukirk et al., 2012; Watkins et al., 1987), which happens in winter in the Northern Hemisphere (Kjeld, 1992) . However, blue whales have been reported to sing year-round in some locations with songs peaking during the summer on feeding grounds (Buchan et al., 2015; Širović et al., 2004; Thomisch et al., 2016) which suggests either a non-spatially and temporally restricted breeding strategy or a different use depending on context. Singular calls are often associated with social interactions or feeding behaviours (Lewis et al., 2018; Širović et al., 2013). Sei whales do not produce songs but they do produce very distinctive calls that occur in doublets or triplets that may act as contact calls between conspecifics (Baumgartner et al., 2008b) . The study of acoustic behaviour, such as seasonal segregation of different call types and their diel patterns, can provide clues to the functions of calls (Baumgartner and Fratantoni, 2008; Lewis et al., 2018; Oleson et al., 2007b), information about animal presence (Buchan et al., 2015; Stafford et al., 2001) and an understanding of biases caused by non-vocalizing animals during specific periods of the day and year. The acoustic behaviour of fin and blue whales has been well studied in feeding areas of the north-eastern Pacific (McDonald et al., 2001; Oleson et al., 2007b; Širović et al., 2017; Stafford et al., 2005), Antarctica (Gavrilov et al., 2011; Shabangu et al., 2019a) and north-eastern Atlantic (Delarue et al., 2009; Simon et al., 2010) but few studies have focused in mid- and north-western Atlantic areas (Akamatsu et al., 2014; Mellinger and Clark, 2003) and even less in migratory temperate habitats. For sei whales, diel patterns in calling have only been investigated in the Gulf of Maine, a springtime feeding ground for this species (Baumgartner and Fratantoni, 2008) .

Here, we investigate the acoustic presence and behaviour of fin, blue and sei whales at a migratory habitat in the Mid-Atlantic, the Azores Archipelago. Using an acoustic dataset collected over 5 years, we describe the seasonal variability in the acoustic presence of these three species and the seasonal and diel patterns of their different calls.

2.2 Materials and methods

2.2.1 Survey area and acoustic recordings

Bottom-mounted Ecological Acoustic Recorders (EARs) (Lammers et al., 2008) were moored at the base of three seamounts in the Azores: Açores, Condor and Gigante (Fig. 2.1) at approximately 190 m depth. Açores seamount, located 40 km south-west from Faial Island, is characterized by a large flat summit with shallow surrounding depths (190-500 m) due to the proximity of other shallow banks to the south. Condor seamount, located 17 km to the WSW of Faial Island, is a two peak shallow-intermediate seamount with a nearly flat summit of 11.6 km^2, steeper slopes and deeper surrounding depths ranging from 700 to 1500 m (Tempera et al., 2012). Gigante seamount is 98 km to the WNW of Faial Island and 6 km east of the Mid-Atlantic Ridge. It is a shallow seamount with a small summit of 0.7 km^2 reaching 161 m depth, steep slopes and surrounding depths similar to Condor seamount.

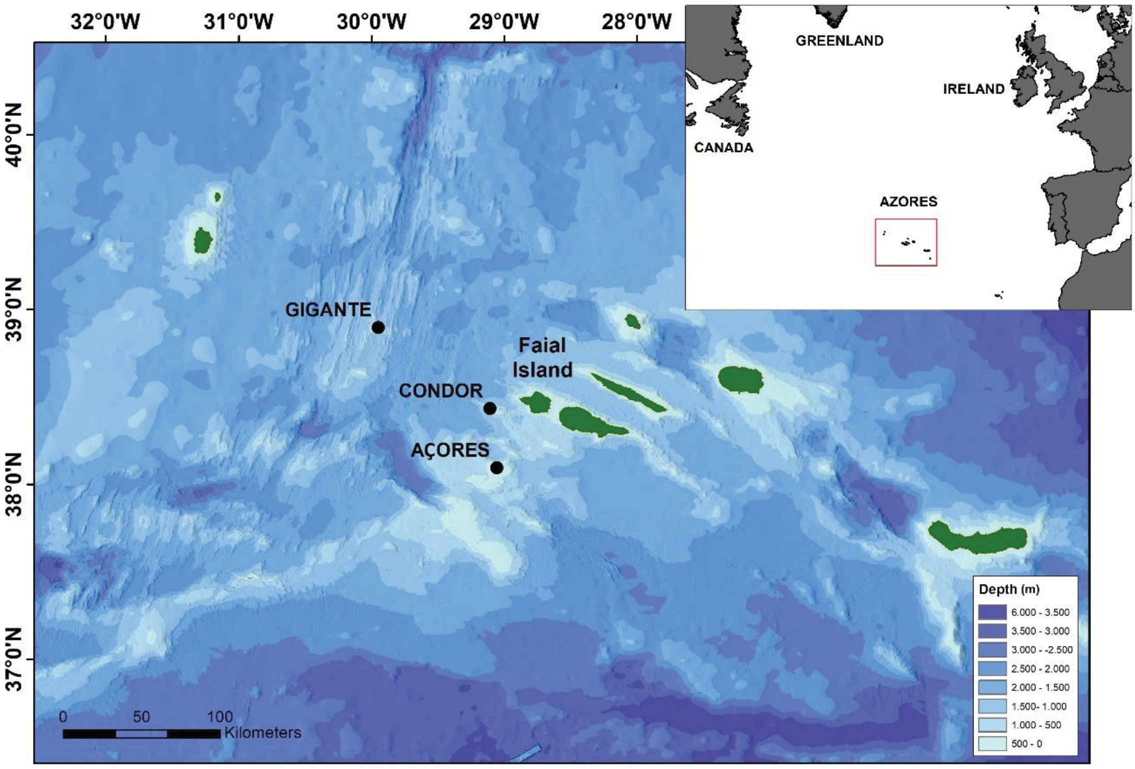


Figure 2.1. Location of the Azores (inset map) and of the hydrophone moorings at three seamounts: Açores, Condor and Gigante in relation to Faial Island. Figure produced with ArcGIS 10.1 (http://www.esri.com).

The EAR consists of a Sensor Technology SQ26-01 hydrophone with a response sensitivity of -193.14/-194.17 dB re 1V/µPa (varying between deployments) for Açores and Condor and -193.64/-193.14 dB for Gigante and a flat frequency response (±1.5 dB) from 18 Hz to 28 kHz. Deployments were set to different duty cycles and sample rates due to multispecies studies and constraints of battery life and data storage capacities. Sampling rates of recordings from Gigante (all deployment) and Condor (March 2008 - February 2011) were of 50 kHz and from Açores (all deployment) and Condor (November 2011 - October 2012) were of 2 kHz. Longer duty cycles (60 min on/138 min off and 60 min on/210 min off) cycled over time so not the same time was recorded every day. Gaps of acoustic recordings found in the time series were caused by maintenance duties and equipment failure. However, all four seasons are well represented in three of the five years sampled (2008, 2010 and 2012) (Fig. 2.2).

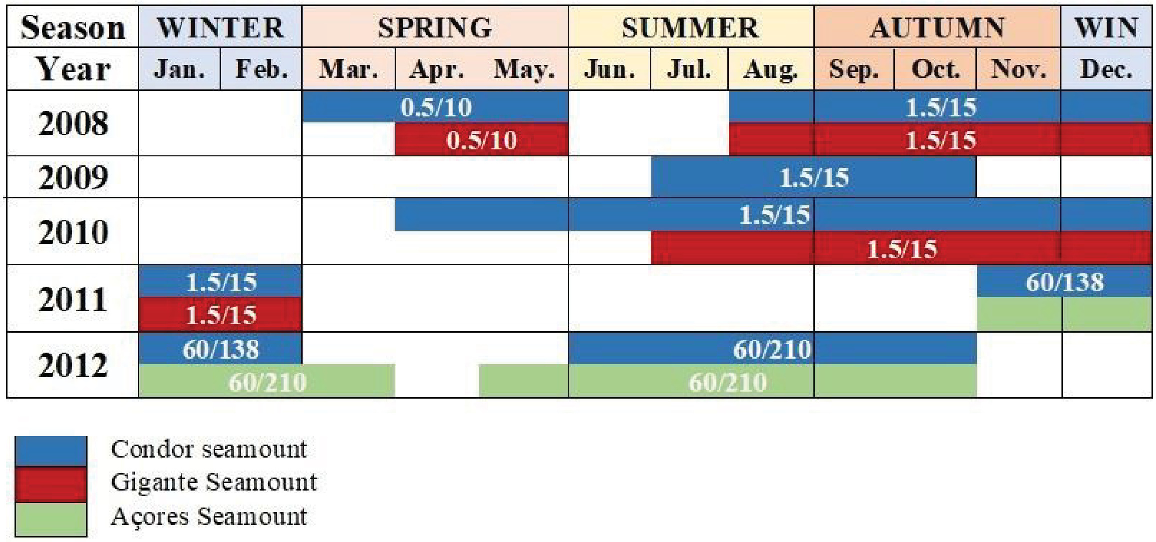


Figure 2.2. Deployment times and duty cycles for each season, month and seamount. Duty cycles for each deployment are in white numbers and indicate recording periods (min on/min off).

2.2.2 Automatic detection of calls

Given the extensive acoustic dataset of this study, a Low Frequency Detection and Classification System (LFDCS)(Baumgartner and Mussoline, 2011) was used to automatically detect and classify calls from fin, and sei whales. A precursor step was the development of a reference call library that contained known calls from fin and sei whales, previously identified and manually extracted from the dataset. Two types of calls from fin whales were included: the 20-Hz pulse, a 1 second downsweep centred at 20 Hz (Watkins et al., 1987), and the 130-Hz upsweep, a higher frequency note from 130 Hz to 140 Hz (Castellote et al., 2012b; Simon et al., 2010). Only one type of call was included for sei whales, the downsweep call, which sweeps from 83 Hz to 34 Hz lasting about 1.4 s (Baumgartner et al., 2008b) . To better visualize how well different call types in the library were separated, scatterplots of attributes of each call type were plotted against one another (Fig. S2.1). EAR recordings were downsampled to a sample rate of 2000 Hz to obtain standardized data covering the frequency range of interest and then processed by the LFDCS. Spectrograms were smoothed using a Gaussian kernel and tonal and broadband noise removed. The resulting filtered spectrograms were then used to find candidate tonal calls using an amplitude threshold. When a candidate call was found, the LFDCS estimated a pitch-track, which characterizes the frequency and amplitude variation of the call over time. For each pitch-track, seven amplitude-weighted attributes were compared to those of each call type in the reference call library, using a quadratic discriminant function analysis (QDFA). The “quality” of a match between the pitch-track and a call type in the call library was assessed with the Mahalanobis distance (Mahalanobis, 1936), which is the distance between the new call and the QDFA-classified call type in the reference library. A previous preliminary manual analysis of the entire dataset, which identified files with and without detections of each call, allowed us to improve the results from the LFDCS by removing false positives detections. Blue whale calls were identified and counted manually due to their low abundance by comparing them with available literature (Mellinger and Clark, 2003; Nieukirk et al., 2004). Calls were differentiated from tonal noise because they decreased in frequency and did not occupy the full file. Even in smaller duty cycled recordings with files that lasted only 30 seconds, we could distinguish separate A calls, a constant-frequency tonal call of about 17 seconds (Mellinger and Clark, 2003).

To assess the performance of the LFDCS, results from one month of recordings were manually analysed for fin and sei whale calls, by logging calls missed by the detector and false positive detections. Months selected for each species were representative in terms of background noise during the rest of the months and years. Potential bias caused by varying background noise levels across months was reduced by spectrogram conditioning which eliminated tonal and broadband noise. Variability in call rates across seasons was reduced by removing false positives. Classifier performance was evaluated using a receiver operating characteristic (ROC) curve as a function of the Mahalanobis distance value. The percentage of false positives (false calls selected by the detector divided by the total number of detections) was plotted against the percentage of true positives (true calls detected by the detectors divided by the total known true calls in the dataset) for each Mahalanobis distance (Fig. S2.1). The chosen Mahalanobis distance was the one that gave the best compromise between false and true positives and false negatives or missed calls (missed true calls by the detector divided by the total number of known true calls in the dataset). A maximum Mahalanobis distance of 5 was used for detecting fin whale 20-Hz (false positives: 0.9%; true positives: 80%; missed calls: 20%) and 130-Hz upsweeps (false positives: 0.7%; true positives: 85%; missed calls: 34%) and 4 for sei whale downsweeps (false positives: 2.7%; true positives: 66%, missed calls: 34%).

2.2.3 Statistical analysis

Assuming that calling behaviour is equally distributed throughout an hour, a correction was applied to call rates to account for the different duty cycles used in this study. Thus, daily call rates were calculated as the total number of detected calls per day divided by the length of recording time during that day (daily call rates/hour). To account for the inter-annual variability we normalised data by dividing each daily call rate by the sum of calls of the corresponding year. Seasonality in the acoustic presence of each species was investigated by averaging the normalized daily call rates over a 5-day period across all years for each whale species (grouping each species call types) and seamount. Seasonality of each call type was examined by averaging daily call rates per season across the three locations. Months were assigned to meteorological seasons reckoned by temperature. In this study, this assignment worked well with the acoustic baleen whale presence in the Azores and the different call usage. Seasons were defined as follows: Spring: March–May, Summer: June–August, Autumn: September–November and Winter: December–February.

Diel patterns for each call type and species were investigated by sorting detections into four light regimes (dawn, day, dusk and night) based on the altitude of the sun, which was obtained from the United States Naval Observatory Astronomical Applications Department website (http://aa.usno.navy.mil). Dawn hours start when the sun is 12º below the horizon and finish at sunrise when light hours start. Dusk corresponds to the period after sunset until the sun is 12º below the horizon. Dark hours are between dusk and dawn. Only days with detections and data with duty cycles covering all hours (Condor and Gigante deployments 2008-2011) were used. Because the duration of light regimes differ and vary over the course of one year, daily number of calls in each light period were divided by the duration of the corresponding time period providing normalized detection rates (detections/hour) for each light regime. Given the variation in the number of calls among days, the resulting normalized detection rates for each light regime and for each day were adjusted by subtracting the mean number of calls during that day(Stafford et al., 2005; Wiggins et al., 2005). To investigate if the number of detections per hour differ between light regimes, we conducted the non-parametric test Kruskal-Wallis followed by a Dunn's multiple comparison test with a Bonferroni adjustment method (Bonferroni, 1936). This test was chosen because data did not follow a normal distribution. Both tests assume independence of observations so data were transformed prior to testing to correct for serial correlation. First, an autocorrelation function was used to check for data autocorrelation and then an auto regressive integrated moving average (ARIMA) model was fitted only to data showing autocorrelation. In each case, the AR order from the ARIMA model was adjusted until getting rid of the autocorrelation. The resulting residuals from the model were used in the Kruskall-Wallis and Dunn's multiple comparison test. This analysis was done with nlme package in R software version 5.4 (R Core team, 2021).

2.3 Results

2.3.1 Vocalisations

In total, 7009 hours of recordings were analysed from the deployments at Açores, Condor and Gigante seamounts. Fin whale 20 Hz pulses were the most commonly recorded baleen whale call. This pulse was found either alone (37% of fin whale calls and 34% of all species calls) or together with upsweeps between 130-135 Hz (63% of fin whale calls and 58% of all species calls) (double pulse call) (Fig. 2.3a). There was an order of magnitude fewer blue and sei whale calls detected as compared to fin whales. The most abundant blue whale call was the A call (81% of blue whale calls and 1.5% of all species calls) very rarely accompanied by a B part (AB calls) (5 % of blue whale calls and 0.1% of all species calls) (Fig.2.3b). Blue whale D calls were also detected sporadically in clusters (14% of blue whale calls and 0.2% of all species calls) (Fig. 2.3c). Only one type of sei whale call was detected, which was the characteristic downsweep call occurring in single, doublets or triplets (6.2% of all species calls) (Fig. 2.3d).

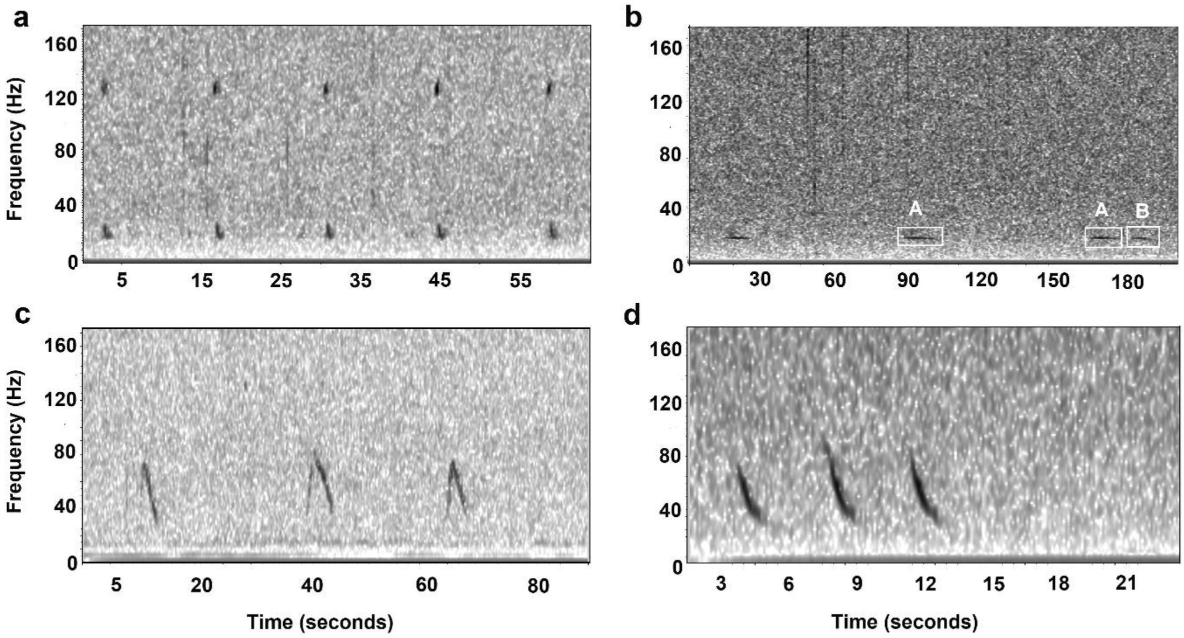


Figure 2.3. Example spectrograms with vocalisations of (a) fin whale double pulse calls, (b) blue whale A and AB calls (c), blue whale D calls and (d) sei whale downsweeps.

2.3.2 Acoustic presence

Acoustic presence of fin, blue and sei whales showed a marked seasonality. A similar pattern was found across years and locations for both fin and blue whales, with increasing daily call rates in autumn, reaching a maximum in winter and decreasing again in spring with no detections in summer (Figs. 2.4a, b and c). Blue whale daily call rates (A-calls + AB-calls + D-calls) (Figs. 2.4d, e and f) increased slightly later (in winter) and decreased earlier (in spring) than fin whales. Sei whales showed a different pattern from that of fin and blue whales with number of calls peaking in spring and autumn in all locations (Figs. 2.4g, h and i). For a visual comparison of datasets, a complete time series for each location and species is provided as supplementary material (Figs. S2.2, S2.3 and S2.4).

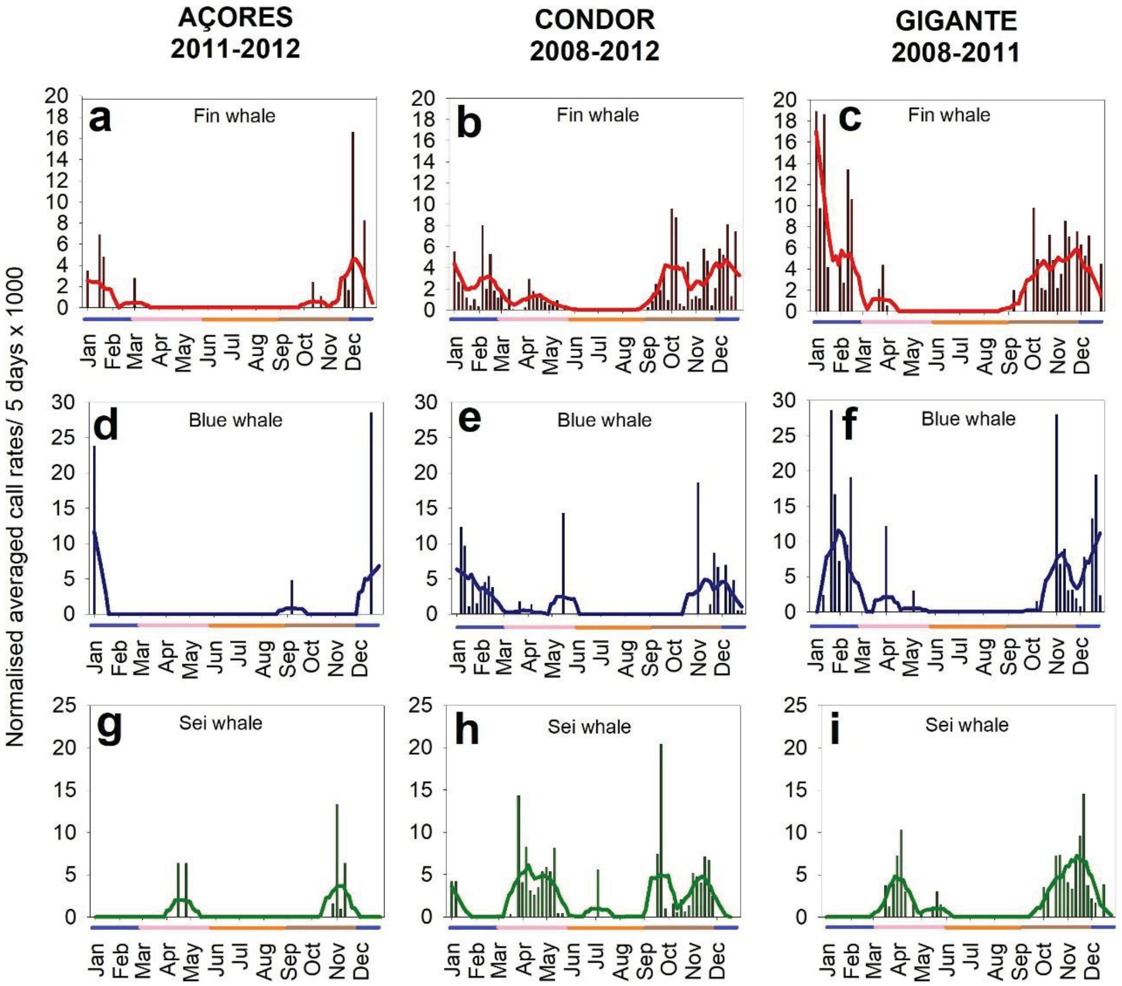


Figure 2.4. Seasonality of acoustic detections of fin (a–c), blue (d–f) and sei whales (g–i) in Açores, Condor and Gigante seamounts. Lines show smoothers (negative exponential) of data for a rapid interpretation of seasonal patterns. Coloured bar below the x-axis show seasons: blue for winter, pink for spring, orange for summer and brown for autumn.

2.3.3 Seasonal and diel patterns by call type

Fin and blue whale call types showed different seasonal patterns. The double pulse call was mostly produced in winter and was the most abundant fin whale call type at this time of the year. The 20-Hz pulse was detected mainly during winter and autumn and showed similar levels to the double pulse call in spring and autumn and much lower levels in winter (Fig. 2.5a). Blue whale A calls also showed a clear seasonality, with a peak in winter and decreasing in autumn and spring. AB calls were mostly found in winter and autumn. In contrast, D calls were detected at similar rates from autumn through spring (Fig. 2.5b).

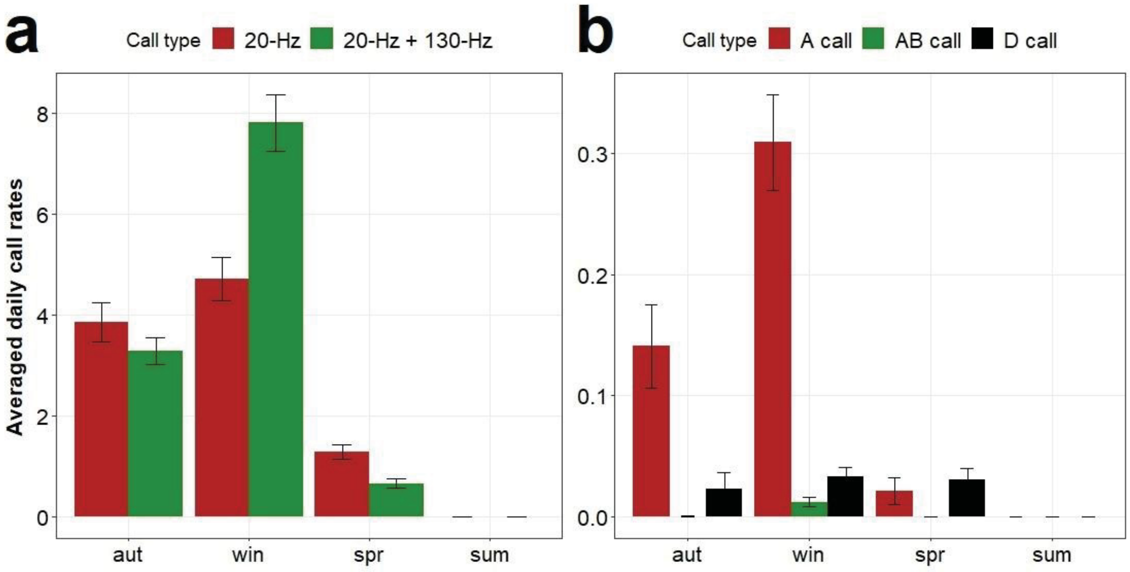


Figure 2.5. Averaged and normalised daily call rates per season at Condor and Gigante seamounts for fin (a) and blue whale (b) call types from 2008 until 2012. Error bars show standard errors. Seasons are defined as: aut – autumn, spr – spring, sum – summer and win – winter.

Fin and blue whale call diel patterns did not show statistically significant differences between autumn and winter seasons (Table S2.1) so they were grouped together for the analysis. Spring had a small number of days with detections (Condor: fin whale 20-Hz pulse=48, fin whale double pulse call=6, blue whale A call=1 and blue whale D call=2; Gigante: fin whale 20-Hz pulse=12, fin whale double pulse call=12, blue whale A call=1 and blue whale D call=2) so was not included in the analysis. Condor and Gigante data were analysed separately due to differences in the diel call patterns of these species.

Results from Kruskal-Wallis tests showed that call numbers are not the same for the four light regimes for both fin whale call types and seamounts (respectively for Condor and Gigante: 20-Hz: KW= 65.5, n=912; KW= 40.4, n = 588 and double pulse call: KW=66.4, n=556; KW=23.9, n=336, all with probability $P < 0.001$). Dunn's Multiple Comparison Test showed that day and night periods are significantly different from one another only in Condor, with more 20-Hz and double pulse calls emitted in daytime than in night-time (20-Hz pulse: Z=3.4, n=912, $P<0.01$; double pulse call: Z=-4.1, n=556, $P<0.001$) (Fig. 2.6a). No differences were found between day and night periods for either call types in Gigante (20-Hz pulse: Z=1.4, n=588, P=0.9; double pulse call: Z=2.2, n=336, P=0.2) (Fig. 2.6b).

Blue whale A and D call numbers showed no differences between day and night-time for either Condor (Fig. 2.6c) or Gigante (Fig. 2.6d) (respectively for Condor and Gigante: A call: Z=-0.7, n=128, P=1; D call: Z=0.4, n=40, P=1; A call: Z=-1.6, n=24, P=0.7; D call: Z=0.4, n=1, p-value=88).

Sei whale diel call patterns showed differences between spring and autumn and between Condor and Gigante and so were analysed separately. In spring, sei whale call numbers are significantly higher during the day than during the night only in Condor (Z=3.7, n=192, P<0.001) (Fig. 2.6e) while in autumn the same pattern occurs in Gigante (Z=-2.9, n=172, P<0.05) (Fig. 2.6f).

Dawn and dusk periods showed a great variance in call numbers with large standard errors of the mean so no clear pattern was found for these intermediate periods.

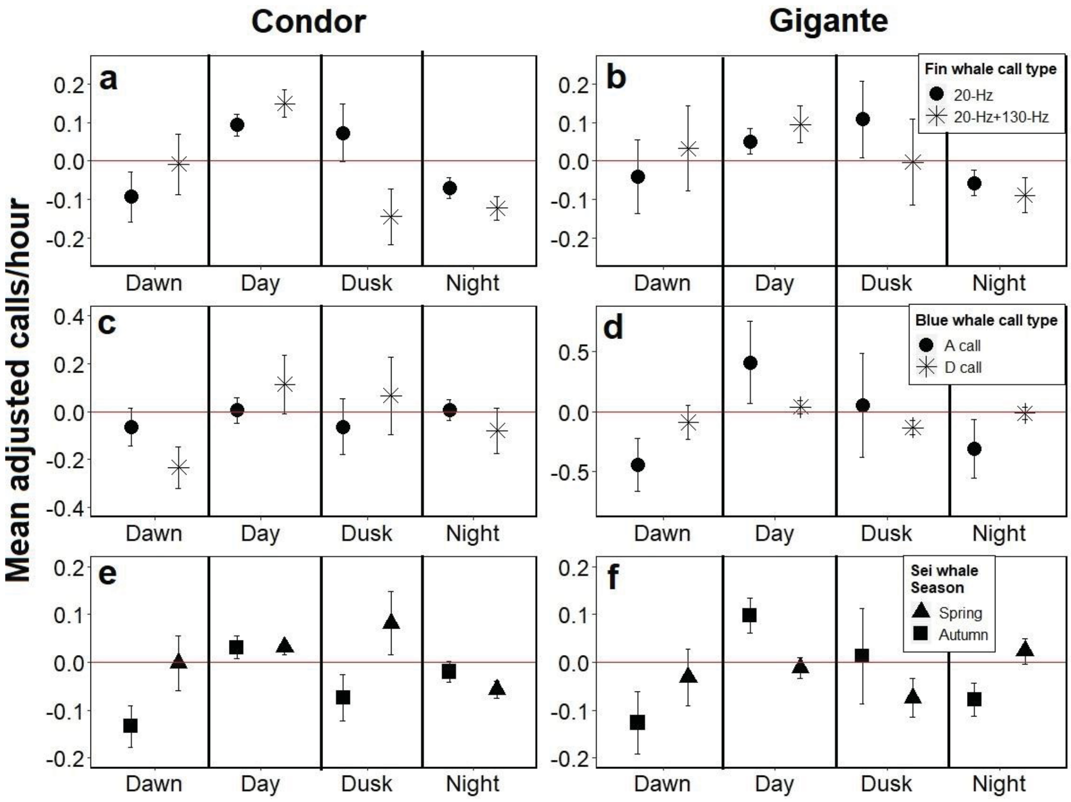


Figure 2.6. Mean adjusted number of calls and standard error by light regime of the fin whale 20-Hz pulse and the double pulse call for autumn and winter months in Condor (a) and

Gigante seamounts (b), blue whale A and D calls for autumn and winter months in Condor (c) and Gigante seamounts (d) and sei whale downsweep call for spring and autumn in Condor (e) and Gigante (f).

2.4 Discussion

This is the first study showing that fin and blue whales are present in the Azores Archipelago during autumn and winter months. Whales were acoustically detected from September until May with no detections during the summer. A similar temporal pattern in the acoustic occurrence of fin and blue whales was found north and south of the Azores between latitudes of 50 º N and 17 ºN, although detections were scarce south of 20ºN (Nieukirk et al., 2004, 2012). Overall, this agrees with whaling and sighting records in the North Atlantic (Kellogg, 1929) and suggests that fin and blue whales occupy a large offshore area in the mid North Atlantic during autumn and winter months (Reeves et al., 2004). The pattern of acoustic detections in spring but decreasing in summer agrees with visual studies documenting a peak in sighting rates from March to June, when whales are seen feeding, and few or no sightings during the summer (Silva et al., 2014). However, the spring peak in sightings does not correspond to a peak in calling; call rates are much lower in spring than autumn or winter. Thus, fin and blue whales change their calling behaviour in spring, dramatically decreasing their call rates and/or switching their call types (Širović et al., 2013; Stafford et al., 2007), either because it is the end of the breeding season and/or because they spend more time foraging (Silva et al., 2013). In the summer, the lack of blue whale calls can be explained by an absence of animals in the archipelago but fin whales may be present throughout the summer in small numbers depending on the year (Silva et al., 2014) and remain undetected acoustically. Fin whales in the summer may be either silent or use other call types not identified in this study (Širović et al., 2013; Stafford et al., 2007). Sei whales show a different acoustic occurrence in the archipelago with two main peaks, one in spring and another one in autumn. This pattern agrees with the presumed migration of the species through the Azores, travelling north to the Labrador Sea during spring (Olsen et al., 2009; Prieto et al., 2014) and south to possible breeding grounds in tropical waters during autumn (Ingebrigtsen A., 1929). We acknowledge that the calling seasonal patterns shown in this study are true only for the years sampled and that some variation may occur in other years.

Fin whale 20-Hz pulses reported in this study were either detected alone or with an upper frequency component, namely the double pulse call, which was mainly detected in autumn and winter months. The presence of these two call types in our recordings could be an artefact due to propagation loss. The double pulse call produced by distant whales may be detected as only a 20-Hz call because higher frequency sounds, like the 130-Hz component, suffer from higher attenuation with distance (Francois and Garrison, 1982). Besides, the 20-Hz pulses have 280 time more energy that the upper component (Simon et al., 2010). If this was true, higher rates of double pulse calls detected in autumn and winter months could be the result of more fin whales being closer to the recorders during these seasons. However, this implies that fin whales may be further away from the recorders in spring, when the double pulse is more scarce, which is not supported by either visual (Silva et al., 2014) nor satellite telemetry data (Silva et al., 2013). Another hypothesis is that fin whales from the same population could be using two call types possibly linked to different behaviours. The double pulse call was mostly detected during the breeding season of fin whales which may represent a male reproductive display, as hypothesized for the 20-Hz pulse songs (Croll et al., 2002; Watkins et al., 1987). Unfortunately, our data from 2008-2011 has small duty cycles do not allow the identification of songs. Alternatively, two distinct acoustic populations could be producing these two call types. In the North Atlantic, this component, also referred as “135-140 Hz upsweep”, has been reported widely from east Greenland to the Alborán basin of the Mediterranean Sea (Castellote et al., 2012b; Garcia et al., 2019; De Vreese et al., 2018). To date, it has not been documented in the North-west Atlantic. It is possible that some fin whales from the North-west Atlantic frequent the Azores during the autumn and winter months. A recent study on stable isotopes identified the Iberian region as a winter feeding area for fin whales that visit the Azores in spring (Silva et al., 2019) but no information exists on the origin of fin whales in the Azores during autumn and winter months.

Diel patterns of both fin whale song-forming call types indicate that more vocalisations are produced during the day than during the night. Although the same diel pattern occurs in both seamounts, it is only in Condor that differences between day and night periods are statistically significant. This contradicts other studies that report higher numbers of 20-Hz calls at night (Simon et al., 2010; Wang et al., 2016; Watkins et al., 1987) which have been associated with either a lower feeding activity during periods when krill is less aggregated (Simon et al., 2010) or on the contrary, associated to feeding when herring fish densities are higher (Wang et al., 2016). In the Azores, satellite tracking data showed enhanced swimming speeds for fin whales engaged in area-restricted search (ARS) behaviour (associated with feeding (Kareiva and Odell, 1987)) at night, with a clear peak at dawn and decreasing shortly after sunrise (Silva et al., 2013). These authors suggest that fin whales feeding over deep waters may need to intensify their foraging effort at night to take advantage of the increased availability of diel vertically migrating prey in surface waters (Silva et al., 2013). If we assume this to be true, then the lower numbers of both call types detected during the night coincide with a higher foraging activity of fin whales inferred from satellite telemetry. However, the fact that Gigante seamount differences between day and night call rates are not statistically different and the discrepancy between other studies (Simon et al., 2010; Wang et al., 2016) may indicate that fin whale call diel patterns may vary depending on the animals' behavioural state, feeding strategy or prey preferences. There is also the possibility of missing 130 Hz pulses due to the animals' location. If this was the case, diel patterns of the double pulse call may not reflect the production of calls but the animal movements with respect to the recorders, as has been hypothesised by other authors in respect to diel patterns (Au et al., 2000). However, the fact that both call types show the same diel patterns makes this hypothesis seem unlikely.

Blue whale vocalisations, described for the first time in the Azores by this study, match the North Atlantic call type, recorded throughout the North Atlantic including the Mid-Atlantic Ridge (Nieukirk et al., 2004) and the North-east (Charif and Clark, 2009) and North-west Atlantic (Berchok et al., 2006; Edds P. L., 1982; Mellinger and Clark, 2003). In this study, AB calls were rarely detected compared to A calls (5.9% of A calls: 94.1% AB). This could be a consequence of a) B calls with lower source levels not being detected by the EARs lower sensitivity below 18 Hz and/or b) missing calls caused by small duty cycles (2008-2011) or c) a true low number of AB calls. While a similar pattern had been reported in the Mid-Atlantic Ridge (Nieukirk et al., 2004) and the Gulf of Saint Lawrence (Edds P. L., 1982) (with a higher percentages of AB calls than in the Azores: 29% and 23% respectively), the opposite had been found for a large offshore area of the North-west Atlantic where AB calls were the most recorded call (65.7%) compared to A calls (33.7%) (Mellinger and Clark, 2003). These differences do not match photo-identification data that suggest the existence of two largely discrete blue whale populations in the North Atlantic (North-east Atlantic and North-west

Atlantic) (Sears et al., 2015). This could be due to: a) different uses of these specific call types are not linked to population identity or b) differences between recorders sensibilities affecting the detectability of B parts. Temporal differences in the production of the three call types, A, AB and D, indicate they may be used in different contexts. A and AB calls were mainly present in autumn and winter months (Nieukirk et al., 2004; Stafford et al., 2001), which agrees with previous studies showing that regularly repeated A or A-B calls forming songs were produced during the hypothesized blue whale breeding season (Lockyer, 1984). In this study though, we cannot differentiate if calls were forming songs or not due the small duty cycles used from 2008 to 2011. D calls were detected in all seasons, except summer, which may relate to the potential multifunctionality of this call. The use of D calls have been described in varying behavioural contexts that include from foraging (Oleson et al., 2007a, 2007b) to social interactions (Lewis et al., 2018; McDonald et al., 2001) and even in competitive behaviour linked to reproduction (Schall et al., 2020).

Diel patterns of blue whale calling activity did not show any significant differences between day or night periods for either A or D calls. Many studies conducted in the North Pacific Ocean have reported a higher number of blue whale A, B or A-B songs during the night, possibly coinciding with lower feeding activity (Lewis et al., 2018; Oleson et al., 2007a; Stafford et al., 2005; Wiggins et al., 2005). The lack of a clear diel pattern in our study may be the result of either the inability to distinguish song fragments from songs due to our duty-cycled data or a true absence of a diel pattern. Blue whale D calls also showed little variation between light regimes. Other studies reported different diel patterns for this call, with more D calls during the day in the North Pacific (Lewis et al., 2018) and during the night in the North-west Atlantic (Wang et al., 2016). D calls have been linked to periods of higher feeding activity but are more likely to be contact calls than foraging calls (Lewis et al., 2018; McDonald et al., 2001; Oleson et al., 2007a). New data suggest that D calls could even be produced in reproductive contexts of male competition (Schall et al., 2020).

Sei whale downsweep calls found in this study had been previously described in the Azores (Romagosa et al., 2015) and showed strong similarities with the ones described in the North-west Atlantic (Baumgartner et al., 2008b). The lack of regional call differences between these two areas agree with satellite and genetic studies indicating that western and central North Atlantic sei whales are part of the same population (Huijser et al., 2018; Prieto et al., 2014).

Sei whales found off the Gulf of Maine vocalize more during the day than at night (Baumgartner and Fratantoni, 2008). Sei whales feed on surface aggregations of highly migrant zooplankton (mainly copepods) during the night, and higher calling activity during the day may serve a social function, maybe to advertise high density prey patches to conspecifics (Baumgartner and Fratantoni, 2008). Detection of sei whale downsweeps in the Azores exhibited the same diel pattern as documented in the Gulf of Maine only in spring at Condor seamount and in autumn at Gigante seamount. This is an interesting result, because behavioural observations, satellite telemetry and stable isotope analysis all indicate that sei whales forage only sporadically in the Azores (Prieto et al., 2014; Silva et al., 2019). Either sei whales feed more often than detected by current observations in those seamounts and seasons and/or downsweeps are not strictly associated with feeding activity and may be also used as contact calls during migration and their diel patterns are affected by unknown variables.

This work emphasizes the importance of the Azores for three species of baleen whales. First, it places the archipelago as part of a large wintering area for fin and blue whales in the mid North Atlantic Ocean. Second, it confirms the relevance of the Azores as a migratory area for sei whales in spring and autumn.

Given the seasonality of these species in the archipelago, a spatial management approach that takes into account a temporal dimension should be considered as the most appropriate conservation strategy. Impacts known to cause disturbance to these species in the short and long-term should be regulated in space and time by integrating near-real time biological information such as habitat use. Noise produced by intense shipping and oil and gas exploration overlaps with baleen whale vocalisations and is known to cause behavioural responses to fin and blue whales (Castellote et al., 2012a; Melcón et al., 2012) which, in the long term, could displace them or affect their survival. More research is needed in autumn and winter months to identify the spatial distribution of fin and blue whales in the Azores as well as the environmental drivers of their presence.

Acknowledgements: This work was supported by Fundação para a Ciência e Tecnologia (FCT), Azores 2020 Operational Programme and Fundo Regional da Ciência e Tecnologia (FRCT) through research projects TRACE (PTDC/MAR/74071/2006), MAPCET

(M2.1.2/F/012/2011) and AWARENESS (PTDC/BIA-BMA/30514/201), co-funded by FEDER, COMPETE, QREN, POPH, ERDF, ESF, the Lisbon Regional Operational Programme, and the Portuguese Ministry for Science and Education. Funding for publication fees was provided by Project AWARENESS (PTDC/BIA-BMA/30514/2017). Okeanos R&D Centre is supported by FCT, through the strategic fund (UIDB/05634/2020). MR was supported by a DRCT doctoral grant (M3.1.a/F/028/2015) and MAS by an FCT-Investigator contract (IF/00943/2013). TAM thanks partial support by CEAUL (funded by FCT - Fundação para a Ciência e a Tecnologia, Portugal, through the project UID/MAT/00006/2013). We are grateful to Rui Prieto, Sérgio Gómez, Norberto Serpa, skilled skippers and crew that participated in the preparation and deployment of EARs at DOP/IMAR and to Ken Sexton and Michael Richlen for their roles in manufacturing the EARs. We are also grateful to Dr. Helena Silva for her feedback on statistical analysis.

Annex II. Supplementary information

Supplementary information associated with this article can be found in the online version at https://www.nature.com/articles/s41598-020-61849-8#Sec11.

Chapter 3

Food talk: 40-Hz fin whale calls are associated with prey biomass[2]

Abstract

Animals use varied acoustic signals that play critical roles in their lives. Understanding the function of these signals may inform about key life history processes relevant for conservation. In the case of fin whales, that produce different call types associated with different behaviours, several hypotheses have emerged regarding call function, but the topic still remains in its infancy. Here, we investigate the potential function of two fin whale vocalisations, the song-forming 20-Hz call and the 40-Hz call, by examining their production in relation to season, year and prey biomass. Our results showed that production of 20-Hz calls was strongly influenced by season, with a clear peak during the breeding months, and secondarily by year, likely due to changes in whale abundance. These results support the reproductive function of the 20-Hz song used as an acoustic display. Conversely, season and year had no effect on variation in 40-Hz calling rates, but prey biomass did. This is the first study linking 40-Hz call activity to prey biomass, supporting the previously suggested food-associated function of this call. Understanding the functions of animal signals can help identifying functional habitats and predict the negative effects of human activities with important implications for conservation.

---

[2] Romagosa, M., Pérez-Jorge, S., Cascão, I., Mouriño, H., Lehodey, P., Pereira, A., Marques, T. A., Matias L. and Silva, M. A. (2021). Food talk: 40-Hz fin whale calls are associated with prey biomass. *Proceedings of the Royal Society B: Biological Sciences*, 288: 20211156. https://doi.org/10.1098/rspb.2021.1156

3.1 Introduction

Animals produce an array of different acoustic signals. These signals can encode various types of information about the signaller's attributes or external environment, and serve various purposes. During the mating season, males of many species produce high intensity and repetitive songs to attract or court females, repel conspecific males, or both (Amorim et al., 2015; Bennet-Clark, 1971; Payne and McVay, 1971). It has been suggested that male songs can convey information about the individual's reproductive status, body size or health (Nowicki and Searcy, 2004; Tregenza et al., 2006), and may be used by females and other males to assess the signaller's quality and competitiveness (Ballentine et al., 2004; De Kort et al., 2009; Moseley et al., 2013). Numerous bird and mammal species produce food-associated calls. These calls can hold information on type, quality or quantity of food available and be used to announce resource ownership or attract others to the food source (Clay et al., 2012). Many species give alarm calls in response to particular predators or predator abundance, thereby informing conspecifics about a threat (Dezecache and Berthet, 2018; Thorley and Clutton-Brock, 2017), while social contact calls are often used to maintain group cohesion, coordinate group activities and mediate social interactions (Kondo and Watanabe, 2009; Marler, 2004). As animal's acoustic signals play a critical role in their reproduction and survival, understanding the context of production and information content of these signals can give valuable insights into key life history processes relevant for conservation (Teixeira et al., 2019).

Fin whales produce distinct vocalisations but knowledge about the functions of their calls is still limited. The most reported fin whale call worldwide is the 20-Hz note (Aulich et al., 2019; Širović et al., 2004; Thompson et al., 1992; Watkins et al., 1987, 2000), a short-frequency downsweep mostly centred around 20 Hz (Watkins et al., 1987). The 20-Hz call can be produced (1) in regular sequences, forming a stereotypical song (Thompson et al., 1992; Watkins et al., 1987); (2) at irregular intervals (Watkins, 1981); and (3) as counter-calls (McDonald et al., 1995). Songs have only been documented from males (Croll et al., 2002) and are produced mainly during the known breeding season of the species (Kjeld, 1992; Ohsumi et al., 1958). Thus, it has been hypothesized that male fin whale song is used to attract females, either as an acoustic display (Watkins et al., 1987) or by advertising patchy food resources (Croll et al., 2002). Non-song counter-calling and irregular 20-Hz calls are normally produced by animals in groups (Watkins, 1981) and probably serve a social function, such as maintaining contact with moving conspecifics (Edds-Walton, 1997; McDonald et al., 1995). Fin whales also produce a 40-Hz call sweeping in frequency from 75 Hz to 40 Hz (Širović et al., 2013; Watkins, 1981; Wiggins and Hildebrand, 2020). The 40-Hz call is mostly detected in late spring and summer in known feeding areas (Širović et al., 2013), in association with complex topographical features (Burnham, 2019; Burnham et al., 2021) and feeding behaviours (Watkins, 1981), suggesting a potential food-associated function.

To investigate the hypothesized fin whale call functions, we examine variation in production rates of song-forming 20-Hz calls and 40-Hz calls with respect to season, year and prey biomass. If males use 20-Hz calls to attract females through acoustic display (Watkins et al., 1987), we expect call production to be mainly driven by season, peaking in winter, the known mating period of the species (Kjeld, 1992; Ohsumi et al., 1958). If, on the other hand, the 20-Hz call is used to attract females via food advertising (Croll et al., 2002), singing activity will be influenced by both season and prey biomass. Finally, if the 40-Hz call is associated with foraging activity, we predict that calling rates will be positively related with prey biomass, comparable with foraging calls of other species (e.g. bottlenose dolphin (*Tursiops truncatus*) bray calls, humpback whale ‘megapclicks’) (Janik, 2000; Stimpert et al., 2007). To test these predictions, we used a 5-year acoustic dataset from bottom-moored hydrophones to extract call detection rates of each call type. In the absence of concurrent measurements of prey biomass, an ecosystem model was used to provide hindcast simulations of low trophic level (mesozooplankton) biomass for the area and period of acoustic recordings (Lehodey et al., 2010, 2015). This approach allowed investigating the direct relationship between fin whale vocal behaviour and predicted prey biomass, avoiding interpretation of relationships with time lagged prey proxies (i.e., chlorophyll).

3.2 Methods

3.2.1 Acoustic data collection and analyses

Passive acoustic monitoring (PAM) data were collected at two locations off the Azores Archipelago (Fig. 3.1a) using Ecological Acoustic Recorders (EARs) (Lammers et al., 2008) deployed at depths of ~200 m. The EAR consists of a Sensor Technology SQ26-01 hydrophone with a response sensitivity ranging from 193 to 194 dB re 1 V/µPa (depending on deployments) and a flat frequency response (±1.5 dB) from 18 Hz to 28 kHz. Hydrophones recorded from March 2008 to October 2012 with several data gaps and duty cycles (Fig. S3.1). Despite gaps in the acoustic dataset, all seasons were well represented across the five sampled years.

Acoustic recordings were analysed for two fin whale vocalisations: the 20-Hz call, a 1 second downsweep centred at 20 Hz (Watkins et al., 1987) (Fig. 3.1b), and the 40-Hz call, a 0.3 s downsweep from 75 Hz to 40 Hz occurring in irregular sequences (Watkins, 1981) (Fig. 3.1c). All acoustic data were downsampled to 1 kHz to facilitate analysis. The 20-Hz call was previously analysed from these recordings and for another study (Romagosa et al., 2020a) by using the Low Frequency Detection and Classification System (LFDCS) (Baumgartner and Mussoline, 2011). Based on a reference call library of manually identified 20-Hz fin whale calls, the LFDCS detected candidate calls and estimated their pitch-track, which characterizes the frequency and amplitude variation of the signal over time. Each candidate call was compared to the reference library using a quadratic discriminant function analysis (QDFA). LFDCS performance was assessed by comparing detector outputs with manually analysed notes, yielding 0.9% of false positives, 80% of true positives and 20% of missed calls (for more details on the methodology (Romagosa et al., 2020a).

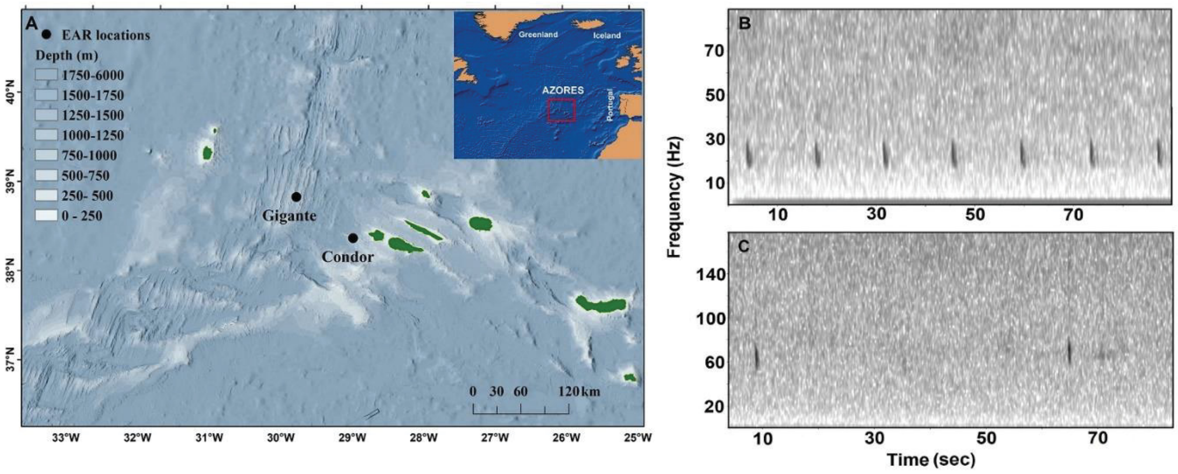


Figure 3.1. (A) Location of the Azores (inset map) and of the hydrophone moorings (black dot) at two locations (Gigante and Condor). Example spectrograms showing (B) the 20-Hz and (C) the 40-Hz call.

Three months (representative of each season) with longer duty cycle recordings (1 hour of continuous recordings) were manually inspected to identify song and non-song 20-Hz calls. Results showed that only 2.5% of the files contained non-song 20-Hz calls (Oct: 0%; Nov: 3.5% and Mar.: 0%). Thus, we assumed that most 20-Hz calls analysed in this study were part of songs. Identification of 40-Hz calls using automatic detectors is challenging because of the frequency overlap with sei and blue whale calls (Širovic et al., 2015). So, 40-Hz calls were detected by visually inspecting spectrograms of the entire dataset (2048-point FFT, Hanning window with 50% overlap) using Adobe Audition 3.0 (Adobe Systems Inc., San Jose, CA) and annotating each call. The 40-Hz call was identified from its acoustic characteristics (Širović et al., 2013; Watkins, 1981), which clearly differentiates it from the 20-Hz call because of the higher frequencies that downsweep from 75 Hz to 40 Hz over 0.3-1s. The 40-Hz call was also easily distinguished manually from blue whale D calls, previously identified in this dataset (Romagosa et al., 2020a), as having a distinctly broader bandwidth and longer duration.

A call rate index was calculated as the total number of 20-Hz or 40-Hz calls detected in a week divided by the recording time, in hours, during that week, to reduce potential bias from the different duty cycles. Hereafter, we will in general refer to 20-Hz or 40-Hz call rates, but these strictly mean the corresponding call rate index.

3.2.2 Zooplankton model

Stable isotope analysis of skin and faeces indicates that fin whales from the study area feed primarily on zooplankton (mainly euphausiids and copepods) (Arregui et al., 2018; Silva et al., 2019). In addition, mesozooplankton biomass derived from a spatial ecosystem and population dynamics model (SEAPODYM) was the most important predictor of the distribution of fin whales in the Azores and across the mid-North Atlantic, whilst micronekton biomass estimates from the same model had no effect on the movements of the species (Pérez-Jorge et al., 2020). Thus, we assumed that zooplankton is the main prey of fin whales in the study area and obtained estimates of zooplankton biomass from the lower trophic level SEAPODYM model (SEAPODYM-LTL) (Lehodey et al., 2010, 2015). The SEAPODYM-LTL is a spatially-explicit ecosystem and population dynamics model that simulates biomass of mesozooplankton organisms within the epipelagic layer defined by the euphotic depth. The model is driven by physical and biological variables and applies a series of advection–diffusion–reaction equations (Lehodey et al., 2010). Physical variables (temperature and currents) were extracted from the ocean reanalysis GLORYS (https://www.mercator-ocean.fr/en/ocean-science/glorys/), produced with the ocean general circulation model NEMO (http://www.nemo-ocean.eu/), in an eddy-permitting configuration (Bernard et al., 2006; Masina et al., 2017; von Schuckmann et al., 2020). Net primary production and euphotic depth were derived from ocean colour satellite data (http://www.science.oregonstate.edu/ocean). Outputs from these models were interpolated onto a weekly time scale and a spatial resolution of 0.25°×0.25° to be used by the SEAPODYM-LTL model. The model predicts weekly mesozooplankton biomass on a global spatial grid (0.25°×0.25°). Predictions for the period 1998-2019 are publicly available (https://marine.copernicus.eu/). The model validation is based on the climatological database COPEPOD that provides standardised mean zooplankton biomass values on a global spatial grid (Masina et al., 2017; von Schuckmann et al., 2020).

3.2.3 Spatial scale of data integration

SEAPODYM-LTL estimates of mesozooplankton biomass (hereafter zooplankton biomass) were extracted for the weeks with acoustic recordings (Fig. S3.1) and averaged across 0.25°× 0.25° grid cells centred around the hydrophone position. To determine the most appropriate spatial scale (i.e., the number of grid cells) for analysing SEAPODYM-LTL data in relation to acoustic data, the maximum detection range of 20-Hz and 40-Hz fin whale calls was estimated using the sonar equation (Lurton, 2002):

$$SNR = SL - TL - NL + 10 \log_{10} BW$$

where SL is the transmitted source level (dB rms re 1 µPa at 1 m), TL is one-way transmission loss (dB), NL is the ambient noise level at the receiver (dB rms re 1 µPa), and BW is the processing bandwidth (Hz). Source levels of 20-Hz and 40-Hz calls were calculated using calls localised by 3 EARs deployed in a nearby area. The propagation Range-dependent Acoustic Model (RAM)(Collins, 1993, 1995) was used for the calculation of TL. Ambient NL were calculated for the frequency band of each call type and for the quietest and noisiest months within the recording period (See Supplementary Text 3.1b for more details).

Finally, a sensitivity test of the scale of data integration was performed by analysing annual and monthly patterns of estimates of zooplankton biomass at a range of scales.

3.2.4 Statistical analyses

Data from summer months (June to August) were excluded because the summer matches the end of fin whale migration through the Azores and whales are rare in the area (Pérez-Jorge et al., 2020; Prieto et al., 2017; Visser et al., 2011); hence lack of acoustic detections in the summer simply reflects the absence of whales and not changes in calling patterns.

The Quasi-Poisson model (a particular case of Generalized Linear Model, GLM) was used to describe the relationship between 20-Hz and 40-Hz call rates and a set of independent variables: year, season (according to meteorological definition) and zooplankton biomass. This modelling tool is especially suited to handle overdispersed count variables because it incorporates an overdispersion parameter that allows for more spread than the standard Poisson mean-variance relationship (Ver Hoef and Boveng, 2007; Zuur et al., 2009). Separate models were built for the 20-Hz and 40-Hz call rates to understand how the same explanatory variables affected each vocalisation type. The variance inflation factor (VIF) was calculated for the complete models to measure the strength of correlation between all predictor variables (season, year and zooplankton biomass). VIF values higher than 5 or 10 are considered too high and could cause misinterpretation of model outputs (Montgomery and Peck, 1992). In our models, VIF values for the three variables were approximately one. Season and year were used to assess intra and inter annual variations in the response variables. Given that zooplankton biomass varied with season, an interaction between these two variables was also included in the models. No interaction between season and year was included because seasonality in calling did not vary with year. Detailed descriptions of the statistical models are given in the Supplementary material (Supplementary Text 3.1c).

The best model was selected based on the lowest Quasi-Akaike's Information Criterion (QAIC). Drop-in deviance tests (based on the F-test to account for overdispersion) were computed for the best model to validate each explanatory variable's statistical significance. The process started with the null model, and each explanatory variable was added sequentially until reaching the best model defined by the QAIC criterion. Moreover, the Wald test was applied to each parameter of the model to test the null hypothesis that the respective parameter is equal to zero.

Model assumptions were verified by plotting residuals versus fitted values to check for heterogeneity of variance and residual QQ plots to check for normality. Half-normal probability plots of the residuals with simulated envelope were computed (Atkinson, 1985) to check whether the choice of the random component of the model was appropriate and identify possible outliers in the data (Demétrio et al., 2014). Additionally, the temporal dependency of the residuals was assessed (Zuur and Ieno, 2016) to detect autocorrelation in the data. An autocorrelation at lag one was detected for the 20-Hz call rates, implying there was a correlation between call rates in successive weeks. To account for the temporal autocorrelation, one-week lagged values of 20-Hz call rates were included in the model as a predictor variable. All statistical analysis were performed using the software R (version 4.0.2)(R Core team, 2021).

3.3 Results

3.3.1 Detection range and zooplankton biomass spatial scale

Median detection ranges at the deployment locations were 64 km for the 20-Hz call and 18 km for the 40-Hz call (Table S3.1). Therefore, SEAPODYM-LTL estimates of zooplankton biomass extracted for the weeks with acoustic recordings (Fig. S3.1) were averaged across 4 grid cells of 0.25°× 0.25° centred around the hydrophone position (55 x 55 km). Changing the number of grid cells to 9 (83 x 83 km) or 16 (194 x 194 km) had little or no effect on the annual and monthly patterns of estimated zooplankton biomass (Fig. S3.2).

3.3.2 Temporal occurrence of calls and zooplankton biomass

Rates of the 20-Hz call increased in autumn, peaked in winter, decreased in spring and were null in summer (Fig. 3.2a). Conversely, 40-Hz call rates were low in autumn, increased in late winter, reached highest values in spring and decreased again in summer (Fig. 3.2b). Zooplankton biomass showed a clear peak in spring (April-May), decreased throughout the summer and early autumn and increased again in winter (Fig. 3.2c).

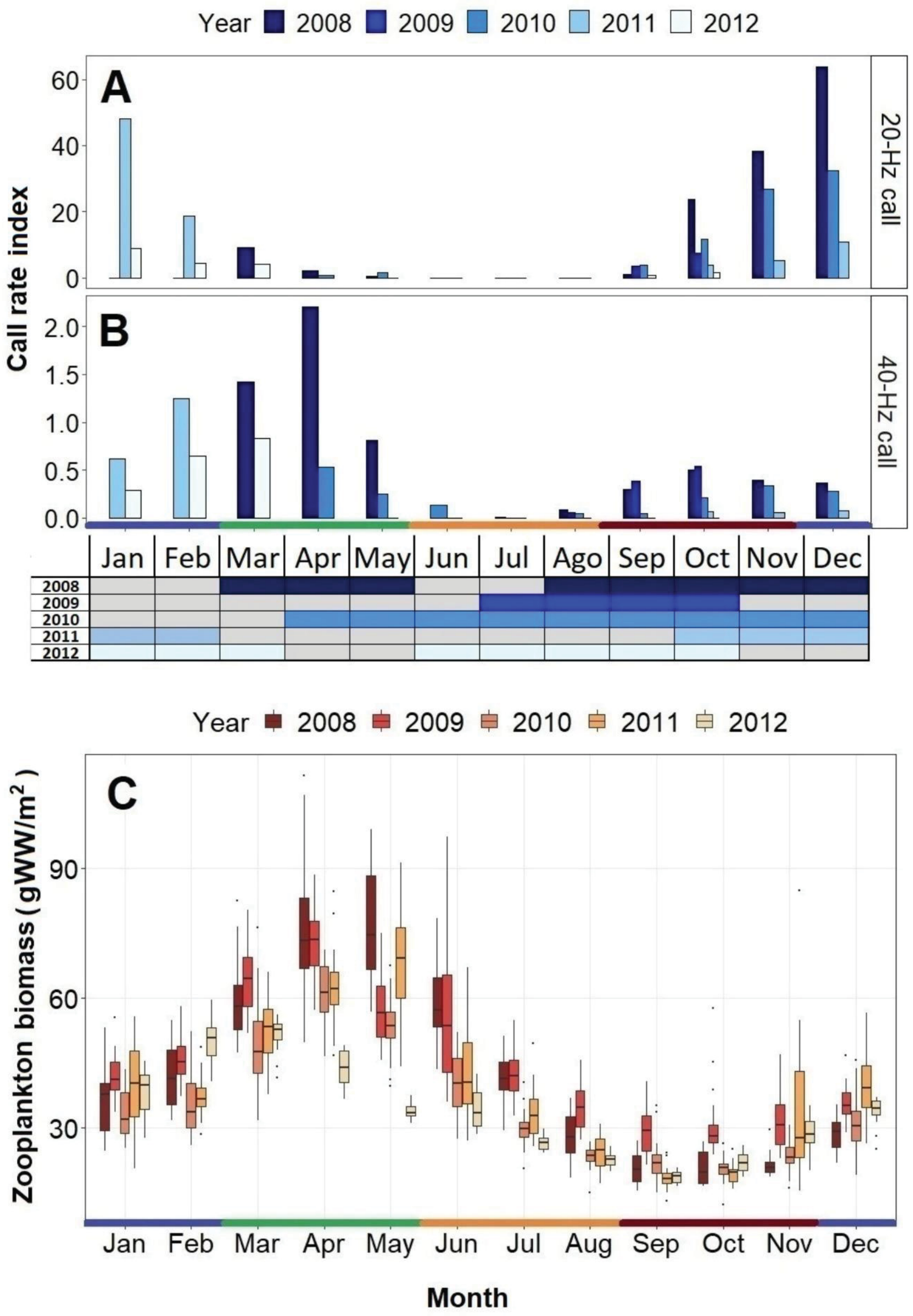


Figure 3.2. Monthly variation in (a) 20-Hz and (b) 40-Hz call rates, and (c) model-based estimates of zooplankton biomass (gWW: gram wet weight), from 2008 to 2012. The graph

on the x-axis in (a) and (b) represents the recording effort by month and year and grey colour indicates no data. Horizontal lines within the boxplots in (c) indicate the median, box boundaries indicate the 25th (lower boundary) and 75th (upper boundary) percentiles, vertical lines indicate the largest (upper whisker) and smallest (lower whisker) values no further than 1.5 times the interquartile range, and black dots represent outliers. Colours on the x-axis indicate seasons: blue—winter, green—spring, orange— summer and brown—autumn. Abbreviations for months are the following: Jan-January, Feb-February, Mar-March, Apr-April, Jun-June, Jul-July, Aug-August, Sep-September, Oct-October, Nov-November, Dec-December.

3.3.3 Model of the 20-Hz call

Season was the most important predictor of the 20-Hz call, followed by year and one- week lagged call rates (57% deviance explained; Table S3.2). Zooplankton biomass had no significant effect on the 20-Hz call (Table 3.1; Table S3.3). Call rate was significantly higher in winter than in autumn and spring but did not differ between these later seasons (Fig. 3.3a). 2012 had significantly lower call rates than all other years except 2009 (Fig. 3.3b; Table S3.3). Overall, the model residuals did not show any pattern, indicating a good fit to the data. Most of the residuals were within the simulated envelope (Fig. S3.3).

Table 3.1. Analysis of deviance (ANOVA) for the best fitting quasi-Poisson model of the 20-Hz call rate. Significant terms ($p<0.05$) are shown in bold. *df* - degrees of freedom, *Dev.* - deviance, *Res. df* - residual df, *Res dev.* - residual deviance.

	df	*Dev.*	*Res.df*	*Res.dev*	*F*	*p-value*
NULL			142	3066.7		
Season	2	955.38	140	2111.3	47.25	**< 0.001**
Year	4	601.36	136	1510.0	14.87	**< 0.001**
Lag-1-call rate	1	209.92	135	1300.0	20.76	**< 0.001**

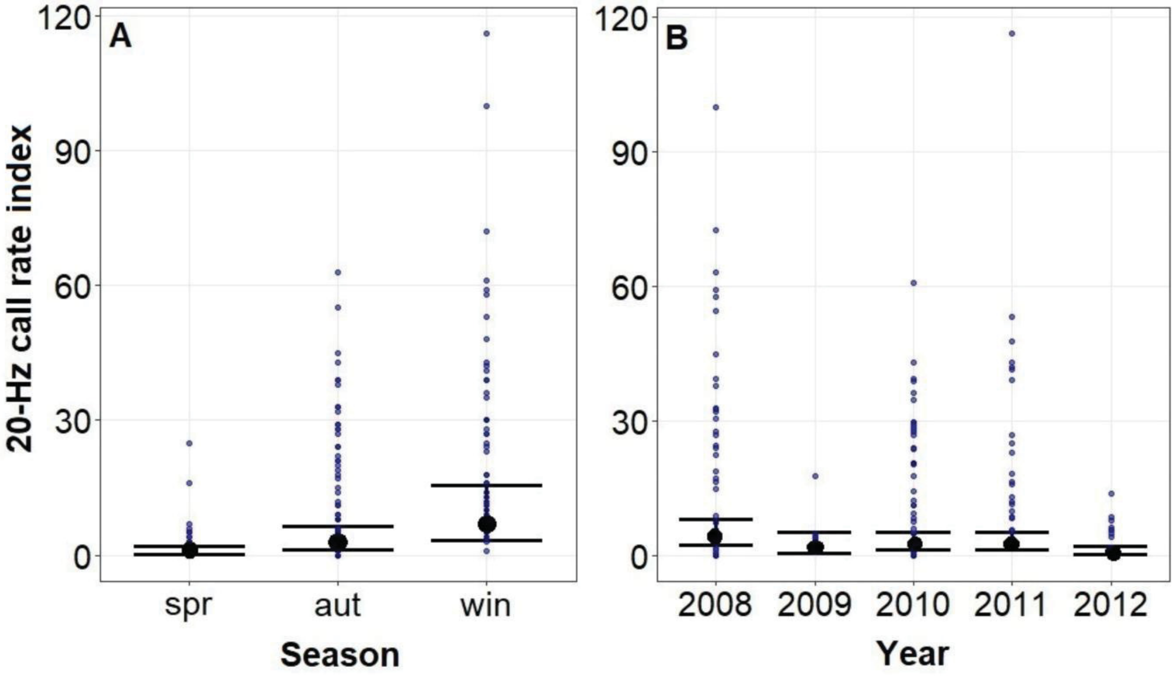


Figure 3.3. Results from the quasi-Poisson model showing the (A) season and (B) year effect on the 20-Hz call rate. Blue points represent observations, error bars represent the mean (black dot) and 95% confidence intervals of fitted values. Seasons are abbreviated as follows: spr-spring, aut-autumn and win-winter.

3.3.4 Model of the 40-Hz call

The best model for the 40-Hz call rate included only zooplankton biomass (20% deviance explained; Table S3.2). Call rate increased with increasing zooplankton biomass (Table 3.2, Fig. 3.4; Table S3.3). Although zooplankton biomass varied seasonally (Fig. 3.2c), the interaction between these two variables had no significant effect on 40-Hz call rates. Model residuals did not show outliers and indicated the model was adequate to describe the data (Fig. S3.4).

Table 3.2. Analysis of deviance (ANOVA) for the best fitting quasi-Poisson model of the 40-Hz call rate. Significant terms ($p<0.05$) are shown in bold. *df* - degrees of freedom, *Dev.* - deviance, *Res. df* - residual df, *Res dev.* - residual deviance.

	df	*Dev.*	*Res.df*	*Res.dev*	*F*	*p-value*
NULL			143	197.81		
Zooplankton	1	39.62	142	158.18	25.94	**< 0.001**

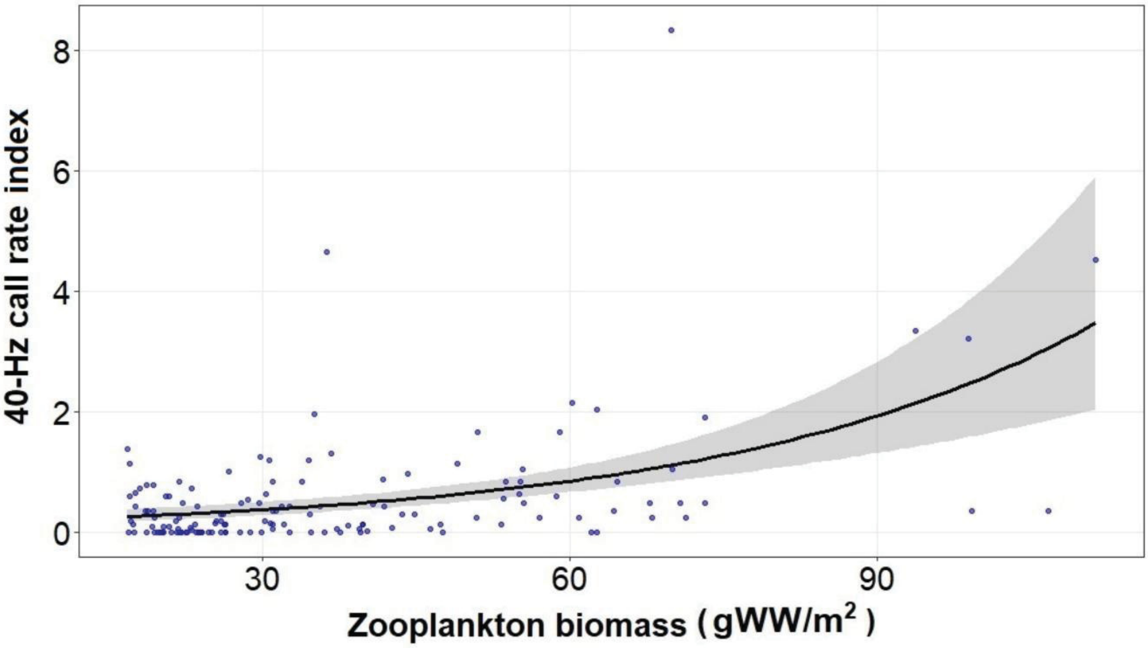


Figure 3.4. Zooplankton biomass effect on the 40-Hz call. Blue points represent observed 40-Hz call rate index. The solid line corresponds to the mean fitted values (i.e., the trend) and the grey shaded area represents the 95% confidence interval.

3.4 Discussion

Our study shows that production of 40-Hz calls in fin whales is positively associated with prey biomass, providing supporting evidence of a food-associated signal, as previously suggested (Burnham, 2019; Burnham et al., 2021; Širović et al., 2013; Watkins, 1981; Wiggins and Hildebrand, 2020). 40-Hz call rates increased with increasing biomass of zooplankton, the main component of fin whale diet (Arregui et al., 2018; Silva et al., 2019). Conversely, production of 20-Hz calls were mainly influenced by season and to a lesser extent by year, but temporal patterns were independent from zooplankton biomass. This finding corroborates the widely accepted view that 20-Hz songs are used in a reproductive context (Croll et al., 2002; Watkins et al., 1987) but suggests their function is independent from food biomass.

3.4.1 20-Hz song function

The winter peak in 20-Hz calls found in this study is consistent with the known seasonality of the fin whale song in the Northern Hemisphere (Nieukirk et al., 2004; Romagosa et al., 2020a; Thompson et al., 1992; Watkins et al., 1987). The fact that the 20-Hz song peaks during the breeding season of the species (Kjeld, 1992; Ohsumi et al., 1958), is produced only by males (Croll et al., 2002), and is well-suited for long-range communication (Payne and Webb, 1971), support the widely accepted hypothesis that fin whale song is a male advertisement signal (Croll et al., 2002; Watkins et al., 1987). Similarly, it has been suggested that male fin whales sing to attract females, mediate interactions with other males, or a combination of both (Croll et al., 2002; Oleson et al., 2014; Watkins et al., 1987). Croll et al. (2002) proposed that male fin whale song could attract females by conveying information on aggregations of patchily distributed prey. In the resident fin whale population of the Gulf of California (López et al., 2019), male singing co-occurs with winter foraging on dense aggregations of krill (Croll et al., 2002, 2001). In this study, zooplankton biomass had no effect on fin whale singing activity, as would be expected if male songs signal food aggregations. Similarly, other studies did not find a relationship between prey proxies (i.e., acoustic backscatter strength) and the production of song-forming 20-Hz calls (Burkhardt et al., 2021; Burnham et al., 2021). Thus, findings from this and previous studies do not support the hypothesis that fin whale song serves to attract females via food advertising. Instead, these results are in line with the hypothesis that singing may be an acoustic display (Watkins et al., 1987) directed towards females or other males. Evidence from a range of taxa indicates that songs can convey honest information on singer's motivation and quality which may be used both by females in mating decisions, and by other males in competitive interactions (Nowicki and Searcy, 2004; Tregenza et al., 2006). However, there are also species in which song traits do not correlate with male quality (Cardoso et al., 2012) and further research is needed to directly test this hypothesis in fin whales.

The effect of year on singing activity was greatly influenced by 2012, which showed significantly lower call rates when compared to 2008, 2010 and 2011. The most plausible explanation is that decreased call rates in 2012 reflect lower numbers of fin whales in the area. This is partly supported by visual observations collected by the Fisheries Observer Program Data showing that fin whale encounter rates (sightings/100 km) were null in 2012, compared to 0.9 in 2010 and 9.2 in 2011. Year-to-year variability in fin whale numbers is usually attributed to environmental changes affecting prey distribution and abundance (Escajeda et al., 2020; Širovic et al., 2015). In this study, models did not show an effect of prey biomass on singing activity. In addition, lower values of modelled zooplankton biomass in 2012 were only found in April and May (Fig. 2C), the end of the singing season. It could also be argued that inter-annual variability in call rates results from differences in call detectability due to variations in background noise from shipping. Although noise levels in the study area did not vary significantly between 2010 and 2012 (Romagosa et al., 2017), effects of shipping noise on call detectability should be investigated in the future.

3.4.2 40-Hz call function

This study confirms the temporal separation between fin whale 40-Hz calls and 20-Hz calls (Širović et al., 2013). More importantly, we demonstrate that production of fin whale 40-Hz calls was best predicted by zooplankton biomass alone across all years and seasons, with call rates increasing with increasing prey biomass. These results lend support to previous suggestions of a food-related function of the 40-Hz call (Burnham, 2019; Burnham et al., 2021; Širović et al., 2013; Watkins, 1981). In the eastern North Pacific, 40-Hz calls peaked in early summer at known important feeding habitats (Širović et al., 2013). In the Canadian Pacific, distance from the shelf break and backscatter intensity (as proxy of potential prey) were important determinants of fin whale 40-Hz calls (Burnham et al., 2021). In addition, 40-Hz calls were generally produced by whales in groups, engaged in long, possibly foraging, dives (Croll et al., 2001) or surface feeding activities (Watkins, 1981). Together, findings from this and previous studies provide strong evidence for the use of 40-Hz calls in a feeding context.

Some food-associated calls are produced only in feeding contexts, with animals adjusting call types or production rates as a function of the type, quality or quantity of food available (Di Bitetti, 2003). More commonly, food-associated calls are given in multiple contexts and are not food-specific (Clay et al., 2012). Irrespective of their degree of context-specificity, there is increasing evidence that food-associated calls provide receivers with information about a food source or feeding event, and often are used to attract them to a foraging site. In many cases, food-associated calling functions to recruit potential mates or kin, increasing the inclusive fitness of callers (Judd and Sherman, 1996), or to recruit non-related partners and allies, potentially enhancing social status and bonds (Slocombe et al., 2010). Attracting conspecifics to a feeding site may also increase foraging efficiency of callers, by facilitating prey capture or defence, or helping with predator vigilance (Sridhar et al., 2009). There are also examples where food-associated calls are not used to attract others but to reduce or mediate competitive interactions over food by establishing resource ownership (Gros-Louis, 2004). Clearly, the ultimate function of food-associated calling varies greatly with the social and ecological environment of animals (Clay et al., 2012).

Fin whales do not live in stable social groups (Whitehead and Carlson, 1988) and the distribution of their prey is ephemeral (Strand et al., 2020). Thus, it is unlikely that fin whale 40-Hz calls serve to attract kin or social partners, either to provide them with increased foraging benefits or to assist defending food patches. Also, the lower detections of fin whale 40-Hz calls during the breeding season reported here and in other studies (Širović et al., 2013; Watkins, 1981), suggests that the primary function of this call is not to attract potential mates, trading-off food for reproductive benefits. In other cetaceans, food-associated vocalisations have been recorded during cooperative foraging behaviours (e.g., humpback whales (D'Vincent et al., 1985), killer whales (*Orcinus orca*) (Guinet, 1992)) and may assist with prey herding and capture (Cerchio and Dahlheim, 2001). With the exception of a single report of fin whales feeding at the surface in perfect synchrony (Canese et al., 2006), there is no evidence of cooperative feeding in fin whales. Nevertheless, attracting other whales to the foraging site may increase the chances of tracking prey movements, thus prolonging feeding opportunities for callers, as suggested for cliff swallows (*Petrochelidon pyrrhonota*) feeding on insect swarms (Brown et al., 1991). Fin whales often occur in temporary foraging aggregations in our study area and elsewhere (Širović et al., 2013; Visser et al., 2011). Fin whale 40-Hz calls could be used to convey information about individual location to regulate spacing between foragers, or establish ownership of food patches, as described for other species (Gros-Louis, 2004). At present though, we do not know the functional significance(s) of the 40-Hz fin whale call when produced in feeding contexts.

The recent description of two acoustically tracked fin whales producing 40-Hz calls while moving pass each other (Wiggins and Hildebrand, 2020), gives some indication that this call might also serve as a contact or social call. In birds and mammals, functionally specific vocalisations, like food or alarm calls, are often used in different behavioural contexts (Clay et al., 2012). Blue whale “D calls” were firstly described as food-associated and social calls because, as the 40-Hz fin whale calls, they were recorded during foraging behaviours in feeding areas (Oleson et al., 2007a, 2007b) and from whales in groups (Lewis et al., 2018; McDonald et al., 2001). Later though, one study reported D calls also produced in a reproductive context where two males were aggressively interacting with each other while escorting a female (Schall et al., 2020). Thus, it is likely that more functions for the 40-Hz call may be revealed with the increasing research effort on fin whale vocal behaviour.

3.5 Conclusion

Our study is the first to show a positive association between the production of the 40-Hz call and modelled biomass of prey, providing additional evidence of the use of this call in feeding contexts. Our findings are also consistent with earlier work indicating that the song-forming 20-Hz call is used in reproductive contexts, but the absence of a relationship with prey biomass does not support the assumption that this call is used by males to advertise a food source and attract potential mates. Instead, the 20-Hz song may be a male acoustic display used in intersexual and intrasexual interactions. Our study also illustrates how spatiotemporally resolved simulations of zooplankton biomass, which is challenging to measure in the field, can provide valuable insights into the environmental context and potential functions of baleen whale vocalisations.

Understanding call function and monitoring vocal behaviours associated to the state of individuals or groups (e.g., reproductive status and success, and social complexity), habitat quality (e.g., food resources) or animal density (e.g., call rates) can help identifying functional habitats, predict negative human impacts and support conservation planning (Teixeira et al., 2019). Information on the temporal and spatial occurrence of fin whale 40-Hz calls may inform when and where animals engage in foraging and provide important clues to the environmental factors promoting foraging behaviour on this species. Similarly, the 20-Hz song may give unique insights into the location and characteristics of the areas used for mating. Studies combining visual and acoustic observations of callers and receivers simultaneously, offering information on the behavioural context of call production along with responses of conspecifics, could significantly advance our understanding of fin whale vocal behaviour.

Acknowledgements: We are grateful to Mark Lammers, for providing the EARs and technical support, and to Rui Prieto, Sérgio Gómez, Norberto Serpa, skilled skippers and crew that participated in the preparation and deployment of the EARs at DOP/IMAR. We also thank the reviewers that significantly improved the original manuscript. Data on fin whale sightings from 2010 - 2012 were kindly provided by the Azores Fisheries Observer Program (POPA) (www.popaobserver.org).

Funding: This work was supported by Fundação para a Ciência e Tecnologia (FCT), Azores 2020 Operational Programme and Fundo Regional da Ciência e Tecnologia (FRCT) through research projects TRACE (PTDC/ MAR/74071/2006), MAPCET (M2.1.2/F/012/2011) and AWARENESS (PTDC/BIA-BMA/30514/2017), co- funded by FEDER, COMPETE, QREN, POPH, ERDF, ESF, the Lisbon Regional Operational Programme, and the Portuguese Ministry for Science and Education. Okeanos R&D Centre is supported by FCT, through the strategic fund (UIDB/05634/2020). MR was supported by a DRCT doctoral grant (M3.1.a/F/028/2015). SPJ was funded by EC funds (SUMMER H2020-EU.3.2.3.1), IC by FCT through AWARENESS – (PTDC/BIA-BMA/30514/2017). HM thanks support by CMAF-CIO (funded by FCT, Portugal, through the projects UID/MAT/00006/2013 and UIDB/04561/2020, respectively). AP was supported by AWARENESS project (PTDC/BIA-BMA/30514/2017) and UIDB/50019/2020 – IDL and TAM by CEAUL and the LMR ACCURATE project (contract number N3943019C2176). MAS was funded by FCT and EC funds (IF/00943/2013, SUMMER H2020-EU.3.2.3.1, GA 817806).

Annex III. Supplementary information

Supplementary information associated with this article can be found in the online version at https://royalsocietypublishing.org/doi/suppl/10.1098/rspb.2021.1156

Chapter 4

Revolutionary and evolutionary changes in fin whale song[3]

Abstract

Cultural transmission, the social learning of information or behaviours from conspecifics, is believed to drive song changes in some bird species and humpback whales. When one song type replaces all others rapidly in a population is revolutionary, while gradual song changes may be evolutionary. Fin whales produce highly stereotyped and repetitive songs, believed to serve in sexual selection, that change over time with all males conforming and maintaining changes, which may indicate they are culturally transmitted. Here, we report two decades of fin whale song changes in the Central and North-eastern Atlantic Ocean. First, we document a rapid replacement of INIs (from 19s to 12s) across a vast area of the Mid-Atlantic Ridge in just four winter seasons. During the transition period, there is co-existence of both song types and hybrid songs as well as a clear south-westerly spatial gradient in percentages of song types, that we attribute to a cultural revolution. Second, we present gradual changes in song characteristics (increase in INIs and decrease of frequencies of the HF component), documented in other ocean basins and for blue whale songs, which may be the result of cultural evolution driven by different interacting selecting pressures. The study of animal culture provides key aspects of the biology and ecology of individuals and populations that should be integrated in conservation strategies.

---

[3] Romagosa, M., Nieukirk, S., Cascão, I., Dziak, R., Perrot, J., O'Brien, J., Pereira, A., Ugalde, A., Papale, E., Rasmussen, M., Mellinger, D., Marques T.A. and M. A. Silva (*In preparation*). Revolutionary and evolutionary changes in fin whale song.

4. 1 Introduction

Many species use songs as mating displays that change over time through evolutionary process (Garland et al., 2011; Otte, 1992; Williams et al., 2013). When environmental causation can be excluded, cultural evolution is the best explanation for the rapid diffusion of novel behaviours throughout a population (Leca, 2015). This process is governed by cultural transmission, the social learning of information or behaviours from conspecifics (Rendell and Whitehead, 2001), and is believed to drive song changes in some bird species and humpback whales (Logue and Leca, 2020; Noad et al., 2000). These changes may be neutrally selected (i.e., cultural evolutionary drift) when they are made by chance (e.g., inaccuracies in song copying) and are neither directional nor indicative of reproductive success (Whiten, 2019). Conversely, cultural evolution through Darwinian selection will favour song variations that best adapt to the species' physical and biotic environments (Whiten, 2019). This selection can be directional and may be caused by either sexual selection, when song traits are linked to males reproductive success (Williams et al., 2013), or cultural selection, when no such link exist. Best example of cultural selection is when it benefits songs that are more effective as communication signals (i.e., selection for optimal sound transmission) (Luther and Baptista, 2010). Selection may also stabilize characters that are beneficial (stabilizing cultural selection) (Whiten, 2019). For example, it may favour species-level song distinctiveness through a process of “reinforcement” and reproductive character displacement (Ptacek, 2000).

Cultural transmission of acoustic signals have been demonstrated for several species of cetaceans (e.g., bottlenose dolphins, killer whales, sperm whales (*Physeter macrocephalus*) and humpback whales) (Whitehead and Rendell, 2015) thus their ability for vocal learning (Janik, 2014). One clear example of song evolution analogous to some birdsong species is the humpback whale song (Garland and McGregor, 2020). Males from this species sing long, complex, stereotyped, and hierarchically structured songs (Payne and McVay, 1971) believed to act in sexual selection (e.g., mate attraction and male-male competition) (Herman, 2016). These songs are clearly culturally transmitted because they change over time, and all males within a population adopt the current version of the display (i.e., conformism), causing geographic variation (Payne et al., 1983; Payne and Payne, 1985). Sometimes, one song type replaces all others in the population in a matter of a just a few years. These drastic changes have been described as whale song revolutions rather than evolutions (Noad et al., 2000) and are only comparable to some species of song birds (Logue and Leca, 2020; Otter et al., 2020).

Although fin whale songs are less complex than those of humpback whales (Watkins et al., 1987), they are also believed to serve as acoustic displays (Thompson et al., 1992; Watkins et al., 1987), are produced only by males (Croll et al., 2002) and change over time (Hatch and Clark, 2004; Leroy et al., 2018; Širović et al., 2017; Weirathmueller et al., 2017). Fin whale songs can consist of single repeating 1-s downsweeps centred around 20 Hz (Watkins et al., 1987) or of two or three alternating notes with different downward-sweeping characters (Širović et al., 2017; Thompson et al., 1992). Fin whale song characteristics vary among geographic areas (Hatch and Clark, 2004) but distributions of inter-note intervals (INIs) are the most significant predictors of region (Hatch and Clark, 2004; Watkins et al., 1987) and have been used differentiate stocks or populations (Delarue et al., 2009; Hatch and Clark, 2004; Širović et al., 2017). In some areas, a higher frequency (~130-Hz) upsweep (hereafter HF note), which frequency varies between regions (Hatch and Clark, 2004; Širović et al., 2004), occurs simultaneously with 20-Hz notes (Hatch and Clark, 2004).

A decent number of studies report how fin whale song change over time (Hatch and Clark, 2004; Leroy et al., 2018; Morano et al., 2012; Širović et al., 2017; Weirathmueller et al., 2017) but none of them specifically focus in causes of song evolution in this species. Here, we analyse two decades of fin whale song variations (INIs and 20-Hz and HF note peak frequencies) in a wide area of the Central and North-east Atlantic Ocean and discuss rapid and slow song changes in the context of cultural evolution.

4.2 Methods

4.2.1 Recording equipment and deployment locations

Acoustic data were collected from 6 different regions of the Central and North-east Atlantic Ocean between 1999-2020 (Fig. 4.1a) with varying sampling periods, sampling rates, duty cycles and deployment depths (Table S4.1; Fig. S4.1). Ocean-Bottom Seismometers (OBS) were used in two regions: the Canaries Islands (2014-2015) and South-west Portugal (SW Portugal) (2007-2008). In the Canary Islands dataset, the hydrophone channel showed good enough quality signals and was selected for the analysis but in the SW Portugal (2007-2008) data, the seismometer channel (vertical component Z) showed higher signal-to-noise ratio

(SNR) signals than the hydrophone channel. Fixed autonomous recorders (ARs) were used in the remaining regions (Table S4.1).

4.2.2 Acoustic analysis

Data with high sampling rates (> 2 kHz) were downsampled to 2 kHz for better spectrogram visualization and consistency with processing across different datasets. Only data from October through March were analysed because fin whale songs are more stable during that period (Hatch and Clark, 2004) and seasonal variation was out of the scope of this study. All datasets were manually inspected to identify days with fin whale 20-Hz notes (Watkins et al., 1987) or double pulsed songs containing the 20-Hz and HF notes (Hatch and Clark, 2004), except for the Azores, where a Low Frequency Detection and Classification System (Baumgartner and Mussoline, 2011) was used following procedures described in Chapter 2. Spectrograms of days with fin whale detections were manually analyzed using Adobe Audition 3.0 software (Adobe Systems Incorporated, CA, USA) to select those periods with good quality notes. The selection criteria was based on: a) a high SNR, b) no masking from noise, c) no overlap with other whale singers and d) notes organized in long series. This last criteria could not be followed for recordings with small duty cycles (Iceland, SW Portugal 2015-2016, Azores 2008-2011 and Ireland) (Table S4.1), but still, regularly spaced notes could be identified and assumed to be part of songs because data comes from the singing season when most of 20-Hz notes form songs (Watkins, 1981; Watkins et al., 1987). Selected days with detections were spaced at least 24 hours to minimize sampling the same animal multiple times.

The number of days with good quality notes varied across locations and months (Fig.S4.1) but when possible, a minimum of 4 days per month were sampled. The small sample rates of some recordings (Canary Islands and SW Portugal - 2006-2007 and North and South MAR) (Table S4.1) did not allow the analysis of the HF component, which frequency (~130-Hz) surpassed maximum frequencies.

Selected days with good quality notes were fed into a band-limited energy detector included in Raven 1.5 (Cornell University, Ithaca, NY) that automatically selected each 20-Hz and HF note in the spectrogram. All selections were re-checked manually by the same analyst to ensure each note was well imbedded in the selection square. For each selected note, the software measured its begin and end time as well as its peak frequency. INIs were calculated by subtracting the time difference between the start time of a 20-Hz note and the start time of the following 20-Hz note (Watkins et al., 1987) (Fig. 4.1b). Peak frequencies were measured for the 20-Hz and the HF notes. The peak frequency is the value at which the maximum energy in the signal occurs. It is considered a robust measurement because is based on the energy within the selection and not the time and frequency boundaries of the selection (Charif et al., 2010).

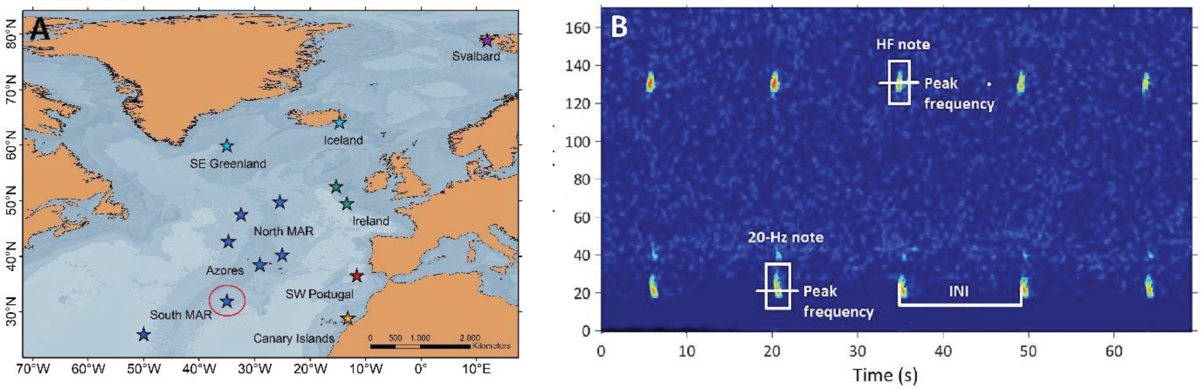


Figure 4.1. (A) Regions of acoustic recordings. Red circle indicates North-eastern (NE) hydrophone from the South Mid-Atlantic Ridge (MAR) region. (B) Example spectrogram of a fin whale song showing the acoustic parameters analysed in this study.

In each selected day, only one continuous sequence of notes was analysed, for which each day represents one sequence of notes or song fragment (hereafter referred as songs). For each day, averaged INIs and peak frequencies of the 20-Hz and HF note as well as standard deviations were calculated. All regions were then plotted in a chronological order to infer into possible trends. A linear regression model was fit to each parameter data using a Gaussian distribution. In the case of INIs, the model was fitted from 2005 to 2020 where a clear linear trend was observed. The slope of the linear trend for these parameters was extracted to represent the changing rate per year.

To illustrate the temporal transition between song types, data from the North-eastern hydrophone of the South MAR region (Fig. 4.1) was analysed to calculate percentages of each song type per singing season (Oct-Mar), from 1998/1999 to 2004/2005. The spatial diffusion of song types was investigated by calculating percentages of song types in the singing season of 2002/2003, where simultaneous data exist for 6 MAR locations.

For comparisons of INIs between regions, only songs within the same singing season in different regions were used given the documented inter-annual variation in fin whale song parameters (Širović et al., 2017; Weirathmueller et al., 2017).

The two types of recorders used in this study, OBS and AR, did not affect INIs measurements but may have affected peak frequencies of the 20-Hz (Supplementary material).

4.3 Results

4.3.1 Sudden song changes

Our results showed a rapid change in INIs across a vast area of the Mid-Atlantic Ridge (MAR/Azores), where the 19s-song was completely replaced by the 12s-song, in just four winter seasons (2000/2001 – 2004/2005) (Fig. 4.2a, b). In 2004, the 19s-song disappeared from all sampled regions, except from one isolated account in 2008. During the transition period, both song types co-existed in the North-eastern hydrophone recordings from the South MAR region, with a notable percentage of hybrid songs (~24% hybrids in 2002/2003) (Fig. 4.2b). Songs were classified as hybrid if they showed both INIs (19s and 12s). In 2002/2003, there was a clear south-westerly spatial gradient in percentages of song types with the new song (12s) being more abundant in the north-eastern locations (Fig. 4.2c).

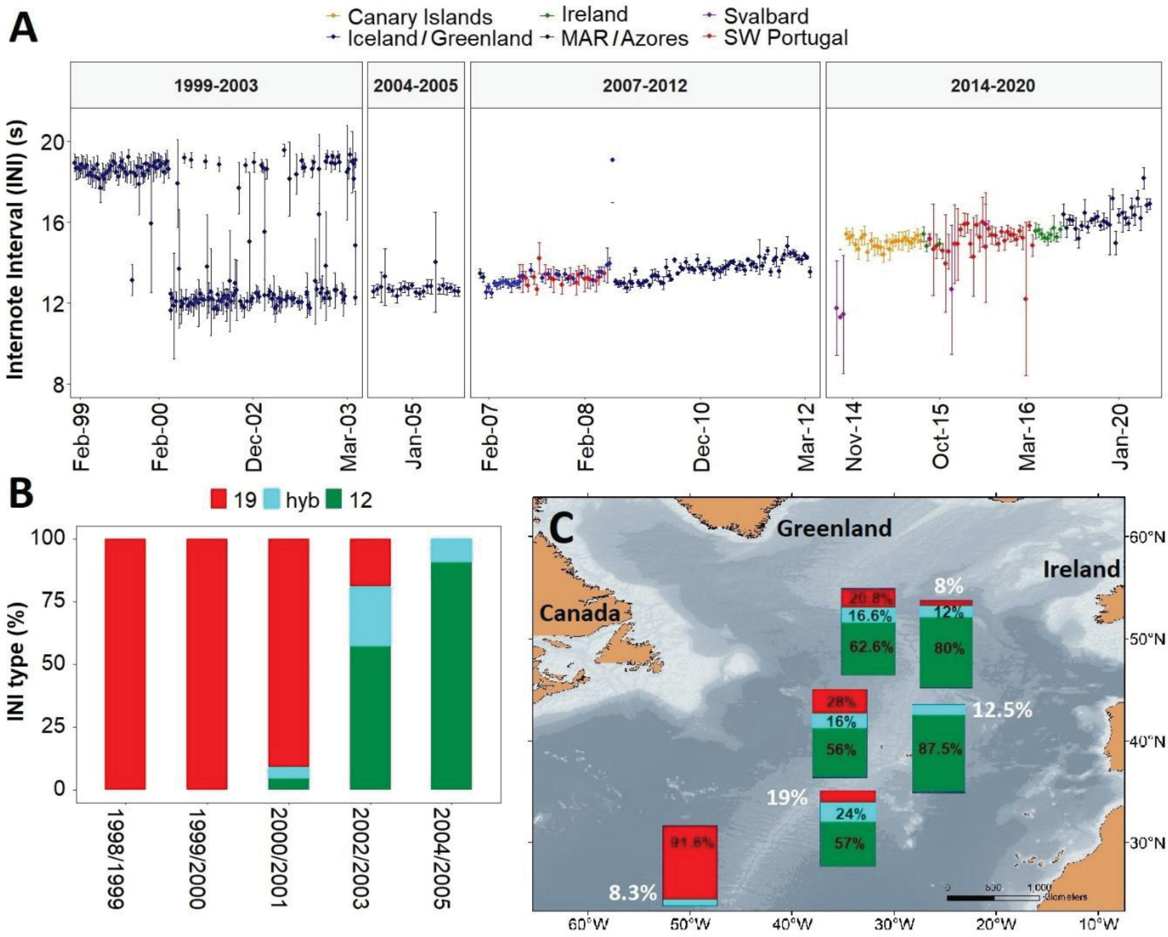


Figure 4.2. (A) Internote intervals (INIs) for all regions sampled (Fig. 4.1a). Points represent averaged INIs per song and error bars are standard deviations. (B) Percentage of each song type in the NE hydrophone of the South MAR region during the song shift from 1999 – 2005 (Hyb; hybrid). (C) Map showing percentages of each song type for North and South MAR hydrophones during the 2002/2003 singing season.

4.3.2 Gradual song changes

This study showed an almost two decade gradual change in some fin whale song characteristics: an increase of INIs (0.24s/yr), a decrease in peak frequencies of HF note (-0.36 Hz/yr) (Fig. 4.3a) and a lack of trend for the 20-Hz note (Fig. 4.3b).

All sampled regions fit within this general trend of increasing INIs (Adj. R-squ. = 0.78) (Fig. 4.2a) and decreasing HF note peak-frequencies (Adj. R-squ. = 0.8) (Fig. 4.3a). Moreover, all recordings with simultaneous data (i.e., same singing season) from different regions (Iceland-Greenland, MAR/Azores, SW Portugal and Ireland) showed unimodal overlapping INI distributions (Fig. 4.4). The only exception was the Svalbard region, sampled in 2014, where songs showed great variability (Table S4.2) and a double pattern of INIs (9s and 14s) (Fig. 4.4). After 2014, some songs (21 %) included 9-10s INIs in SW Portugal and variability in INIs increased in the Azores region (Fig. 4.2a; Table S4.2).

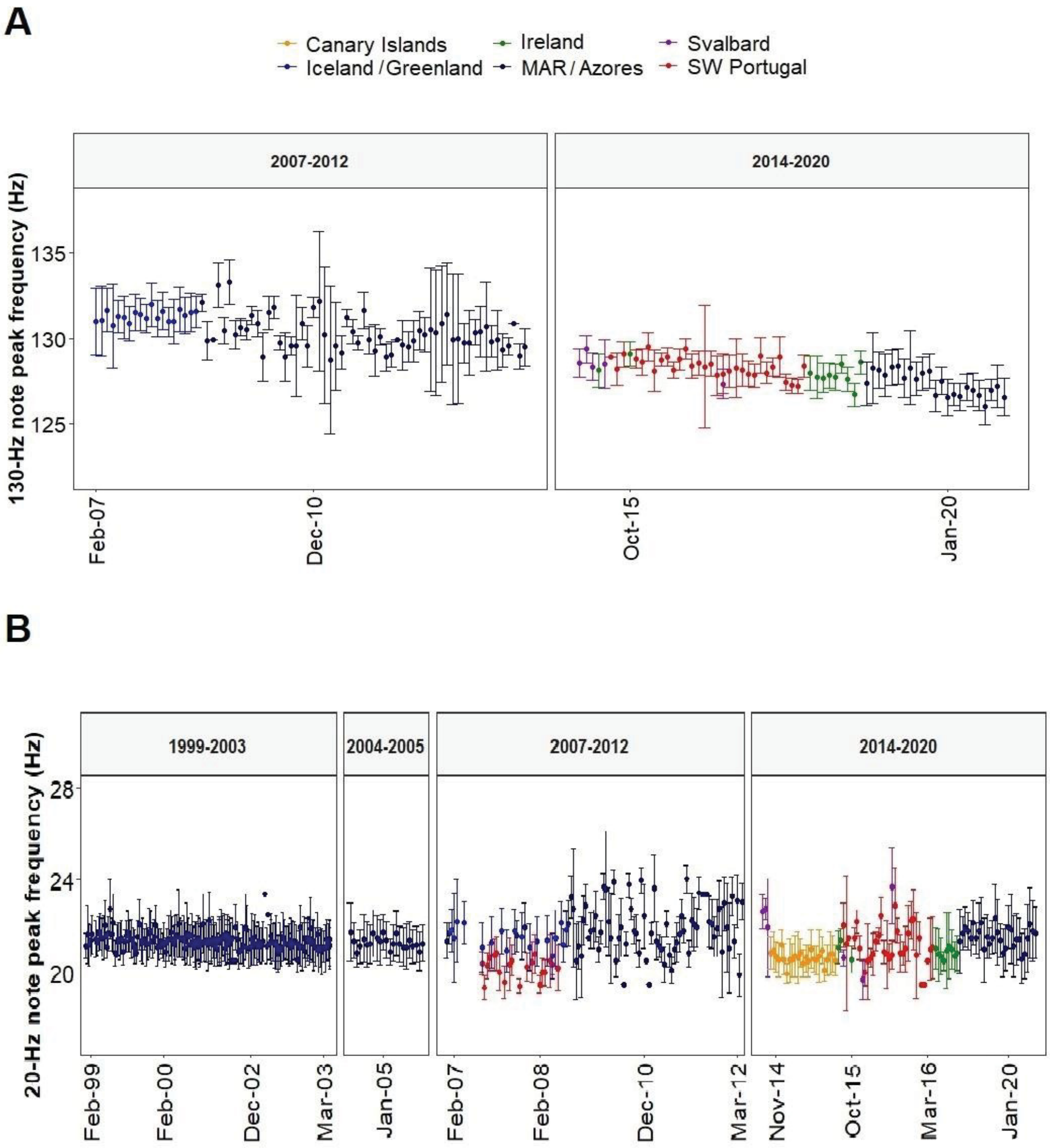


Figure 4.3. Peak frequencies of the HF note (A) and 20-Hz note (B) for the regions sampled. Points represent averaged peak frequencies per song and error bars are standard deviations.

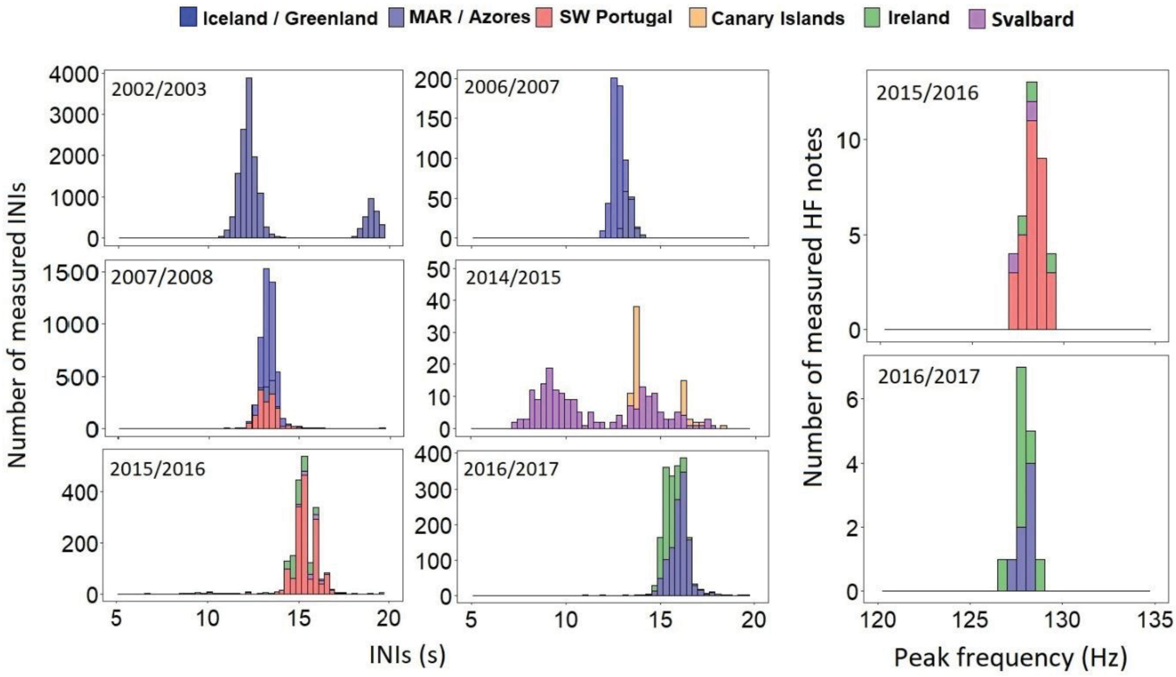


Figure 4.4. Histograms showing INIs (left) and peak frequencies of the HF note (right) by singing season (Oct-Mar) and from regions with simultaneous data.

4.4 Discussion

4.4.1 Revolutionary change in song INIs

The rapid change in INIs across a vast area of the Mid-Atlantic Ridge (MAR/Azores), where the 19s-song was completely replaced by the 12s-song, in just four winter seasons (2000/2001 – 2004/2005) cannot be explained by a change in habitat use of distinct acoustic populations (with different INIs). First, if these two INI types were exclusively used by two distinct fin whale acoustic populations, we would not expect to find hybrid songs during the transition period. One study that attributes changes in song INIs to population shifts found that each song pattern was very conserved and no intermediate songs existed (Širović et al., 2017). Second, if a population replacement was the cause for the change in INIs then we would expect some degree of co-existence of INIs in posterior years, but we report a complete disappearance of the old INI song. Finally, the same fin whale song shift reported here in the MAR/Azores region seemed to occur simultaneously at northern latitude feeding grounds, in the so-called North-east North Atlantic (NENA) region (Hatch and Clark, 2004). Thus, a large-scale population change in such a vast area including migratory and feeding habitats is very unlikely.

The reported unequal spatial distribution of song INIs in the same winter singing season over a region with similar environmental conditions also excludes the hypotheses that song changes may be caused by environmental drivers, thus cultural revolution may be the most probable explanation (Leca, 2015).

Cultural transmission is the motor of cultural revolution and involves vocal learning. The existence of hybrid songs found here together with the ability of individual fin whales to switch between song types (Helble et al., 2020) suggest a greater fin whale song plasticity than previously thought and opens the possibility of learning by imitation in this species. Vocal learning is known to occur in bottlenose dolphins (Richards et al., 1984) and very likely to happen in killer whales, bowhead (*Eubalaena glacialis*) (Janik, 2014) and humpback whales (Rendell and Whitehead, 2001). Sperm whales are able to match their codas in duets by overlapping their clicking patterns (Weilgart, 1990). This synchronization would require imitative learning in some form (Whitehead and Rendell, 2015). Similarly, fin whales may imitate songs with new INIs by overlapping notes with conspecifics.

Like in some bird species, humpback whale songs are clearly culturally transmitted because they evolve through time and all males in a population conform to song changes (Payne and Payne, 1985) and maintain them (Mundinger, 1980). Male fin whale songs are also regionally distinctive (Castellote et al., 2012b; Delarue et al., 2009; Hatch and Clark, 2004; Širović et al., 2017), go through changes over time (Delarue et al., 2009; Leroy et al., 2018; Širović et al., 2017; Weirathmueller et al., 2017) and all males in a population adopt and maintain these changes (Oleson et al., 2014)(this study), which adds supporting evidence to cultural evolution in fin whale song.

Cultural revolutions have been triggered by overlapping bird dialects in migratory areas (Logue and Leca, 2020) or by a small number of immigrant humpback whale individuals into a new area (Noad et al., 2000). Assuming the rapid song change reported here is the result of a cultural revolution, fin whales singing the old 19s-song must have overlapped in time and space with 12s-song singers for the song transfer to occur. The spatial gradient in song types suggest the new song (12s) may have originated somewhere in the Eastern North Atlantic and spread south-westerly. An overlap between Mediterranean and North Atlantic fin whales is believed to occur either inside of the Mediterranean basin (Castellote et al., 2012b) or off the Strait of Gibraltar (Gauffier et al., 2018; Pereira et al., 2020) but the INI of Mediterranean fin whale song was 14s at the time of the song shift (Clark et al., 2002). The only documented 12s-song type was from the Western North Atlantic, in the Gulf of Saint Lawrence (GSL), in 2006/2007 (Delarue et al., 2009). Given the reported inter-annual variability in fin whale INIs (Delarue et al., 2009; Hatch and Clark, 2004) we cannot assume that back in the 2000s this population may have had this same INIs. What is certain is that the same fin whale song shift reported here in the MAR/Azores region occurred simultaneously in a northern latitude summer feeding area (NENA) (Hatch and Clark, 2004; Víkingsson et al., 2015). More data are needed to determine if the new 12s-song came from an eastern unsampled region or from overlapping populations in feeding grounds.

4.4.2 Directional evolutionary song changes

After the rapid song shift, our results indicate that fin whales from all other sampled regions share the same song characteristics and maintain changes over time, with the only exception of the Svalbard region, sampled in 2014. The fact that SW Portugal songs include Svalbard INIs only after 2014 but not in 2007/2008 and that Azores INIs increase their variability after that year, may suggest a link between these regions. Satellite telemetry tracking data shows that some fin whales summering in Svalbard migrate to SW Portugal in fall and winter (Lydersen et al., 2020). Also, stable isotope data (majority from 2014) from fin whales visiting the Azores in spring show that these animals had been feeding off Iberia in winter (Silva et al., 2019).

The fin whale song trends found in this study of increasing INIs and decreasing HF peak-frequencies are in line with global trends of decreasing frequencies (Leroy et al., 2018; Malige et al., 2020; McDonald et al., 2009; Weirathmueller et al., 2017) and increasing inter unit intervals (Jolliffe et al., 2019; Malige et al., 2020; Morano et al., 2012; Širović et al., 2017; Weirathmueller et al., 2017) described not only in fin whales but also in blue whales. These common directional song changes require a global explanation applicable to both species.

While cultural or genetic drift drive song changes by chance, cultural, natural and sexual selection favour those changes that confer advantages to singers in response to external factors (e.g., environment, animal density and female preferences) and can cause population-wide shifts in the frequency and temporal properties of songs (Podos et al., 2004). The best illustration of cultural selection is the acoustic adaptation hypotheses, which states that there is a selection for optimal sound transmission (Ey and Fischer, 2009). For example, bird song frequencies and timings can change in response to changes in anthropogenic noise (Job et al., 2016; Luther and Baptista, 2010; Parks et al., 2007; Williams et al., 2013). The increased levels of low-frequency shipping noise (Andrew et al., 2002; McDonald et al., 2006a) have been postulated as potential drivers of the decreasing frequencies of blue whale songs but was discarded since a change of few Hz was not sufficient to counteract noise (McDonald et al., 2009). Moreover, to effectively avoid masking from shipping, blue whales should increase their tonal frequencies, as described for several bird species (Luther and Baptista, 2010), belugas (*Delphinapterus leucas*) (Lesage et al., 1999) and right whales (*Eubalaena glacialis*) (Parks et al., 2009). Finally, some studies report a lack of relationship between noise levels and decreasing frequencies (Miksis-Olds et al., 2018) and trends in noise levels are not the same worldwide with even decreasing trends in some parts of the Indian Ocean (Leroy et al., 2018).

Alternatively, changes in sound propagation conditions may be causing changes in fin and blue whale song frequencies and tempos. Most acoustically active species are able to adapt their signals to optimize communication dependent on the environment (Bradbury and Vehrencamp, 1998). For example, bird populations adapt their song characteristics in forest versus open-country environments to overcome propagation challenges (Boncoraglio and Saino, 2007). Similarly, changes in water sound propagation conditions caused by global warming (increased ocean temperatures and acidity) could potentially drive fin and blue whale song changes. While some authors argue that changes are too small (0.02%) to account for the observed decrease in blue whale song frequencies (20%)(McDonald et al., 2009), others state that these changes may indeed reflect the progressive ocean acidification (Leroy et al., 2018) that increases propagation ranges for low-frequency sounds (<200 Hz) (Ilyina et al., 2010). This phenomena could also explain the increase in inter-unit intervals reported here and elsewhere for fin (Širović et al., 2017; Weirathmueller et al., 2017) and blue whale songs (Malige et al., 2020). Improved sound propagation conditions may decrease repetition rates because songs travel faster and animals do not need to call as often to be heard. We ignore to what extent fin and blue whales are able to perceive small changes in sound propagation conditions but, for such widely dispersed and nomadic species, attracting the female may be the major task for a singing male. In fact, songs seem specially adapted for long-range communication (Payne and Webb, 1971), thus it is conceivable that even small changes in water characteristics may have an effect on fin and blue whale songs.

Sexual selection postulates that song variants that are more effective in mate competition or attraction are retained over evolutionary time, and that female preferences evolve together with male display traits (Andersson, 1994). Evidence from different taxa suggests that bigger males can sing lower pitch songs (Gillooly and Ophir, 2010; Hall et al., 2013; Hoskin et al., 2009) and that females prefer larger males (Searcy and Andersson, 1986). If this also applies to fin and blue whales, sexual selection may explain the song frequency shift observed in these species. However, the rate of change of blue whale song frequencies seem too fast for standard genetic sexual selection and the conformism in blue whale frequencies discards a variation-based selection, where singing blue whales may adjust their own frequencies when seeing others singing lower frequencies being more successful (Whitehead and Rendell, 2015).

An increase in post-whaling population abundance could also drive a decrease in song frequencies, based on the assumption that lower amplitudes imply lower frequencies (McDonald et al., 2009). If whales can acoustically sense changes in population densities, an increase in the number of singing males would, on one side, increase the intensity of the sexual selection towards lower frequencies, and on the other, decrease the intensity of selection towards long-distance communications allowing males to calling quietly (i.e., lower amplitudes). Authors calculate the theoretic change that densities would cause to song source levels and coincided with real data. This may also explain the observed increase in inter-unit intervals. Jolliffe et al. (2019) attributes the increase in pygmy blue whale song repetition interval to a higher abundance of animals in the area that cause a reduction in singing frequency. Birds reduce song interference by other singers by using longer inter-song pauses and singing shorter songs in species rich habitats (Sorjonen, 1986). Overall, fin whales have increased in the North Atlantic possibly due to recovering from past whaling and environmental changes (Víkingsson et al., 2015) and this may be a plausible hypotheses to explain the fin whale song changes reported here. However, the link between song frequency and intensity is still uncertain. In the last few decades, blue whales from different regions have either increased (Gavrilov et al., 2012) or stabilized their source levels (Miksis-Olds et al., 2018) and bowhead whale calls minimum frequency has decreased while source levels have remained stable (Thode et al., 2017).

Whatever is the cause of these fin and blue whale song variations, all individuals in the population conform to the same song characteristics (frequencies and INIs) at any one time. Cultural song conformity is a social learning strategy, described in birds and mammals, where individuals are more likely to share song variants with nearby individuals than with more distant ones (Morganand and Laland, 2012). Some authors suggest that it may be advantageous for blue whales, and also for fin whales, in a population to sing using the same frequencies because it may facilitate male singers to be localised by females using the Doppler effect (Hoffman et al., 2010). This means that, a female could know if she is approaching or going away from a male over large distances by detecting differences in received frequencies, which is only possible if all males use the same singing frequencies.

This study also documents different frequency trends for two fin whale song notes, with no trend for the 20-Hz note and a decreasing trend for the HF component. These results can be comparable to the differential changing rates found in frequencies of two song units of the Sri Lankan pygmy blue whale song, which authors attribute to the unit's different functions (Miksis-Olds et al., 2018). In some bird species, parts of the same song inform about species or individual identification while others encode information on individual characteristics or location of the singer (Marler, 1957; Williams et al., 2013). In fin whales, the 20-Hz note has remained unchanged over 50 years (Watkins et al., 1987) and is used by all known fin whale populations (Leroy et al., 2018; Shabangu et al., 2017; Thompson et al., 1992; Watkins et al., 1987) while frequencies of the HF component vary geographically (Hatch and Clark, 2004; Širović et al., 2004). Perhaps, the 20-Hz note informs about species identification and is under a strong stabilizing selective pressure to remain unchanged over time while the HF component is not.

Song evolution often does not respond to single pressures but likely results from the complex interplay between drift, selective pressures and vocal constraints (Ey and Fischer, 2009; Mahler and Gil, 2009; Podos et al., 2004). The functional mechanisms of fin whale songs (e.g., female attraction and male-male competition mechanisms) remain unknown which makes debates on sources of song variation more speculative and based on comparative analysis with other taxa. More research is needed to firstly understand the link between fin whale song structure and function to then infer into the causes of their variation.

4.5 Conclusion

The rapid and complete replacement of song INIs and subsequent conformism shown here for a wide area of the North Atlantic resembles cultural revolutions described for birds and humpback whale songs (Garland et al., 2011; Logue and Leca, 2020; Noad et al., 2000; Otter et al., 2020) and suggest that fin whale songs may also be culturally transmitted. The gradual change in fin whale song properties may be the result of cultural evolution driven by different interacting selecting pressures such as environment, animal density and female preferences. Overall, this study adds further evidence to the great plasticity in fin whale song, which may suggest the ability of this species to respond to different selective pressures. However, if pressure driving song changes surpasses the ability of the species to adapt or compensate (e.g., anthropogenic noise), then song function may be compromised. For example, if the frequency decrease of already very low-frequency songs continues, it could reach the physiological limit of sound production in fin and blue whales. Studies on long-term song variations within and across populations in relation to physical or biotic factors may provide clues into the selective pressures driving song evolution and help predicting the effects of anthropogenic habitat degradation.

Annex IV. Supplementary information

Chapter 5

Underwater ambient noise in a baleen whale migratory habitat off the Azores[4]

Abstract

Assessment of underwater noise is of particular interest given the increase in noise-generating human activities and the potential negative effects on marine mammals which depend on sound for many vital processes. The Azores archipelago is an important migratory and feeding habitat for blue, fin and sei whales en route to summering grounds in northern Atlantic waters. High levels of low frequency noise in this area could displace whales or interfere with foraging behavior, impacting energy intake during a critical stage of their annual cycle. In this study, bottom-mounted Ecological Acoustic Recorders were deployed at three Azorean seamounts (Condor, Açores, and Gigante) to measure temporal variations in background noise levels and ship noise in the 18–1,000 Hz frequency band, used by baleen whales to emit and receive sounds. Monthly average noise levels ranged from 90.3 dB re 1 µPa (Açores seamount) to 103.1 dB re 1 µPa (Condor seamount) and local ship noise was present up to 13% of the recording time in Condor. At this location, average contribution of local boat noise to background noise levels is almost 10 dB higher than wind contribution, which might temporally affect detection ranges for baleen whale calls and make communication difficult at long ranges. Given the low time percentage with noise levels above 120 dB re 1 µPa found here (3.3% at Condor), we would expect limited behavioral responses to ships from baleen whales. Sound pressure levels measured in the Azores are lower than those reported for the Mediterranean basin and the Strait of Gibraltar. However, the currently unknown effects of baleen whale vocalization masking and the increasing presence of boats at the monitored sites underline the need for continuous monitoring to understand any long-term impacts on whales.

---

[4] Romagosa, M., Cascão, I., Merchant, N. D., Lammers, M. O., Giacomello, E., Marques, T. A. and Silva, M. A. (2017). Underwater ambient noise in a baleen whale migratory habitat off the Azores. *Frontiers in Marine* Science. **4**, 109. https://doi.org/10.3389/fmars.2017.00109

5.1 Introduction

Marine acoustic pollution has become an issue of special concern over recent decades. Measurements from the North Atlantic show that average noise at 50 Hz has increased about 5.5 dB per decade from 1950 to 1970 (Ross, 2005) and about 2.8 dB from 1966 to 2013 (Širović et al., 2016). A similar trend has been found in the North Pacific with noise increasing at an average rate of 2.5–3 dB per decade at 30–50 Hz since the 1960s (Andrew et al., 2002; Chapman and Price, 2011; McDonald et al., 2006a). This rise has been mainly due to shipping and together with seismic surveys has become one of the principal sources of ambient noise below ~1 kHz (Andrew et al., 2002; Hildebrand, 2009; Klinck et al., 2012; McDonald et al., 2006a; Nieukirk et al., 2012; Wenz, 1962). Shipping noise contribution can be at very low frequencies below 200 Hz (Ross, 1976), when is given by the summation of many distant large ships scattered throughout an ocean basin. When a ship passes nearby, however, it increases temporarily and substantially noise levels at that location at much greater frequencies since propagation removes the high frequency portion of the spectrum (Hildebrand, 2009; Wenz, 1962).

Baleen whales emit sounds with fundamental frequencies below 1 kHz (Richardson et al., 1995b) which overlap with peak power in ship noise (Hildebrand, 2009; Wenz, 1962). The production and reception of baleen whale vocalisations have been associated to vital biological processes such as feeding, mating, group cohesion and social interaction (Dudzinski, K.A., Thomas, J.A. and Douaze, 2009; Payne and Webb, 1971) which make these animals especially vulnerable to this source. Noise in the environment can limit the range for successful detection of signals through masking, thus significantly affecting the acoustic communication in large whales (Erbe et al., 2015; Hatch et al., 2012; Ponce et al., 2012; Samaran et al., 2010). Blue whales have shown increased source levels of their D calls (<100 Hz) as well as increased multiple callers when ships are nearby (McKenna, 2011; Melcón et al., 2012) and North Atlantic right whales call louder with increasing background noise levels (Parks et al., 2010). Following the mounting evidence of noise impact on marine mammals, the U.S. National Research Council (NRC) established the 120 dB re 1 μPa as the noise level above which marine mammals might be adversely affected by sound (NRC, 2005). Vessel avoidance behavior has been documented for some species of baleen whales at received sound pressure levels (SPLs) of 92.8–148.6 dB re 1 μPa, but especially above 120 dB re 1 μPa

(Richardson et al., 1995; Richardson and Würsig, 1997; Southall et al., 2007). In addition, in the presence of shipping noise, North Atlantic right whales have been shown to exhibit increased stress levels (Rolland et al., 2012) and humpback whales changed their foraging activity (Blair et al., 2016).

In the long term, behavioral disturbance and physiological stress caused by noise could lead to population-level effects. Changes in vocal behavior in response to noise during feeding, socializing (Di Iorio and Clark, 2010) and breeding (Miller et al., 2000) may have energetic costs, and potential avoidance of noisy foraging/breeding/resting areas (Castellote et al., 2012a) could reduce energy intake and disrupt behavior at key life stages. These effects could have a negative impact at a population level by affecting growth, survival and reproductive success of individual animals. However, determining a causal link between noise exposure through effects on individual vital rates to population consequences is extremely difficult and further studies are needed and models developed to answer these questions.

Although research on noise levels and the impacts on marine life have been increasing over recent years (Williams et al., 2015), most studies have focused on whales' feeding grounds and coastal continental areas (Dunlop, 2016; Parks et al., 2010) with fewer studies on open ocean waters (Bittencourt et al., 2016; Dziak et al., 2015). In the central Atlantic area, only one measurement has been made north of the Azores archipelago (Castellote et al., 2012a) and only one study has been published documenting airgun seismic noise in mid-Atlantic waters (Nieukirk et al., 2012).

The region around the Azores is a migratory habitat for several species of baleen whales. Blue and fin whales interrupt their journeys to northern latitudes to feed in the archipelago every spring and early summer (Silva et al., 2014, 2013). Sei whales travel through the archipelago in spring on their way up to the Labrador Sea but they do not seem to forage routinely in the area (Prieto et al., 2014). Moreover, preliminary acoustic data suggest the presence of fin whale (Silva et al., 2011) and blue whale calls also during the winter (Chapter 2). This finding is in accordance with a study documenting winter calling by fin and blue whales around the mid-Atlantic ridge, south of the Azores (Nieukirk et al., 2004). Therefore, the region around the Azores may be an important habitat for these species in the central North Atlantic and noise pollution should be carefully monitored to inform effective management of human activities in these waters.

This work investigates low-frequency underwater noise levels at an important baleen whale habitat in the North Atlantic, the Azores archipelago by: (a) investigating the spatial and temporal variability within the 18–1,000 Hz frequency band (calling range of most baleen whales), (b) determining the contribution of local ship and wind driven noise (c) describing noise levels above 120 dB re 1 µPa, reported to cause behavioral responses to baleen whales (NRC, 2005) and (d) discuss potential effects of these results on baleen whales in the Azores. In addition, we investigated variability of noise levels in one-third octave bands centered at 63 and 125 Hz, which have been specifically proposed by EU Marine Strategy Framework Directive (MSFD) as a measure of noise from distant shipping (2008/56/EC, European Commission 2008).

5.2 Material and methods

5.2.1 Deployment locations

The three deployment locations are seamounts and were chosen for their distinct importance for baleen whales and their differences in anthropogenic usage. Condor seamount, located 17 km south-west of Faial Island, became a scientific observatory in 2008 when local authorities, researchers, fisherman and other stakeholders agreed on designating it as a protected area for scientific research. Since 2010, demersal fisheries are banned, tuna and big game fishing are permitted upon prior authorisation and scientific and recreational activities (such as shark diving) are allowed (Giacomello et al., 2013; Ressurreição and Giacomello, 2013). Açores seamount, located 40 km south-west off Faial Island, is frequented by small commercial fishing and recreational activities, although to a much lesser extent than Condor (Fig. 5.1). Gigante seamount, located 100 km west-north-west of Faial Island along the Mid-Atlantic Ridge, is used by commercial fisheries and lies close to major marine traffic lanes.

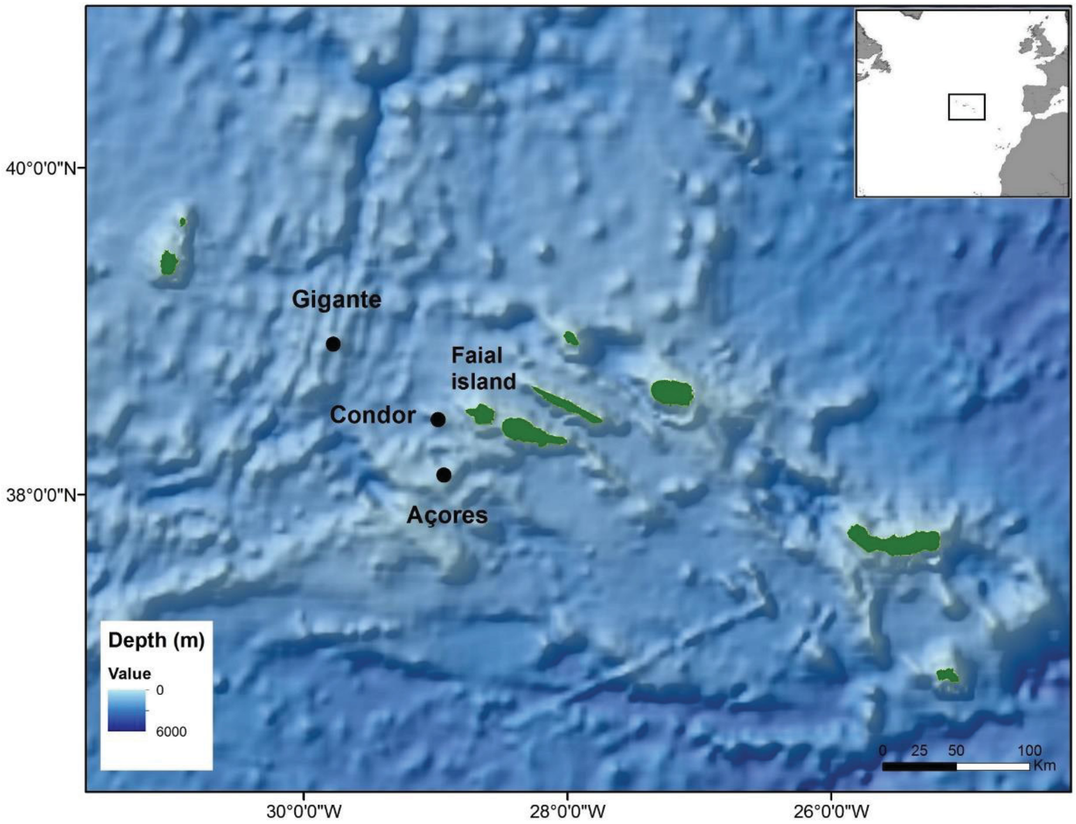


Figure 5.1. Ecological Acoustic Recorders (EARs) deployment locations in the Azores archipelago (black dots).

The areas around Condor and Açores seamounts are frequently used by blue and fin whales for foraging (Silva et al., 2014, 2013) and by sei whales for migrating (Prieto et al., 2014). Gigante seamount is close to a transit area for the three species, and occasional feeding may also occur there. Other species of baleen whales may also occasionally occur in these areas (Silva et al., 2014).

5.2.2 Acoustic data

Bottom-mounted Ecological Acoustic Recorders (EARs; Lammers et al., 2008) were deployed at the three seamounts at an approximate depth of 190 m. The EAR consists of a sensor Technology SQ26-01 hydrophone with a response sensitivity of −193.14/−194.17 dB re 1 V/μPa (varying between deployments) for Condor and Açores and −193.64/−193.14 dB for Gigante and a flat frequency response (±1.5 dB) from 18 Hz to 28 kHz. A Burr-Brown ADS8344 A/D converter was used with a zero-to-peak voltage of 1.25. A total system gain of 47.5 dB re

1 μPa was used during all recordings resulting in a noise floor of 89 dB re 1 μPa (18–1,000 Hz), 65.5 dB re 1 μPa (63 Hz octave band) and 66.7 dB re 1 μPa (125 Hz octave band). Dynamic range of the instrument was of 57 dB re 1 μPa reaching saturation at 146 dB re 1 μPa.

EARs recorded from March 2008 to October 2012 at Condor, from November 2011 to October 2012 at Açores and from April 2008 to February 2011 at Gigante with several gaps due to equipment failure or maintenance duties. Sampling rates and duty cycles were constrained by battery life and disk space limitations, given programmed deployment durations (Table 5.1).

Table 5.1. Summary of acoustic data used in this work including recording dates, deployment depth, sampling rate, duty cycle and total recording time.

Location	Dates of recording	Depth (m)	Sampling rate (Hz)	Minutes on/every x min	Total recording time (hours)
Condor	Mar 2008 –May 2008	189	50000	0.5/10	88.6
	Aug 2008 – Dec 2008	190	50000	1.5/15	326.5
	Jul 2009 – Oct 2009	190	50000	1.5/15	295.2
	Apr 2010 – Feb 2011	190	50000	1.5/15	746.2
	Nov 2011 – Feb 2012	195	2000	60/138	1361
	Jun 2012 – Oct 2012	195	2000	60/210	948
Total					**376.5**
Açores	Nov 2011 – Mar 2012	190	2000	60/210	830
	May 2012 – Oct 2012	190	2000	60/210	1262
Total					**2092**
Gigante	Apr 2008 – May 2008	175	50000	0.5/10	70.8
	Aug 2008 – Nov 2008	190	50000	1.5/15	279.6
	Jul 2010 – Aug 2010	190	50000	1.5/15	135.6
	Oct 2010 – Feb 2011	190	50000	1.5/15	343
Total					**829**

5.2.3 Noise measurements

Recordings with sample rates of 50 kHz were re-sampled to 2 kHz using Adobe Audition 3.0 software (Adobe Systems Incorporated, CA, USA) to standardize all acoustic data from 18 to

1,000 Hz, which is the bandwidth dominated by anthropogenic noise (Wenz, 1962) and overlaps the vocalizing range of balaenopterids. Self-system tonal noise within the frequency band of interest was identified only in recordings with sampling rates of 2,000 Hz which correspond to deployments at Condor and Açores from 2011 and 2012. 1-Hz Spectrogram Power Density (SPD) plots were made for each month to precisely identify which frequency bins were affected so they could be removed before computing broadband SPLs. Given that all self-system noise identified was highly tonal, removing these few frequency bins is likely to have a negligible effect on averaged broadband SPLs and on the characterization of shipping noise, which spreads across a wide range of frequencies. Moreover, self-system noise removed was found in frequencies well above the one-third octave bands analyzed in this study (63 and 125 Hz). From the SPD plots we can say that data were not clipped since there is no flat line of data points at high noise levels clustered at the limit value of 146 dB where the system saturates (see Figure 5.4 from results section).

Each month of recordings was grouped and concatenated to form a single file to be analyzed with Matlab code written by Merchant et al. (2015). The time-series of every signal was divided into *m 1-s* segments of consecutive samples overlapping in time (50% overlap). Each segment was then multiplied by a Hann window and transformed to the frequency domain via the Discrete Fourier Transform (DFT). Spectra were then averaged to a 90-s resolution via the standard Welch method (Welch, 1967). The power spectrum (P) was then computed from the DFT, which for the mth segment, of signal X at frequency f and for N number of samples in each segment is given by:

$$P^{(m)}(f) = \left|\frac{X^{m}(f)}{N}\right|^{2}$$

For each deployment, calibration data from the EAR, including the hydrophone sensitivity (Mh), system gain (G) and the zero-to-peak voltage of the analog-to-digital converter (VADC), were used to calculate a correction factor (S(f)) computed by:

$$S(f) = M_h + G(f) + 20log_{10}\left(\frac{1}{V_{ADC}}\right) + 20log_{10}(2^{N_{bit}-1})$$

where N_{bit} is the bit-depth of the digital signal (16 bits). S(f) was then used to obtain SPLs in the bandwidth from 18 to 1000 Hz by:

$$SPL_{(m)} = 10log_{10}\left(\frac{1}{P_{ref}^2}\sum_{f'=f_{low}}^{f'=f_{high}}\frac{P^{(m)}(f')}{B}\right) - S$$

where p_{ref} is the reference pressure of 1 μPa for underwater measurements, f_{low} and f_{high} are the lower and upper bounds of the frequency range under consideration and B is the noise power bandwidth of the window function, which corrects for the energy added through spectral leakage.

5.2.4 Noise data analysis

The effect of different duty cycles on the calculation of monthly average background noise levels was investigated by concatenating a full month of data (May 2008 from Condor), treating it as a continuous recording, and then subsampling it according to the different duty cycles used in this study (Table 5.1). To test for statistical differences in SPLs between different duty cycles, a first order autoregressive model was fitted to the SPL time series of mean SPL per sample for each duty cycle. Then, based on the estimated parameters and corresponding standard errors, 95% confidence intervals for each duty cycle mean SPLs were derived, assuming a Gaussian distribution for the parameter estimates. Number of samples (N) was the number of files resulting from the different duty cycles applied.

To investigate differences in noise levels between locations, only Condor's data from 2011 and 2012 were analyzed to compare with time series of similar length from Açores and Gigante. For every location, the arithmetic mean (AM) over the period considered was calculated. For N samples $P^2 rms$, AM is given by:

$$AM = 10log_{10}\left(\frac{\frac{1}{N}\sum_{i=1}^{N}p_{rms,i}^2}{p_{ref}^2}\right)$$

where $p_{rms,i}^2$ is the *i*th value of the mean squared pressure given by:

$$p_{rms}^2 = \sum_{f'=f_{low}}^{f'=f_{high}}\frac{P^{(m)}(f')}{B}$$

To test for statistical differences in SPLs between locations, a first order autoregressive model was fitted to the SPL time series of each location (containing daily averaged SPLs). Then, based on the estimated parameters and corresponding standard errors, confidence intervals (95%CI) for each location mean SPLs were derived, assuming a Gaussian distribution for the parameter estimates. Number of samples (N) was the number of days.

Variability in noise levels for every location was analyzed using the coefficient of variation (CV), which allows comparison between datasets with different means.

Within each location, temporal variability of noise levels was explored by calculating hourly and monthly averaged, median and 5th, 75th, and 95th percentiles SPLs for the frequency band of 18–1,000 Hz. Also, hourly and monthly averaged one-third octave bands centered in 63 and 125 Hz were calculated to specifically measure the contribution of distant ship noise to ambient noise as suggested by the MSFD (2008/56/EC, European Commission 2008).

Seasons were defined according to the location (North-East Atlantic) as follows: Spring: March–May, Summer: June–August, Autumn: September–November and Winter: December–February.

To allow for comparisons, average SPLs were calculated for the three noisiest months in Condor (July-September, 2010), Açores (May-July, 2011) and Gigante (May–September, 2008) in the frequency band of 10–585 Hz to be compared to SPLs found in the Mediterranean by (Castellote et al., 2012a). Also, median levels in the frequency band of 10–25,000 Hz were measured in Condor (July-September, 2010) to compare it with levels found in another oceanic archipelago by Bittencourt et al. (2016).

5.2.5 Ship noise analysis

In the absence of an operative antenna in the area for receiving information from Automatic Information System (AIS) installed in ships during the recording period, a methodology was used to study the contribution of local ship noise to general background noise levels. Using the broadband (18–1,000 Hz) noise background levels for every recording, an Adaptive Threshold Level (ATL; Merchant et al., 2012b) was obtained to identify local intermittent ship noise. The ATL was calculated by computing the minimum SPL in a certain period of time (W) and summing a tolerance above this minimum, a threshold ceiling (C) in dB re 1 μPa:

$$ATL(t) = \min\ SPL(t)_{t-\frac{w}{2}}^{t+\frac{W}{2}} + C$$

Due to differences in background noise levels and duty cycles in this study compared with Merchant et al. (2012b), two different periods of time (W) (1 and 7 hours of recordings) and 4 different threshold ceilings (C) (from 4, 6, 8, and to 12 dB) were tested. Firstly, an appropriate time period, W, was selected by visually inspecting plots of SPL values and thresholds and selecting the one that best discriminated wind-wave driven noise from intermittent noise. Once W had been specified, results from the ATL applying different values of C were compared to visually confirmed boats in the spectrogram for one chosen month per location (July 2012 for Condor, May 2012 for Açores and July 2010 for Gigante). Those parameters that resulted in the best compromise between visually confirmed boats detected by the ATL (true positives) and detections by the ATL not corresponding to boats (false positives) were selected.

Once W and C were set, ATL was calculated for every month and location. Time with levels above the threshold was summed and divided by the total recording time to obtain the Percentage of Time with noise levels Above the Threshold Level (PT-ATL). The PT-ATL was then used to investigate spatial variations in boat presence using a Kruskal-Wallis ANOVA and a post-hoc Dunn test for multiple comparisons.

To test the efficiency of the methodology at detecting the presence of vessels, a comparison was made between monthly PT-ATLs and the number of days per month with boat presence in Condor. Data on boat presence were obtained from logbooks that contained information on the number of boats and type of activity conducted at the Condor seamount area per day from 2008 to 2012. The type of boats' activities recorded were: recreational activities, such as big-game fishing and shark diving, with data logged by the operators themselves; scientific research, based on information provided by scientists conducting research at Condor; and tuna fishing, based on data recorded by onboard observers under the Azorean Fisheries Observer Programme (POPA).

5.2.6 Contribution of wind-wave and vessel-driven noise

An analysis of wind-wave driven noise and intermittent ship noise was implemented to compare the relative contribution of natural and anthropogenic sources to background noise levels in this region. Windiest months were selected for the three locations and daily averaged SPLs and wind speeds calculated. Days with maximum and minimum SPLs coincided with maximum and minimum wind speeds. For every month, averaged SPLs were calculated from 10 min sound files free of ship noise (visually inspected spectrograms) selected from 2 days, one with maximum and one with minimum wind speed. Similarly, for all months and for all locations, average SPLs were calculated for periods of time above the threshold and compared to those with minimum wind conditions. Differences between quietest average and noisiest average were then calculated for the wind and for the ship contribution. Daily averaged wind speeds (km/s) were obtained from Weather Underground historical data (www.wunderground.com) for each location.

5.2.7 Noise levels above 120 dB re 1 µPa

Since baleen whales have been shown to avoid vessels at noise levels above 120 dB re 1 μPa (Richardson et al., 1995b; Richardson and Würsig, 1997; Southall et al., 2007a), percentage of time with SPL above this level was also calculated for every month of study. To do so, broadband average SPL for every month and location were used to calculate the amount of time with noise levels above 120 dB re 1 μPa and divide that by total recording time.

5.3 Results

5.3.1 Ship noise analysis

The only anthropogenic noise source found in the recordings was ship noise, which had the maximum energy above 100 Hz for boats with higher noise levels, or in the bandwidth of 10–100 Hz for boats with lower noise levels.

The ATL only detected local boat noise that increased noise levels significantly and intermittently (Fig. 5.2). The most adequate time period (W) to calculate minimum SPLs was 1 h of recordings for both duty cycles as this discriminated well between wind-driven and intermittent noise. The best compromise considering a minimum of 90% of visually confirmed boats in the spectrogram detected by the ATL, and a maximum of 5% of false positives was obtained using a threshold ceiling C = 4 dB for duty cycle of 3,600 s every 12,600 s, and C = 8 dB for the 90 and 30 s duty cycle (Table 5.2). False positives were mainly caused by loud biological sounds consisting of low frequency clicks produced by delphinids and sperm whales.

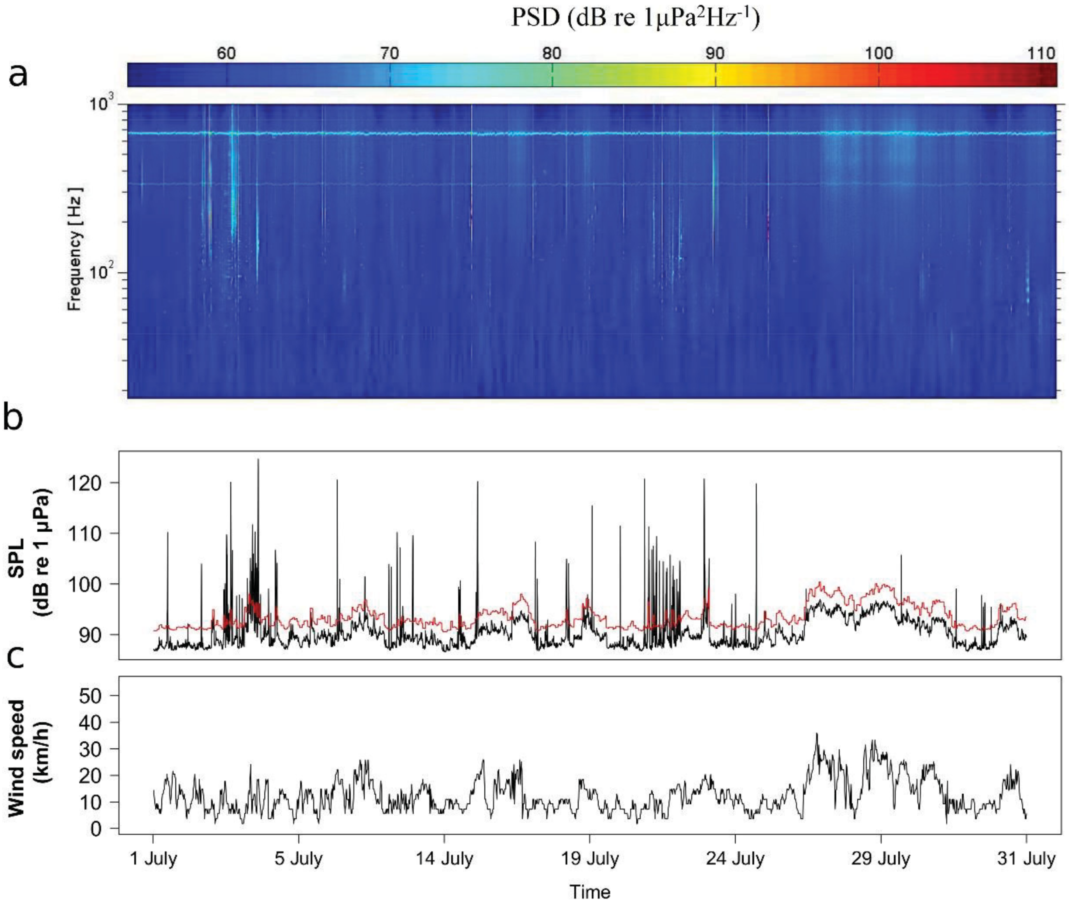


Figure 5.2. Example of a time-series analysis of intermittent noise for July 2012 at Condor seamount. (A) Spectrogram composed of Power Spectral Densities (PSDs) with 1-s time segments; (B) Broadband (18–1,000 Hz) SPLs measurements and threshold (red line) for boat detection and; (C) 30-min interval wind speed measured in Castelo Branco, Faial Island.

Table 5.2. Percentages of True Positives (TP), False Positives (FP) and False Negatives (FN) resulting from the comparison between boat detections applying the ATL function with different threshold ceilings (C) and visually confirmed boats in the spectrogram. Results are for July 2012 in Condor, May 2012 in Açores and July 2010 in Gigante.

Threshold ceilings (dB)	**CONDOR**			**AÇORES**			**GIGANTE**		
	TP	**FP**	**FN**	**TP**	**FP**	**FN**	**TP**	**FP**	**FN**
4	98.3	11.1	1.6	91.3	4.6	8.7	97.2	8.7	2.8
6	95.9	8.5	4.1	82.6	3.4	17.4	95.3	5.6	4.7
8	90.9	4.5	9.1	69.6	2.3	30.4	90.6	4	9.4
10	81	2.8	19	56.5	2.2	43.5	72.6	4.5	27.4
12	74.4	3.1	25.6	45.6	0	54.4	58.5	4.5	41.5

Logbook data from Condor was compared to the acoustic recordings resulting in 19 months of simultaneous data. There was a weak correlation ($R2 = 0.354$, $p < 0.05$, $n = 19$) between boat presence from logbooks and PT-ATL from 2008 to 2012, mainly because the high peak in PT-ATL in June was not matched by a higher presence of boats (Figure 5.3). Removing June 2012 from the analysis resulted in a stronger correlation ($R2 = 0.582$, $p < 0.001$, $n = 18$). Recordings from this month were visually inspected and boat noise detected by the ATL was confirmed to be mainly present during daylight hours.

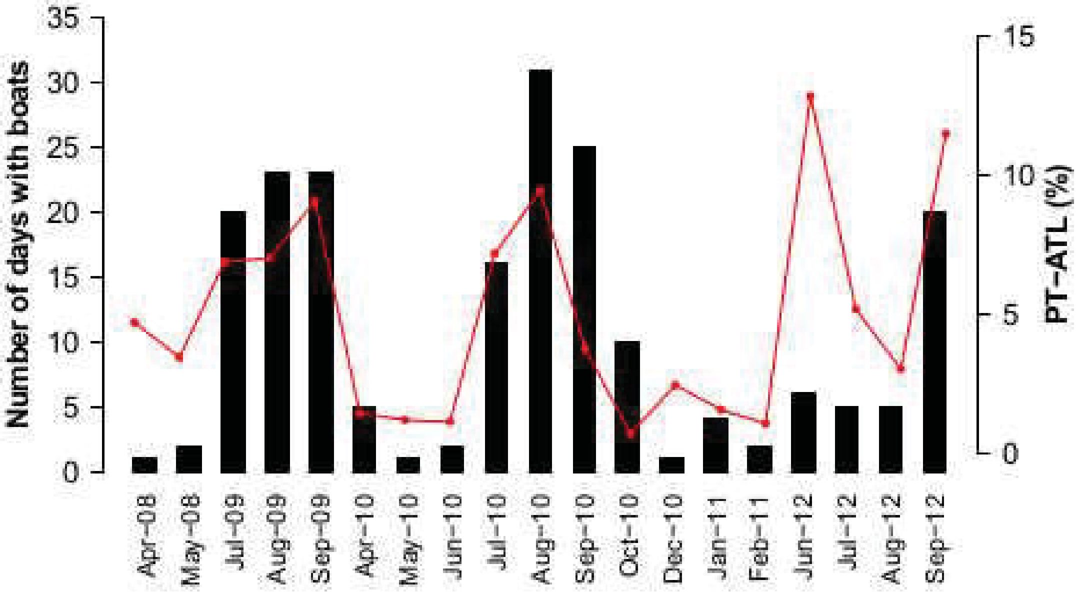


Figure 5.3. Number of days with boats registered in logbooks (bars) and PT-ATL from the acoustic data (red line).

5.3.2 Spatial variability in ambient noise levels and peak-generating vessels

The different duty cycles used in this study did not significantly affect the average monthly SPLs. Differences between the assumed "continuous" recording (AM = 91.8, 95%CI = 91.78–91.82) and the different duty cycles were very small (1.5/15: AM = 91.9, 95%CI = 91.72–92.02; 0.5/10: AM = 91.6, 95%CI = 91.45–91.62; 60/138: AM = 91.4, 95%CI = 91.40–91.47; 60/210: AM = 91, 95%CI = 90.99–91.08), as were differences between duty cycles. Therefore, comparison of noise levels between deployments and locations with different duty cycles should remain valid.

The arithmetic mean of SPLs was calculated for the 18–1,000 Hz band for Condor, Açores and Gigante over 9, 11, and 14 months, respectively. Açores had the lowest value (92.9 dB re 1 µPa), followed by Gigante (95.9 dB re 1 µPa), with higher mean SPL in Condor (97.6 dB re 1 µPa). Higher variability was found in Condor (CV = 0.098) followed by Gigante (CV = 0.085) and Açores (CV = 0.071). Median values of noise levels were higher for Condor and Gigante (93.1dB re 1 µPa and 91.6 dB re 1 µPa, respectively) and lower for Açores (90.1 dB re 1 µPa). Averaged noise levels for the 63 and 125 Hz one-third octave bands were also lower in Açores (70.2 dB re 1 µPa and 74.6 dB re 1 µPa, respectively), while the highest levels at the 63 Hz band were found in Gigante (73.6 dB re 1 µPa) and for the 125 Hz band in Condor (79.5 dB re 1 µPa; Table 5.3). There was no overlap in the 95%CI of SPL within the 18–1,000 Hz, the 63 Hz and the 125 Hz one-third octave bands for Condor, Açores and Gigante, suggesting differences in average ambient noise levels between the three locations were highly significant (see Table S5.1 for details on 95%CI values).

Table 5.3. Arithmetic mean (AM) (±SD) and median SPL at broadband levels (18-1000 Hz) and one-third octave bands 63 Hz and 125 Hz, and total PT-ATL for Condor, Açores and Gigante calculated over 9, 11 and 14 months respectively.

Location	**Broadband noise levels (1-1000 Hz)**		**63 Hz**	**125 Hz**	**PT-ATL (%)**
	AM±SD	**Median**	**AM ±SD**	**AM ±SD**	**Total**
Condor	97.6±8.5	93.1	72.4±5.6	79.5±10.2	4.5
Açores	92.9±6.6	90.1	70.2±9.2	74.6±9.8	1.9
Gigante	95.9±8.2	91.6	73.6±12.8	76.0±11	6.0

Differences in average noise levels for the 63 and 125 Hz one-third octave bands are supported by the spectral characteristics of sound for every location. Looking at the noisiest months, we can see that Gigante showed higher levels of noise from ships <100 Hz (Fig. 5.4c) while Condor and Açores had higher ship noise levels >100 Hz (Figs. 5.4a,b).

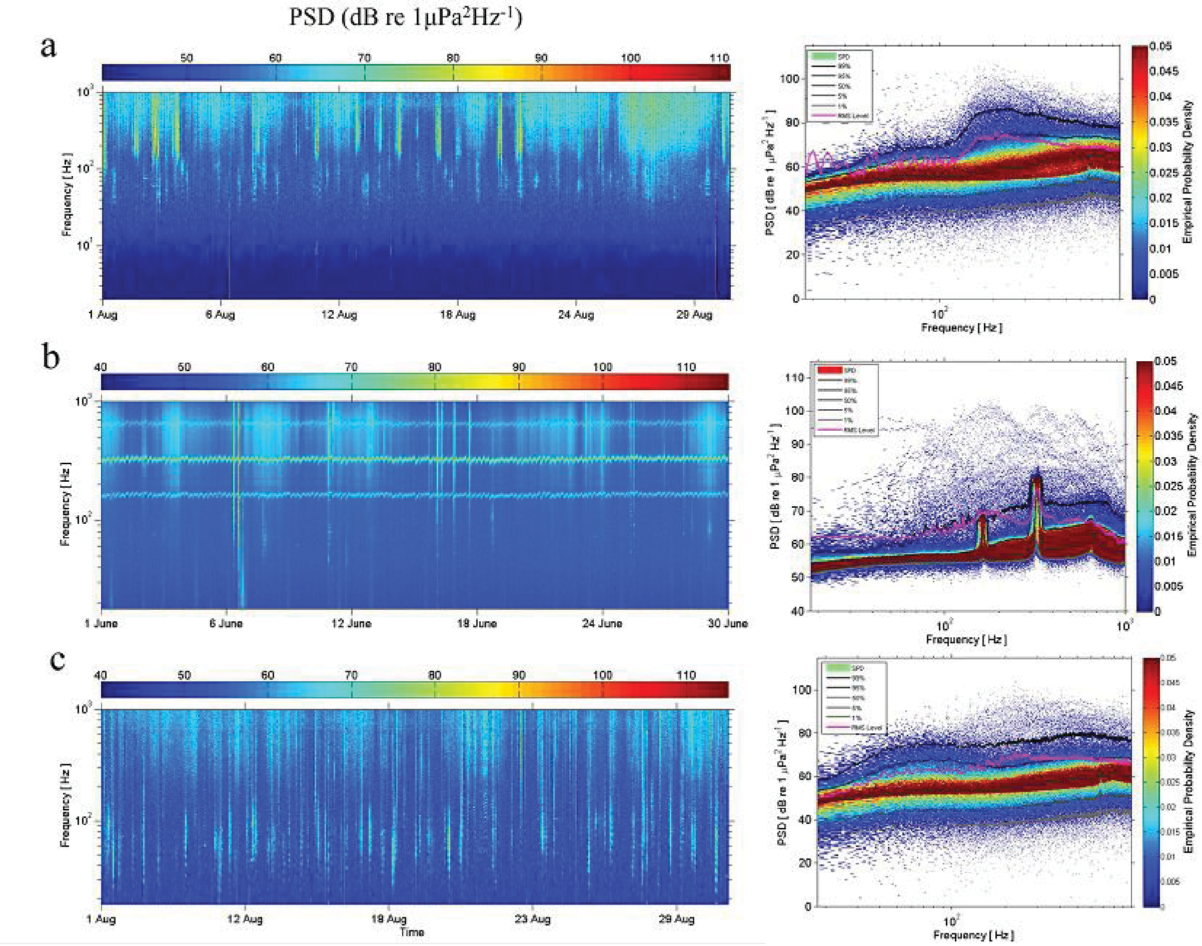


Figure 5.4. Spectrograms composed of PSDs with 1-s time segments (left) and spectral probability densities (SPDs), percentiles and root-mean-square (RMS) level (right) of 1 month of recordings for (a) Condor; (b) Açores; and (c) Gigante.

PT-ATL averaged across the same months showed that Gigante had the highest percentage of boat noise followed by Condor and Açores (Table 5.3). However, Condor showed a much higher variability (CV = 0.97) than Açores (CV = 0.4) and Gigante (CV = 0.3). PT-ATLs differed between locations (Kruskal-Wallis H = 13.806, df = 2, $p < 0.01$) but only differences between Gigante and Açores ($p < 0.001$) and Gigante and Condor ($p < 0.05$) were statistically significant.

5.3.3 Temporal variability in ambient noise levels and peak-generating vessels

In Condor seamount, percentage of time with boats peaked during the summer months (June–August) extending to September in some years (Fig. 5.5d). This is well illustrated by increased broadband and 125 Hz octave band noise levels at these periods (Figs. 5.5a,c). Açores seamount also showed higher PTL-ATL during summer months, especially in June, with another peak seen in November (Fig. 5.6d). These peaks are well reflected in the higher average broadband and 63 and 125 Hz octave band noise levels (Figs. 5.6a,c). In Gigante, values of PTL-ATL tended to be greater in summer months or in September, although differences to other seasons were not as obvious as in Condor and Açores (Fig. 5.6d). In this case, temporal patterns in broadband and one-third octave bands SPLs did not match those of boat time (Figs. 5.6 a,c,d).

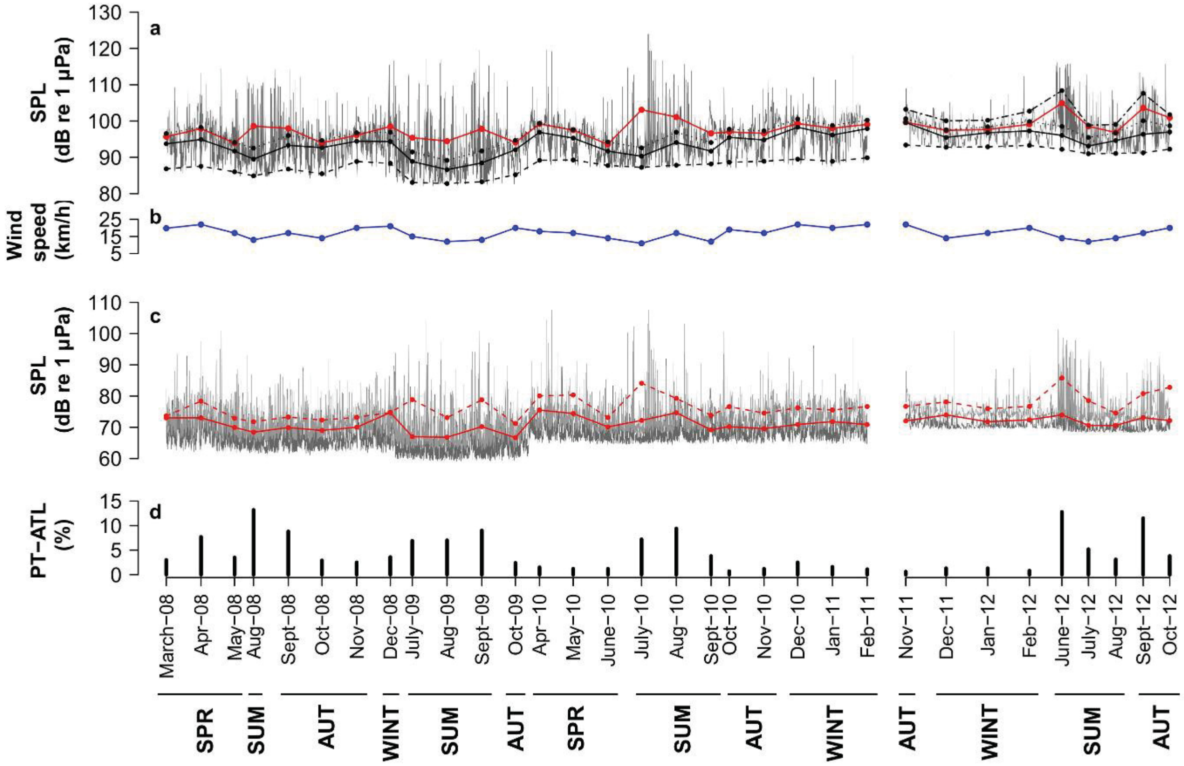


Figure 5.5. Condor seamount: (A) hourly (gray lines) and monthly averages (red lines), medians (black lines) and 5th, 75th, and 95th percentiles (dashed black lines from bottom to top) SPLs in the 18–1,000Hz frequency band. (B) monthly averaged wind speed (blue line). (C) hourly SPLs in the 63Hz (dark gray lines) and 125Hz (light gray lines) one-third octave bands and monthly averages (63Hz: red line and 125 Hz: dashed red line). (D) monthly PT-ATL. Months are grouped in seasons below the x axis. Seasons are described as follows: SPR, Spring (March–May); SUM, Summer (June–August); AUT, Autumn (September–November) and WINT, Winter (December–February).

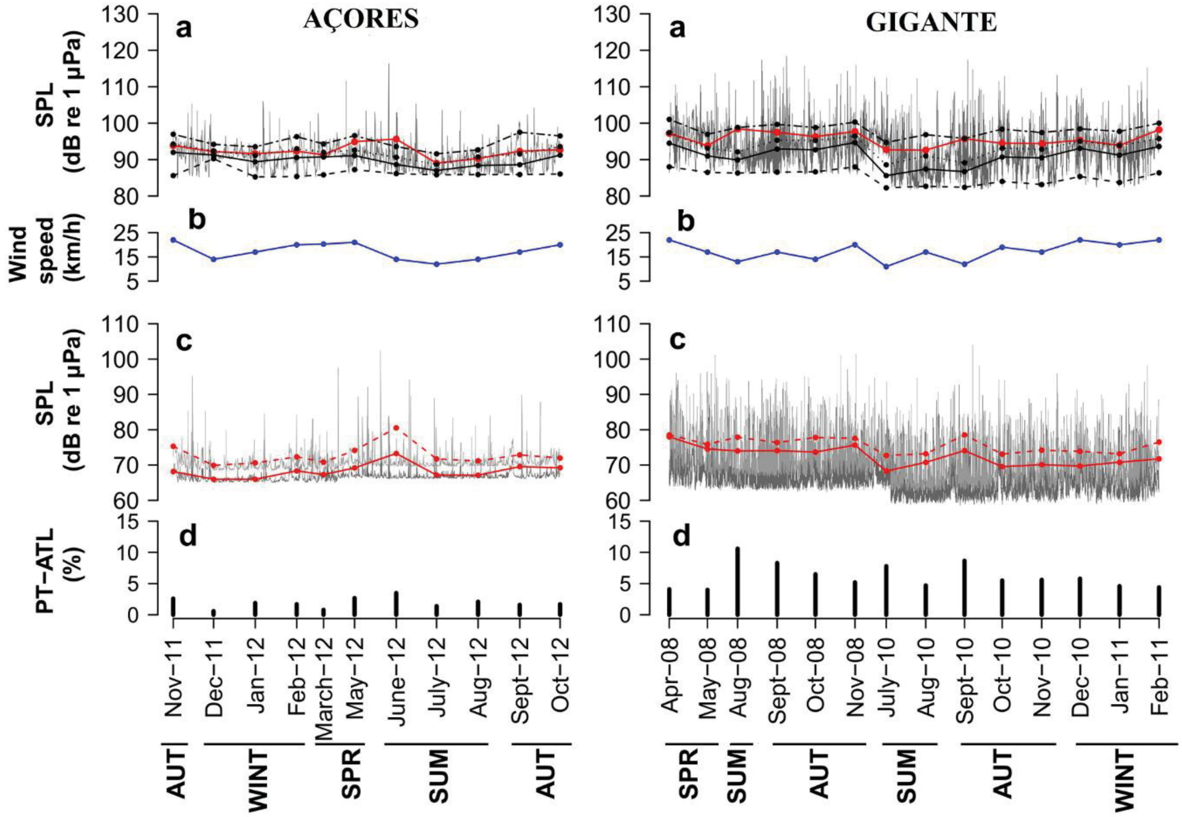


Figure 5.6. Açores and Gigante seamount: (A) hourly (gray lines) and monthly averages (red lines), medians (black lines) and 5th, 75th, and 95th percentiles (dashed black lines from bottom to top) SPLs in the 1–1,000Hz frequency band. (B) monthly averaged wind speed (blue line). (C) hourly SPLs in the 63Hz (light gray lines) and 125Hz (dark gray lines) one-third octave bands and monthly averages (63Hz: red line and 125 Hz: dashed red line). (D) monthly PT-ATL. Months are grouped in seasons below the x axis. Seasons are described as follows: SPR, Spring (March–May); SUM, Summer (June–August); AUT, Autumn (September–November) and WINT, Winter (December–February).

Note that fluctuations in the 75th percentile noise levels are still highly affected by wind-driven noise in all locations (Figs. 5.5b, 5.6b) and only the 95th percentile is affected by the presence of boats in accordance to the low PT-ATL found in all areas (Figs. 5.5d, 5.6d). Average levels (AM) are more affected by brief and high amplitude events such as ships and might not represent the real average of noise data which has a highly skewed distribution. However, average levels are a robust metric that can be used to assess shipping noise if presented in combination with other metrics that identify loud events, such as the PT-ATL used here (Merchant et al., 2012a).

Annual trends in PT-ATL values for Condor averaged within seasons showed a decrease of boats from 2008 to 2010 in spring (Figure 5.7a), an increase between 2008 and 2010 in the summer (Fig. 5.7b), a decrease from 2008 to 2011 and a subsequent increase in 2011 and 2012 in autumn (Fig. 5.7c) and little variation over time in winter (Fig. 5.7d).

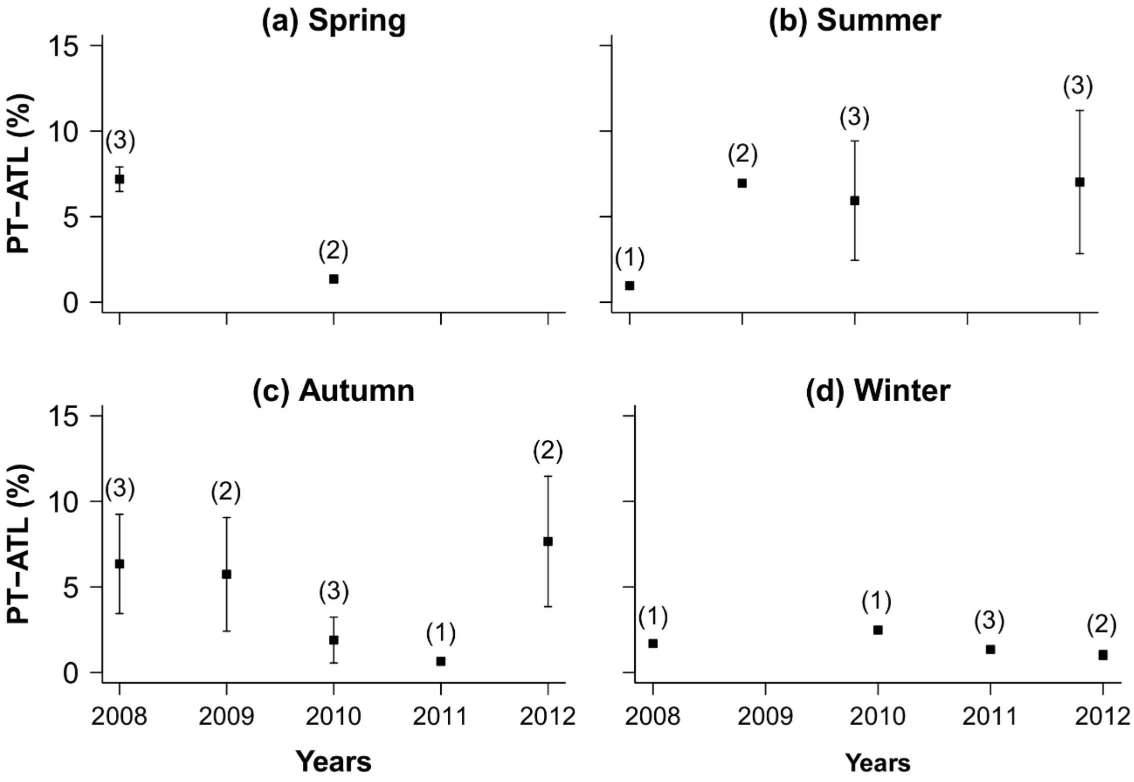


Figure 5.7. Inter-annual variability in averaged seasonal PT-ATL values for Condor seamount and standard deviations (error bars). Numbers in brackets are number of months with data representing each of the following seasons: (A) Spring: March–June; (B) Summer: June–September; (C) Autumn: October–November; (D) Winter: December–February.

5.3.4 Contribution of wind-wave and vessel-driven noise

A strong correlation was found between daily averaged noise levels and wind speed for the windiest months (November) in Condor (R2 = 0.8, $p < 0.001$, n = 30) and Açores (R2 = 0.6, $p < 0.001$, n = 30) and a weak correlation for Gigante (R2 = 0.3, $p < 0.001$, n = 30). Average contribution of wind noise to background noise levels was of 10.8 ± 3 dB in Condor (n = 25), 7.7 ± 2.5 dB in Açores (n = 8) and 11.7 ± 3.4 dB in Gigante (n = 11).

Months with higher boat presence (August 2010 for Condor, June 2012 for Açores and August 2008 for Gigante) showed no or only a weak correlation between daily SPLs and wind speeds (Condor: R2 = 0.11, p = 0.003, n = 31; Açores: R2 = −0.03, p = 0.9, n = 30; Gigante: R2 = 0.06, p = 0.1, n = 26). On average, SPLs for intermittent noise increased background noise levels in 19.3 ± 3.6 dB in Condor (n = 32), 16.2 ± 3 dB in Açores (n = 11) and 18.3 ± 3 dB in Gigante (n = 14) with a maximum value of 29.1 dB for Condor in July of 2010.

5.3.5 Noise levels above 120 dB re 1µPa

Percentage of time with noise levels >120 dB re 1 µPa was higher in Condor with a maximum of 3.3% in July of 2010. In 13 out of 32 months sampled, noise levels were always <120 dB and for the remaining months, time with boats varied from 0.007 to 0.4%, with greater percentages in summer and autumn. In Açores, noise levels >120 dB were recorded only in the noisiest months, May (0.03%) and June (0.07%) of 2012, while in Gigante, values >120 dB were recorded in 2008, with a maximum value of 0.12% in August, and in February 2011.

5.4 Discussion

This work provides the first long-term characterization of low-frequency underwater noise levels at an important baleen whale mid-ocean habitat and discusses potential adverse effects on this cetacean group.

Noise levels at Condor seamount were higher than at Gigante and Açores seamounts and rises in monthly average broadband noise levels were mainly due to the presence of intermittent loud events such as boats. Median noise levels were more affected by wind-driven noise. In the absence of boats or with few boats, median and average levels were similar and wind became a major contributor to background noise.

The ATL methodology developed by Merchant et al. (2012b); to detect intermittent loud noise events attributed to boat presence has been successfully tested and applied in this study. Time period (W) over which minimum SPLs are calculated and threshold ceiling (C) are parameters that need readjustment depending on environmental acoustic characteristics and system duty cycle. We found that increasing C caused a decrease on the percentage of true and false positives but the extent of this variation differed between locations, depending on the acoustic characteristics of the environment. In our case, the same W worked well for all duty cycles but the adequate threshold ceiling was lower for higher duty cycles than for lower duty cycles (Table 5.2). In general, environments with a high presence of loud intermittent events and systems with lower duty cycles should require smaller W and higher C than quieter places and higher duty cycles in order to detect these events above minimum SPLs. The high correlation between boat presence at Condor seamount from logbook data and PT-ATL values from 2009 to 2011 indicates that this methodology can be used to describe boat presence in the study area. The lack of correlation in 2012 is likely explained by the limitations in boat detection distance using these methods and the fact that not all boat activity was registered in logbooks. We suspect that the high PT-ATL values found in June 2012 could be due to an increase in recreational activities.

The monthly variability in PT-ATL values found in Condor reflects this area's main recreational uses during late spring and summer. Also, the annual decrease in PT-ATL values in winter can be explained by the designation of the temporary protected area for research in force since 2010. Since this was implemented, demersal fisheries, which operate year round, are prohibited, thus explaining the lower presence of boats during the winter. On the other hand, recreational activities are gaining importance, particularly shark diving, an activity which started experimentally in 2009 and that mostly operate in spring and summer (Ressurreição and Giacomello, 2013). The expeditions to dive with sharks at Condor were reported to double between 2011 and 2012 (Ressurreição and Giacomello, 2013), which might well explain why PT-ATL values increased in 2012. This activity also takes place in the Açores seamount, but to a lesser extent, which is reflected by a lower boat presence than in Condor. Gigante seamount shows a higher presence of boats throughout the year, as a result of the proximity of a marine traffic route used by commercial shipping and the presence of commercial fishing year-round in Gigante. Therefore, there is a great potential for using passive acoustic techniques to monitor boat activity in specific areas such as the ones in the study. This methodology, however, cannot be used to detect distant vessels and might not be adequate for areas with higher ship traffic where separation between continuous and intermittent events might not be possible.

For measuring the contribution of distant ship noise, the European MSFD (2008/56/EC, European Commission 2008) suggests the use of one-third octave bands, centered at 63 Hz and 125 Hz, which are included as indicators to assess the Good Environmental Status (GES) of the marine environment. In this study, Gigante shows the highest noise levels in the 63 Hz one-third octave band which can be explained by the proximity of a shipping lane mentioned in the above paragraph. Noise levels measured in the 125 Hz octave band better reflect local boat presence at Condor and Açores while at Gigante the difference between the two octave bands (63 and 125 Hz) is not very clear. This is mainly due to the difference in the type of vessels and distance of those to the hydrophone at each location. Comparison of spectrum levels indicates that Gigante has higher noise levels below 100 Hz, which is typical of distant large vessels such as tankers, while Condor and Açores have higher levels above 100 Hz, which is characteristic of smaller boats. Performance of one-third octave bands with distant shipping could not be assessed in this study because AIS data were not available for this period.

The maximum percentage of time with presence of boats found in this study is relatively low (13%). However, our results show that contribution of local boat noise to background noise levels ranged from 16–19 dB, depending on the study area, and on average was nearly 10 dB higher than wind contribution. This value is similar to those described in the literature where it is documented that below 1 kHz ship traffic regularly increases noise levels by 25 dB above background levels(Bassett et al., 2012). These increases in ambient noise might be sufficient to mask baleen whale calls unless they are able to compensate vocally, which is known as the Lombard effect (Lombard, 1911). There is some evidence that several species of mysticetes can, but sometimes do not, modify their vocalization's characteristics in response to shipping noise. Blue whales have been found to change the interval, types and amplitudes of their calls(McKenna, 2011; Melcón et al., 2012) while male fin whales seem to change their song characteristics (Castellote et al., 2012a). Other baleen whale species such as gray whales (*Eschrichtius robustus*) also modify calling rates, received levels and percentage of calls (Dahlheim and Castellote, 2016), humpback whales sing shorter versions of their songs (Sousa-lima et al., 2002) and North Atlantic right whales show short- and long-term changes in their calling behavior in response to increased low-frequency noise (Parks et al., 2007, 2009, 2010). However, other studies show that humpback whales respond to increases of noise levels produced by wind but do not compensate for higher levels of noise from vessels (Dunlop, 2016).

Auditory masking reduces the effective communication space between sender and receiver (Clark et al., 2009). A model developed by Tennessen and Parks (2016) demonstrated that a right whale is not able to hear an upcall from another whale if a ship passes at less than 25 km, unless the calling whale increases the amplitude of the calls by 20 dB. Despite differences in call source levels between right whales and blue, fin and sei whales, they share similarities in call frequency ranges (Parks and Tyack, 2005; Romagosa et al., 2015; Širović et al., 2007). Detection ranges of calls for these three species might be affected by passing ships in similar ways, which is of concern given the dependence of balaenoperids on long range communication (Payne and Webb, 1971). Although their calls have been mainly attributed to male reproductive displays, whales also produce sounds outside their breeding grounds and season (Clark et al., 2002; Oleson et al., 2007a; Vu et al., 2012). Blue whales are known to produce D calls during foraging within groups (Calambokidis et al., 2007; McDonald et al., 2001; Stafford et al., 2005) and fin whales produce “20-Hz pulse” calls that are likely to have a social purpose or a contact maintaining function when produced irregularly or as call-counter calls (Edds-Walton, 1997; McDonald et al., 1995). Baleen whale long-range calls could also be used for orientation purposes, as suggested by Payne and Webb (1971). In the Azores, preliminary analysis of acoustic data shows that blue and fin whales produce these types of calls when they are seen in spring as well as reproductive songs during the winter (unpublished data). Sei whales also vocalize during their migratory journey (Olsen et al., 2009; Prieto et al., 2014) through the Azores producing a well-known downsweep call for this species (Romagosa et al., 2015). Several studies indicate that blue, fin and sei whales are present around the archipelago, including in the deployment areas, mostly from February to May (Prieto et al., 2017; Silva et al., 2014) which coincides with a lower presence of boats at Condor but with a higher presence of boats at Açores. As for the transiting area (Gigante), due to its more constant vessel traffic throughout the year, an overlap exists with the baleen whale northward migration in spring and summer, and possibly with the southward journey in late autumn.

The biological implications of masking for these three species, whether they compensate it by modifying vocal behavior or not, are still unclear. However, given the association of vocalisations to such vital processes (e.g., social, foraging, navigation, reproduction), masking could reduce the chance of finding partners to mate, the ability of finding food or even their navigational skills thus negatively affecting their reproductive success and ultimately its survival. Although some efforts have been made to develop masking models that can be incorporated into regulation strategies, more research is needed to better understand potential effects of this complex phenomena, hearing characteristics from different species and anti-masking strategies used by free-ranging animals (Clark et al., 2009; Erbe, 2002).

Ship noise can also cause behavioral responses to cetaceans and Southall et al., (2007) suggests using SPLs to assess it. This metric might not be the most appropriate way to look for consistent patterns of response but it is often measured or estimated because it is required by law in many European countries and the USA as part of their noise mitigation regulations. Also, many other variables such as location, nature and behavior of noise sources and characteristics and activity of the individual animal among others, can affect the nature and extent of responses (Ellison et al., 2012). Therefore, the percentage of time with SPL levels above 120 dB re 1 μPa was calculated based on the model from the (NRC, 2005) that established that marine mammals exposed to levels above this value might be affected by sound. The maximum monthly percentage time with levels above 120 dB re 1 μPa was 3.3% (at Condor seamount) which is very low considering that an animal is unlikely to remain in the same location for the entire month. However, deployment depth affect noise levels received by the hydrophone and percentages with levels above 120 dB re 1 μPa are certainly higher closer to the source which in this case is found at the surface. While this is a simplistic and limited approach, it can nevertheless give an initial sense of the time that noise levels in an area could induce behavioral responses on baleen whales.

Comparatively, average noise levels for the three noisiest months at Condor (100.1 ± 17.2 dB re 1 μPa), Açores (95.9 ± 7 dB re 1 μPa) and Gigante (96.2 ± 13 dB re 1 μPa) for the frequency band of 10–585 Hz are lower than those measured by (Castellote et al., 2012a) in areas of the Mediterranean, such as the Provençal (106.9 ± 5.3 dB re 1 μPa), Alboran (103.7 ± 2.5 dB re 1 μPa) and Balearic (105.2 ± 1.2 dB re 1 μPa) basins and the Strait of Gibraltar (112.5 ± 4 dB re 1 μPa). Also, median noise levels within the 10–25,000 Hz measured in winter at Trindade-Martin Vaz archipelago (113.7 ± 11.4 dB re 1 μPa), another oceanic archipelago in the South-western Atlantic, are higher than those of Condor (105.3 ± 11.4 dB re 1 μPa) for the same frequency band (Bittencourt et al., 2016). Differences in this case might be explained by presence of snapping shrimp found to be an important noise contributor in shallow waters (Hildebrand, 2009).

Despite our findings suggesting the Azores is characterized by reduced underwater noise, we expect other areas in the archipelago closer to ferry routes, commercial shipping routes or routinely used by whale watching boats to be considerably noisier. Therefore, these measurements are representative only of these locations and further measurements and sound propagation modeling in other areas will be necessary to produce a detailed soundscape for the entire archipelago.

Acknowledgments: We are grateful to Rui Prieto, the skippers and crew members that helped with the deployment of the EARs. Data on boat presence were kindly provided by the Azores Fisheries Observer Program (POPA) (www.popaobserver.org) and by tourism operators (in the latter case an output of the projects CONDOR (EEA Grants PT-0040/2008) and SMaRT (M.2.1.2/029/2011)). We are also grateful to Ricardo Serrão Santos for his support and useful comments. Comments and suggestions from two reviewers significantly improved the present paper. This work is an output of research projects TRACE-PTDC/MAR/74071/2006, MAPCET-M2.1.2/F/012/2011, and of the FCT-Exploratory project IF/00943/2013/CP1199/CT0001. **Funding:** Fundação para a Ciência e a Tecnologia (FCT) and Fundo Regional da Ciência e Tecnologia (FRCT), through research projects TRACE-PTDC/MAR/74071/2006 and MAPCET-M2.1.2/F/012/2011 [FEDER, the Competitiveness Factors Operational (COMPETE), QREN European Social Fund, and Proconvergencia Açores/EU Program]. We also acknowledge funds provided by FCT to MARE, through the strategic project UID/MAR/04292/2013. IC was supported by a FCT doctoral grant (SFRH/BD/41192/2007) and MAS is supported by an FCT-Investigator contract (IF/00943/2013). TAM is a member of CEA/UL (Funded by FCT - Fundação para a Ciência e a Tecnologia, Portugal, through the project UID/MAT/00006/2013). Fees for this open access publication were supported by the FCT Exploratory project (IF/00943/2013/CP1199/CT0001) that as (IF/00943/2013) is funded by POPH, QREN European Social Fund and the Portuguese Ministry for Science and Education.

Annex V. Supplementary data

The Supplementary Material for this article can be found online at:

https://www.frontiersin.org/article/10.3389/fmars.2017.00109/full#supplementary-material

Chapter 6

Discussion

This dissertation contributes to the knowledge on the vocal behaviour of three species of baleen whales, with a focus on the migratory phase, a poorly understood period of their annual life cycles.

Through the analysis of a large acoustic dataset collected over a period of five years, this study provides, in Chapter 2, the first insights into the vocal behaviour of fin, blue and sei whales in a migratory and foraging habitat, the Azores archipelago. Main findings included a seasonal shift in fin and blue whale calling behaviours that reflected a change from reproductive to foraging behaviours, and a sei whale bi-seasonal calling pattern, coincidental with the migration timing of the species through the region. It also investigated diel calling patterns and found a higher diurnal fin whale singing activity, a lack of diel patterns for the two blue whale call types and higher sei whale calling activity during the day. Finally, fin and blue whale song structures identified here were identical to those previously described in the North Atlantic while irregular calls had also been described in other ocean basins, including those of sei whales.

In Chapter 3 of this thesis, this work focused on fin whales, and used the same acoustic dataset as in Chapter 2 to investigate the function of two call types by assessing their relationship with year, season and the modelled zooplankton biomass, the main prey of this species. Results showed, for the first time, a positive relationship between the 40-Hz call and prey biomass, the only variable found to have a statistically significant effect on this call. Conversely, song-forming 20-Hz note activity was best predicted by season and year and not influenced by zooplankton biomass.

The following chapter (Chapter 4) compiled two decades of acoustic data from six different regions of the North Atlantic to investigate changes in two fin whale song parameters (INIs and peak frequencies). This study reported a rapid change in song INIs in just four winter seasons in a vast area of the Mid- North Atlantic. After this change, a gradual increase in INIs and decrease in peak frequencies of the HF note occurred across the whole sampled region.

Finally, Chapter 5 used the same dataset from Chapters 2 and 3 to analyse low-frequency (<1 kHz) noise levels and shipping noise in three offshore areas of the Azores archipelago. Results indicated that noise levels and shipping noise were low compared to other areas but emphasize the need to continue monitoring noise levels.

The main findings of all chapters are combined and contextualised into an integrated discussion to advance knowledge on the vocal behaviour and ecology of these three species.

6.1 Seasonal variations in vocal behaviour

Chapter 2 reports a temporal segregation of fin and blue whale vocal behaviour from intensive singing to irregular calling and a sei whale bi-seasonal calling activity in spring and autumn.

This study found that fin whale and blue whale songs peaked in late autumn and winter during the known mating season of these species (Mizroch et al., 1984; Ohsumi et al., 1958). This agrees with the widely documented seasonality in singing activity that matches the presumed breeding season of these species (Tripovich et al., 2015; Watkins et al., 1987). The clear seasonality in singing, together with the song production by males (Croll et al., 2002; McDonald et al., 2001; Oleson et al., 2007a), has led to the generally accepted assumption that fin and blue whale songs are used in reproductive contexts (Oleson et al., 2007a; Watkins et al., 1987). Thus, our findings indicate that both species are engaged in reproductive behaviours from late autumn to early spring in a mid-latitude area. Similar seasonal patterns in fin and blue whale singing have been documented along the Mid-Atlantic Ridge between 17°N and 50°N (Nieukirk et al., 2004, 2012), between south-eastern Iceland and west of the British Isles (Charif and Clark, 2009) and in high latitude feeding grounds (Davis et al., 2020; Simon et al., 2010). Overall, the seasonal detection of blue and fin whale songs in a vast area of the central and North-eastern Atlantic suggests a lack of a winter breeding aggregations and adds further evidence for a partial and differential migration in both species (Branch et al., 2007; Geijer et al., 2016; Kellogg, 1929).

Individuals that do migrate though, are known to time their northward spring migration with the North Atlantic spring bloom (Pérez-Jorge et al., 2020; Visser et al., 2011) and stop their journey to forage in mid-latitude habitats, such as the Azores archipelago (Silva et al., 2013). During spring and early summer, this study found a notable decrease in fin and blue whale singing activity (Chapter 2) replaced by the production of other non-song irregular calls. In Chapter 3, this work documented an increase in the activity of the fin whale 40-Hz call in spring matching the timing of the spring bloom and showing a positive association with zooplankton biomass, the main component of fin whale diet (Arregui et al., 2018; Silva et al., 2019). This finding also provided the first direct evidence of a previously suggested food-associated function of the 40-Hz fin whale call (Burnham et al., 2021; Širović et al., 2013; Watkins, 1981). Similarly, in Chapter 2 this work reports non-song irregular calls in blue whales, named D calls, but their frequency was similar in spring, autumn and winter. Although this call type, like the fin whale 40-Hz call, has been associated to foraging behaviours (Oleson et al., 2007a, 2007b), it has also been recorded in social (Lewis et al., 2018; McDonald et al., 2001) and even reproductive contexts (Schall et al., 2020), which may explain why blue whale D calls were used evenly across the seasons. The change in vocal behaviour from singing to calling, also reported in other studies (Oleson et al., 2007b; Širović et al., 2013), clearly reflects a behavioural shift in both species.

The bi-seasonal pattern of sei whale calling activity in spring and autumn (Chapter 2) agrees well the timing of migration of this species through the Azores. Sei whales travel north in spring (Silva et al., 2014) towards the Labrador sea (Olsen et al., 2009; Prieto et al., 2014), and south in autumn, towards wintering grounds off north-western Africa (Prieto et al., 2014; Silva et al., 2019). The production of downsweep calls by migratory sei whales that seldom feed in the archipelago (Prieto et al., 2014) suggests these calls are not produced in a feeding context but may serve as contact calls (Baumgartner and Fratantoni, 2008) or even represent reproductive displays. Recent work described sequences of sei whale vocalisations with a song-like structure but further studies are required to confirm it (Tremblay et al., 2019).

6.2 Diel patterns in vocal behaviour

Diel patterns in vocal behaviour were investigated for the three species (Chapter 2) showing a higher diurnal fin whale calling rates, a lack of diel pattern for singing and calling blue whales and increased sei whale calling during the day.

Decreased fin and blue whale singing activity in spring found in this study may be caused by changes in male hormonal levels (Kjeld, 1992) and/or by a trade-off between singing and feeding. When foraging, both species perform lunge-feeding behaviours with increased swimming speeds (Goldbogen et al., 2006, 2013) and deep dives to feed on densely aggregated prey patches (Croll et al., 2001). In contrast, singing fin and blue whales are often travelling (Oleson et al., 2007a; Watkins, 1981) and engaged in non-lunging, long, stereotypically ‘U-shaped dives’ to a consistent shallow depth (10 -30 m) with little body movement (Lewis et al., 2018; Stimpert et al., 2015). The fact that singing fin and blue whales do not perform dives with vertical lunges and that sound production occurs at shallow depths suggest that feeding and singing behaviours may be incompatible (Oleson et al., 2007a, 2007b; Stafford et al., 2005; Wiggins et al., 2005).

In Chapter 2, this work reported greater diurnal fin whale singing activity in autumn and winter months. In the North Atlantic, fin whales mostly feed during the night in spring and summer months (Silva et al., 2013; Víkingsson, 1997b). If this pattern in foraging behaviour also occurs during the rest of the year, then more singing during the day could be attributed to more intense feeding during the night. However, an opposite pattern (more singing at night) was reported from fin whales at higher latitudes during the winter (Simon et al., 2010) and related to higher densities of herring in autumn in the North-west Atlantic (Wang et al., 2016). Similarly, studies in different regions of the North Pacific reported different fin whale diel singing patterns. While in northern latitudes (i.e., Bering Sea) more singing occurred during the day, further south in the Gulf of California, higher singing activity was reported during the night (Širović et al., 2013). In Antarctica, one study reported that diel pattern varied seasonally (Shabangu et al., 2020) and another found no diel pattern at all (Burkhardt et al., 2021). These diverse and often contradictory results may have different explanations. First, some of these studies did not distinguish between fin whale song-forming and non-song irregular 20-Hz calls (Širović et al., 2013; Wang et al., 2016). Irregular 20-Hz calls have been recorded from whales often engaged in foraging (Watkins, 1981). Combining song and irregular 20-Hz calls into one metric may therefore obscure and confound diel patterns. Second, fin whales may time their feeding activity for optimum efficiency (e.g., to benefit from densely aggregated prey) which may vary spatially and seasonally depending on the prey species, given that the presence and amplitude of the diel vertical migration of krill and their aggregation varies greatly across regions and seasons (Gaten et al., 2008; Santora et al., 2012).

In this study, blue whales did not show any significant singing (AB song) or calling (D calls) diel patterns. This may be caused either by the small sample size (i.e., low number of calls) of our study or by a true pattern. In the North Pacific, blue whale singing activity (B songs) was higher at night (Oleson et al., 2007b; Stafford et al., 2005) while D calls were produced more often during the day (Oleson et al., 2007b), when whales are known to feed on densely aggregated krill (Tershy, 1992). In Antarctica though, blue whale singing activity (Z song) was higher during the day (Leroy et al., 2016) while in Australia an opposite pattern was reported by Tripovich et al.(2015). As in fin whales, different prey species and behaviours may determine blue whale feeding strategies, which may affect their singing and calling diel patterns.

Sei whale calling activity was higher during the day than at night in spring, in Condor, and in autumn, in Gigante (Chapter 2). The same pattern was found in the Gulf of Maine (Baumgartner and Fratantoni, 2008; Wang et al., 2016) and was attributed to sei whales feeding on surface aggregations of highly migrant copepods during the night (Baumgartner and Fratantoni, 2008). Authors suggested that diurnal sei whale calling may serve a social function and signal food resources to conspecifics (Baumgartner and Fratantoni, 2008). Behavioural observations, satellite telemetry and stable isotope analysis indicate that sei whales forage only sporadically in the Azores (Prieto et al., 2014; Silva et al., 2019). Thus, either sei whales feed more often than detected by current observations and/or downsweeps are not strictly associated with foraging activity but could also be used as contact calls during migration. Still, the underlying reason for the diel patterns in sei whale calling remains to be explained.

6.3 Geographic variations in song and call structure

Fin and blue whale song structures identified in Chapter 2 were identical to those previously described in the North Atlantic but differed from songs reported in other ocean basins. Irregular calls produced by these species, including sei whales, were similar to those described in other ocean basins.

Songs used as reproductive displays show geographically distinct structures in many species (Campbell et al., 2010; Davidson and Wilkinson, 2002; Irwin, 2000; Simmons et al., 2001) and are believed to be the by-product of specific learning mechanisms and dispersal patterns (Podos and Warren, 2007). Blue and fin whale songs show a remarkable geographic variation that has been used to distinguish populations or stocks (Hatch and Clark, 2004; McDonald et al., 2006b). In Chapter 2, this work described blue whale song A and B units belonging to the North Atlantic type (McDonald et al., 2006b), which has been previously documented in both eastern (Berchok et al., 2006; Edds P. L., 1982; Mellinger and Clark, 2003) and western regions (Charif and Clark, 2009). However, photo-identification data suggests that the North-west Atlantic blue whale population is separate from the north-east Atlantic population (Sears et al., 2015). Previous acoustic studies have found differential usage in AB, A and B units in blue whale songs between Mid-Atlantic (Nieukirk et al., 2004) and North-west Atlantic (Berchok et al., 2006; Mellinger and Clark, 2003), suggesting that these units may indicate distinct blue whale populations. Our results showing differential use in song units, with AB calls being rarely detected (5.9%) compared to single A units (94.1%), were inconclusive due to the EAR's poor sensibility at low frequencies (<18-Hz) compromising B unit detection.

Fin whale songs described here showed two simultaneous pulses, a downsweep centred at 20-Hz and an upsweep around 130-Hz (hereafter HF component). The HF component of the fin whale song has been detected in regions of the eastern and western North Atlantic (Castellote et al., 2012b; Garcia et al., 2019; Hatch and Clark, 2004; Simon et al., 2010; De Vreese et al., 2018) but its frequency differs from songs recorded in the eastern Antarctic (~99 Hz) (Širović et al., 2004), and the western Antarctic Peninsula and the Scotia Sea (~89 Hz) (Širović et al., 2009).

In Chapter 4, this study analysed two decades of acoustic data and measured fin whale song properties (INIs and peak frequencies of the 20-Hz and HF notes) across six regions of the central and eastern North Atlantic. Our results showed a 12-year (2008-2020) gradual decrease in the frequencies of the fin whale song HF component across the central and North-eastern Atlantic, with songs from Iceland, Greenland, Ireland, Svalbard, South-west Portugal and Azores fitting the same linear trend. This suggests that fin whales from these regions have the same song HF component frequencies. Similarly, INIs (i.e., the time interval between two consecutive 20-Hz notes) in fin whale songs gradually increased over the same period (2008-2020) and all sampled regions fitted the trend. Moreover, regions with simultaneous data (same singing season) showed similar INIs as indicated by their unimodal overlapping distributions. The only exception was Svalbard, where INIs differed from the rest of the sampled regions. The fact that the HF component in Svalbard was similar to the rest of the sampled region area while INIs were not, may indicate that frequencies of the HF component may only differ between very distant populations while INIs may indicate finer scale differences. In fact, Delarue et al. (2009) showed differences in INIs between relatively close regions from the Norwest Atlantic (Gulf of St Lawrence and the Gulf of Maine) that were indicative of different populations. Except from Svalbard data, results on variation in song parameters found in Chapter 4 agree with genetic data stating that eastern North Atlantic fin whales may belong to the same population but differ from western North Atlantic fin whales (Bérubé et al., 1998). One explanation for the different INIs detected in Svalbard could be a recently geographic isolated fin whale population. However, satellite telemetry data show that at least some of the fin whales that feed around Svalbard in the summer disperse in fall and winter, with some individuals travelling to Iceland and others to SW Portugal (Lydersen et al., 2020). Alternatively, this new song type could have emerged from a recent population mixture or change driven by the new ice-free passages resulting from ocean warming. Distribution shifts in several baleen whale species have already been documented as a consequence of ice retrieval (Davis et al., 2020; Nieukirk et al., 2020).

Downsweep calls from sei whales documented in Chapter 2 in the Azores were identical to those reported off the North eastern coast of North America (Baumgartner et al., 2008b) and Fram Strait (between Greenland and Svalbard) (Nieukirk et al., 2020). Satellite telemetry data indicate a link between animals migrating through the Azores and foraging off the coast of Maine, in the US (Prieto et al., 2014), and genetic studies show low genetic divergence among these locations, suggesting that North Atlantic sei whales may constitute a unique population (Huijser et al., 2018). However, the same call type was also described for sei whales from the North and South Pacific Oceans (Español-Jiménez et al., 2019; Rankin and Barlow, 2007) indicating that sei whale downsweeps are not geographically distinct. Similarly, blue whale D calls and fin whale 40-Hz calls described for the Azores (Chapters 2 and 3, respectively) were comparable to calls from other regions within the North Atlantic (Boisseau et al., 2008; Mellinger and Clark, 2003; Watkins, 1981), the North Pacific (Oleson et al., 2007a; Širović et al., 2013; Wiggins and Hildebrand, 2020) and Antarctica (Shabangu et al., 2020). Unlike songs, calls are genetically predetermined and apparently stereotyped within species; thus, animals are able to produce them without intensive learning (Marler, 2004). This could explain why in some species these calls are not geographically distinct.

6.4 Call Function

In Chapter 3 this work inferred into the potential functions of the fin whale song-forming 20-Hz note and the 40-Hz call by investigating their production in relation to year, season and the simulated zooplankton biomass, the main prey of this species (Arregui et al., 2018; Silva et al., 2019). Our results showed that the production of song-forming 20-Hz calls was strongly influenced by season, with a clear peak during the breeding months, and secondarily by year, likely due to changes in local whale abundance. This suggests that fin whale songs do not serve to advertise food resources to potential mates, as some authors suggested (Croll et al., 2002). Instead they may be used as acoustic displays in intersexual and intrasexual interactions, as proposed for humpback whale songs (Cholewiak et al., 2018b; Smith et al., 2008). Male humpback whales were more likely to sing after joining mother-calf pairs if no other males were around and stopped singing when joining other males, indicating that songs may be directed towards females (intersexual interaction) (Smith et al., 2008). Another study found that males altered their songs in the presence of other singers and that changes in distance between singers influenced singing activity, indicating that song may also mediate male-male competition (intrasexual interaction) (Cholewiak et al., 2018b).

Unlike the song-forming 20-Hz call, the 40-Hz call was strongly influenced by zooplankton biomass. This work showed a positive association between this call type and prey biomass, which provides the first direct evidence of a previously suggested food-associated function of the 40-Hz call (Širović et al., 2013; Watkins, 1981). Food associated calls are widely used in many species of birds and mammals and may provide information about a food source or feeding event to attract receivers to a foraging site (Clay et al., 2012). Fin whales are solitary or form temporary aggregations (Whitehead and Carlson, 1988) and do not generally show cooperative feeding behaviour (Aguilar, 2009). Thus, it is unlikely that fin whale 40-Hz calls serve to attract kin or social partners, either to provide them with increased foraging benefits or to assist defending food patches. Instead, fin whale 40-Hz calls may be used to convey information about the individual location, for example, to regulate spacing between foragers, or establish ownership of food patches, as described for other species (Gros-Louis, 2004). However, at this moment, we ignore the functional significance(s) of the 40-Hz fin whale call when produced in feeding contexts.

In birds and mammals, food calls are also often used in different behavioural contexts (Clay et al., 2012). A recent study documented two acoustically tracked fin whales producing 40-Hz calls in a loosely coordinated call sequence and showing converging tracks that passed within ~500 m of each other (Wiggins and Hildebrand, 2020), suggesting that this call may also serve as a contact or social call.

Low variation in blue whale D call activity across seasons (Chapter 2) supports the multifunctionality of this call. D calls were first described as food-associated and social calls because, as the 40-Hz fin whale calls, were recorded in feeding areas during foraging activity (Oleson et al., 2007a, 2007b) and from whales in groups (Lewis et al., 2018; McDonald et al., 2001). However, recent reports of D calls produced by males competing for a female (Schall et al., 2020), indicates that these calls may be used for different purposes.

6.5 Fin whale song evolution and revolution

Although geographic differences in baleen whale song have been used as a proxy for stock identity (Delarue et al., 2009; McDonald et al., 2006b), some researchers argue that vocal displays are too susceptible to ecological (e.g., habitat adaptation) and social (e.g., social learning and imitation) factors to successfully reflect population and genetic relationships (Harvey and Purvis, 1991). In Chapter 4, this study analysed two decades (1999-2020) of acoustic data including six regions in the central and eastern North Atlantic (MAR/Azores, Iceland/Greenland, Svalbard, Ireland, SW Portugal and the Canary Islands) and measured two fin whale song parameters (INIs and peak frequencies of the 20-Hz and HF notes).

Results showed a rapid change in INIs across a vast area of the central North Atlantic (MAR/Azores), where the 19s-INI song was completely replaced by the 12s-INI song, in just four winter seasons (2000/2001 – 2004/2005). In 2004, the 19s-INI song disappeared from all sampled regions, except from one isolated account in 2008. During the transition period, songs with both INIs co-existed with a notable percentage of hybrid songs, that included both INIs (~24% hybrids in 2002/2003). In 2002/2003, there was a clear south-westerly gradient in the percentage of each INI type, with the new INIs (12s) being more abundant in north-eastern locations. This unequal spatial distribution of song types in the same winter singing season over a region with similar environmental conditions exclude the hypothesis that INI changes were driven by environmental drivers.

When environmental causation can be excluded, cultural evolution is the best explanation for the rapid diffusion of novel behaviours throughout a population (Leca, 2015). Cultural transmission is the motor of cultural revolution and involves vocal learning. The existence of hybrid songs found here together with the ability of individual fin whales to switch between song types (Helble et al., 2020), suggest a greater fin whale song plasticity than previously thought and opens the possibility of learning by imitation in this species. Vocal learning is known to occur in several species of cetaceans (e.g., bottlenose dolphins, killer whales, bowhead and humpback whales) (Rendell and Whitehead, 2001).

Humpback whale songs are clearly culturally transmitted because they evolve through time and all males in a population conform to song changes (Payne and Payne, 1985) and maintain them (Mundinger, 1980). Male fin whale songs are also regionally distinctive (Castellote et al., 2012b; Delarue et al., 2009; Hatch and Clark, 2004; Širović et al., 2017), go through changes over time (Delarue et al., 2009; Leroy et al., 2018; Širović et al., 2017; Weirathmueller et al., 2017) and all males adopt and maintain these changes (Oleson et al., 2014) (this study), which supports the notion of cultural evolution in fin whale song. Assuming the rapid song change reported here is the result of a cultural revolution, fin whales singing the old 19s-INI song must have overlapped in time and space with 12s-INI song singers for the song transfer to occur. The spatial gradient in song types suggest the new song (12s-INI) may have originated somewhere in the eastern North Atlantic and spread south-westerly. The same fin whale song shift reported in Chapter4 in the MAR/Azores region occurred simultaneously in a northern latitude summer feeding area (NENA) (Hatch and Clark, 2004; Víkingsson et al., 2015). Simultaneous data from more regions would be needed to determine if the new 12s-INI song came from an eastern unsampled region or from overlapping populations in feeding grounds.

After the rapid change in INIs, this study also reports a 12-year gradual increase in INIs, a decrease in peak frequencies of the HF note and a lack of trend in peak frequencies of the 20-Hz note for the central and eastern North Atlantic. These song changes reported here are in line with the worldwide gradual trends of decreasing frequencies (Leroy et al., 2018; Malige et al., 2020; McDonald et al., 2009; Weirathmueller et al., 2017) and increasing inter unit intervals (Jolliffe et al., 2019; Malige et al., 2020; Morano et al., 2012; Širović et al., 2017; Weirathmueller et al., 2017) described not only in fin whales but also in blue whales. Although authors have postulated several hypotheses to explain these common directional changes, none of them is free of opposing arguments. In Chapter 4, this work further discussed the potential drivers of song changes that include: sexual selection (female preference for larger males able to sing lower pitch songs), increased levels of shipping noise, increased whale density (McDonald et al., 2009) and changes in water sound propagation conditions caused by ocean warming (Leroy et al., 2018). Song evolution often does not result from a single driver but from the complex interplay between drift, selective pressures and vocal constraints (Ey and Fischer, 2009; Mahler and Gil, 2009; Podos et al., 2004). In addition, the functional mechanisms of fin and blue whale songs remain unknown, which makes debates on sources of song variation strongly speculative and based on comparative analysis with other taxa.

The great fin whale song plasticity documented in Chapter 4 suggests an ability of this species to respond to different selective pressures. However, if pressure driving song changes surpasses the ability of the species to adapt or compensate (e.g., anthropogenic noise), then song function may be compromised. For example, if the frequency decrease of already very low-frequency songs continues, it could reach the physiological limit of sound production in fin and blue whales, with unforeseeable consequences for the survival of these species.

6.6 Impact of noise on baleen whale vocal behaviour

In Chapter 5, low-frequency (< 1 kHz) noise levels and boat presence (time with ship noise) were measured over a period of five years (2008-2012) at three Azorean offshore seamounts (Condor, Gigante and Açores) that are part of a baleen whale migratory habitat.

Results showed noise levels that were comparatively lower than, for example, in the Mediterranean Sea or in the Strait of Gibraltar (Castellote et al., 2012a). Shipping noise was identified as the main source of anthropogenic noise in our study area, but presence of boat noise was relatively low, with a maximum of 13% of recording time with boat noise. However, these results should not be extrapolated to the entire archipelago, as other areas are known to have higher shipping traffic (Soares et al., 2020). In fact, daily presence of shipping noise in the vicinity of Faial and Pico Islands reached a maximum of 60% of time with boat noise in spring (Romagosa et al., 2020b). During this season, satellite telemetry, visual and acoustic data show that blue, fin and sei whales use these areas as foraging spots or migratory corridors during their journey to northern latitudes (Olsen et al., 2009; Prieto et al., 2014; Silva et al., 2014, 2013). At that time, they produce different types of vocalisations associated to reproductive, feeding and social behaviours (Chapter 2 and 3), with frequencies overlapping those of shipping noise (Ross, 1976).

Shipping noise can directly disrupt baleen whale behaviours, such as interrupting foraging activities in bowhead (*Balaena mysticetus*) (John Richardson et al., 1985) and humpback whales (Blair et al., 2016), or mask their vocalisations (Erbe et al., 2015, 2019). In Chapter 5, this study found that the contribution of local boat noise to background noise levels was nearly 10 dB higher than wind contribution. This increase in ambient noise might be sufficient to mask baleen whale calls unless they are able to compensate vocally. In response to shipping noise, male fin whales can change their song characteristics (Castellote et al., 2012a) while blue whales have been found to modify the interval, types and amplitudes of their calls (McKenna, 2011; Melcón et al., 2012). Vocal compensation may come with a substantial increase in energy expenditure, as shown for other taxa (Currie et al., 2020). But they may not even be able to compensate. Humpback whales, for example, respond to increased noise levels produced by the wind but do not compensate for higher levels of noise from vessels (Dunlop, 2016).

When noise compensation mechanisms do not exist, then a reduction of the animal's communication space occurs (i.e., acoustic masking) hindering the transmission of information between individuals (Clark et al., 2009). In addition to masking, chronic noise exposure can result in increased stress levels in animals, as documented for right whales (Rolland et al., 2012), and reported to have many costs across terrestrial species (Barber et al., 2010). Recent studies document declines in reproductive success (Habib et al., 2007), density and diversity of several bird species due to noise (Slabbekoorn and Ripmeester, 2008). The long-term noise effects on the heath of a population or species are extremely difficult to quantify, especially in elusive, long-lived and slowly reproducing animals like baleen whales. In any case, the reported losses of communication space for fin whales due to shipping (Cholewiak et al., 2018a; Williams et al., 2014) are worrying enough to highlight the need for decision makers to adopt strategies for noise management in the marine environment.

6.7 Implications for PAM

Studies on the vocal behaviour of baleen whales are indispensable for improving their monitoring through passive acoustics techniques. When seasonal and diel differences in acoustic behaviour (Chapter 2) can be linked to different behavioural activity patterns (i.e., call function) (Chapter 3), PAM becomes a powerful tool to study the ecology and biology of such cryptic and highly mobile marine species (Baumann-Pickering et al., 2015; Bridges and Dorcas, 2000; Kamimura and Tatsuki, 1993).

Passive acoustic density estimation (PADE) is becoming a common technique to obtain estimates of cetacean density (e.g., Marques et al., 2013). Call production rate, i.e., the number of calls of interest produced per animal per unit time is a fundamental multiplier in PADE. Baleen whale call production rates depend on the animals' behavioural and environmental context that vary with day-night phases, seasons, locations and years. For example, in Chapter 2, this work documents seasonal and diel differences in calling rates of singing fin and blue whales. We also report different calling rates by call type (Chapter 2 and 3) and sudden and gradual changes in fin whale song INIs over time that also affect call production rates (Chapter 4). Thus, this dissertation further emphasizes that for fin, blue and sei whale populations, no single species-specific call production rate could be applied to estimate density across the distribution range of these species. Further studies investigating and describing call production rates, understanding what drives them, are therefore fundamental for PAM density estimation.

6.8 Future research

One of the major knowledge gaps in baleen whale vocal behaviour is the context and content of signals' production. Understanding why animals produce certain calls in certain circumstances is an essential step for accurate interpretation of acoustic data and evaluation of human impacts. More effort should be placed into simultaneous visual and acoustic surveys, using acoustic recording tags, behavioural observations and biopsy sampling, to document calls from specific individuals and their associated behaviours. The few studies using these methodologies have greatly contributed to fill in this knowledge gap (Lewis et al., 2018; Oleson et al., 2007a; Stimpert et al., 2015) especially in blue whales, but more studies are needed in fin and sei whales. For example, information on sex-specific calling rates or types is not available for these species and neither is the context of fin whale 40-Hz or sei whale downsweep call production. These studies would also provide valuable information on calling rates by gender, behaviour and call type, an essential variable to accurately estimate animal density through acoustic methods.

Playback experiments have been extensively used to study vocal behaviour in several species of terrestrial animals (Di Bitetti, 2003; Bohn et al., 2013; Grafe, 1999; Moseley et al., 2013) but their use in baleen whales is limited to a few studies on humpback whales (Mobley et al., 1988; Tyack, 1983). Yet, these experiments are essential to understand how receiver's respond to a signal, which could provide clues on the function of the signal. For example, playing a male reproductive song in the presence of males and females while observing their reactions may inform about the attraction or deterrent effect of songs. In addition, by investigating other male's vocal responses to song playbacks, the potential competition mechanism may be revealed (e.g., song synchronisation or alternation).

Finally, more studies are needed on the masking effects of various noise sources on different baleen whale call types. The modelling-frameworks used in some studies (Cholewiak et al., 2018a; Clark et al., 2009) are a good approach to calculate loss of communication space but it is still necessary to really understand how much noise is necessary to disrupt communication. This is a key information for defining a noise threshold, which can inform conservation and management efforts.

6.9 Final considerations

Outcomes from this dissertation highlight the potential of using animal vocal behaviour to infer into behavioural and ecological aspects that are relevant for conservation. The recent advances in software to process large acoustic datasets and in recorder technology will promote the long-term acoustic monitoring of baleen whale populations at ocean scales. In the current global warming context, information on population trends and distribution are needed to understand how populations and individuals are adapting, or not, to these rapid changes.

To achieve this goal, a better understanding of the proximate and ultimate functions of singing and calling are required. This thesis contributes to the knowledge on fin whale call function by using model-based estimates of prey biomass. This methodology offers a cost-effective way of exploring vocal behaviour in feeding contexts and may help predicting foraging spots by just studying the occurrence of call types. If a relationship between call detection rates and prey biomass can be found, then calling activity may also inform about ecosystem quality.

Baleen whale vocal behaviour has adapted to an optimum transmission between senders and receivers. Changes in sound propagation conditions caused by climate change (e.g., ocean warming and acidity) and increased anthropogenic noise may already be affecting the communication space in these species, with adverse effects on baleen whale communication, which can ultimately impact their long-term reproduction and survival success.

References

Abecassis, M., Senina, I., Lehodey, P., Gaspar, P., Parker, D., Balazs, G., and Polovina, J. (**2013**). "A Model of Loggerhead Sea Turtle (*Caretta caretta*) Habitat and Movement in the Oceanic North Pacific," PLoS One, **8**, e73274. doi:10.1371/journal.pone.0073274

Afonso, P., Fontes, J., Giacomello, E., Magalhães, M. C., Martins, H. R., Morato, T., Neves, V., et al. (**2020**). "The Azores: A Mid-Atlantic Hotspot for Marine Megafauna Research and Conservation," Front. Mar. Sci., **6**, 1–8. doi:10.3389/fmars.2019.00826

Aguilar, A. (**2009**). "Fin Whale: *Balaenoptera physalus*," In W. F. Perrin, B. Würsig, and J. G. M. Thewissen (Eds.), Encycl. Mar. Mamm. (Second Ed., Academic Press, London, Second Edi., pp. 433–437. doi:https://doi.org/10.1016/B978-0-12-373553-9.00102-4

Akamatsu, T., Rasmussen, M. H., and Iversen, M. (**2014**). "Acoustically invisible feeding blue whales in Northern Icelandic waters," J. Acoust. Soc. Am., **136**, 939–944. doi:10.1121/1.4887439

Amorim, M. C. P., Vasconcelos, R. O., and Fonseca, P. J. (**2015**). "Fish sounds and mate choice," In F. Ladich (Ed.), Sound Commun. fishes, Springer-Verlag, Wien, Vol. 4, pp. 1–33. doi:10.1007/978-3-7091-1846-7

Andersson, M. (**1994**). *Sexual Selection*, Princeton University Press, Vol. 72. doi:10.2307/j.ctvs32s1x

Andrew, R. K., Howe, B. M., Mercer, J. a., and Dzieciuch, M. a. (**2002**). "Ocean ambient sound: Comparing the 1960s with the 1990s for a receiver off the California coast," Acoust. Res. Lett. Online, **3**, 65. doi:10.1121/1.1461915

Archer, F. I., Rankin, S., Stafford, K. M., Castellote, M., and Delarue, J. (**2020**). "Quantifying spatial and temporal variation of North Pacific fin whale (*Balaenoptera physalus*) acoustic behavior," Mar. Mammal Sci., **36**, 224–245. doi:10.1111/mms.12640

Arregui, M., Borrell, A., Víkingsson, G., Ólafsdóttir, D., and Aguilar, A. (**2018**). "Stable isotope analysis of fecal material provides insight into the diet of fin whales," Mar. Mammal Sci., **34**, 1059–1069. doi:10.1111/mms.12504

Atkinson, A. C. (**1985**). *Plots, Transformations, and Regression: An Introduction to Graphical Methods of Diagnostic Regression Analysis*, Clarendon Press, Oxford.

Au, W. W. L., Mobley, J., Burgess, W. C., and Lammers, M. O. (**2000**). "Seasonal and diurnal trends of chorusing humpback whales wintering in waters off western Maui," Mar. Mammal Sci., **16**, 530–544.

Aulich, M. G., McCauley, R. D., Saunders, B. J., and Parsons, M. J. G. (**2019**). "Fin whale (*Balaenoptera physalus*) migration in Australian waters using passive acoustic monitoring," Sci. Rep., **9**, 1–12. doi:10.1038/s41598-019-45321-w

Baines, M. E., and Reichelt, M. (**2014**). "Upwellings, canyons and whales: An important winter habitat for balaenopterid whales off Mauritania, northwest Africa," J. Cetacean Res. Manag., **14**, 57–67.

Baines, M., Reichelt, M., and Griffin, D. (**2017**). "An autumn aggregation of fin (*Balaenoptera physalus*) and blue whales (*B musculus*) in the Porcupine Seabight, southwest of Ireland," Deep. Res. Part II Top. Stud. Oceanogr., **141**, 168–177. doi:10.1016/j.dsr2.2017.03.007

Balcazar, N. E., Tripovich, J. S., Klinck, H., Nieukirk, S. L., Mellinger, D. K., Dziak, R. P., and Rogers, T. L. (**2015**). "Calls reveal population structure of blue whales across the Southeast Indian Ocean and the Southwest Pacific Ocean," J. Mammal., **96**, 1184–1193. doi:10.1093/jmammal/gyv126

Ballentine, B., Hyman, J., and Nowicki, S. (**2004**). "Vocal performance influences female response to male bird song: An experimental test," Behav. Ecol., **15**, 163–168. doi:10.1093/beheco/arg090

Bannister, J. L. (**2009**). "Baleen Whales (Mysticetes)," In W. F. Perrin, B. Würsig, and J. G. M. B. T.-E. of M. M. (Second E. Thewissen (Eds.), Encycl. Mar. Mamm. (Second Ed., Academic Press, London, pp. 80–89. doi:https://doi.org/10.1016/B978-0-12-373553-9.00024-9

Barber, J. R., Crooks, K. R., and Fristrup, K. M. (**2010**). "The costs of chronic noise exposure for terrestrial organisms," Trends Ecol. Evol., **25**, 180–189. doi:10.1016/j.tree.2009.08.002

Bassett, C., Polagye, B., Holt, M., and Thomson, J. (**2012**). "A vessel noise budget for Admiralty Inlet, Puget Sound, Washington (USA)," J. Acoust. Soc. Am., **132**, 3706–3719.

doi:10.1121/1.4763548

Baumann-Pickering, S., Roch, M. A., Wiggins, S. M., Schnitzler, H. U., and Hildebrand, J. A. (**2015**). "Acoustic behavior of melon-headed whales varies on a diel cycle," Behav. Ecol. Sociobiol., **69**, 1553–1563. doi:10.1007/s00265-015-1967-0

Baumgartner, M. F., and Fratantoni, D. M. (**2008**). "Diel periodicity in both sei whale vocalization rates and the vertical migration of their copepod prey observed from ocean gliders," Limnol. Oceanogr., **53**, 2197–2209. doi:10.4319/lo.2008.53.5_part_2.2197

Baumgartner, M. F., Freitag, L., Partan, J., Ball, keenan R., and Prada, K. E. (**2008a**). "Tracking large marine predators in three dimensions: The real-time acoustic tracking system," IEEE J. Ocean. Eng., **33**, 146–157. doi:10.1109/JOE.2007.912496

Baumgartner, M. F., and Mussoline, S. E. (**2011**). "A generalized baleen whale call detection and classification system," J. Acoust. Soc. Am., **129**, 2889–2902. doi:10.1121/1.3562166

Baumgartner, M. F., Van Parijs, S. M., Wenzel, F. W., Tremblay, C. J., Carter Esch, H., and Warde, A. M. (**2008b**). "Low frequency vocalizations attributed to sei whales (*Balaenoptera borealis*)," J. Acoust. Soc. Am., **124**, 1339–1349. doi:10.1121/1.2945155

Bennet-Clark, H. C. (**1971**). "Acoustics of Insect Song," Nature, **234**, 255–259. doi:10.1038/234255a0

Berchok, C. L., Bradley, D. L., and Gabrielson, T. B. (**2006**). "St Lawrence blue whale vocalizations revisited: Characterization of calls detected from 1998 to 2001," J. Acoust. Soc. Am., **120**, 2340–2354. doi:10.1121/1.2335676

Bernard, B., Madec, G., Penduff, T., Molines, J.-M., Treguier, A.-M., Le Sommer, J., Beckmann, A., et al. (**2006**). "Impact of partial steps and momentum advection schemes in a global ocean circulation model at eddy-permitting resolution," Ocean Dyn., **56**, 543–567. doi:10.1007/s10236-006-0082-1

Bérubé, M., Aguilar, A., Dendanto, D., Larsen, F., Notarbartolo Di Sciara, G., Sears, R., Sigurjónsson, J., et al. (**1998**). "Population genetic structure of North Atlantic, Mediterranean Sea and Sea of Cortez fin whales, *Balaenoptera physalus* (Linnaeus 1758): Analysis of mitochondrial and nuclear loci," Mol. Ecol., **7**, 585–599. doi:10.1046/j.1365-

294x.1998.00359.x

Bérubé, M., Urbán-Ramírez, J., Dizon, A. E., Brownell, R. L., and Palsbøll, P. J. (**2002**). “Genetic identification of a small and highly isolated population of fin whales (*Balaenoptera physalus*) in the Sea of Cortez, M´exico,” Conserv. Genet., **3**, 183–190. doi:10.1023/A

Di Bitetti, M. S. (**2003**). “Food-Associated Calls of Tufted Capuchin Monkeys (*Cebus apella nigritus*) Are Functionally Referential Signals,” Behaviour, **140**, 565–592. Retrieved from http://www.jstor.org/stable/4536046

Bittencourt, L., Barbosa, M., Secchi, E., and Azevedo, A. (**2016**). “Acoustic habitat of an oceanic archipelago in the Southwestern Atlantic,” Deep. Res. Part I Oceanogr. Res. Pap., **115**, 103–111. doi:10.1016/j.dsr.2016.06.001

Blair, H. B., Merchant, N. D., Friedlaender, A. S., Wiley, D. N., and Parks, S. E. (**2016**). “Evidence for ship noise impacts on humpback whale foraging behaviour,” Biol. Lett., **12**, 20160005. doi:10.1098/rsbl.2016.0005

Bohn, K. M., Smarsh, G. C., and Smotherman, M. (**2013**). “Social context evokes rapid changes in bat song syntax,” Anim. Behav., **85**, 1485–1491. doi:10.1016/j.anbehav.2013.04.002

Boisseau, O., Gillespie, D., Leaper, R., and Moscrop, A. (**2008**). “Blue (*Balaenoptera musculus*) and fin (B physalus) whale vocalisations measured from northern latitudes of the Atlantic Ocean,” J. Cetacean Res. Manag., **10**, 23–30.

Boncoraglio, G., and Saino, N. (**2007**). “Habitat structure and the evolution of bird song: A meta-analysis of the evidence for the acoustic adaptation hypothesis,” Funct. Ecol., **21**, 134–142. doi:10.1111/j.1365-2435.2006.01207.x

Bonferroni, C. E. (**1936**). “Teoria statistica delle classi e calcolo delle probabilità,” R Ist. Super. di Sci. Econ. e Commer. di Firenze,.

Bradbury, J. W., and Vehrencamp, S. L. (**1998**). *Principles of Animal Communication*, Sinauer.

Branch, T. A., Stafford, K. M., Palacios, D. M., Allison, C., Bannister, J. L., Burton, C. L. K., Cabrera, E., et al. (**2007**). “Past and present distribution, densities and movements of blue whales *Balaenoptera musculus* in the Southern Hemisphere and northern Indian Ocean,” Mamm. Rev., **37**, 116–175. doi:10.1111/j.1365-2907.2007.00106.x

Bridges, A. S., and Dorcas, M. E. (**2000**). “Temporal Variation in Anuran Calling Behavior: Implications for Surveys and Monitoring Programs,” Copeia, **2**, 587–592. doi:10.1643/0045-8511(2000)000

Brown, C. R., Brown, M. B., and Shaffer, M. L. (**1991**). “Food-sharing signals among socially foraging cliff swallows,” Anim. Behav., **42**, 551–564. doi:10.1016/S0003-3472(05)80239-8

Buchan, S. J., Stafford, K. M., and Hucke-Gaete, R. (**2015**). “Seasonal occurrence of southeast pacific blue whale songs in southern chile and the eastern tropical pacific,” Mar. Mammal Sci., **31**, 440–458. doi:10.1111/mms.12173

Burkhardt, E., Van Opzeeland, I., Cisewski, B., Mattmüller, R., Meister, M., Schall, E., Spiesecke, S., et al. (**2021**). “Seasonal and diel cycles of fin whale acoustic occurrence near Elephant Island, Antarctica,” R. Soc. Open Sci., **8**, 201142. doi:10.1098/rsos.201142

Burnham, R. E. (**2019**). “Fin Whale Call Presence and Type Used to Describe Temporal Distribution and Possible Area Use of Clayoquot Sound,” Northwest Sci., **93**, 66–74. doi:10.3955/046.093.0106

Burnham, R. E., Duffus, D. A., and Ross, T. (**2021**). “Remote sensing and mapping habitat features pertinent to fin whale life histories in coastal and offshore waters of Vancouver Island, British Columbia,” J. Exp. Mar. Bio. Ecol., **537**, 151511. doi:10.1016/j.jembe.2021.151511

Burtenshaw, J. C., Oleson, E. M., Hildebrand, J. A., McDonald, M. A., Andrew, R. K., Howe, B. M., and Mercer, J. A. (**2004**). “Acoustic and satellite remote sensing of blue whale seasonality and habitat in the Northeast Pacific,” Deep. Res. Part II Top. Stud. Oceanogr., **51**, 967–986. doi:10.1016/j.dsr2.2004.06.020

Calambokidis, J., Schorr, G. S., Steiger, G. H., Francis, J., Bakhtiari, M., Marshall, G., Oleson, E. M., et al. (**2007**). “Insights into the underwater diving, feeding, and calling behavior of blue whales from a suction-cup-attached video-imaging tag (CRITTERCAM),” Mar. Technol. Soc. J., **41**, 19–29. doi:10.4031/002533207787441980

Caldeira, R. M. A., and Reis, J. C. (**2017**). “The Azores Confluence Zone,” Front. Mar. Sci., **4**, 1–14. doi:10.3389/fmars.2017.00037

Calderan, S., Miller, B., Collins, K., Ensor, P., Double, M., Leaper, R., and Barlow, J. (**2014**). " Low-frequency vocalizations of sei whales (*Balaenoptera borealis*) in the Southern Ocean ," J. Acoust. Soc. Am., **136**, EL418–EL423. doi:10.1121/1.4902422

Calupca, T. A., Fristrup, K. M., and Clark, C. W. (**2000**). "A compact digital recording system for autonomous bio- acoustic monitoring," J. Acoust. Soc. Am., **108**, 2582–2582. Retrieved from https://doi.org/10.1121/1.4743595

Campbell, P., Pasch, B., Pino, J. L., Crino, O. L., Phillips, M., and Phelps, S. M. (**2010**). "Geographic variation in the songs of neotropical singing mice: Testing the relative importance of drift and local adaptation," Evolution (N. Y)., **64**, 1955–1972. doi:10.1111/j.1558-5646.2010.00962.x

Canese, S., Cardinali, A., Fortuna, C. M., Giusti, M., Lauriano, G., Salvati, E., and Greco, S. (**2006**). "The first identified winter feeding ground of fin whales (*Balaenoptera physalus*) in the Mediterranean Sea," J. Mar. Biol. Assoc. United Kingdom, **86**, 903–907. doi:10.1017/S0025315406013853

Cardoso, G. C., Atwell, J. W., Hu, Y., Ketterson, E. D., and Price, T. D. (**2012**). "No Correlation Between Three Selected Trade-Offs in Birdsong Performance and Male Quality for a Species With Song Repertoires," Ethology, **118**, 584–593. doi:10.1111/j.1439-0310.2012.02047.x

Castellote, M., Clark, C. W., and Lammers, M. O. (**2012**). "Acoustic and behavioural changes by fin whales (*Balaenoptera physalus*) in response to shipping and airgun noise," Biol. Conserv., **147**, 115–122. doi:10.1016/j.biocon.2011.12.021

Castellote, M., Clark, C. W., and Lammers, M. O. (**2012**). "Fin whale (*Balaenoptera physalus*) population identity in the western Mediterranean Sea," Mar. Mammal Sci., **28**, 325–344. doi:10.1111/j.1748-7692.2011.00491.x

Cerchio, S., and Dahlheim, M. (**2001**). "Variation in feeding vocalizations of humpback whales *Megaptera novaeangliae* from southeast Alaska," Bioacoustics, **11**, 277–295. doi:10.1080/09524622.2001.9753468

Chapman, N. R., and Price, A. (**2011**). "Low frequency deep ocean ambient noise trend in the Northeast Pacific Ocean," JASA Express Lett., **129**, 161–165. doi:10.1121/1.3567084

Charif, R. A., Waack, A. M., and Strickman, L. M. (**2010**). “Raven Pro 14 User’s Manual The Cornell Lab of Ornithology,.” Retrieved from https://ravensoundsoftware.com/software/raven-pro/

Charif, R. a, and Clark, C. W. (**2009**). *Acoustic monitoring of large whales in deep waters north and west of the British Isles: 1996-2005* Cornell Lab Ornithol.,Vol. 08, 40 pages. doi:10.1578/AM.35.3.2009.313

Cheney, D. L., and Seyfarth, R. M. (**2018**). “Flexible usage and social function in primate vocalizations,” Proc. Natl. Acad. Sci. U. S. A., **115**, 1974–1979. doi:10.1073/pnas.1717572115

Cholewiak, D., Clark, C. W., Ponirakis, D., Frankel, A., Hatch, L. T., Risch, D., Stanistreet, J. E., et al. (**2018**). “Communicating amidst the noise: Modeling the aggregate influence of ambient and vessel noise on baleen whale communication space in a national marine sanctuary,” Endanger. Species Res., **36**, 59–75. doi:10.3354/ESR00875

Cholewiak, D. M., Cerchio, S., Jacobsen, J. K., Urbán-R., J., and Clark, C. W. (**2018**). “Songbird dynamics under the sea: Acoustic interactions between humpback whales suggest song mediates male interactions,” R. Soc. Open Sci., **5**, 171298. doi:10.1098/rsos.171298

Clapham, P. J. (**2016**). “Managing leviathan: Conservation challenges for the great whales in a post-whaling world,” Oceanography, **29**, 214–225. doi:10.5670/oceanog.2016.70

Clark, C. W., Borsani, J. F., and Notarbartolo-Di-Sciara, G. (**2002**). “Vocal activity of fin whales, *Balaenoptera physalus*, in the Ligurian Sea,” Mar. Mammal Sci., **18**, 286–295. doi:10.1111/j.1748-7692.2002.tb01035.x

Clark, C. W., Ellison, W. T., Southall, B. L., Hatch, L., Van Parijs, S. M., Frankel, A., and Ponirakis, D. (**2009**). “Acoustic masking in marine ecosystems: Intuitions, analysis, and implication,” Mar. Ecol. Prog. Ser., **395**, 201–222. doi:10.3354/meps08402

Clay, Z., Smith, C. L., and Blumstein, D. T. (**2012**). “Food-associated vocalizations in mammals and birds: What do these calls really mean?,” Anim. Behav., **83**, 323–330. doi:10.1016/j.anbehav.2011.12.008

Collins, M. D. (**1993**). “A split-step Padé solution for the parabolic equation method,” J.

Acoust. Soc. Am., **93**, 1736–1742.

Collins, M. D. (**1995**). *User’s guide for RAM versions 1.0 and 1.0p* Washington, D.C.

Crance, J. L., Berchok, C. L., Bonnel, J., and Thode, A. M. (**2015**). “Northeasternmost record of a North Pacific fin whale (*Balaenoptera physalus*) in the Alaskan Chukchi Sea,” Polar Biol., **38**, 1767–1773. doi:10.1007/s00300-015-1719-7

Croll, A. D., Clark, C. W., Acevedo, A., Tershy, B., Flores, S., Gedamke, J., and Urban, J. (**2002**). “Only male fin whales sing loud songs,” Nature, **417**, 5–7. doi:10.1038/417809a

Croll, D. A., Acevedo-Gutiérrez, A., Tershy, B. R., and Urbán-Ramírez, J. (**2001**). “The diving behavior of blue and fin whales: Is dive duration shorter than expected based on oxygen stores?,” Comp. Biochem. Physiol. - A Mol. Integr. Physiol., **129**, 797–809. doi:10.1016/S1095-6433(01)00348-8

Currie, S. E., Boonman, A., Troxell, S., Yovel, Y., and Voigt, C. C. (**2020**). “Echolocation at high intensity imposes metabolic costs on flying bats,” Nat. Ecol. Evol., **4**, 1174–1177. doi:10.1038/s41559-020-1249-8

D’Vincent, C. G., Nilson, R. M., and Hanna, R. E. (**1985**). “Vocalization and coordinated feeding behavior of the humpback whale *Megaptera novaeangliae* in Southeastern Alaska, USA,” Sci. Reports Whale Res. Inst. Tokyo, **36**, 41–47.

Dahlheim, M., and Castellote, M. (**2016**). “Changes in the acoustic behavior of gray whales *Eschrichtius robustus* in response to noise,” Endanger. Species Res., **31**, 227–242. doi:10.3354/esr00759

Davidson, S. M., and Wilkinson, G. S. (**2002**). “Geographic and individual variation in vocalizations by male Saccopteryx bilineata (Chiroptera: Emballonuridae),” J. Mammal., **83**, 526–535. doi:10.1644/1545-1542(2002)083<0526:GAIVIV>2.0.CO;2

Davis, G. E., Baumgartner, M. F., Bonnell, J. M., Bell, J., Berchok, C., Bort Thornton, J., Brault, S., et al. (**2017**). “Long-term passive acoustic recordings track the changing distribution of North Atlantic right whales (*Eubalaena glacialis*) from 2004 to 2014,” Sci. Rep., **7**, 13460. doi:10.1038/s41598-017-13359-3

Davis, G. E., Baumgartner, M. F., Corkeron, P. J., Bell, J., Berchok, C., Bonnell, J. M., Bort

Thornton, J., et al. (**2020**). “Exploring movement patterns and changing distributions of baleen whales in the western North Atlantic using a decade of passive acoustic data,” Glob. Chang. Biol., **26**, 4812– 4840. doi:10.1111/gcb.15191

Dekeling, R. P. A., Tasker, M. L., Van der Graaf, A. J., Ainslie, M. ., Andersson, M. H., André, M., Borsani, J. F., et al. (**2014**). *Monitoring Guidance for Underwater Noise in European Seas, Part II: Monitoring Guidance Specifications, JRC Scientific and Policy Report EUR 26555 EN, Publications Office of the European Union, Luxembourg, 2014, doi: 10.2788/27158*, 49 pages. doi:10.2788/27158

Delarue, J., Todd, S. K., Van Parijs, S. M., and Di Iorio, L. (**2009**). “Geographic variation in Northwest Atlantic fin whale (*Balaenoptera physalus*) song: Implications for stock structure assessment,” J. Acoust. Soc. Am., **125**, 1774–1782. doi:10.1121/1.3068454

Demétrio, C. G. B., Hinde, J., and Moral, R. A. (**2014**). “Models for Overdispersed Data in Entomology,” In C. P. Ferreira and W. A. C. Godoy (Eds.), Ecol. Model. Appl. to Entomol., Springer-Verlag, pp. 219–259.

Dezecache, G., and Berthet, M. (**2018**). “Working hypotheses on the meaning of general alarm calls,” Anim. Behav., **142**, 113–118. doi:10.1016/j.anbehav.2018.06.008

Dingle, H., and Drake, A. V. (**2007**). “What is migration?,” Bioscience, **57**, 113–121. doi:10.1641/B570206

Dudzinski, K.A., Thomas, J.A. and Douaze, E. (**2009**). *Communication in Encyclopedia of Marine Mammals*, (W. F. Perrin, B. Wursig, and J. G. M. Thewissen, Eds.) Academic Press, San Diego, 2nd Editio., 248–268 pages.

Dunlop, R. A. (**2016**). “The effect of vessel noise on humpback whale, *Megaptera novaeangliae*, communication behaviour,” Anim. Behav., **111**, 13–21. doi:10.1016/j.anbehav.2015.10.002

Dziak, R. P., Bohnenstiehl, D. R., Stafford, K. M., Matsumoto, H., Park, M., Lee, W. S., Fowler, M. J., et al. (**2015**). “Sources and Levels of Ambient Ocean Sound near the Antarctic Peninsula,” PLoS One, **10**, e0123425. doi:10.1371/journal.pone.0123425

Edds-Walton, P. L. (**1997**). “Acoustic communication signals of mysticete whales,” Bioacoustics, **8**, 47–60. doi:10.1080/09524622.1997.9753353

Edds P. L. (**1982**). “Vocalizations of the Blue Whale, *Balaenoptera musculus*, in the St Lawrence River,” J. Mammal., **63**, 345–347.

Edds, P. L. (**1988**). “Characteristics of finback *Balaenoptera physalus* vocalisations in the St Lawrence Estuary,” Bioacoustics, **1**, 131–149. doi:10.1080/09524622.1988.9753087

Ellison, W. T., Southall, B. L., Clark, C. W., and Frankel, A. S. (**2012**). “A New Context-Based Approach to Assess Marine Mammal Behavioral Responses to Anthropogenic Sounds,” Conserv. Biol., **26**, 21–28. doi:10.1111/j.1523-1739.2011.01803.x

Erbe, C. (**2002**). “Hearing Abilities of Baleen Whales Defence R & D Canada,” Atlantic,.

Erbe, C., Marley, S. A., Schoeman, R. P., Smith, J. N., Trigg, L. E., and Embling, C. B. (**2019**). “The Effects of Ship Noise on Marine Mammals—A Review,” Front. Mar. Sci., **6**, 606. doi:10.3389/fmars.2019.00606

Erbe, C., Reichmuth, C., Cunningham, K., Lucke, K., and Dooling, R. (**2015**). “Communication masking in marine mammals: A review and research strategy,” Mar. Pollut. Bull., **103**, 15–38. doi:10.1016/j.marpolbul.2015.12.007

Escajeda, E., Stafford, K. M., Woodgate, R. A., and Laidre, K. L. (**2020**). “Variability in fin whale (*Balaenoptera physalus*) occurrence in the Bering Strait and southern Chukchi Sea in relation to environmental factors,” Deep. Res. Part II Top. Stud. Oceanogr., **177**, 104782. doi:10.1016/j.dsr2.2020.104782

Español-Jiménez, S., Bahamonde, P. A., Chiang, G., and Häussermann, V. (**2019**). “Discovering sounds in Patagonia: Characterizing sei whale (*Balaenoptera borealis*) downsweeps in the south-eastern Pacific Ocean,” Ocean Sci., **15**, 75–82. doi:10.5194/os-15-75-2019

Ey, E., and Fischer, J. (**2009**). “The ‘acoustic adaptation hypothesis’—a review of the evidence from birds, anurans and mammals,” Bioacoustics, **19**, 21–48. doi:10.1080/09524622.2009.9753613

Fox, C. G., Matsumoto, H., and Lau, T.-K. (**2001**). “Monitoring Pacific Ocean seismicity from an autonomous hydrophone array Christopher,” J. Geophys. Res., **106**, 4183–4206. doi:10.1533/9781782422723.41

Francois, R. E., and Garrison, R. G. (**1982**). “Sound absorption based on ocean measurements Part II: Boric acid contribution and equation for total absorption,” J. Acoust. Soc. Am., **72**, 1879–1890.

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,” Mar. Mammal Sci., **18**, 644–662. doi:10.1111/j.1748-7692.2002.tb01064.x

Garcia, H. A., Zhu, C., Schinault, M. E., Kaplan, A. I., Handegard, N. O., Godø, O. R., Ahonen, H., et al. (**2019**). “Temporal-spatial, spectral, and source level distributions of fin whale vocalizations in the Norwegian Sea observed with a coherent hydrophone array,” ICES J. Mar. Sci., **76**, 268–283. doi:10.1093/icesjms/fsy127

Garcia, M., and Favaro, L. (**2017**). “Animal vocal communication : function , structures , and production mechanisms,” Curr. Zool., **63**, 417–419. doi:10.1093/cz/zox040

Garland, E. C., Goldizen, A. W., Rekdahl, M. L., Constantine, R., Garrigue, C., Hauser, N. D., Poole, M. M., et al. (**2011**). “Dynamic horizontal cultural transmission of humpback whale song at the ocean basin scale,” Curr. Biol., **21**, 687–691. doi:10.1016/j.cub.2011.03.019

Garland, E. C., and McGregor, P. K. (**2020**). “Cultural Transmission, Evolution, and Revolution in Vocal Displays: Insights From Bird and Whale Song,” Front. Psychol., **11**, 544929. doi:10.3389/fpsyg.2020.544929

Gaten, E., Tarling, G., Dowse, H., Kyriacou, C., and Rosato, E. (**2008**). “Is vertical migration in Antarctic krill (*Euphausia superba*) influenced by an underlying circadian rhythm?,” J. Genet., **87**, 473–483. doi:10.1007/s12041-008-0070-y

Gauffier, P., Verborgh, P., Giménez, J., Esteban, R., Sierra, J. M. S., and De Stephanis, R. (**2018**). “Contemporary migration of fin whales through the Strait of Gibraltar,” Mar. Ecol. Prog. Ser., **588**, 215–228. doi:10.3354/meps12449

Gavrilchuk, K., Lesage, V., Ramp, C., Sears, R., Bérubé, M., Bearhop, S., and Beauplet, G. (**2014**). “Trophic niche partitioning among sympatric baleen whale species following the collapse of groundfish stocks in the Northwest Atlantic,” Mar. Ecol. Prog. Ser., **497**, 285–301. doi:10.3354/meps10578

Gavrilov, A. N., McCauley, R. D., and Gedamke, J. (**2012**). “Steady inter and intra-annual decrease in the vocalization frequency of Antarctic blue whales,” J. Acoust. Soc. Am., **131**, 4476–4480. doi:10.1121/1.4707425

Gavrilov, A. N., McCauley, R. D., Salgado-Kent, C., Tripovich, J., and Burton, C. (**2011**). “Vocal characteristics of pygmy blue whales and their change over time,” J. Acoust. Soc. Am., **130**, 3651–3660. doi:10.1121/1.3651817

Gedamke, J., and Robinson, S. M. (**2010**). “Acoustic survey for marine mammal occurrence and distribution off East Antarctica (30-80°E) in January-February 2006,” Deep. Res. Part II Top. Stud. Oceanogr., **57**, 968–981. doi:10.1016/j.dsr2.2008.10.042

Geijer, C. K. A., Notarbartolo di Sciara, G., and Panigada, S. (**2016**). “Mysticete migration revisited: are Mediterranean fin whales an anomaly?,” Mamm. Rev., **46**, 284–296. doi:10.1111/mam.12069

Giacomello, E., Menezes, G., and Bergstad, O. (**2013**). “An integrated approach for studying seamounts: CONDOR observatory,” Deep. Res. Part Ii-topical Stud. Oceanogr., **98**, 1–6.

Gillooly, J. F., and Ophir, A. G. (**2010**). “The energetic basis of acoustic communication,” Proc. R. Soc. B Biol. Sci., **277**, 1325–1331. doi:10.1098/rspb.2009.2134

Goldbogen, J. a., Cade, D., Calambokidis, J., Friedlaender, A. S., Potvin, J., Segre, P. S., and Werth, A. J. (**2017**). “How Baleen Whales Feed: The Biomechanics of Engulfment and Filtration,” Ann. Rev. Mar. Sci., **9**, annurev–marine–122414–033905. doi:10.1146/annurev-marine-122414-033905

Goldbogen, J. A., Calambokidis, J., Friedlaender, A. S., Francis, J., DeRuiter, S. L., Stimpert, A. K., Falcone, E., et al. (**2013**). “Underwater acrobatics by the world’s largest predator: 360° rolling manoeuvres by lunge-feeding blue whales,” Biol. Lett., **9**, 20120986. doi:10.1098/rsbl.2012.0986

Goldbogen, J. A., Calambokidis, J., Shadwick, R. E., Oleson, E. M., McDonald, M. A., and Hildebrand, J. A. (**2006**). “Kinematics of foraging dives and lunge-feeding in fin whales,” J. Exp. Biol., **209**, 1231–1244. doi:10.1242/jeb.02135

Grafe, T. U. (**1999**). “A function of synchronous chorusing and a novel female preference shift in an anuran," Proc. R. Soc. B Biol. Sci., **266**, 2331–2336. doi:10.1098/rspb.1999.0927

Green, D. B., Bestley, S., Trebilco, R., Corney, S. P., Lehodey, P., McMahon, C. R., Guinet, C., et al. (**2020**). "Modelled mid-trophic pelagic prey fields improve understanding of marine predator foraging behaviour," Ecography (Cop.)., **43**, 1014–1026. doi:10.1111/ecog.04939

Grémillet, D., Lewis, S., Drapeau, L., Van Der Lingen, C. D., Huggett, J. A., Coetzee, J. C., Verheye, H. M., et al. (**2008**). "Spatial match-mismatch in the Benguela upwelling zone: Should we expect chlorophyll and sea-surface temperature to predict marine predator distributions?," J. Appl. Ecol., **45**, 610–621. doi:10.1111/j.1365-2664.2007.01447.x

Gros-Louis, J. (**2004**). "The function of food-associated calls in white-faced capuchin monkeys, *Cebus capucinus*, from the perspective of the signaller," Anim. Behav., **67**, 431–440. doi:https://doi.org/10.1016/j.anbehav.2003.04.009

Guinet, C. (**1992**). "Predatory behaviour of killer whales (*Orcinus orca*) around the Crozet Islands," Can. J. Zool., **70**, 1656–1667. doi:10.1139/z92-231

Habib, L., Bayne, E. M., and Boutin, S. (**2007**). "Chronic industrial noise affects pairing success and age structure of ovenbirds Seiurus aurocapilla," J. Appl. Ecol., **44**, 176–184. doi:10.1111/j.1365-2664.2006.01234.x

Hall, M. L., Kingma, S. A., and Peters, A. (**2013**). "Male Songbird Indicates Body Size with Low-Pitched Advertising Songs," PLoS One, **8**, 1–5. doi:10.1371/journal.pone.0056717

Harvey, P. H., and Purvis, A. (**1991**). "Comparative methods for explaining adaptations," Nature, **351**, 619–624. doi:10.1038/351619a0

Hatch, L., Oceanic, N., Clark, C. W., Parijs, S. Van, and Oceanic, N. (**2012**). "Quantifying Loss of Acoustic Communication Space for Right Whales in and around a U S National," Conserv. Biol., **26**, 983–994. doi:10.1111/j.1523-1739.2012.01908.x

Hatch, L. T., and Clark, C. W. (**2004**). "Acoustic differentiation between fin whales in both the North Atlantic and North Pacific Oceans , and integration with genetic estimates of divergence," Pap. Present. to IWC Sci. Committee, Sorrento, Italy, July, **SC/56/SD6**, 1–37.

Helble, T. A., Guazzo, R. A., Alongi, G. C., Martin, C. R., Martin, S. W., and Henderson, E. E. (**2020**). “Fin Whale Song Patterns Shift Over Time in the Central North Pacific,” Front. Mar. Sci., **7**, 1–16. doi:10.3389/fmars.2020.587110

Herman, L. M. (**2016**). “The multiple functions of male song within the humpback whale (*Megaptera novaeangliae*) mating system: review, evaluation, and synthesis,” Biol. Rev., **92**, 1795–1818. doi:10.1111/brv.12309

Herman, L. M., Pack, A. a., Spitz, S. S., Herman, E. Y. K., Rose, K., Hakala, S., and Deakos, M. H. (**2013**). “Humpback whale song: Who sings?,” Behav. Ecol. Sociobiol., **67**, 1653–1663. doi:10.1007/s00265-013-1576-8

Herzing, D. L. (**1996**). “Vocalizations and associated underwater behavior of free-ranging Atlantic spotted dolphins, Stenella frontalis and bottlenose dolphins, *Tursiops truncatus*,” Aquat. Mamm., **22**, 61–79.

Hildebrand, J. A. (**2009**). “Anthropogenic and natural sources of ambient noise in the ocean,” Mar. Ecol. Prog. Ser., **395**, 5–20. doi:10.3354/meps08353

Ver Hoef, J. M., and Boveng, P. L. (**2007**). “Quasi-poisson vs negative binomial regression: How should we model overdispersed count data?,” Ecology, **88**, 2766–2772. doi:10.1890/07-0043.1

Hoffman, M. D., Garfield, N., and Bland, R. W. (**2010**). “Frequency synchronization of blue whale calls near Pioneer Seamount,” J. Acoust. Soc. Am., **128**, 490–494. doi:10.1121/1.3446099

Hood, J. D., Flogeras, D. G., and Theriault, J. a. (**2016**). “Improved passive acoustic band-limited energy detection for cetaceans,” Appl. Acoust., **106**, 36–41. doi:10.1016/j.apacoust.2015.12.011

Horwood, J. (**2009**). “Sei Whale: *Balaenoptera borealis*,” In W. F. Perrin, B. Würsig, and J. G. M. B. T.-E. of M. M. (Second E. Thewissen (Eds.), Academic Press, London, pp. 1001–1003. doi:https://doi.org/10.1016/B978-0-12-373553-9.00231-5

Hoskin, C. J., James, S., and Grigg, G. C. (**2009**). “Ecology and taxonomy-driven deviations in the frog call-body size relationship across the diverse Australian frog fauna,” J. Zool., **278**, 36–41. doi:10.1111/j.1469-7998.2009.00550.x

Huijser, L. A. E., Bérubé, M., Cabrera, A. A., Prieto, R., Silva, M. A., Robbins, J., Kanda, N., et al. (**2018**). "Population structure of North Atlantic and North Pacific sei whales (*Balaenoptera borealis*) inferred from mitochondrial control region DNA sequences and microsatellite genotypes," Conserv. Genet., **19**, 1007–1024. doi:10.1007/s10592-018-1076-5

Ilyina, T., Zeebe, R. E., and Brewer, P. G. (**2010**). "Future ocean increasingly transparent to low-frequency sound owing to carbon dioxideemissions," Nat. Geosci., **3**, 18–22. doi:10.1038/ngeo719

Ingebrigtsen A. (**1929**). "Whales captured in the North Atlantic and other seas," Rapp P-V Reun Cons Int Explor Mer, **56**, 1–26.

Di Iorio, L., and Clark, C. W. (**2010**). "Exposure to seismic survey alters blue whale acoustic communication," Biol. Lett., **6**, 334–335. doi:10.1098/rsbl.2009.0967

Irwin, D. E. (**2000**). "Song variation in an avian ring species," Evolution (N. Y)., **54**, 998–1010. doi:10.1111/j.0014-3820.2000.tb00099.x

Janik, V. M. (**2000**). "Food-related bray calls in wild bottlenose dolphins (*Tursiops truncatus*)," Proc. R. Soc. B Biol. Sci., **267**, 923–927. doi:10.1098/rspb.2000.1091

Janik, V. M. (**2014**). "Cetacean vocal learning and communication," Curr. Opin. Neurobiol., **28**, 60–65. doi:10.1016/j.conb.2014.06.010

Jefferson, T. A., Stacey, P. J., and Baird, R. W. (**1991**). "A review of Killer Whale interactions with other marine mammals: predation to co-existence," Mamm. Rev., **21**, 151–180. doi:10.1111/j.1365-2907.1991.tb00291.x

Job, J. R., Kohler, S. L., and Gill, S. A. (**2016**). "Song adjustments by an open habitat bird to anthropogenic noise, urban structure, and vegetation," Behav. Ecol., **27**, 1734–1744. doi:10.1093/beheco/arw105

John Richardson, W., Fraker, M. A., Würsig, B., and Wells, R. S. (**1985**). "Behaviour of Bowhead Whales *Balaena mysticetus* summering in the Beaufort Sea: Reactions to industrial activities," Biol. Conserv., **32**, 195–230. doi:https://doi.org/10.1016/0006-

3207(85)90111-9

Jolliffe, C. D., McCauley, R. D., Gavrilov, A. N., Jenner, C. S. K., Jenner, M. N. M., and Duncan, A. J. (**2019**). “Song variation of the South Eastern Indian Ocean pygmy blue whale population in the Perth Canyon, Western Australia,” PLoS One, **14**, 1–26. doi:10.1371/journal.pone.0208619

Judd, T. M., and Sherman, P. W. (**1996**). “Naked mole-rats recruit colony mates to food sources,” Anim. Behav., **52**, 957–969. doi:10.1006/anbe.1996.0244

Juliano, M. F., and Alves, M. L. G. R. (**2007**). “The atlantic subtropical front/current systems of Azores and St Helena,” J. Phys. Oceanogr., **37**, 2573–2598. doi:10.1175/2007JPO3150.1

Kamimura, M., and Tatsuki, S. (**1993**). “Diel rhythms of calling behavior and pheromone production of oriental tobacco budworm moth, *Helicoverpa assulta* (Lepidoptera: Noctuidae),” J. Chem. Ecol., **19**, 2953–2963. doi:10.1007/BF00980595

Kareiva, P., and Odell, G. (**1987**). “Swarms of predators exhibit ‘“preytaxis”’ if individual predators use area restricted search,” Am. Nat., **130**, 233–270.

Kellogg, R. (**1929**). “What is known of the migrations of some of the whalebone whales,” Smithson. Inst. Ann. Rep., **1929**, 467–494.

Kjeld, M. J. (**1992**). “Sex hormone concentrations in blood serum from the north Atlantic fin whale (*Balaenoptera physalus*),” J. Endocrinol., **134**, 405–413. doi:10.1677/joe.0.1340405.

Klinck, H., Nieukirk, S. L., and Mellinger, D. K. (**2012**). “Seasonal presence of cetaceans and ambient noise levels in polar waters of the North Atlantic,” JASA Express Lett., **132**, 176–181. doi:10.1121/1.4740226

Knowlton, A., Clark, C. W., and Kraus, S. (**1991**). “ Sounds recorded in the presence of sei whale, *Balaenoptera borealis* ,” J. Acoust. Soc. Am., **89**, 1968–1968. doi:10.1121/1.2029710

Kondo, N., and Watanabe, S. (**2009**). “Contact calls: Information and social function,” Jpn. Psychol. Res., **51**, 197–208. doi:10.1111/j.1468-5884.2009.00399.x

De Kort, S. R., Eldermire, E. R. B., Cramer, E. R. A., and Vehrencamp, S. L. (**2009**). “The deterrent effect of bird song in territory defense," Behav. Ecol., **20**, 200–206. doi:10.1093/beheco/arn135

Kowarski, K. A., and Moors-Murphy, H. (**2020**). "A review of big data analysis methods for baleen whale passive acoustic monitoring," Mar. Mammal Sci., **37**, 652– 673. doi:10.1111/mms.12758

Kroodsma, D. E., and Byers, B. E. (**1991**). "The function(s) of bird song," Integr. Comp. Biol., **31**, 318–328. doi:10.1093/icb/31.2.318

Laist, D. W., Knowlton, A. R., Mead, J. G., Collet, A. S., and Podesta, M. (**2001**). "Collisions between ships and whales," Mar. Mammal Sci., **17**, 35–75. doi:10.1111/j.1748-7692.2001.tb00980.x

Lambert, C., Mannocci, L., Lehodey, P., and Ridoux, V. (**2014**). "Predicting cetacean habitats from their energetic needs and the distribution of their prey in two contrasted tropical regions," PLoS One, **9**, e105958. doi:10.1371/journal.pone.0105958

Lammers, M. O., Brainard, R. E., Au, W. W. L., Mooney, T. A., and Wong, K. B. (**2008**). "An ecological acoustic recorder (EAR) for long-term monitoring of biological and anthropogenic sounds on coral reefs and other marine habitats," J. Acoust. Soc. Am., **123**, 1720–1728. doi:10.1121/1.2836780

Lascelles, B., Notarbartolo Di Sciara, G., Agardy, T., Cuttelod, A., Eckert, S., Glowka, L., Hoyt, E., et al. (**2014**). "Migratory marine species: Their status, threats and conservation management needs," Aquat. Conserv. Mar. Freshw. Ecosyst., **24**, 111–127. doi:10.1002/aqc.2512

Leca, J. B. (**2015**). "Arbitrary Cultural Behavior Patterns Are Not Unique to Humans," Curr. Anthropol., **56**, 112–113.

Lehodey, P., Conchon, A., Senina, I., Domokos, R., Calmettes, B., Jouanno, J., Hernandez, O., et al. (**2015**). "Optimization of a micronekton model with acoustic data," ICES J. Mar. Sci., **72**, 1399–1412. doi:10.1093/icesjms/fsu233

Lehodey, P., Murtugudde, R., and Senina, I. (**2010**). "Bridging the gap from ocean models to population dynamics of large marine predators: A model of mid-trophic functional groups," Prog. Oceanogr., **84**, 69–84. doi:10.1016/j.pocean.2009.09.008

Leroy, E. C., Royer, J. Y., Alling, A., Maslen, B., and Rogers, T. L. (**2021**). "Multiple pygmy blue whale acoustic populations in the Indian Ocean : whale song identifies a possible new population," Sci. Rep., **11**, 8762. doi:10.1038/s41598-021-88062-5

Leroy, E. C., Royer, J. Y., Bonnel, J., and Samaran, F. (**2018**). "Long-Term and Seasonal Changes of Large Whale Call Frequency in the Southern Indian Ocean," J. Geophys. Res. Ocean., **123**, 8568–8580. doi:10.1029/2018JC014352

Leroy, E. C., Samaran, F., Bonnel, J., and Royer, J.-Y. (**2016**). "Seasonal and Diel Vocalization Patterns of Antarctic Blue Whale (*Balaenoptera musculus intermedia*) in the Southern Indian Ocean: A Multi-Year and Multi-Site Study," PLoS One, **11**, e0163587. doi:10.1371/journal.pone.0163587

Lesage, V., Barrette, C., Kingsley, M. C. S., and Sjare, B. (**1999**). "The effect of vessel noise on the vocal behavior of belugas in the St Lawrence River estuary, Canada," Mar. Mammal Sci., **15**, 65–84. doi:10.1111/j.1748-7692.1999.tb00782.x

Lesage, V., Gavrilchuk, K., Andrews, R. D., and Sears, R. (**2017**). "Foraging areas, migratory movements and winter destinations of blue whales from the western North Atlantic," Endanger. Species Res., **34**, 27–43. doi:10.3354/esr00838

Levitus, S. (**1983**). "Climatological Atlas of the World Ocean," Eos, Trans. Am. Geophys. Union, **64**, 962–963. doi:https://doi.org/10.1029/EO064i049p00962-02

Lewis, L. A., Calambokidis, J., Stimpert, A. K., Fahlbusch, J., Friedlaender, A. S., McKenna, M. F., Mesnick, S. L., et al. (**2018**). "Context-dependent variability in blue whale acoustic behaviour," R. Soc. Open Sci., **5**, 180241. doi:10.1098/rsos.180241

Lockyer, C. (**1984**). "Review of baleen whale (Mysticeti) reproduction and implications for management," Int. Whal. Comm., **6**, 27–50.

Logue, D. M., and Leca, J. B. (**2020**). "Animal Culture: How a New Birdsong Went Viral," Curr. Biol., **30**, R957–R959. doi:10.1016/j.cub.2020.06.055

Lombard, É. (**1911**). "Le signe de l'élévation de la voix," Ann. des Mal. L'Oreille du Larynx, **XXXVII**, 101–109.

López, M. E. J., Palacios, D. M., Legorreta, A. J., Urbán, J. R., and Mate, B. R. (**2019**). “Fin whale movements in the Gulf of California, Mexico, from satellite telemetry,” PLoS One, **14**, e0209324. doi:10.1371/journal.pone.0209324

Lurton, X. (**2002**). *An Introduction to Underwater Acoustics: Principles and Applications*, Praxis publishing; UK.

Luther, D., and Baptista, L. (**2010**). “Urban noise and the cultural evolution of bird songs,” Proc. R. Soc. B Biol. Sci., **277**, 469–473. doi:10.1098/rspb.2009.1571

Lydersen, C., Garcia, J. V., Peter, M., Jørgensen, H., and Øien, N. (**2020**). “Autumn movements of fin whales (*Balaenoptera physalus*) from Svalbard , Norway , revealed by satellite tracking,” Sci. Rep., **10**, 16966. doi:10.1038/s41598-020-73996-z

Mahalanobis, C. P. (**1936**). “On the generalised distance in statistics,” Proc. Natl. Inst. Sci. India, **2**, 49–55.

Mahler, B., and Gil, D. (**2009**). *Chapter 2 The Evolution of Song in the Phylloscopus Leaf Warblers (Aves: Sylviidae). A Tale of Sexual Selection, Habitat Adaptation, and Morphological Constraints*, Adv. Study Behav., Elsevier Inc., 1st ed., Vol. 40, 35–66 pages. doi:10.1016/S0065-3454(09)40002-0

Malige, F., Patris, J., Buchan, S., Stafford, K. M., Shabangu, F., Findlay, K. P., Hucke-Gaete, R., et al. (**2020**). “Inter-annual decrease in pulse rate and peak frequency of Southeast Pacific blue whale song types,” Sci. Rep., **10**, 8121. doi:10.1038/s41598-020-64613-0

Marler, P. (**1957**). “Specific Distinctiveness in the Communication Signals of Birds,” Behaviour, **11**, 13–39.

Marler, P. (**2004**). “Bird Calls: Their Potential for Behavioral Neurobiology,” Ann. N. Y. Acad. Sci., **1016**, 31–44. doi:10.1196/annals.1298.034

Marques, T. a, Thomas, L., Martin, S. W., Mellinger, D. K., Ward, J. a, Moretti, D. J., Harris, D., et al. (**2013**). “Estimating animal population density using passive acoustics,” Biol. Rev. Camb. Philos. Soc., **88**, 287–309. doi:10.1111/brv.12001

Masina, S., Storto, A., Ferry, N., Valdivieso, M., Haines, K., Balmaseda, M., Zuo, H., et al. (**2017**). “An ensemble of eddy-permitting global ocean reanalyses from the MyOcean project,” Clim. Dyn., **49**, 813–841. doi:10.1007/s00382-015-2728-5

Mate, B. R., Lagerquist, B. A., and Calambokidis, J. (**1999**). “Movements of North Pacific blue whales during the feeding season off Southern California and their southern fall migration,” Mar. Mammal Sci., **15**, 1246–1527.

McCauley, R. D., Gavrilov, A. N., Jolliffe, C. D., Ward, R., and Gill, P. C. (**2018**). “Pygmy blue and Antarctic blue whale presence, distribution and population parameters in southern Australia based on passive acoustics,” Deep. Res. Part II Top. Stud. Oceanogr., **157**–**158**, 154–168. doi:10.1016/j.dsr2.2018.09.006

Mcdonald, M. A. (**1999**). “Passive acoustic methods applied to fin whale population density estimation,” J. Acoust. Soc. Am., **105**, 2643.

McDonald, M. A., Calambokidis, J., Teranishi, A. M., and Hildebrand, J. A. (**2001**). “The acoustic calls of blue whales off California with gender data,” J. Acoust. Soc. Am., **109**, 1728–1735. doi:10.1121/1.1353593

McDonald, M. A., Hildebrand, J. A., and Webb, S. C. (**1995**). “Blue and fin whales observed on a seafloor array in the Northeast Pacific,” J. Acoust. Soc. Am., **98**, 712–721. doi:10.1121/1.413565

McDonald, M. a., Hildebrand, J. a., and Wiggins, S. M. (**2006**). “Increases in deep ocean ambient noise in the Northeast Pacific west of San Nicolas Island, California,” J. Acoust. Soc. Am., **120**, 711–718. doi:10.1121/1.2216565

McDonald, M. a., Hildebrand, J. a., Wiggins, S. M., Thiele, D., Glasgow, D., and Moore, S. E. (**2005**). “Sei whale sounds recorded in the Antarctic,” J. Acoust. Soc. Am., **118**, 3941. doi:10.1121/1.2130944

McDonald, M. A., Mesnick, S. L., and Hildebrand, J. A. (**2006**). “Biogeographic characterisation of blue whale song worldwide: using song to identify populations,” J. Cetacean Res. Manag., **8**, 55–65. doi:10.1029/2006WR005124.DOI

McDonald, M., Hildebrand, J., and Mesnick, S. (**2009**). “Worldwide decline in tonal frequencies of blue whale songs,” Endanger. Species Res., **9**, 13–21. doi:10.3354/esr00217

McKenna, M. F. (**2011**). *Blue whale response to underwater noise from commercial ships*

University of California, San Diego, 215 pages.

Melcón, M. L., Cummins, A. J., Kerosky, S. M., Roche, L. K., Wiggins, S. M., and Hildebrand, J. A. (**2012**). "Blue whales respond to anthropogenic noise," PLoS One, **7**, 1–6. doi:10.1371/journal.pone.0032681

Mellinger, D. K., and Clark, C. W. (**2003**). "Blue whale (*Balaenoptera musculus*) sounds from the North Atlantic," J. Acoust. Soc. Am., **114**, 1108. doi:10.1121/1.1593066

Mellinger, D. K., Stafford, K. M., Moore, S. E., Dziak, R. P., and Matsumoto, H. (**2007**). "An overview of fixed passive acoustic observation methods for Cetaceans," Oceanography, **20**, 36–45. doi:10.5670/oceanog.2007.03

Merchant, N. D., Blondel, P., Dakin, D. T., and Dorocicz, J. (**2012**). "Averaging underwater noise levels for environmental assessment of shipping," J. Acoust. Soc. Am., **132**, EL343–EL349. doi:10.1121/1.4754429

Merchant, N. D., Fristrup, K. M., Johnson, M. P., Tyack, P. L., Matthew, J., Blondel, P., and Parks, S. E. (**2015**). "Measuring acoustic habitats," Methods Ecol. Evol., **6**, 257–265. doi:10.1111/2041-210X.12330

Merchant, N. D., Witt, M. J., Blondel, P., Godley, B. J., and Smith, G. H. (**2012**). "Assessing sound exposure from shipping in coastal waters using a single hydrophone and Automatic Identification System (AIS) data," Mar. Pollut. Bull., **64**, 1320–1329. doi:10.1016/j.marpolbul.2012.05.004

Miksis-Olds, J. L., Harris, D. V., and Mouw, C. (**2019**). "Interpreting fin whale (*Balaenoptera physalus*) call behavior in the context of environmental conditions," Aquat. Mamm., **45**, 691–705. doi:10.1578/AM.45.6.2019.691

Miksis-Olds, J. L., Nieukirk, S. L., and Harris, D. V. (**2018**). "Two unit analysis of Sri Lankan pygmy blue whale song over a decade," J. Acoust. Soc. Am., **144**, 3618–3626. doi:10.1121/1.5084269

Miller, P. J. O., Biassoni, N., Samuels, A., Tyack, P. L., Daniel, F., Rice, A. L., and Biology, C. (**2000**). "Whale songs lengthen in response to sonar," Nature, **405**, 903.

Mizroch, S. A., Rice, D. W., Zwiefelhofer, D., Waite, J., and Perryman, W. L. (**2009**).

"Distribution and movements of fin whales in the North Pacific Ocean," Mamm. Rev., **39**, 193–227. doi:10.1111/j.1365-2907.2009.00147.x

Mizroch, S. a, Rice, D. W., and Breiwick, J. M. (**1984**). "The Blue Whale , *Balaenoptera musculus*," Mar. Fish. Rev., **46**, 15–19.

Mobley, J. R., Herman, L. M., and Frankel, A. S. (**1988**). "Responses of wintering humpback whales (*Megaptera novaeangliae*) to playback of recordings of winter and summer vocalizations and of synthetic sound," Behav. Ecol. Sociobiol., **23**, 211–223. doi:10.1007/BF00302944

Montgomery, D. C., and Peck, E. A. (**1992**). *Introduction to linear regression analysis*, Willey, New York, 504 pages.

Moore, S. E., Stafford, K. M., Dahlheim, M. E., Fox, C. G., Braham, H. W., Polovina, J. J., and Bain, D. E. (**1998**). "Seasonal variation in reception of fin whale calls at five geographic areas in the north pacific," Mar. Mammal Sci., **14**, 617–627. doi:10.1111/j.1748-7692.1998.tb00749.x

Moore, S. E., Stafford, K. M., Mellinger, D. K., and Hildebrand, J. a. (**2006**). "Listening for Large Whales in the Offshore Waters of Alaska," Bioscience, **56**, 49. doi:10.1641/0006-3568(2006)056[0049:LFLWIT]2.0.CO;2

Morano, J. L., Salisbury, D. P., Rice, A. N., Conklin, K. L., Falk, K. L., and Clark, C. W. (**2012**). "Seasonal and geographical patterns of fin whale song in the western North Atlantic Ocean," J. Acoust. Soc. Am., **132**, 1207–1212. doi:10.1121/1.4730890

Morato, T., Machete, M., Kitchingman, A., Tempera, F., Lai, S., Menezes, G., Pitcher, T. J., et al. (**2008a**). "Abundance and distribution of seamounts in the Azores," Mar. Ecol. Prog. Ser., **357**, 17–21. doi:10.3354/meps07268

Morato, T., Varkey, D. A., Damaso, C., Machete, M., Santos, M., Prieto, R., Santos, R. S., et al. (**2008b**). "Evidence of a seamount effect on aggregating visitors," Mar. Ecol. Prog. Ser., **357**, 23–32. doi:10.3354/meps07269

Morganand, T. J. H., and Laland, K. N. (**2012**). "The biological bases of conformity," Front. Neurosci., **6**, 1–7. doi:10.3389/fnins.2012.00087

Moseley, D. L., Lahti, D. C., and Podos, J. (**2013**). “Responses to song playback vary with the vocal performance of both signal senders and receivers,” Proc. R. Soc. B Biol. Sci., **280**, 20131401. doi:10.1098/rspb.2013.1401

Mundinger, P. C. (**1980**). “Animal cultures and a general theory of cultural evolution,” Ethol. Sociobiol., **1**, 183–223. doi:https://doi.org/10.1016/0162-3095(80)90008-4

National Research Council (**2005**). *Marine Mammal Populations and Ocean Noise: Determining When Noise Causes Biologically Significant Effects*, The National Academies Press, Washington, DC. doi:10.17226/11147

Nieukirk, S. L., Mellinger, D. K., Dziak, R. P., Matsumoto, H., and Klinck, H. (**2020**). “Multi-year occurrence of sei whale calls in North Atlantic polar waters,” J. Acoust. Soc. Am., **147**, 1842–1850. doi:10.1121/10.0000931

Nieukirk, S. L., Mellinger, D. K., Moore, S. E., Klinck, K., Dziak, R. P., and Goslin, J. (**2012**). “Sounds from airguns and fin whales recorded in the mid-Atlantic Ocean, 1999–2009,” J. Acoust. Soc. Am., **131**, 1102–1112. doi:10.1121/1.3672648

Nieukirk, S. L., Stafford, K. M., Mellinger, D. K., Dziak, R. P., and Fox, C. G. (**2004**). “Low-frequency whale and seismic airgun sounds recorded in the mid-Atlantic Ocean,” J. Acoust. Soc. Am., **115**, 1832. doi:10.1121/1.1675816

Noad, M. J., Cato, D. H., Bryden, M. M., Jenner, M.-N., and Jenner, K. C. S. (**2000**). “Cultural revolution in whale songs,” Nature, **408**, 537–537. doi:10.1038/35046199

Nowacek, D. P., Christiansen, F., Bejder, L., Goldbogen, J. A., and Friedlaender, A. S. (**2016**). “Studying cetacean behaviour: new technological approaches and conservation applications,” Anim. Behav., **120**, 235–244. doi:10.1016/j.anbehav.2016.07.019

Nowacek, D. P., Thorne, L. H., Johnston, D. W., and Tyack, P. L. (**2007**). “Responses of cetaceans to anthropogenic noise,” Mamm. Rev., **37**, 81–115. doi:10.1111/j.1365-2907.2007.00104.x

Nowicki, S., and Searcy, W. A. (**2004**). “Song function and the evolution of female preferences: Why birds sing, why brains matter,” Ann. N. Y. Acad. Sci., **1016**, 704–723. doi:10.1196/annals.1298.012

Oestreich, W. K., Fahlbusch, J. A., Cade, D. E., Southall, B. L., Goldbogen, J. A., Ryan, J. P., Oestreich, W. K., et al. (**2020**). “Animal-Borne Metrics Enable Acoustic Detection of Blue Whale Migration,” Curr. Biol., **30**, 1–7. doi:10.1016/j.cub.2020.08.105

Ohsumi, S., Nishiwaki, M., and Hibiya, T. (**1958**). “Growth of fin whale in the Northern Pacific,” Sci. Reports Whales Res. Inst., **13**, 97–133.

Oleson, E., Calambokidis, J., Burgess, W., McDonald, M., LeDuc, C., and Hildebrand, J. (**2007a**). “Behavioral context of call production by eastern North Pacific blue whales,” Mar. Ecol. Prog. Ser., **330**, 269–284. doi:10.3354/meps330269

Oleson, E. M., Širović, A., Bayless, A. R., and Hildebr, J. A. (**2014**). “Synchronous seasonal change in fin whale song in the North Pacific,” PLoS One, **9**, 1–18. doi:10.1371/journal.pone.0115678

Oleson, E. M., Wiggins, S. M., and Hildebrand, J. A. (**2007b**). “Temporal separation of blue whale call types on a southern California feeding ground,” Anim. Behav., **74**, 881–894. doi:10.1016/j.anbehav.2007.01.022

Olsen, E., Budgell, W. P., Head, E., Kleivane, L., Nøttestad, L., Prieto, R., Silva, M. A., et al. (**2009**). “First satellite-tracked long-distance movement of a sei whale (*Balaenoptera borealis*) in the North Atlantic,” Aquat. Mamm., **35**, 313–318. doi:10.1578/AM.35.3.2009.313

Otte, D. (**1992**). “Evolution of cricket songs,” J. Orthoptera Res., **1**, 25–49.

Otter, K. A., Mckenna, A., LaZerte, S. E., and Ramsay, S. M. (**2020**). “Continent-wide Shifts in Song Dialects of White-Throated Sparrows,” Curr. Biol., **30**, 3231-3235.e3. doi:10.1016/j.cub.2020.05.084

Van Parijs, S. M., Clark, C. W., Sousa-Lima, R. S., Parks, S. E., Rankin, S., Risch, D., and Van Opzeeland, I. C. (**2009**). “Management and research applications of real-time and archival passive acoustic sensors over varying temporal and spatial scales,” Mar. Ecol. Prog. Ser., **395**, 21–36. doi:10.3354/meps08123

Parks, S. E., Clark, C. W., and Tyack, P. L. (**2007**). “Short- and long-term changes in right whale calling behavior: the potential effects of noise on acoustic communication,” J. Acoust.

Soc. Am., **122**, 3725–3731. doi:10.1121/1.2799904

Parks, S. E., Johnson, M., Nowacek, D., and Tyack, P. L. (**2010**). “Individual right whales call louder in increased environmental noise Subject collect,” Biol. Lett., **7**, 33–35.

Parks, S. E., and Tyack, P. L. (**2005**). “Sound production by North Atlantic right whales (*Eubalaena glacialis*) in surface active groups,” J. Acoust. Soc. Am., **117**, 3297–3306. doi:10.1121/1.1882946

Parks, S. E., Urazghildiiev, I., and Clark, C. W. (**2009**). “Variability in ambient noise levels and call parameters of North Atlantic right whales in three habitat areas,” J Acoust Soc Am, **125**, 1230–1239. doi:10.1121/1.3050282

Payne, K., and Payne, R. (**1985**). “Large Scale Changes over 19 Years in Songs of Humpback Whales in Bermuda,” Z. Tierpsychol., **68**, 89–114. doi:https://doi.org/10.1111/j.1439-0310.1985.tb00118.x

Payne, K., Tyack, P., and Payne, R. S. (**1983**). “Progressive changes in the songs of humpback whales *Megaptera novaeangliae* : A detailed analysis of two seasons in Hawaii,” In R. Payne (Ed.), Commun. Behav. whales, Boulder, Colorado:Westview Press, Westview, Boulder, CO., pp. 9–57.

Payne, R. S., and McVay, S. (**1971**). “Songs of Humpback Whales,” Science (80-.)., **173**, 585–597. doi:10.1126/science.173.3997.585

Payne, R., and Webb, D. (**1971**). “Orientation By Means of Long Range Acoustic Signaling in Baleen Whales,” Ann. N. Y. Acad. Sci., **188**, 110–141. doi:10.1111/j.1749-6632.1971.tb13093.x

Pen, O., Fournet, M. E. H., Matthews, L. P., Gabriele, C. M., Haver, S., Mellinger, D. K., and Klinck, H. (**2018**). “Humpback whales *Megaptera novaeangliae* alter calling behavior in response to natural sounds and vessel noise,” Mar. Ecol. Prog. Ser., **607**, 251–268.

Pereira, A., Harris, D., Tyack, P., and Matias, L. (**2020**). “Fin whale acoustic presence and song characteristics in seas to the southwest of Portugal,” J Acoust Soc Am, **147**, 2235–2249. doi:10.1121/10.0001066

Pérez-Jorge, S., Tobeña, M., Prieto, R., Vandeperre, F., Calmettes, B., Lehodey, P., and Silva,

M. A. (**2020**). “Environmental drivers of large-scale movements of baleen whales in the mid-North Atlantic Ocean,” Divers. Distrib., **26**, 1–16. doi:10.1111/ddi.13038

Pirotta, E., Booth, C. G., Calambokidis, J., Costa, D. P., Fahlbusch, J. A., Friedlaender, A. S., Goldbogen, J. A., et al. (**2022**). “From individual responses to population effects: Integrating a decade of multidisciplinary research on blue whales and sonar,” Anim. Conserv., , doi: 10.1111/acv.12785. doi:10.1111/acv.12785

Podos, J., Huber, S. K., and Taft, B. (**2004**). “Bird song: The interface of evolution and mechanism,” Annu. Rev. Ecol. Evol. Syst., **35**, 55–87. doi:10.1146/annurev.ecolsys.35.021103.105719

Podos, J., and Warren, P. S. (**2007**). “The Evolution of Geographic Variation in Birdsong,” Adv. Study Behav., **37**, 403–458. doi:10.1016/S0065-3454(07)37009-5

Ponce, D., Thode, A. M., Guerra, M., Urbán R., J., and Swartz, S. (**2012**). “ Relationship between visual counts and call detection rates of gray whales (*Eschrichtius robustus*) in Laguna San Ignacio, Mexico ,” J. Acoust. Soc. Am., **131**, 2700–2713. doi:10.1121/1.3689851

Prieto, R., Janiger, D., Silva, M. A., Waring, G. T., and Gonçalves, J. M. (**2012**). “The forgotten whale: A bibliometric analysis and literature review of the North Atlantic sei whale *Balaenoptera borealis*,” Mamm. Rev., **42**, 235–272. doi:10.1111/j.1365-2907.2011.00195.x

Prieto, R., Silva, M. A., Waring, G. T., and Gonçalves, J. M. A. (**2014**). “Sei whale movements and behaviour in the North Atlantic inferred from satellite telemetry,” Endanger. Species Res., **26**, 103–113. doi:10.3354/esr00630

Prieto, R., Tobeña, M., and Silva, M. A. (**2017**). “Habitat preferences of baleen whales in a mid-latitude habitat,” Deep. Res. Part II Top. Stud. Oceanogr., **141**, 155–167. doi:10.1016/j.dsr2.2016.07.015

Ptacek, M. B. (**2000**). “The role of mating preferences in shaping interspecific divergence in mating signals in vertebrates,” Behav. Processes, **51**, 111–134. doi:https://doi.org/10.1016/S0376-6357(00)00123-6

Putland, R. L., Merchant, N. D., Farcas, A., and Radford, C. A. (**2018**). “Vessel noise cuts down communication space for vocalizing fish and marine mammals,” Glob. Chang. Biol., **24**, 1708–1721. doi:10.1111/gcb.13996

R Core team (**2021**). “R: A language and environment for statistical computing R Foundation for Statistical Computing, Vienna, Austria.,” Retrieved from https://www.r-project.org/

Rankin, S., and Barlow, J. A. Y. (**2007**). “Vocalisations of the sei whale *Balaenoptera borealis* off the Hawaiian Islands,” Bioacoustics, **16**, 137–145.

Redfern, J. V, Ferguson, M. C., Becker, E. A., Hyrenbach, K. D., Good, C., Barlow, J., Kaschner, K., et al. (**2006**). “Techniques for cetacean – habitat modeling,” Mar. Ecol. Prog. Ser., **310**, 271–295.

Reeves, R. R., McClellan, K., and Werner, T. B. (**2013**). “Marine mammal bycatch in gillnet and other entangling net fisheries, 1990 to 2011,” Endanger. Species Res., **20**, 71–97. doi:10.3354/esr00481

Reeves, R. R., Smith, T. D., Josephson, E. a., Clapham, P. J., and Woolmer, G. (**2004**). “Historical Observations of Humpback and Blue Whales in the North Atlantic Ocean: Clues To Migratory Routes and Possibly Additional Feeding Grounds,” Mar. Mammal Sci., **20**, 774–786. doi:10.1111/j.1748-7692.2004.tb01192.x

Rendell, L., and Whitehead, H. (**2001**). “Culture in whales and dolphins,” Behav. Brain Sci., **24**, 309–382. doi:10.1016/B978-0-12-373553-9.00068-7

Ressurreição, A., and Giacomello, E. (**2013**). “Quantifying the direct use value of Condor seamount,” Deep. Res. Part II Top. Stud. Oceanogr., **98**, 209–217. doi:10.1016/j.dsr2.2013.08.005

Richards, D. G., Wolz, J. P., and Herman, L. M. (**1984**). “Vocal mimicry of computer-generated sounds and vocal labeling of objects by a bottlenosed dolphin, *Tursiops truncatus*,” J. Comp. Psychol., **98**, 10–28. doi:10.1037/0735-7036.98.1.10

Richardson, W. J., Greene, C. R., Malme, C. I., and Thomson, D. H. (**1995**). *Marine mammals and noise*, Academaic Press, San Diego: CA.

Richardson, W. J., Greene, C. R., Malme, C. I., and Thomson, D. H. (**1995**). “CHAPTER 7 - MARINE MAMMAL SOUNDS11By Denis H Thomson and W John Richardson, LGL Ltd,” In

W. J. Richardson, C. R. Greene, C. I. Malme, and D. H. B. T.-M. M. and N. Thomson (Eds.), Mar. Mamm. noise, Academic Press, San Diego, pp. 159–204. doi:https://doi.org/10.1016/B978-0-08-057303-8.50010-0

Richardson, W. J., and Würsig, B. (**1997**). "Influences of man - made noise and other human actions on cetacean behaviour," Mar. Freshw. Behav. Phy, **29**, 183–209. doi:10.1080/10236249709379006

Roch, M. a., Batchelor, H., Baumann-Pickering, S., Berchok, C. L., Cholewiak, D., Fujioka, E., Garland, E. C., et al. (**2016**). "Management of acoustic metadata for bioacoustics," Ecol. Inform., **31**, 122–136. doi:10.1016/j.ecoinf.2015.12.002

Rolland, R. M., Parks, S. E., Hunt, K. E., Castellote, M., Corkeron, P. J., Nowacek, D. P., Wasser, S. K., et al. (**2012**). "Evidence that ship noise increases stress in right whales," Proc. R. Soc. B Biol. Sci., **279**, 2363–2368. doi:10.1098/rspb.2011.2429

Romagosa, M., Baumgartner, M., Cascão, I., Lammers, M. O., Marques, T. A., Santos, R. S., and Silva, M. A. (**2020**). "Baleen whale acoustic presence and behaviour at a Mid-Atlantic migratory habitat, the Azores Archipelago," Sci. Rep., **10**, 1–11. doi:10.1038/s41598-020-61849-8

Romagosa, M., Boisseau, O., Cucknell, A.-C., Moscrop, A., and McLanaghan, R. (**2015**). "Source level estimates for sei whale (*Balaenoptera borealis*) vocalizations off the Azores," J. Acoust. Soc. Am., **138**, 2367–2372. doi:10.1121/1.4930900

Romagosa, M., Cascão, I., Merchant, N. D., Lammers, M. O., Giacomello, E., Marques, T. A., and Silva, M. A. (**2017**). "Underwater Ambient Noise in a Baleen Whale Migratory Habitat Off the Azores," Front. Mar. Sci., **4**, 1–14. doi:10.3389/fmars.2017.00109

Romagosa, M., Cascão, I., and Silva, M. A. (**2020**). "Underwater noise levels and shipping off the Faial-Pico channel, Azores, in relation to the acoustic presence of baleen whales," Acústica 2020/XI Congr. Ibérico Acústica/51º Congr. Esp. Acústica - Tec. 2020. Online Ed. 21-23 October, 2020, 1–9.

Ross, D. (**1976**). "Chapter 8 - Propeller cavitation noise," In D. B. T.-M. of U. N. ROSS (Ed.), Pergamon, pp. 253–287. doi:https://doi.org/10.1016/B978-0-08-021182-4.50014-3

Ross, D. (**2005**). “Ship sources of ambient noise,” IEEE J. Ocean. Eng., **30**, 257–261. doi:10.1109/JOE.2005.850879

Samaran, F., Adam, O., and Guinet, C. (**2010**). “Detection range modeling of blue whale calls in Southwestern Indian Ocean,” Appl. Acoust., **71**, 1099–1106. doi:10.1016/j.apacoust.2010.05.014

Samaran, F., Stafford, K. M., Branch, T. a, Gedamke, J., Royer, J.-Y., Dziak, R. P., and Guinet, C. (**2013**). “Seasonal and geographic variation of southern blue whale subspecies in the Indian Ocean,” PLoS One, **8**, e71561. doi:10.1371/journal.pone.0071561

Santora, J. a, Sydeman, W. J., Schroeder, I. D., Reiss, C. S., Wells, B. K., Field, J. C., Cossio, A. M., et al. (**2012**). “Krill space: a comparative assessment of mesoscale structuring in polar and temperate marine ecosystems,” ICES J. Mar. Sci., **69**, 1317–1327.

Santos, M., Moita, M. T., Bashmachnikov, I., Menezes, G. M., Carmo, V., Loureiro, C. M., Mendonça, A., et al. (**2013**). “Phytoplankton variability and oceanographic conditions at Condor seamount, Azores (NE Atlantic),” Deep. Res. Part II Top. Stud. Oceanogr., **98**, 52–62. doi:10.1016/j.dsr2.2013.05.037

Santos, R. S., Hawkins, S., Monteiro, L. R., Alves, M., and Isidro, E. J. (**1995**). “Marine research, resources and conservation in the Azores,” Aquat. Conserv. Mar. Freshw. Ecosyst., **5**, 311–354. doi:10.1002/aqc.3270050406

Schall, E., Di Iorio, L., Berchok, C., Filún, D., Bedriñana-Romano, L., Buchan, S. J., Van Opzeeland, I., et al. (**2020**). “Visual and passive acoustic observations of blue whale trios from two distinct populations,” Mar. Mammal Sci., **36**, 365–374. doi:10.1111/mms.12643

Von Schuckmann, K., Le Traon, P.-Y., Smith, N., Pascual, A., Djavidnia, S., Gattuso, J.-P., Grégoire, M., et al. (**2020**). “Copernicus Marine Service Ocean State Report, Issue 4,” J. Oper. Oceanogr., **13**, S1–S172. doi:10.1080/1755876X.2020.1785097

Schwartz, J. J. (**1994**). “Male advertisement and female choice in frogs: Recent findings and new approaches to the study of communication in a dynamic acoustic environment,” Integr. Comp. Biol., **34**, 616–624. doi:10.1093/icb/34.6.616

Searcy, W. A., and Andersson, M. (**1986**). “Sexual selection and the evolution of song,” Annu. Rev. Ecol. Syst., **17**, 507–533. doi:10.1146/annurev.es.17.110186.002451

Sears, R., and Perrin, W. F. (**2009**). “Blue Whale: *Balaenoptera musculus*,” In W. F. Perrin, B. Würsig, and J. G. M. B. T.-E. of M. M. (Second E. Thewissen (Eds.), Academic Press, London, pp. 120–124. doi:https://doi.org/10.1016/B978-0-12-373553-9.00033-X

Sears, R., Vikingsson, G., Santos, R., Steiner, L., Silva, M., and Ramp, C. (**2015**). “Comparison of northwest Atlantic (NWA) and northeast Atlantic (NEA) blue whale (*Balaenoptera musculus*) photo-identification catalogues,” 21st Bienn. Conf. Biol. Mar. Mamm., 13-18 December, 2015. San Francisco CA.

Senina, I., Lehodey, P., Sibert, J., and Hampton, J. (**2020**). “Improving predictions of a spatially explicit fish population dynamics model using tagging data,” Can. Jorunal Aquat. Fish. Sci., **77**, 576–593. doi:https://doi.org/10.1139/cjfas-2018-0470

Shabangu, F. W., Andrew, R. K., Yemane, D., and Findlay, K. P. (**2020**). “Acoustic seasonality, behaviour and detection ranges of Antarctic blue and fin whales under different sea ice conditions off Antarctica,” Endanger. Species Res., **43**, 21–37. doi:10.3354/esr01050

Shabangu, F. W., Findlay, K. P., Yemane, D., Stafford, K. M., van den Berg, M., Blows, B., and Andrew, R. K. (**2019**). “Seasonal occurrence and diel calling behaviour of Antarctic blue whales and fin whales in relation to environmental conditions off the west coast of South Africa,” J. Mar. Syst., **190**, 25–39. doi:10.1016/j.jmarsys.2018.11.002

Shabangu, F. W., Findlay, K. P., Yemane, D., Stafford, K. M., van den Berg, M., Blows, B., and Andrew, R. K. (**2019**). “Seasonal occurrence and diel calling behaviour of Antarctic blue whales and fin whales in relation to environmental conditions off the west coast of South Africa,” J. Mar. Syst., **190**, 25–39. doi:10.1016/j.jmarsys.2018.11.002

Shabangu, F. W., Yemane, D., Stafford, K. M., Ensor, P., and Findlay, K. P. (**2017**). “Modelling the effects of environmental conditions on the acoustic occurrence and behaviour of Antarctic blue whales,” PLoS One, **12**, e0172705. doi:10.1371/journal.pone.0172705

Sibert, J., Senina, I., Lehodey, P., and Hampton, J. (**2012**). “Shifting from marine reserves to maritime zoning for conservation of Pacific bigeye tuna (*Thunnus obesus*),” Proc. Natl. Acad. Sci. U. S. A., **109**, 18221–18225. doi:10.1073/pnas.1209468109

Sigurjónsson, J., and Víkingsson, G. A. (**1997**). “Seasonal abundance of the estimated food consumption by cetaceans in Icelandic and adjacent waters,” J. Northwest Atl. Fish. Sci., **22**, 271–287. doi:10.2960/J.v22.a20

Silva, M. A., Borrell, A., Prieto, R., Gauffier, P., Bérubé, M., Palsbøl, P. J., and Colaço, A. (**2019**). “Stable isotopes reveal winter feeding in different habitats in blue, fin and sei whales migrating through the Azores,” R. Soc. Open Sci., **6**, 181800. doi:10.1098/rsos.181800

Silva, M. A., Prieto, R., Cascão, I., Oliveira, C., Vaz, J., Lammers, M., Jonsen, I., et al. (**2011**). “Fin whale migration in the North Atlantic : placing the Azores into the big picture,” 19th Bienn. Conf. Biol. Mar. Mamm., Tampa, FLorida, USA.

Silva, M. A., Prieto, R., Cascão, I., Seabra, M. I., Machete, M., Baumgartner, M. F., and Santos, R. S. (**2014**). “Spatial and temporal distribution of cetaceans in the mid-Atlantic waters around the Azores,” Mar. Biol. Res., **10**, 123–137. doi:10.1080/17451000.2013.793814

Silva, M. a, Prieto, R., Jonsen, I., Baumgartner, M. F., and Santos, R. S. (**2013**). “North Atlantic blue and fin whales suspend their spring migration to forage in middle latitudes: building up energy reserves for the journey?,” PLoS One, **8**, e76507. doi:10.1371/journal.pone.0076507

Silva, S. D. M. M. F. da (**2017**). *Strain partitioning and the seismicity distribution within a transpressive plate boundary: SW Iberia-NW Nubia* University of Lisbon.

Simmons, L. W., Zuk, M., and Rotenberry, J. T. (**2001**). “Geographic variation in female preference functions and male songs of the field cricket Teleogryllus oceanicus,” Evolution (N. Y)., **55**, 1386–1394. doi:10.1111/j.0014-3820.2001.tb00660.x

Simon, M., Stafford, K. M., Beedholm, K., Lee, C. M., and Madsen, P. T. (**2010**). “Singing behavior of fin whales in the Davis Strait with implications for mating, migration and foraging,” J. Acoust. Soc. Am., **128**, 3200–3210. doi:10.1121/1.3495946

Širović, A., and Hildebrand, J. A. (**2011**). “Using passive acoustics to model blue whale habitat off the Western Antarctic Peninsula,” Deep. Res. Part II Top. Stud. Oceanogr., **58**, 1719–1728. doi:10.1016/j.dsr2.2010.08.019

Širović, A., Hildebrand, J. a., and McDonald, M. a. (**2016**). “Ocean ambient sound south of

Bermuda and Panama Canal traffic," J. Acoust. Soc. Am., **139**, 2417–2423. doi:10.1121/1.4947517

Širović, A., Hildebrand, J. A., and Wiggins, S. M. (**2007**). "Blue and fin whale call source levels and propagation range in the Southern Ocean," J. Acoust. Soc. Am., **122**, 1208–1215. doi:10.1121/1.2749452

Širović, A., Hildebrand, J. A., Wiggins, S. M., McDonald, M. A., Moore, S. E., and Thiele, D. (**2004**). "Seasonality of blue and fin whale calls and the influence of sea ice in the Western Antarctic Peninsula," Deep. Res. Part II Top. Stud. Oceanogr., **51**, 2327–2344. doi:10.1016/j.dsr2.2004.08.005

Širović, A., Hildebrand, J. A., Wiggins, S. M., and Thiele, D. (**2009**). "Blue and fin whale acoustic presence around Antarctica during 2003 and 2004," Mar. Mammal Sci., **25**, 125–136. doi:10.1111/j.1748-7692.2008.00239.x

Širović, A., Oleson, E. M., Buccowich, J., Rice, A., and Bayless, A. R. (**2017**). "Fin whale song variability in southern California and the Gulf of California," Sci. Rep., **7**, 1–11. doi:10.1038/s41598-017-09979-4

Širović, A., Rice, A., Chou, E., Hildebrand, J. A., Wiggins, S. M., and Roch, M. A. (**2015**). "Seven years of blue and fin whale call abundance in the Southern California Bight," Endanger. Species Res., **28**, 61–76. doi:10.3354/esr00676

Širović, A., Williams, L. N., Kerosky, S. M., Wiggins, S. M., and Hildebrand, J. A. (**2013**). "Temporal separation of two fin whale call types across the eastern North Pacific," Mar. Biol., **160**, 47–57. doi:10.1007/s00227-012-2061-z

Slabbekoorn, H., and Ripmeester, E. A. P. (**2008**). "Birdsong and anthropogenic noise: Implications and applications for conservation," Mol. Ecol., **17**, 72–83. doi:10.1111/j.1365-294X.2007.03487.x

Slocombe, K. E., Kaller, T., Turman, L., Townsend, S. W., Papworth, S., Squibbs, P., and Zuberbühler, K. (**2010**). "Production of food-associated calls in wild male chimpanzees is dependent on the composition of the audience," Behav. Ecol. Sociobiol., **64**, 1959–1966. doi:10.1007/s00265-010-1006-0

Smith, J. N., Goldizen, A. W., Dunlop, R. A., and Noad, M. J. (**2008**). “Songs of male humpback whales, *Megaptera novaeangliae*, are involved in intersexual interactions,” Anim. Behav., **76**, 467–477. doi:10.1016/j.anbehav.2008.02.013

Soares, C., Zabel, F., Silva, A., and Jesus, M. (**2020**). “Shipping noise predictions from AIS in the Faial-Pico area , Azores archipelago,” Glob. Ocean. 2020 Singapore – U.S. Gulf Coast, 2020, 1–6. doi:10.1109/IEEECONF38699.2020.9389442.

Sorjonen, J. (**1986**). “Factors Affecting the Structure of Song and the Singing Behaviour of Some Northern European Passerine Birds,” Behaviour, **98**, 286–304. Retrieved from http://www.jstor.org/stable/4534546

Soule, D. C., and Wilcock, W. S. D. (**2013**). “Fin whale tracks recorded by a seismic network on the Juan de Fuca Ridge, Northeast Pacific Ocean,” J. Acoust. Soc. Am., **133**, 1751–1761. doi:10.1121/1.4774275

Sousa-Lima, R. (**2013**). “A Review and Inventory of Fixed Autonomous Recorders for Passive Acoustic Monitoring of Marine Mammals,” Aquat. Mamm., **39**, 23–53. doi:10.1578/AM.39.1.2013.23

Sousa-lima, R. S., Morete, M. E., Freitas, A., and Engel, M. H. (**2002**). “Impact of boats on the vocal behavior of humpback whales off Brazil,” J. Acoust. Soc. Am., **112**, 2430–2431. doi:10.1121/1.4779974

Southall, B. L., Bowles, A. E., Ellison, W. T., Finneran, J., Gentry, R. L., Greene, C. R. J., Kastak, D., et al. (**2007**). “Marine Mammal Noise Exposure Criteria ,” Aquat. Mamm., **33**, 411–521.

Southall, B. L., Bowles, A. E., Ellison, W. T., Finneran, J. J., Gentry, R. L., Jr, C. R. G., Kastak, D., et al. (**2007**). “Marine Mammal Noise Exposure Criteria: Initial Scientific Recommendations,” Aquat. Mamm., **33**, 1–434.

Southall, E. B. L., Finneran, J. J., Reichmuth, C., Nachtigall, P. E., Ketten, D. R., Bowles, A. E., Ellison, W. T., et al. (**2019**). “Marine mammal noise exposure criteria: Updated scientific recommendations for residual hearing effects,” Aquat. Mamm., **45**, 125–232. doi:10.1578/AM.45.2.2019.125

Sridhar, H., Beauchamp, G., and Shanker, K. (**2009**). “Why do birds participate in mixed-species foraging flocks? A large-scale synthesis,” Anim. Behav., **78**, 337–347. doi:10.1016/j.anbehav.2009.05.008

Stafford, K. M. (**2003**). “Two types of blue whale calls recorded in the Gulf of Alaska,” Mar. Mammal Sci., **19**, 682–693. doi:10.1111/j.1748-7692.2003.tb01124.x

Stafford, K. M., Mellinger, D. K., Moore, S. E., and Fox, C. G. (**2007**). “Seasonal variability and detection range modeling of baleen whale calls in the Gulf of Alaska, 1999-2002,” J. Acoust. Soc. Am., **122**, 3378–3390. doi:10.1121/1.2799905

Stafford, K. M., Moore, S. E., and Fox, C. G. (**2005**). “Diel variation in blue whale calls recorded in the eastern tropical Pacific,” Anim. Behav., **69**, 951–958. doi:10.1016/j.anbehav.2004.06.025

Stafford, K., Nieukirk, S., and Fox, C. (**2001**). “Geographic and seasonal variation of blue whale calls in the North Pacific,” J. Cetacean Res. Manag., **3**, 65–76.

Stimpert, A. K., Deruiter, S. L., Falcone, E. A., Joseph, J., Douglas, A. B., Moretti, D. J., Friedlaender, A. S., et al. (**2015**). “Sound production and associated behavior of tagged fin whales (*Balaenoptera physalus*) in the Southern California Bight,” Anim. Biotelemetry, **3**, 1–12. doi:10.1186/s40317-015-0058-3

Stimpert, A. K., Wiley, D. N., Au, W. W. L., Johnson, M. P., and Arsenault, R. (**2007**). “‘ Megapclicks ’: acoustic click trains and buzzes produced during night-time foraging of humpback whales (*Megaptera novaeangliae*),” Biol. Lett., **3**, 467–470. doi:10.1098/rsbl.2007.0281

Strand, E., Klevjer, T., Knutsen, T., and Melle, W. (**2020**). “Ecology of mesozooplankton across four North Atlantic basins,” Deep Sea Res. Part II Top. Stud. Oceanogr., **180**, 104844. doi:https://doi.org/10.1016/j.dsr2.2020.104844

Teixeira, D., Maron, M., and Rensburg, B. J. (**2019**). “Bioacoustic monitoring of animal vocal behavior for conservation,” Conserv. Sci. Pract., **1**, 1–15. doi:10.1111/csp2.72

Tempera, F., Giacomello, E., Mitchell, N., and Campos, A. S. (**2012**). “Mapping Condor Seamount Seafloor Environment and Associated Biological Assemblages (Azores, NE

Atlantic),” Seafloor Geomorphol. as Benthic Habitat Geohab Atlas Seafloor Geomorphic Featur. Benthic Habitats, Elsevier, p. 58.

Tennessen, J., and Parks, S. (**2016**). “Acoustic propagation modeling indicates vocal compensation in noise improves communication range for North Atlantic right whales,” Endanger. Species Res., **30**, 225–237. doi:10.3354/esr00738

Tershy, B. R. (**1992**). “Body size, diet, habitat use, and social behavior of Balaenoptera whales in the Gulf of California,” J. Mammal., **73**, 477–486. doi:10.2307/1382013

Thode, A. M., Blackwell, S. B., Conrad, A. S., Kim, K. H., and Michael Macrander, A. (**2017**). “Decadal-scale frequency shift of migrating bowhead whale calls in the shallow Beaufort Sea,” J. Acoust. Soc. Am., **142**, 1482–1502. doi:10.1121/1.5001064

Thode, A. M., D’Spain, G. L., and Kuperman, W. A. (**2000**). “Matched-field processing, geoacoustic inversion, and source signature recovery of blue whale vocalizations,” J. Acoust. Soc. Am., **107**, 1286–1300. doi:10.1121/1.428417

Thomas, P. O., Reeves, R. R., and Brownell, R. L. (**2015**). “Status of the world’s baleen whales,” Mar. Mammal Sci., **32**, 682–734. doi:10.1111/mms.12281

Thomisch, K., Boebel, O., Clark, C. W., Hagen, W., Spiesecke, S., Zitterbart, D. P., and Van Opzeeland, I. (**2016**). “Spatio-temporal patterns in acoustic presence and distribution of Antarctic blue whales *Balaenoptera musculus* intermedia in the Weddell Sea,” Endanger. Species Res., **30**, 239–253. doi:10.3354/esr00739

Thompson, P. O., Findley, L. T., and Vidal, O. (**1992**). “20-Hz pulses and other vocalizations of fin whales, *Balaenoptera physalus*, in the Gulf of California, Mexico,” J. Acoust. Soc. Am., **92**, 3051–3057. doi:10.1121/1.404201

Thompson, P. O., Findley, L. T., Vidal, O., and Cummings, W. C. (**1996**). “Underwater sounds of blue whales, *Balaenoptera musculus*, in the Gulf of California, Mexico,” Mar. Mammal Sci., **12**, 288–293.

Thompson, T. J., Winn, H. E., and Perkins, P. J. (**1979**). “Mysticete Sounds BT - Behavior of Marine Animals: Current Perspectives in Research,” In H. E. Winn and B. L. Olla (Eds.), Springer US, Boston, MA, pp. 403–431. doi:10.1007/978-1-4684-2985-5_12

Thorley, J. B., and Clutton-Brock, T. (**2017**). “Kalahari vulture declines, through the eyes of meerkats,” Ostrich, **88**, 177–181. doi:10.2989/00306525.2016.1257516

Tregenza, T., Simmons, L. W., Wedell, N., and Zuk, M. (**2006**). “Female preference for male courtship song and its role as a signal of immune function and condition,” Anim. Behav., **72**, 809–818. doi:https://doi.org/10.1016/j.anbehav.2006.01.019

Tremblay, C. J., Van Parijs, S. M., and Cholewiak, D. (**2019**). “ 50 to 30-Hz triplet and singlet down sweep vocalizations produced by sei whales (*Balaenoptera borealis*) in the western North Atlantic Ocean ,” J. Acoust. Soc. Am., **145**, 3351–3358. doi:10.1121/1.5110713

Tripovich, J. S., Klinck, H., Nieukirk, S. L., Adams, T., Mellinger, D. K., Balcazar, N. E., Klinck, K., et al. (**2015**). “Temporal Segregation of the Australian and Antarctic Blue Whale Call Types (*Balaenoptera musculus spp*),” J. Mammal., **96**, 603–610. doi:10.1093/jmammal/gyv065

Tsujii, K., Akamatsu, T., Okamoto, R., Mori, K., Mitani, Y., and Umeda, N. (**2018**). “Change in singing behavior of humpback whales caused by shipping noise,” PLoS One, **13**, 1–16. doi:10.1371/journal.pone.0204112

Tulloch, V. J. D., Plagányi, É. E., Brown, C., Richardson, A. J., and Matear, R. (**2019**). “Future recovery of baleen whales is imperiled by climate change,” Glob. Chang. Biol., **25**, 1263–1281. doi:10.1111/gcb.14573

Tyack, P. (**1983**). “Differential response of humpback whales, *Megaptera novaeangliae*, to playback of song or social sounds,” Behav. Ecol. Sociobiol., **13**, 49–55. doi:10.1007/BF00295075

Víkingsson, G. A. (**1997**). “Feeding of fin whales (*Balaenoptera physalus*) off Iceland - diurnal and seasonal variation and possible rates,” J. Northwest Atl. Fish. Sci., **22**, 77–89. doi:10.2960/J.v22.a7

Víkingsson, G. A., Pike, D. G., Valdimarsson, H., Schleimer, A., Gunnlaugsson, T., Silva, T., Elvarsson, B. P., et al. (**2015**). “Distribution, abundance, and feeding ecology of baleen whales in Icelandic waters: Have recent environmental changes had an effect?,” Front. Ecol. Evol., **3**, 1–18. doi:10.3389/fevo.2015.00006

Visser, F., Hartman, K. L., Pierce, G. J., Valavanis, V. D., and Huisman, J. (**2011**). “Timing of migratory baleen whales at the azores in relation to the north atlantic spring bloom,” Mar. Ecol. Prog. Ser., **440**, 267–279. doi:10.3354/meps09349

De Vreese, S., van der Schaar, M., Weissenberger, J., Erbs, F., Kosecka, M., Solé, M., and André, M. (**2018**). “Marine mammal acoustic detections in the Greenland and Barents Sea, 2013 – 2014 seasons,” Sci. Rep., **8**, 2013–2014. doi:10.1038/s41598-018-34624-z

Vu, E., Risch, D., Clark, C., Gaylord, S., Hatch, L., Thompson, M., Wiley, D., et al. (**2012**). “Humpback whale song occurs extensively on feeding grounds in the western North Atlantic Ocean,” Aquat. Biol., **14**, 175–183. doi:10.3354/ab00390

Wang, D., Garcia, H., Huang, W., Tran, D. D., Jain, A. D., Yi, D. H., Gong, Z., et al. (**2016**). “Vast assembly of vocal marine mammals from diverse species on fish spawning ground,” Nature, **531**, 366–370. doi:10.1038/nature16960

Watkins, W. A. (**1981**). “Activities and underwater sounds of fin whales,” Sci. Rep. Whale Res. Inst., **33**, 83–117.

Watkins, W. A., Daher, M. A., Reppucci, G. M., George, J. E., Martin, D. L., DiMarzio, N. A., and Gannon, D. P. (**2000**). “Seasonality and distribution of whale calls in the North Pacific,” Oceanography, **13**, 62–67. doi:10.5670/oceanog.2000.54

Watkins, W. A., and Schevill, W. E. (**1979**). “Aerial Observation of Feeding Behavior in Four Baleen Whales: *Eubalaena glacialis*, *Balaenoptera borealis*, *Megaptera novaeangliae*, and *Balaenoptera physalus*,” J. Mammal., **60**, 155–163. doi:10.2307/1379766

Watkins, W. A., Tyack, P., Moore, K. E., and Bird, J. E. (**1987**). “The 20-Hz signals of finback whales (*Balaenoptera physalus*),” J. Acoust. Soc. Am., **82**, 1901–1912. doi:https://doi.org/10.1121/1.395685

Weilgart, L. S. (**1990**). *Vocalizations of the sperm whale (Physeter macrocephalus) off the Galápagos Islands as related to behavioral and circumstantial variables* Dalhousie University, Halifax, Nova Scotia.

Weirathmueller, M. J., Stafford, K. M., Wilcock, W. S. D., Hilmo, R. S., Dziak, R. P., and Tréhu, A. M. (**2017**). “Spatial and temporal trends in fin whale vocalizations recorded in the NE

Pacific Ocean between 2003-2013," PLoS One, **12**, e0186127. doi:10.1371/journal.pone.0186127

Weirathmueller, M. J., Wilcock, W. S. D., and Soule, D. C. (**2013**). "Source levels of fin whale 20 Hz pulses measured in the Northeast Pacific Ocean," J. Acoust. Soc. Am., **133**, 741–749. doi:10.1121/1.4773277

Welch, P. D. (**1967**). "The Use of Fast Fourier Transform for the Estimation of Power Spectra: A Method Based on Time Aver aging Over Short, Modified Periodograms," IEEE Trans. audio Electroacoust., **15**, 70–73.

Wensveen, P. J., Kvadsheim, P. H., Lam, F. P. A., Von Benda-Beckmann, A. M., Sivle, L. D., Visser, F., Cure, C., et al. (**2017**). "Lack of behavioural responses of humpback whales (*Megaptera novaeangliae*) indicate limited effectiveness of sonar mitigation," J. Exp. Biol., **220**, 4150–4161. doi:10.1242/jeb.161232

Wenz, G. M. (**1962**). "Acoustic Ambient Noise in the Ocean: Spectra and Sources," J. Acoust. Soc. Am., **34**, 1936–1956. doi:10.1121/1.1909155

Whitehead, H., and Carlson, C. (**1988**). "Social behaviour of feeding finback whales off Newfoundland: comparisons with the sympatric humpback whale," Can. J. Zool., **66**, 217–221. doi:10.1139/z88-031

Whitehead, H., and Rendell, L. (**2015**). *The Cultural Lives of Whales and Dolphins*, University of Chicago Press; Reprint edition. doi:10.7208/chicago/9780226187426.001.0001

Whiten, A. (**2019**). "Cultural Evolution in Animals," Annu. Rev. Ecol. Evol. Syst., **50**, 27–48. doi:10.1146/annurev-ecolsys-110218-025040

Wiggins, S. M., and Hildebrand, J. A. (**2020**). "Fin whale 40-Hz calling behavior studied with an acoustic tracking array," **36**, 964– 971. doi:10.1111/mms.12680

Wiggins, S. M., Oleson, E. M., McDonald, M. a., and Hildebrand, J. a. (**2005**). "Blue Whale (*Balaenoptera musculus*) Diel Call Patterns Offshore of Southern California," Aquat. Mamm., **31**, 161–168. doi:10.1578/AM.31.2.2005.161

Wilcock, W. S. D. (**2012**). "Tracking fin whales in the northeast Pacific Ocean with a seafloor seismic network," J. Acoust. Soc. Am., **132**, 2408–2419. doi:10.1121/1.4747017

Williams, H., Levin, I. I., Norris, D. R., Newman, A. E. M., and Wheelwright, N. T. (**2013**). “Three decades of cultural evolution in Savannah sparrow songs,” Anim. Behav., **85**, 213–223. doi:10.1016/j.anbehav.2012.10.028

Williams, R., Clark, C. W., Ponirakis, D., and Ashe, E. (**2014**). “Acoustic quality of critical habitats for three threatened whale populations,” Anim. Conserv., **17**, 174–185. doi:10.1111/acv.12076

Williams, R., Wright, A. J., Ashe, E., Blight, L. K., Bruintjes, R., Canessa, R., Clark, C. W., et al. (**2015**). “Impacts of anthropogenic noise on marine life: Publication patterns, new discoveries, and future directions in research and management,” Ocean Coast. Manag., **115**, 17–24. doi:10.1016/j.ocecoaman.2015.05.021

Zuur, A. F., and Ieno, E. N. (**2016**). “A protocol for conducting and presenting results of regression-type analyses,” Methods Ecol. Evol., **7**, 636–645. doi:10.1111/2041-210X.12577

Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A., and Smith, G. M. (**2009**). *Mixed Effects Models and Extensions in Ecology with R*, (M. Gail, K. Krickeberg, J. M. Samet, A. Tsiatis, and W. Wong, Eds.) Springer, Springer, Berlin.

List of figures and tables

Figures

Tables

Annex I. Contribution to material published during this thesis, other publications and training

a. Contribution to material published during the preparation of this thesis

Chapter 2:

Romagosa, M., Baumgartner, M., Cascão, I. Lammers, M. O., Marques, T. A., Santos, R. S. and Silva, M. A. (2020). Baleen whale acoustic presence and behaviour at a Mid-Atlantic migratory habitat, the Azores Archipelago. Scientific Reports 10: 4766. https://doi.org/10.1038/s41598-020-61849-8

Contribution: MR designed the study in collaboration with MAS, did the all analysis and graphs and wrote the original draft manuscript integrating suggestions from the other authors.

Chapter 3:

Romagosa, M., Pérez-Jorge, S., Cascão, I., Mouriño, H., Lehodey, P., Pereira, A., Marques, T. A., Matias L. and Silva, M. A. (2021). Food talk: 40-Hz fin whale calls are associated with prey biomass. Proceedings of the Royal Society B: Biological Sciences, 288: 20211156. https://doi.org/10.1098/rspb.2021.1156.

Contribution: MR designed the study in collaboration with MAS, processed the data, conducted the analysis, graphical outputs and wrote the original draft manuscript under the supervision of all other authors.

Chapter 5:

Romagosa, M., Cascão, I., Merchant, N. D., Lammers, M. O., Giacomello, E., Marques, T. A. and Silva, M. A. Underwater Ambient Noise in a Baleen Whale Migratory Habitat Off the Azores. Frontiers in Marine Science. 4, 109 (2017). https://doi.org/10.3389/fmars.2017.00109.

Contribution: MR designed the study in collaboration MAS. MR analysed the data, did all graphs and develop the original paper integrating other author's suggestions.

b. Other publications

Romagosa, M., Lucas, C., Pérez-Jorge, S., Tobeña, M., Lehodey, P., Reis, J., Cascão, I., Lammers, M.O., Caldeira, R.M.A., and Silva, M.A. (2019). Differences in regional oceanography and prey biomass influence the presence of foraging odontocetes at two Atlantic seamounts. *Marine Mammal Science*, *36*, 158–179. https://doi.org/10.1111/mms.12626.

Pereira, A., **Romagosa, M.**, Corela, C., Silva, M.A., and Matias, L. (2021). Source Levels of 20 Hz Fin Whale Notes Measured as Sound Pressure and Particle Velocity from Ocean-Bottom Seismometers in the North Atlantic. Journal of Marine Science and Engineering. 9, 646. https://doi.org/10.3390/jmse9060646.

Soares, C., Duarte, R., Silva, M. A., **Romagosa, M**. and Jesus. Shipping noise in the Azores: a threat to the Faial-Pico cetacean community? Int. Conf. on Underwater Acoustics - ICUA'2020, Southampton (UK), September. https://doi.org/10.1121/2.0001313

Ryan, C., **Romagosa, M.**, Boisseau, O., Moscrop, A., and McLanaghan, R. (2019). Humpback whale (*Megaptera novaeangliae*) song detected at the Cape Verde Islands during boreal and austral spring. *Marine Mammal Science*, *35*, 336–344. https://doi.org/10.1111/mms.12523.

c. Conference papers

Oral communications

Romagosa, M., Pérez-Jorge, S., Cascão, I., Mouriño, H., Lehodey, P., Pereira, A., Marques, T. A., Matias L. and Silva, M. A. Food talk: 40-Hz fin whale calls are associated with prey biomass. 24th Biennial Conference on the Biology of Marine Mammals. The Society of Marine Mammology. December 13-17, 2021. West Palm Beach, Florida, USA.

Romagosa, M., Cascão, I. and Silva, M. A. (2020). Undewater noise levels and shipping off the Faial-Pico channel, Azores, in relation to the acoustic presence of baleen whales. ACÚSTICA 2020. XI Congresso Ibérico de Acústica. 51° Congresso Español de Acústica. October 21-23, 2020. Online.

Posters

Romagosa, M., Merchant, N., Lammers, M., Marques, T. A., Silva, M.A. (2016). Underwater noise levels in a critical habitat for North Atlantic baleen whales. 30th Conference of the European Cetacean Sociey. 14-16 March. Funchal. Madeira.

Romagosa, M., Baumgartner, M., Lammers, M., Marques, T. A., Santos, R. S. and Silva M. A. Intra- and inter-annual variation in fin whale song parameters in the North Atlantic Ocean. 22nd Biennial Conference of the Society of Marine Mammology. October 22-29, 2017. Halifax, Nova Scotia, Canada

d. Projects

BIOMETORE - Biodiversity in seamounts: the Madeira-Tore and Great Meteor (EAA-PT02 PA).

RAGES - Risk-based approaches to Good Environmental Status (GA 110661/2018/794607/SUB/ENV.C.2 DG ENV/MSFD).

AWARENESS - Assessing vocal behaviour of fin whales for robust density estimation from passive acoustics (FCT - PTDC/BIA-BMA/30514/2017).

e. Research stays

Woods Hole Oceanographic Institution. Woods Hole. Massachussets, USA. (Sep-Oct, 2017). Supervisor: Mark Baumgartner. Funded by a FLAD/University of the Azores grant FC/FLAD/FMF/RLT/2017/010.

Annex II. Supplementary data – Chapter 2

Baleen whale acoustic presence and behaviour at a Mid-Atlantic migratory habitat, the Azores Archipelago

The following supplementary material is available online: Materials and methods – Automatic detection of calls (Fig. S.2.1), Results - Acoustic presence (Figs. S.2.2 – S.2.4), Results - Seasonal and diel patterns by call type (Table S.2.1).

1. Materials and Methods – Automatic detection of calls

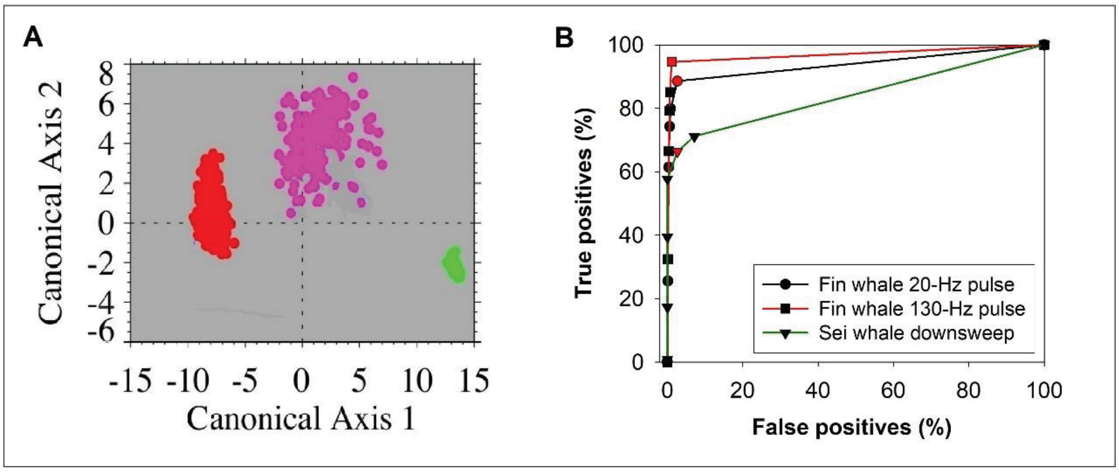


Figure S2.1. (A) Scatterplots for fin whale 20-Hz pulse (red), 130-Hz upsweep (green) and sei whale downsweep (pink) resulting from a canonical discriminant function analysis. For better visualization, scatterplots of attributes of each call type were plotted against one another by reducing the 7 attribute dimensions down to 2 through a canonical discriminant functional analysis (CDFA), (B) ROC curves showing the performance of the LFDCS for varying Mahalanobis distance (0 – >5) for calls of fin and sei whales. Red dots show the chosen Mahalanobis distance for this study.

2. Results – Acoustic presence

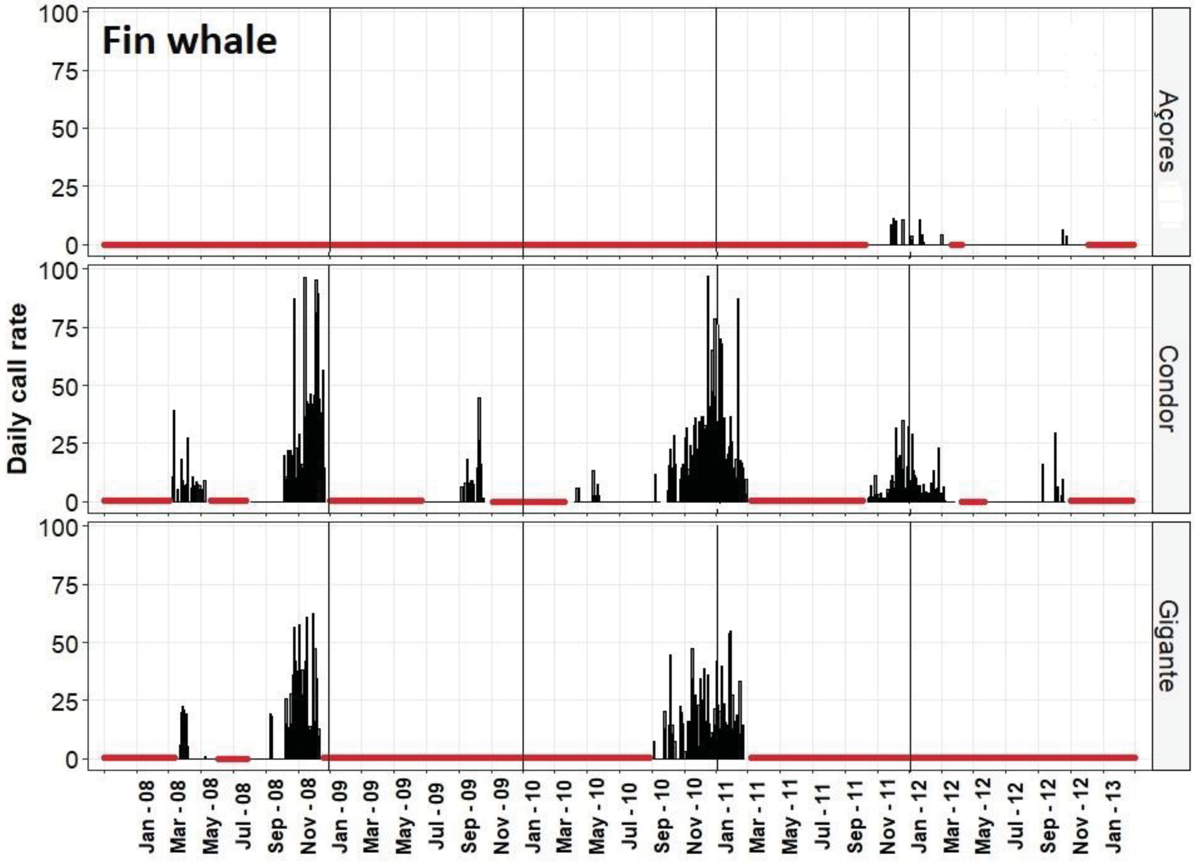


Figure S2.2. Fin whale daily call rates in Açores, Condor and Gigante seamounts from 2008 until 2012. Red line shows periods with no data.

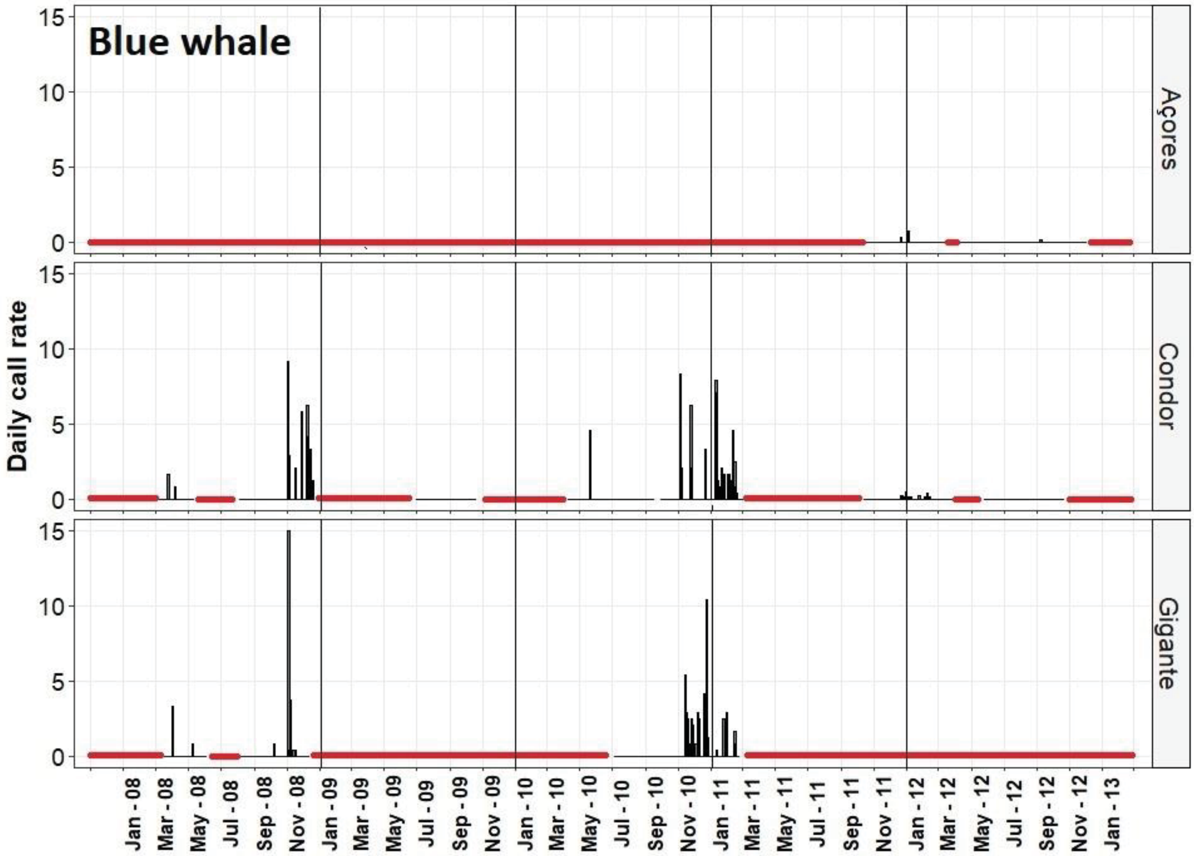


Figure S2.3. Blue whale daily call rates in Açores, Condor and Gigante seamounts from 2008 until 2012. Red line shows periods with no data.

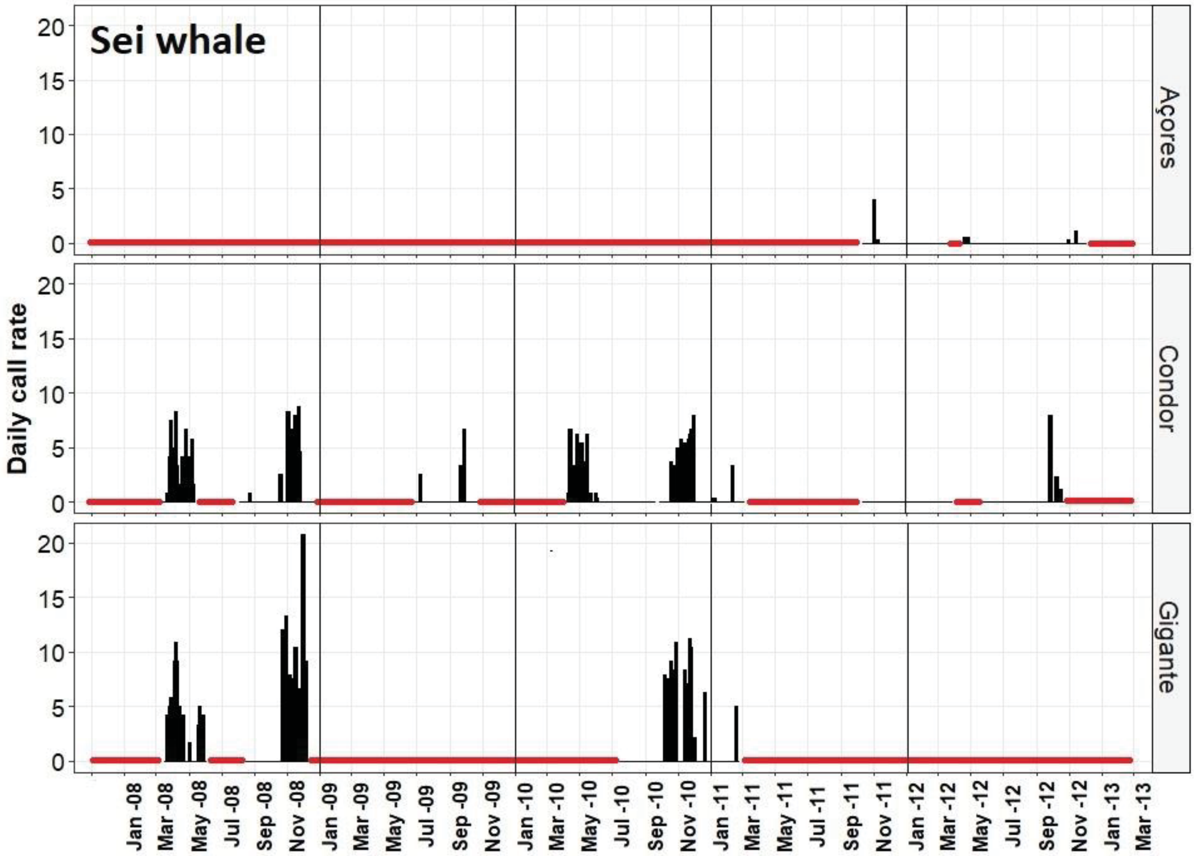


Figure S2.4. Sei whale daily call rates in Açores, Condor and Gigante seamounts from 2008 until 2012. Red line shows periods with no data.

3. Results - Seasonal and diel patterns by call type

Table S2.1 Results form Kruskal-Wallis tests comparing diel patterns of autumn and winter for each seamount and species call.

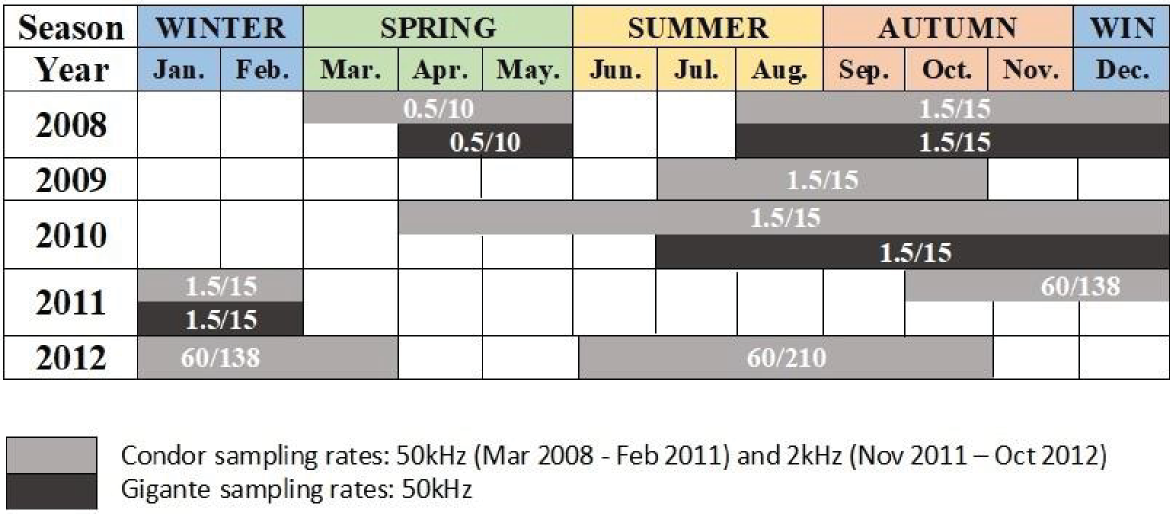
KW test for diel patterns of autumn and winter months	**CONDOR**	**GIGANTE**
Fin 20-Hz call	Naut.=548, Nwin.=364 Chi square= 0.05, df=1, p-value=0.82	Naut.=472, Nwin.=452 Chi square = 0.3, df=1, p-value=0.1
Fin whale 20-Hz + 135-Hz call	Naut.=280, Nwin.=276 Chi square = 0.08, df=1 p-value=0.8	Naut.=160, Nwin.=176 Chi square = 0.05, df=1p-value=0.82
Blue whale A call	Naut=40, Nwin=128 Chi square = 1.5, df=1, p-value=0.2	Naut=40, Nwin=72 Chi square = 0.7, df=1, p-value=0.4
Blue whale D call	Naut=16 Nwin=24 Chi square = 4.6, df=1, p-value=0.05	Naut=28 Nwin=60 Chi square = 1.5, df=1, p-value=0.21

Annex III. Supplementary data – Chapter 3

Food talk: 40-Hz fin whale calls are associated with prey biomass

3.1 METHODS

(a) Acoustic data collection and analyses



Season	WINTER		SPRING			SUMMER			AUTUMN			WIN
Year	Jan.	Feb.	Mar.	Apr.	May.	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.
2008			0.5/10					1.5/15				
				0.5/10				1.5/15				
2009							1.5/15					
2010				1.5/15								
							1.5/15					
2011	1.5/15									60/138		
	1.5/15											
2012	60/138					60/210						

Condor sampling rates: 50kHz (Mar 2008 - Feb 2011) and 2kHz (Nov 2011 – Oct 2012)
Gigante sampling rates: 50kHz

Figure S3.1. Deployment times, duty cycles and sampling rates for each season, month and location. Duty cycles for each deployment are in white numbers and indicate recording periods (min on/every x min). Gaps in the time series were caused by maintenance duties and equipment failure.

(b) Spatial scale of data integration

Detection range estimation

The maximum range at which the two types of fin whale vocalizations could be detected was estimated theoretically using the sonar equation and other mathematical models. For passive sonar, signal-to-noise ratio SNR (dB) of a signal is defined as (Lurton, 2002):

$$SNR = SL - TL - NL + 10\log_{10} BW \qquad \text{Eq. (1)}$$

where SL is the transmitted source level (dB rms re 1 µPa at 1 m), TL is one-way transmission loss (dB), NL is the ambient noise level at the receiver (dB rms re 1 µPa), and BW is the processing bandwidth (Hz). Knowing SL, NL, BW and SNR, TL can be calculated using Eq. (1). By matching the calculated TL in the TL model obtained for the study area, we can then obtain a theoretical maximum range at which a fin whale calls could be detected.

The Range-dependent Acoustic Model (RAM)(Collins, 1993, 1995) is a parabolic equation model that was used to model the propagation loss estimates along the range-depth plane from source to receiver. We developed propagation loss models based on the frequency of each fin whale vocalization along 12 bathymetric transects from each EAR position, obtained every 30º measured from North. Since seasonal changes can cause differences in the water column and affect propagation conditions, we used sound speed profiles for winter and summer months (January and June for Condor and January and September for Gigante). In total, we developed 96 propagation loss models up to 180 km, with a 50 m range step, 24 for each fin whale call in each area. Additional information and parameters for the propagation loss modelling are described below:

Frequency and depth of the vocalizing whale: We used the centre frequency of a sample of fin whale calls recorded around the Azores area. The centre frequency was estimated to be of 25 Hz for the 20-Hz call and 62 Hz for the 40-Hz call. The depth of the vocalizing whale was estimated to be 50 m and was obtained from the literature (Watkins et al., 1987).

Depth of the hydrophones: The two EARS were deployed in Condor and Gigante at similar depths (190 m).

Sound speed profile: The sound speed profiles for January, June and September were extracted from the Levitus climatological database (Levitus, 1983). The profiles were obtained for one point between Condor and Gigante.

Ocean bottom composition: Since there were no direct measurements of sediment properties in the two areas, we used an average sound speed in the sediments of 1700 m/s and a seabed density of 1500 kg/m^3.

Bathymetry along the transmission path: The bathymetric relief of transects around the EARS were obtained from the European Marine Observation and Data Network (EMODnet) (https://portal.emodnet-bathymetry.eu/).

For the TL calculation using Eq. (1) we also used the following data:

Source level: We calculated average source level estimates for a sample of fin whale 20-Hz (n = 139) and 40-Hz (n = 42) calls recorded in 3 EARS deployed off Faial-Pico Island, close to the study area, and located using Time-of-Arrival-Differences (TOADs) (Baumgartner et al., 2008a). Source level estimates were calculated using the “inband power” feature in RAVEN PRO 2.0 (Bioacoustics Research Program) and root-mean-squared (RMS) received levels were extracted in the measured bandwidth of the vocalizations. Then we used the passive sonar equation by adding the received levels of the transmitted signal in the EARS and the associated transmission loss. The average estimated source levels for the 20-Hz call was 147.4 dB rms re 1 µPa at 1 m (± 15.5) and for the 40-Hz call was 144.3 dB rms re 1 µPa at 1 m (± 3.6).

Ambient noise level: Received ambient noise levels for the noisiest and quietest month, previously identified in this dataset(Romagosa et al., 2017), were calculated in 1/3 octave bands centred at the target frequencies for each fin whale call: centred at 20 Hz (14.15 - 28.3 Hz) and 62 Hz (44 - 88 Hz). Measurements were made using PAMGuide (Merchant et al., 2015) by entering the manufacturer's specifications for the end-to-end sensitivity of the instrument (−193.14/-194.17 re 1 V/µPa; depending on deployment), a gain of 47.5 dB and a 0-peak voltage of 1.25 V.

Signal-to-noise ratio (SNR): Since the automatic detection process for the 20-Hz fin whale call was based on a detection threshold of 10 dB, we used this value to indicate the detectability of this call type and conservatively assumed the same SNR for manually detected 40-Hz calls.

(c) Statistical analyses

Model information

Let X_{it} be a random variable that represents the *i-th* call type (corresponding to 20-Hz song call and 40-Hz call, respectively) at week t, $t=1,\ldots,144$. Assuming that $E\left(X_{it}\right)=\mu_{it}$, the basic log link function that describes the relationship between the mean and the explanatory variables takes the form:

$$\log(\mu_{it})=\alpha_{0i}+\alpha_{1i}\ \text{zoo\_biomass}_{it}+\alpha_{2i}\ \text{season\_aut}_{it}+\alpha_{3i}\ \text{zoo\_biomass}_{it}\times\text{season\_aut}_{it}+$$
$$+\alpha_{4i}\ \text{zoo\_biomass}_{it}\times\text{season\_spr}_{it}+\sum_{j=1}^{4}\gamma_{ji}\ year_{ijt},\quad i=1,2;\ t=1,\ldots,144.$$

where μ_{it} represents the mean of the Poisson distribution for the *i-th* call type ($i=1,2,$ corresponding to 20-Hz and 40-Hz calls, respectively) at week t, $t=1,\ldots,144$. The variable $zoo\_biomass_{it}$ describes zooplankton biomass at week t, for the *i-th* call type; the variables $season\_aut_{it}$ and $season\_spr_{it}$ are the season indicators, for the *i-th* call type: $season\_aut_{it}$ is equal to 1 if week t belongs to autumn, and 0 otherwise; $season\_spr_{it}$ is equal to 1 if week t belongs to spring, and 0 otherwise; the reference category is the winter season. The interaction terms between zooplankton biomass and the season of the year were also included in the model. The dummy variable $year_{ijt}$ is the year indicator, equal to 1 if week t belongs to year j ($j=1,2,3,4,$ corresponding to year 2008, 2009, 2010, 2011, respectively); the reference category is the year 2012. The vector of the parameters for the *i*-th model is given by

$\boldsymbol{\theta}=\left(\alpha_{0i}\quad\alpha_{1i}\quad\alpha_{2i}\quad\alpha_{3i}\quad\alpha_{4i}\quad\gamma_{1i}\quad\gamma_{2i}\quad\gamma_{3i}\quad\gamma_{4i}\right)^{T}$, where α_{0i} is the intercept, $i=1,2.$

For the quasi-Poisson model, it is assumed that the variance is equal to the mean multiplied by a dispersion parameter (denoted by $\phi,\ \phi\neq 1$), that is, $Var\left(X_{it}\right)=\phi\ \mu_{it}$. In this work, we considered $\phi>1$ because the datasets were overdispersed. The parameters of the model are obtained by maximum quasi-likelihood estimation, where only the relationship between the mean value and the variance is specified. Thus, there is no need to establish the form of the underlying probability distribution.

Model fitting relies upon the quasi-Poisson models, which means that we are working in the quasi-likelihood framework. Therefore, we used the Quasi-Akaike's Information Criterion (QAIC) instead of the well-known AIC, which is given by

$$\mathrm{QAIC} = 2k - \frac{2\ln\left(\hat{L}\right)}{\hat{\phi}},$$

where k is the number of parameters in the model; $\hat{L}$ represents the quasi-likelihood function evaluated at the maximum quasi-likelihood estimators; $\hat{\phi}$ is the estimate of the variance inflation factor that accommodates overdispersion.

3.2 RESULTS

(a) Detection range and zooplankton biomass spatial scale

Table S3.1. Summary table showing averaged source levels, ambient noise levels, transmission loss and average detection ranges for each vocalization type and noise conditions. SL –Source levels, BW – Bandwidth, NL-Noise levels and TL-Transmission loss.

Type	SL (dB re 1 µPa at 1 m)	BW	Location	Month	Description	NL (RMS) (dB re 1 µPa)	TL (dB)	Average detection range (km)
20-Hz note	147.3	14	Condor	Jan-12	Quietest	69.7	79.1	70
				Jun-12	Noisiest	71	77.8	58
			Gigante	Jan-11	Quietest	62.2	86.6	149
				Sep-10	Noisiest	77.4	71.4	20
40-Hz call	144.3	44	Condor	Jan-12	Quietest	78.7	72	26
				Jun-12	Noisiest	82.4	68.3	11
			Gigante	Jan-11	Quietest	77.7	73	34
				Sep-10	Noisiest	83.5	67.2	11

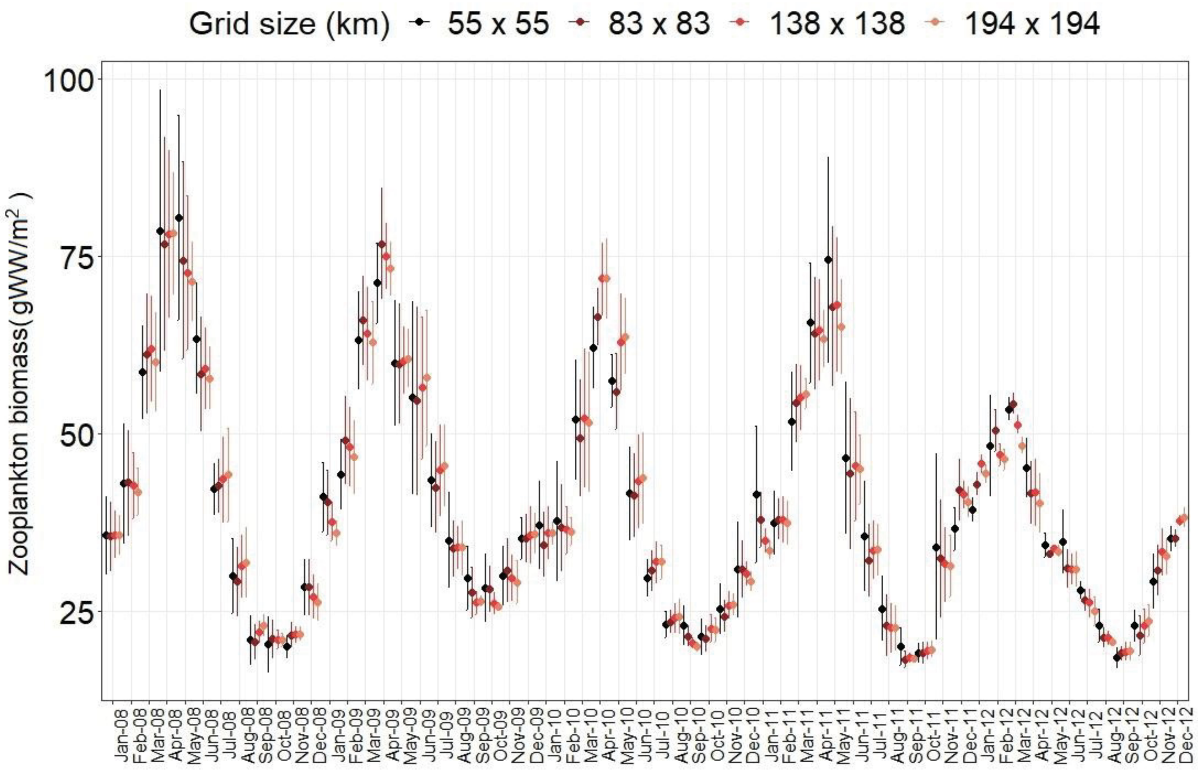


Figure S3.2. Monthly averaged modelled zooplankton biomass by grid size. Points represent averaged values and error bars represent standard deviations.

(a) Models of the 20-Hz and 40-Hz call

Table S3.2. Model selection results for the 20-Hz and 40-Hz call ordered by lowest QAIC. Best model is shown in bold.

ID	Model	Number of parameters	QAIC	∆(QAIC)	Weight (QAIC)
20-Hz call					
1	**season + year**	**7**	**186.8**	**0**	**0.69**
2	zoo+season+year	8	188.8	1.9	0.25
3	zoo+season+year+zoo×season	10	191.8	5.0	0.05
4	zoo+season	4	224.3	37.4	0
5	zoo+season+zoo × season	6	226.3	39.5	0
6	season	3	230.0	43.1	0

7	zoo+year	6	265.0	78.1	0
8	year	5	283.1	96.3	0
9	zoo	2	288.9	102.1	0
40-Hz call					
1	**zoo**	**2**	**176.0**	**0**	**0.57**
2	zoo+year	6	178.0	2	0.21
3	zoo+season	4	179.5	3.5	0.1
4	zoo+season+year	8	181	4.9	0.05
5	zoo+season+zoo×season	6	182.3	6.3	0.02
6	season+year	7	182.4	6.4	0.02
7	zoo+season+zoo×season	10	183.1	7.2	0.02
8	season	3	184.8	8.8	0.01
9	year	5	193.2	17.3	0

QAIC: Quasi-Akaike Information Criteria

Δ(QAIC) = QAIC of the current model – QAIC of the best model (i.e., the model with the lowest QAIC)

Weight(QAIC): is the relative likelihood of the current model, when compared to the other models under consideration, and can be obtained by

$$\text{Weight}(\text{QAIC}_i) = \frac{\exp(-0.5\Delta(\text{QAIC}_i))}{\sum_{j=1}^{k}\exp(-0.5\Delta(\text{QAIC}_k))}$$

, where QAIC_i is the QAIC of model i ($i = 1,\ldots,k$), k is the number of models under analysis.

Table S3.3. Estimation results from the quasi-Poisson best selected models for the 20-Hz and 40-Hz call: point and interval estimates for each parameter and respective estimate of the standard error; test statistic and *p*-value from the Wald test.

	Estimate	Std. error	t-value	P-value	95% CI
20-Hz call					
Intercept	-0615	0.531	-1.159	0.248	(-1.748, 0.348)
Season_spr	Reference				
Season_aut	1.471	0.362	4.057	**<0.001**	(0.816, 2.254)
Season_win	2.379	0.381	6.237	**<0.001**	(1.680, 3.192)
Year2008	1.816	0.424	4.281	**<0.001**	(1.056, 2.745)
Year2009	0.770	0.659	1.168	0.24	(-0.637, 2.033)

Year2010	1.323	0.422	3.132	**<0.01**	(1.056, 2.745)
Year2011	1.250	0.415	3.009	**<0.01**	(0.567, 2.250)
Year 2012	Reference				
20rate_lag_1	0.012	0.002	4.834	**<0.001**	(0.008, 0.018)
Dispersion parameter	10.11	0.156*	—	—	(6.549,13.817)
40-Hz call					
Intercept	-2.076	0.322	-6.441	**<0.001**	(-2.735, -1.467)
Zooplankton	0.029	0.005	5.641	**<0.001**	(0.019, 0.039)
Dispersion parameter	1.527	0.024	—	—	(1.052, 2.160)

* Results obtained by parametric bootstrap based on 1000 replications

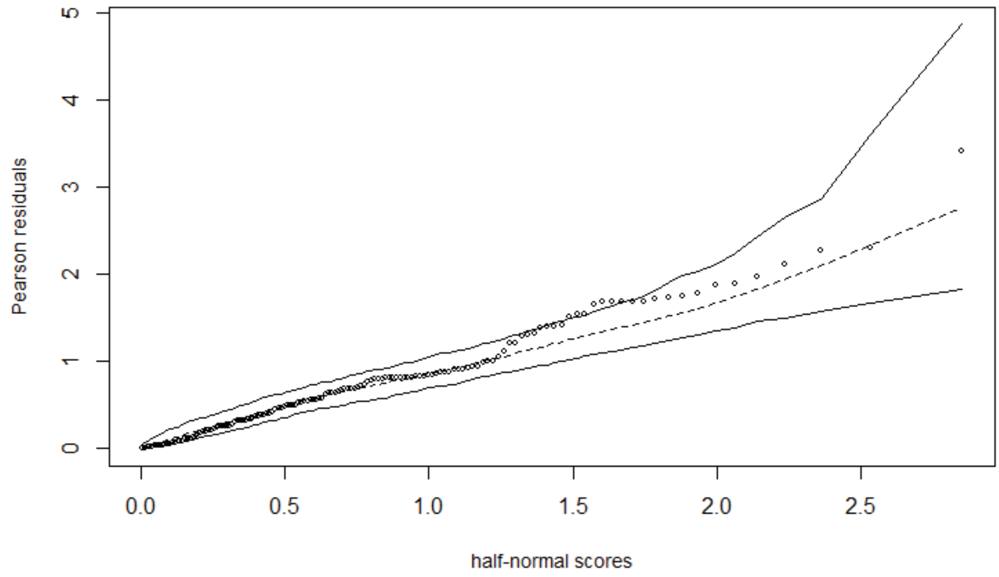


Figure S3.3. Quasi-Poisson fitted to the 20-Hz call rate: half-normal plot of the Pearson residuals, with simulation envelope based on 1000 runs. The scatter points (represented by circles) correspond to the ordered absolute values of the Pearson residuals *versus* the expected order statistics of the half-normal distribution. Solid lines indicate the 99% limits of the simulated envelope.

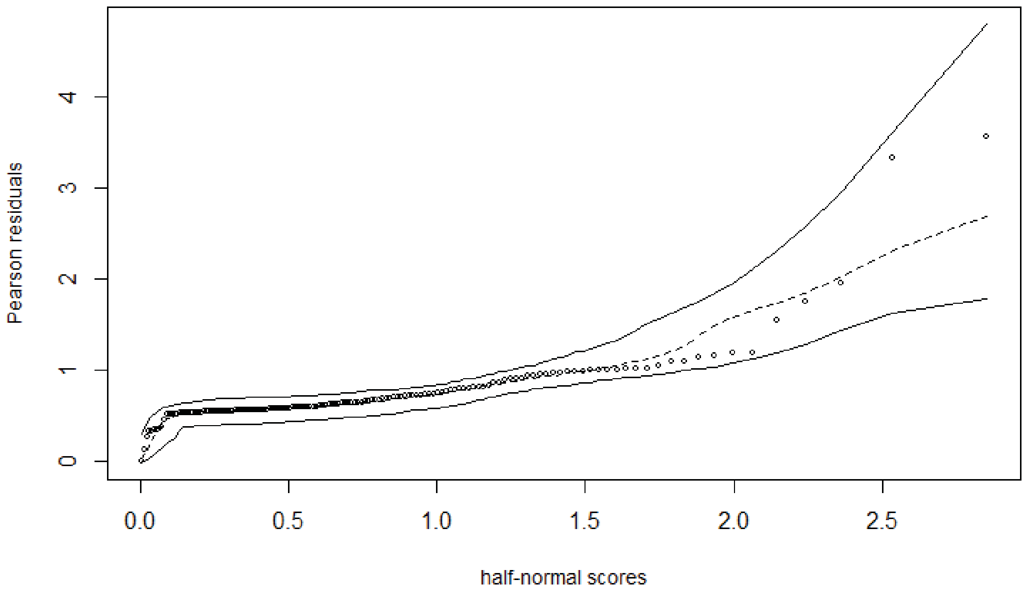


Figure S3.4. Quasi-Poisson fitted to the 40-Hz call rate: half-normal plot of the Pearson residuals, with simulation envelope based on 1000 runs. The scatter points (represented by circles) correspond to the ordered absolute values of the Pearson residuals *versus* the expected order statistics of the half-normal distribution. Solid lines indicate the 99% limits of the simulated envelope. Model residuals reveal that the model is adequate to describe the data and does not show the existence of outliers, with the residuals placed inside the envelope.

Annex IV. Supplementary data – Chapter 4

Revolutionary and evolutionary changes in fin whale song

The effect of recording equipment on fin whale song parameters

When comparing data from multiple sensors an obvious question is whether the results might be dependent on the specific sensors considered. To investigate the influence of the acoustic recorder type, OBS or ARs, on the song parameters, we analysed the same song fragment, consisting of 209 notes, recorded by the hydrophone channel of an OBS and an AR, specifically an Ecological Acoustic Recorder (EAR)(Lammers et al., 2008). The two instruments were deployed ~6 km from each other in the Azores region in spring of 2019. Measurements of INIs and 20-Hz peak frequencies of songs recorded by each instrument were compared using a non-parametric paired samples Wilcoxon Test. Differences in HF note peak frequencies could not be tested because of limitations in the sampling rate of the OBS. Results showed that median INIs measured from OBS (16.52) and EARs (16.42) were not significantly different (p-value = 0.43) but median peak frequencies of the 20-Hz note (median OBS = 23.4; EARs = 21.1) were (p-value < 0.001). Thus, the use of different recorders did not affect INI measurements but influenced measurements of 20-Hz peak frequencies. The effect of the distance to the source in the analysed fin whale song parameters is included in this study, given than these two recorders were positioned at different distances to the singer All statistical analyses were performed using the software R (v. 4.0.2)(R Core team, 2021).

Table S4.1. Recoding equipment, positions, depths, sampling rates and duty cycles per location sampled.

Regions	**Sub regions**	**Recording equipment (AR or OBS)**	**Locations**	**Latitude and longitude (°)**	**Aprox. depth (m)**	**Sampling rate (Hz)**	**Duty cycle on/off (min)**
Mid-Atlantic Ridge (MAR)	North MAR	AR (Fox et al., 2001)	NE (S4)	49.8554°N 25.4541°W	~4200	260	Cont.
			NW (S3)	47.5941°N - 32.4500°W	~4100		Cont.
			SE (S1)	40.3365°N 25.0350°W	~3300		Cont.
			SW (S2)	42.7188°N 34.7226°W	~3970		Cont.
	Azores	AR EARs (Lammers et al., 2008)	Gigante	38.9863°N 29.8823°W	~300	50000	1.5/10
			Condor	38.5396°N 29.0434°W	~300	2000	0.5/10 1.5/15
			Condor	38.5396°N 29.0434°W	~ 300	2000	60/210
			Pico-Faial Chanel	38.4555°N 28.5630°W	~ 500	2000	360/1080

	South MAR	AR (Fox et al., 2001)	NE	32° N 35° W	~ 926	110	Cont.
			SW	26°N 50°W			
Iceland-Greenland	Iceland	AR (Calupca et al., 2000)	Iceland	64.185° N 14.686° W	~ 60	4000	Cont.
	SE Greenland	AR (Fox et al., 2001)	SE Greenland	60° N 35° W	~ 800	2000	Cont.
SW Portugal	SW Portugal	OBS (Silva, 2017)	SW Portugal	35.7798°N 10.3584°W	~1993-5100	100	Cont.
	Gorringe bank	AR EARs (Lammers et al., 2008)	Gorringe bank	36.5753° N 11.5969° W	~ 255	2000	3/12
Ireland	North Porcupine	AR AMARs (JASCO Applied Sciences, Halifax, Canada)	North Porcupine	52.6221° N 15.3045° W	~1700	32000	2/18
	South Porcupine		South Porcupine	49.5478°N 13.3723°W			
Canary Island	East Lanzarote	OBS	East Lanzarote	28.8997°N 13.2003°W	~1350	100	Cont.

Days (INIs)	January	February	March	October	November	December
1999		4 (411)	4 (267)	4 (1609)	4 (466)	4 (755)
2000	4 (701)	4 (468)	4 (489)	2 (433)	4 (399)	4 (595)
2001	5 (503)	4(543)	4 (420)			
2002				1 (160)	4 (534)	4 (749)
				4 (625)	4 (603)	4 (652)
				4 (440)	4 (756)	5 (458)
				4 (338)	4 (571)	4 (623)
				4 (571)	4 (464)	5 (568)
						1 (40)
2003	4 (556)	4 (696)	4 (310)			
	4 (463)	4 (581)	4 (548)			
	4 (511)	4 (462)	4 (482)			
	4 (217)	4 (474)	4 (607)			
	4 (428)	4 (405)	4 (274)			
	3 (445)	4 (603)	4 (456)			
2004				1 (134)	4 (883)	4 (730)
2005	5 (942)	4 (436)	4 (418)		1 (162)	
2006						
2007	2 (135)					
						7 (300)
		2 (371)	1 (107)			
				6 (497)	3 (248)	4 (971)
2008	2 (115)					1 (162)
				8 (45)	4 (17)	4 (19)
	7 (535)	6 (593)				
	4 (845)	4 (455)	3 (111)			
2009				4 (21)		
2010				3 (11)	7 (31)	8 (39)
2011	8 (37)	3 (12)		1 (36)	2 (70)	4 (251)
2012	5 (356)	5 (201)	2 (85)	2 (11)		
2013						
2014					9 (808)	7 (609)
					3 (199)	
2015				5 (43)	1 (7)	6 (49)
	8 (881)					
				1 (13)	1 (22)	
				3 (39)		
2016	10 (94)	7 (53)	3 (19)			
			1 (21)	7 (181)	1 (20)	
	1 (13)					
2017		2 (127)	7 (1019)			2 (194)
2018	4 (191)					
2019			1 (48)			2 (69)
2020	3 (255)	5 (684)	3 (171)			

Region	Location
South_MAR	NE
	CW
North-MAR	SE
	SW
	NW
	NE
Azores	AZORES
Sw Portugal	SW Portugal
Canary Islands	Canary Islands
Iceland-Greenland	Iceland
	SE Greenland
Ireland-Greenland	Ireland
Svalbard	Svalbard

Fig. S4.1. Days sampled and INIs measured (in brackets) for each location and year sampled.

Table S4.2. Coefficient of variation of INIs by singing season and region.

Region	Singing season	CV
MAR/Azores	1998/1999	2.657221
	1999/2000	3.046693
	2000/2001	9.166669
	2002/2003	20.00352
	2004/2005	5.343912
	2006/2007	1.812738
	2007/2008	1.769775
	2008/2009	2.202547
	2009/2010	3.3381
	2010/2011	2.025955
	2011/2012	2.758649
	2012/2013	3.048037
	2016/2017	3.564225
	2017/2018	2.171907
	2018/2019	9.185202
	2019/2020	4.396421
Iceland/Greenland	2006/2007	2.022589
	2007/2008	4.212161
Canary Islands	2014/2015	3.0130331
Svalbard	2014/2015	23.99678
	2015/2016	13.77192
SW Portugal	2007/2008	4.430923
	2015/2016	8.293319
Ireland	2015/2016	3.057298
	2016/2017	2.674506

Annex V. Supplementary data – Chapter 5

Underwater Ambient Noise in a Baleen Whale Migratory Habitat Off the Azores

Table S5.1. Mean and 95% confidence interval (95% CI) in brackets calculated for broadband

Location	Broadband noise levels (18-1000 Hz)	63 Hz	125Hz
Condor	97.6 (97.3 - 98.6)	72.4 (71.9 - 72.7)	79.5 (79.2 - 80.9)
Açores	92.9 (92.3 - 93.4)	70.2 (69.4 - 71)	74.6 (73.8 - 75.4)
Gigante	95.9 (95.5 - 96.4)	73.6 (73- 74.1)	76 (75.5 - 76.6)

(18-1000 Hz) and 63 Hz and 125 Hz one-third octave bands noise levels at the three locations. N is number of days (Condor: n = 261, Açores; n = 305; Gigante n = 391).

UNIVERSIDADE DOS AÇORES

Faculdade de Ciências e Tecnologia

Rua Professor Doutor Frederico Machado, N.º 4

9901-862 Horta

Açores, Portugal

Noise exposure and vocal behaviour of baleen whales

Miriam Romagosa Vergés

TD

SICUT AURORA SCIENTIA LUCET
UNIVERSIDADE DOS AÇORES

2021