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Dedicated to my family

Summary

Antarctic minke whales (AMW) have a circum-antarctic distribution and are known to occur in both open and ice-covered waters of the Southern Ocean (SO). They are a pagophilic species and are regularly observed in heavily sea-ice covered areas. Because of this, current knowledge about Antarctic minke whales is scarce and limited to austral summer and ice-free regions where the majority of visual survey data have been collected. Hence, very little is known on their winter distribution in high latitude waters and to what extent the wintering individuals that are occasionally observed in Antarctic waters represent single observations or a structurally present behavioral trait of the species. Likewise, AMW population structure is poorly known. As most baleen whale species, AMWs are known to undertake annual migrations between high latitude feeding areas and low latitude breeding areas. However, available data to date suggest that for AMWs, migrations seem more protracted and complex than in other baleen whale species. The recent identification of vocalizations produced by AMWs ("bio-duck call") now makes it possible to also use passive acoustic technology to study occurrence patterns and behavior. Passive acoustic monitoring (PAM) offers a versatile technology with which long-term archival data can be collected on sound-producing species using autonomous recording units. Acoustic observation has the additional advantages that it can continue data collection independent of light conditions and under poor weather conditions. Furthermore, it can monitor large areas at the same time, since it collects data omnidirectionally, and it can collect data over extended periods (i.e., multi-year time scales) through the use of autonomous devices.

In the scope of this doctoral thesis, I analysed passive acoustic data from high and low latitudes collected in the Atlantic Ocean sector of the Southern Ocean (Weddell Sea) and southern Atlantic Ocean, to investigate spatio-temporal patterns in the acoustic presence and vocal behaviour of AMWs.

In **Chapter I**, I investigate year-round spatial- temporal patterns in AMW occurrence in ice-covered areas. Our analysis was based on a 9-year passive acoustic dataset (2008- 2016) from 21 locations throughout the Weddell Sea (WS). AMW bio-duck calls were detected acoustically at all mooring locations from May to December, with the highest presence between August and November (bio-duck calls present at more than 80% of days). At the southernmost recording locations, bio-duck calls were present up to 10 months of the year. We identified a substantial inter-annual variation in the seasonality of vocal activity correlated to variation in

local ice concentration. Our analysis indicates that part of the AMW population stays in the Weddell Sea during austral winter.

In **Chapter II**, I used PAM data from 6 positions located along the WS during 2013 as well as three consecutive years of PAM data (2015-2016-2017) recorded at the stationary coastal acoustic observatory PALAOA to study both spatial and inter-annual variability in the acoustic behavior of AMWs. During 2013, between May and December throughout the WS, we detected 11 different bio-duck call types. The comparative analyses of the AMW bio-duck call repertoire throughout the WS showed that these 11 call types can be attributed to four call type groups. Furthermore, multi-year data from PALAOA on AMW repertoire composition showed an inter-annual difference in bio-duck call type usage. The observed patterns in AMW vocal behavior show that AMW vocal behavior matches the definition of song, exhibiting regional differences and highly dynamic revolutions over time. This study provides new information to potentially explore stock structures and movement patterns using passive acoustic methods.

In **Chapter III**, my work addressed the occurrence of the AMW through bio-duck acoustic detections in the Santos Basin, South-Southeastern Brazil (22° and 28° S / 42° and 48° W), recorded between 12 November and 19 December 19, 2015, utilizing advanced passive acoustic technologies, i.e., an autonomous underwater vehicle (SeaGlider), for sampling. AMW calls were detected during 12 days. We detected and classified 9 different bio-duck calls in Brazilian coastal waters, evidencing a highly diverse acoustic behavior on this potential Antarctic minke whale breeding ground.

Finally, in **Chapter IV**, our study investigated the temporal patterns of acoustic occurrence of baleen whales in a presumed baleen whale breeding area off Namibia. Our results show seasonal acoustic presence of humpback whales, fin whales and Antarctic minke whales from November to January and from June to August. Their acoustic absence from February to May possibly indicates that most animals migrated to other areas (presumably in higher latitudes) in austral summer to feed. Our findings support the presumed ecological importance of the oceanic area off Namibia, providing (part of) a suitable cetacean wintering and, possibly, breeding range or migratory corridor. Furthermore, the occurrence of Antarctic blue and minke whales off Namibia, concurrent with their reported acoustic presence in high-latitude feeding areas, adds to growing evidence that baleen whale migration is not obligate but much more dynamic than previously assumed.

Overall, this PhD thesis highlights the significance of using long-term and large-scale datasets for the investigation of distribution patterns, habitat preferences, behavior and the effects of environmental variation on AMW distribution. The results present new information about fundamental and ecological knowledge of AMWs that can be implemented for the conservation and management of populations and ecosystems.

Zusammenfassung

Antarktische Zwergwale (AMW) sind in der gesamten Antarktis verbreitet und kommen sowohl in offenen als auch in eisbedeckten Gewässern des Südlichen Ozeans (SO) vor. Sie sind eine pagophile Art und werden regelmäßig in stark mit Meereis bedeckten Gebieten beobachtet. Aus diesem Grund ist das derzeitige Wissen über antarktische Zwergwale spärlich und beschränkt sich auf den australischen Sommer und eisfreie Regionen, wo die meisten visuellen Erhebungen durchgeführt wurden. Daher weiß man nur sehr wenig über ihre Winterverbreitung in den Gewässern der hohen Breiten und darüber. Inwieweit es sich bei den gelegentlich in antarktischen Gewässern beobachteten überwinternden Individuen um Einzelbeobachtungen oder um ein strukturell vorhandenes Verhaltensmerkmal der Art handelt ist bisher ungeklärt. Auch die Populationsstruktur der AMW ist kaum erforscht. Wie bei den meisten Bartenwalen ist bekannt, dass AMWs jährliche Wanderungen zwischen den Nahrungsgebieten in hohen Breiten und den Brutgebieten in niedrigen Breiten unternehmen. Die bisher vorliegenden Daten deuten jedoch darauf hin, dass die Wanderungen von AMWs länger und komplexer sind als bei anderen Bartenwalen. Die kürzlich erfolgte Identifizierung von Lauten, die von AMWs erzeugt werden ("Bio-duck"), macht es nun möglich, auch passive akustische Technologien einzusetzen, um Vorkommensmuster und Verhalten zu untersuchen. Das passive akustische Monitoring (PAM) bietet eine vielseitige Technologie, mit der durch autonome Aufzeichnungseinheiten Langzeitarchivierungsdaten über geräuschproduzierende Arten gesammelt werden können. Die akustische Beobachtung hat den zusätzlichen Vorteil, dass sie unabhängig von den Lichtverhältnissen und unter schlechten Wetterbedingungen fortgesetzt werden kann. Außerdem können große Gebiete gleichzeitig überwacht werden, da die Daten omnidirektional erfasst werden, und durch den Einsatz autonomer Geräte können Daten über längere Zeiträume (d. h. auf mehrjährigen Skalen) gesammelt werden.

Im Rahmen dieser Doktorarbeit analysierte ich passive akustische Daten aus hohen und niedrigen Breiten, die im atlantischen Sektor des Südlichen Ozeans (Weddellmeer) und Südatlantik gesammelt wurden, um raum-zeitliche Muster der akustischen Präsenz und des Stimmverhaltens von antarktischen Zwergwalen zu untersuchen.

In **Kapitel I** beschreibe ich ganzjährige räumlich-zeitliche Muster im Auftreten von AMW in eisbedeckten Gebieten. Unsere Analyse basiert auf einem 9-jährigen passiven akustischen Datensatz (2008-2016) von 21 Orten im Weddellmeer (WS). Bio-duck Rufe von AMW wurden

von Mai bis Dezember an allen Verankerungsorten akustisch erfasst, wobei die höchste Präsenz zwischen August und November zu verzeichnen war (Bio-duck Rufe an mehr als 80 % der Tage). An den südlichsten Verankerungsorten waren Bio-duck Rufe in bis zu 10 Monaten des Jahres zu hören. Wir konnten erhebliche jahreszeitliche Schwankungen in der Aktivität der Rufe feststellen, die mit den Schwankungen der lokalen Eiskonzentration zusammenhängen. Unsere Analyse zeigt, dass ein Teil der AMW-Population während des australischen Winters im Weddellmeer bleibt.

In **Kapitel II** habe ich PAM-Daten von 6 Positionen entlang der WS im Jahr 2013 sowie drei aufeinanderfolgende Jahre von PAM-Daten (2015-2016-2017), die am PALAOA-Observatorium aufgezeichnet wurden, verwendet, um sowohl die räumliche als auch die inter-annuelle Variabilität im akustischen Verhalten der AMWs zu untersuchen. Im Jahr 2013 haben wir zwischen Mai und Dezember im gesamten WS 11 verschiedene Arten von Bio-duck Rufen festgestellt. Die vergleichende Analyse des AMW-Bio-duck Rufrepertoires im gesamten WS zeigte, dass diese 11 Ruftypen vier Ruftypengruppen zugeordnet werden können. Darüber hinaus zeigten die mehrjährigen Daten von PALAOA über die Zusammensetzung des AMW-Rufrepertoires, dass es zwischen den einzelnen Jahren Unterschiede in der Verwendung der Bio-duck Rufe gibt. Die beobachteten Muster im Gesangsverhalten von AMW zeigen, dass das Gesangsverhalten von AMW der Definition von Gesang entspricht und regionale Unterschiede sowie hochdynamische Umwälzungen im zeitlichen Verlauf aufweist. Diese Studie liefert neue Informationen zur möglichen Erforschung von Bestandsstrukturen und Bewegungsmustern mit Hilfe passiver akustischer Methoden.

In **Kapitel III** befasste sich meine Arbeit mit dem Vorkommen der AMW durch akustische Erfassungen von Bio-duck Rufen im Santos-Becken im Süd-Südosten Brasiliens (22° und 28° S / 42° und 48° W), die zwischen dem 12. November und dem 19. Dezember 2015 unter Verwendung fortschrittlicher passiver akustischer Technologien und autonomer Unterwasserfahrzeuge (SeaGlider) aufgezeichnet wurden. AMW-Rufe wurden an 12 Tagen erfasst. Wir entdeckten und klassifizierten 9 verschiedene Bio-duck Rufe in den brasilianischen Küstengewässern, was auf ein äußerst vielfältiges akustisches Verhalten in diesem potenziellen Brutgebiet der antarktischen Zwergwale hindeutet.

In **Kapitel IV** schließlich untersuchte unsere Studie die zeitlichen Muster des akustischen Auftretens von Bartenwalen in einem mutmaßlichen Bartenwal-Brutgebiet vor Namibia. Unsere Ergebnisse zeigen die saisonale akustische Präsenz von Buckelwalen, Finnwalen und antarktischen Zwergwalen von November bis Januar und von Juni bis August. Ihre akustische

Abwesenheit von Februar bis Mai deutet möglicherweise darauf hin, dass die meisten Tiere im australischen Sommer zur Nahrungsaufnahme in andere Gebiete (vermutlich in höheren Breiten) abwandern. Unsere Ergebnisse stützen die vermutete ökologische Bedeutung des Meeresgebiets vor Namibia, das (einen Teil) eines geeigneten Überwinterungs- und möglicherweise auch Brutgebiets oder eines Wanderkorridors für Wale darstellt. Das Vorkommen von antarktischen Blau- und Zwergwalen vor Namibia und ihre akustische Präsenz in Futtergebieten in hohen Breitengraden ist ein weiterer Beleg dafür, dass die Wanderung von Bartenwalen nicht obligatorisch, sondern vielmehr dynamisch ist.

Insgesamt unterstreicht diese Doktorarbeit die Bedeutung der Verwendung langfristiger und groß angelegter Datensätze für die Untersuchung von Verbreitungsmustern, Habitatpräferenzen, Verhalten und den Auswirkungen von Umweltveränderungen auf die Verbreitung von AMWs. Die Ergebnisse liefern neue grundlegende und ökologische Erkenntnisse über AMWs, die für die Erhaltung und das Management von Populationen und Ökosystemen genutzt werden können.

Abbreviation & Acronyms

SO	Southern Ocean
WS	Weddell Sea
ACC	Antarctic Circumpolar Current
UCDW	Upper Circumpolar Deep Water
PAM	Passive Acoustic Monitoring
AMW	Antarctic Minke Whale
IWC	International Whaling Commission
B.	*Balaenoptera*
E.	*Euphausia*
FFT	Fast Fourier Transformation
Ovlp	Overlap
SR	Sampling Rate
FR	Frequency Resolution
TR	Time Resolution
AWI	Alfred Wegener Institute
GM	Greenwich Meridian
WAP	Western Antarctic Peninsula
IUCN	International Union for Conservation of Nature

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Introduction

The Southern Ocean

The Antarctic environment is a biodiversity hotspot area, showing distinctive biogeographic features and high environmental variability (Knox, 2006; De Broyer et al., 2014). Variation in nutrient dynamics, variation in summer light availability, influenced by latitude and factors such as ice cover and sediment load, and variation in salinity and glacier runoff that in turn also affects sedimentation and turbidity, all contribute from small to large spatial scales to the region's unique terrestrial and marine environmental heterogeneity (Thomas, 2014). Habitats in sea ice vary over small spatial scales due to vertical light gradients and strong salinity changes over both spatial and temporal scales (Convey and Peck, 2019). The large environmental variability also makes that the Antarctic environment constitutes a productive and dynamic habitat for many unique migratory and resident species, ranging from zooplankton, fish and birds to marine mammals (Knox, 2006).

The Antarctic continent is surrounded by the Southern Ocean (SO) which is seasonally ice-covered, comprising 3–4 million km^2 in summer and up to 20 million km^2 in austral winter (Figure 1). The occurrence of sea ice with its seasonally drastically varying extent hence probably is the most pronounced feature of the Southern Ocean (Knox, 2006). The seasonal cycle of formation and melt is in itself of high significance to the Antarctic marine ecosystem, particularly for krill (i.e., *Euphausia superba, E. crystallorophias*) (Atkinson et al., 2019). Krill occupies a key position in the SO food web, acting as a direct link between primary producers and predators (e.g., Ryabov et al., 2017). The Southern Ocean's sea ice environment furthermore offers substantial habitat heterogeneity; even in heavy sea ice, open water areas constantly are formed and reformed, enhancing phytoplankton blooms, which attract first order consumers such as krill (*e.g.*, Anderson et al., 1993). These open water areas therefore provide local prey patches for higher trophic levels (Gordon and Comiso, 1988).

During austral summer when the retreating sea-ice exposes large quantities of patchily distributed krill, high densities of various krill consumers aggregate in the ice edge region to feed (Daly and Macaulay, 1988; Saunders and Brierley, 2007; Nicol et al., 2008). Evidence is furthermore increasing that many species remain in Antarctic waters during winter in spite of heavy sea-ice cover, exploiting food resources under the ice and in open water patches (Melnikov and Spiridonov, 1996; Atkinson et al., 2008; Flores et al., 2012). For Antarctic krill, one of the world's most abundant species and foundation of the SO food web, information on winter distribution and sea-ice habitat preferences is virtually lacking because survey ships are typically insufficiently ice-strengthened to break winter or multi-year sea-ice to perform a structural sampling (Williams et al., 2014; Branch and Butterworth, 2001; Friedlaender et al., 2006; Bengtson et al., 2018). Although many aspects of the relationship between krill abundance and sea ice are still under discussion, it is generally believed that ice-edge algal blooms form an important and predictable food source for krill, while under-ice biota provide krill protection from predators and a food source during austral winter and spring (Smetacek et al., 1990; Reiss et al., 2017). Antarctic krill occurs on a circumpolar scale in large concentrations and high densities, mainly associated with the continental shelf break (Nicol, 2006). The reproductive strategy and life cycle of the Antarctic krill is entirely adapted to the environmental conditions of the Southern Ocean including sea ice dynamics, ocean circulations and light availability, allowing for an optimized recruitment of krill populations (Nicol, 2006; Flores et al., 2012b). Given its important role as the food base for many marine mammal species, krill is thought to be one of the important drivers behind marine mammal distribution in the SO (Erbe et al., 2019).

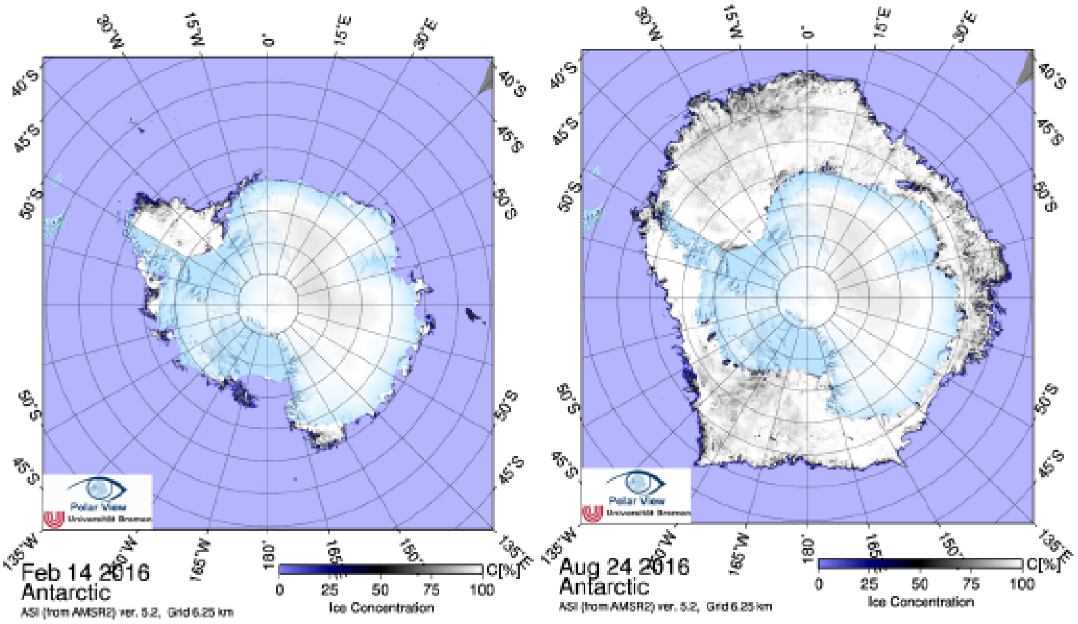

Figure 1. Map of the sea-ice concentration around the Antarctic continent during February 14th (left) and August 24th (right) of 2016.

The Weddell Sea

The sea ice is an important component of the Antarctic marine ecosystem. Every austral winter, a vast ice sheet forms over previously open waters in the Southern Ocean (Zwally, 1983). Around most of the Antarctic continent, the ice edge retreats to the coast in summer, except in the western Weddell Sea (WS) and the Bellingshausen–Amundsen Seas, where multi-year ice sheet largely remains in-tact year-round (Zwally 2002).

Sea ice provides a nutrient-rich substrate on and within which microbial communities can develop over winter (Arrigo et al., 2008; Ryan et al., 2011) and these communities are thought to provide over-wintering food sources for herbivores and to support the development of open ocean blooms in spring (Brierley and Thomas, 2002). During the summer, primary productivity in Antarctic waters increases as the ice melts and retreats. The microbial communities in the ice fertilize the surface water layer with iron and other nutrients. (Smetacek and Nicol, 2005). The melting process leads to the formation of a low salinity, stable surface layer which prevents deep mixing of phytoplankton cells retaining them at optimum light concentrations resulting in large blooms (Falkowski et al., 1998). The duration and extent of ice cover has been linked to the spawning and recruitment success of krill (Siegel, 2005).

The Weddell Sea ecosystem is dominated by dynamic sea ice, the eastward-flowing Antarctic Circumpolar Current (ACC) and its associated fronts, and the Weddell Sea Gyre (Deacon 1979). The Southern Boundary of the ACC creates various productivity hotspots around the Antarctic continent due to its high concentration of nutrient-rich Upper Circumpolar Deep Water (UCDW) (Tynan, 1998). The Weddell Gyre acts as an insulating current system which regulates temperature in the Weddell Sea and efficiently circulates nutrients, phytoplankton and zooplankton (Deacon, 1979; Daly and Macaulay, 1988). The Southern Boundary forms a critical trophic structure in the function of the Southern Ocean ecosystem, determining the broad circumpolar distribution of productivity and the resulting cascade of trophic dynamics (Tynan, 1998).

In comparison to other sectors of the Southern Ocean (i.e., Indian Ocean sector and Pacific sector), the WS is colder, more productive (in terms of primary production), and sustaining greater densities of Antarctic krill (Conil and Menéndez, 2006). Although many aspects of the relationship between krill abundance and sea ice are still under discussion (see Siegel, 2005 for a review), it is generally believed that ice-edge algal blooms form an important and predictable food source for krill, while under-ice biota provide krill protection from predators and a food source during austral winter and spring (Knox, 2006).

Spatial temporal distribution of species in the SO

The SO sea ice environment represents a critical habitat for many threatened migratory and resident species (Erbe et al., 2019) and is in many ways not comparable to other ocean basins (Boyd 2009). Many migratory mysticete whale species frequent this region during the austral summer for feeding (e.g. Schall et al., 2021; Thomisch et al., 2016; Burkhardt et al., 2021). During this time, they take in the larger proportion of their annual energy requirements and store substantial amounts of lipids (Lockyer, 1981; Reilly et al., 2004). Ice-breeding seals critically rely on pack- or fast ice for reproduction, moult and haul out, exhibiting species-specific preferences in the sea ice characteristics that they associate to (e.g., Siniff, 1991). In terms of biodiversity, the Antarctic marine realm is home to a range of marine species that cannot be found elsewhere on the globe (Erbe et al., 2019).

Information on marine species' spatio-temporal distribution and their relationship to the environment is essential for well-informed, proactive management strategies and conservation actions (Becker et al., 2016; Guisan et al., 2013), particularly in the light of ongoing climate-induced changes (e.g., Clem et al., 2020). However, obtaining sufficient data on marine mammal distribution across large spatial scales is challenging due to financial and logistic constraints, particularly in remote oceans such as the SO (Kaschner et al., 2012). Spatio-temporal information on species distributions from the SO, necessary for conservation planning and management, is therefore particularly patchy for the SO. Research efforts are generally biased towards relatively small areas of the SO (e.g. the West Antarctic Peninsula), repetitive ship tracks (e.g. to and from Antarctic stations) and limited to mainly the austral summer months (Erbe et al., 2019). Consequently, deep-sea and remote regions (e.g. the Bellingshausen and Amundsen Seas) remain largely underinvestigated (De Broyer et al., 2014). Most research vessels that operate in the SO are biased towards the operationally safe ice-free waters and do not engage in the risk and costs of going deep into the sea ice (Herr et al., 2019; Bombosch et al., 2014; El-Gabbas et al., 2021a; Williams et al., 2014). This results in substantial seasonal and spatial biases in the available data that need to be overcome by technologies such as remote sensing techniques to answer pressing questions on the effects of climate-induced changes on Antarctic ecosystems.

Passive Acoustic Monitoring (PAM)

In recent years, passive acoustic monitoring (PAM) has become an important tool for monitoring marine mammals (Van Parijs et al., 2009). Sound plays an important role for many marine mammal species, as visibility is often restricted underwater and water has excellent sound transmission properties. Marine mammals use sound passively by listening to their acoustic environment exploiting biotic and abiotic cues for example to orientate or localize prey and predators (Roger Payne and Webb, 1971; Au, 1993). Active sound production is used for various behavioral purposes, such as mother-calf communication (Parks et al., 2019) as well as intra- and inter-sexual communication in reproductive contexts. This makes passive acoustic recording techniques a suitable tool to remotely monitor presence and study marine mammal behaviour, in particular for polar species inhabiting regions that are largely seasonally inaccessible (Bombosch et al., 2014).

Furthermore, visual observations, which was long the traditional tool of choice for data collection on marine mammals, depend on favourable weather and light conditions and the presence of an observation team on-site. In polar areas, weather conditions can be particularly adverse year-round with heavy storms and fog. Outside the summer period, favourable sighting conditions are further restricted by limited daylight hours (Williams et al., 2014; Bombosch et al., 2014; Herr et al., 2019).

In contrast to visual observation, acoustic recorders can, as mentioned previously, be operated autonomously, are quasi-omnidirectional and independent of weather and light conditions, providing the option to study animals over longer time frames (i.e., years), at night and under conditions where visual observation is not possible. By coupling in-situ measured or remote sensing environmental data to recordings, it is possible to combine on-site measurements of acoustic activity with biological or oceanographical features to monitor responses of marine mammals to environmental change on various time and spatial scales (e.g., Stafford et al., 2009; Thomisch et al., 2016; Menze et al., 2017; Williamson et al., 2017; Buchan et al., 2018; Shabangu et al., 2020; Schall et al., 2021).

Acoustic recordings can be valuable tools for monitoring populations of marine mammals since many species produce loud and distinctive calls. In some species, recordings can furthermore be used to identify stocks on the basis of regional dialects, providing information on movement and association patterns of animals (Noad et al., 2000).

Passive acoustic methods are furthermore also being increasingly used to estimate animal population density (Küsel et al., 2011). Most density estimation methods are based on estimates of the probability of detecting calls as functions of distance (Barlow and Taylor, 2005; Marques et al., 2009, 2013). Typically these are obtained using receivers capable of localizing calls or from studies of tagged animals (Marques et al., 2009). The estimated detection function is integrated over the area of interest, which is equivalent to averaging over distance, assuming that animals are uniformly distributed around the sensors, to derive the estimated average probability of detection. This relatively novel method is applied increasingly often to better understand a particular species' distribution and population density in a given geographic area (McDonald and Fox, 1999; Moretti et al., 2006; Marques et al., 2009; Küsel et al., 2011; Hildebrand et al., 2016).

Figure 2. Deployment of an acoustic recorder (Sonovault) in the Weddell Sea.

Despite the many benefits of the PAM methodology, it is also important to consider its limitations when designing a monitoring study. Those can be attributed to the specification of the acoustic recording device e.g., due to its depth limits or, the most common one, the operational deployment duration, which is directly determined by data storage capacity and battery capacity of the recorder (e.g., Sousa-Lima et al., 2013). Particularly in polar environments, high logistic and financial costs limit the frequency with which recorders can be refurbished and longer recordings times are preferred. Increasing the operational deployment time requires increasing storage capacities of the instrument and increasing power consumption. Increased power consumption in turn, affects the number, and possibly type, of batteries that are needed to cover the requirements, thereby in turn potentially increasing both instrument size and hence flotation requirements (Wiggins and Hildebrand, 2007). Instrument size may also affect its installation on the mooring infrastructure and recovery of the equipment (Figure 2).

Another issue that needs to be taken into account when collecting passive acoustic data, can be that sometimes the target sounds can also be masked by non-target sounds, from anthropogenic sources as well as other (non-target) vocalizing animals (Gibb et al., 2019). The effective sampling area around an acoustic sensor therefore varies among species and call types, and across space and time (Marques et al., 2013). If unaccounted for, any resulting detection biases (e.g., towards animals that call at higher amplitudes and/or lower frequencies) may cause biased population, acoustic presence or diversity estimates (Marques et al., 2013; Gibb et al., 2019).

It also needs to be considered that the signature or characteristic sound of the study species is sufficiently known and well-described. Attributing a sound to a species is not an easy task, especially with marine mammals, which are pelagic animals that can move over large areas and not all species spend a lot of time on the surface (i.e., cetaceans). The attribution of a specific sound has been accomplished through studies of animals in captivity (seals, porpoises, etc.), (Rogers et al., 1996; Kastelein et al., 2006; Teilmann et al., 2006) or using hydrophones with visual confirmation of the species and knowing that there are no other individuals in the area (Edds-Walton, 1997; Parks et al., 2019). To date, there are still sounds of which the origin has not yet been attributed and of which the source is still unknown (e.g. Gedamke & Robinson, 2010). Last but not least, it is essential to have knowledge about the behavior of the target species; not all animals produce sounds all the time, some are only vocally active during a certain period of the year. To successfully study the presence or behavior of animals using passive acoustic techniques, it is a prerequisite for the animals to produce sound, as silent individuals will go unnoticed.

With the advance of technology, new sounds have been recorded and attributed to species or abiotic sound sources, as for example the case of the Antarctic minke whales (*Balaenoptera bonaerensis*) (AMW) in the heavily ice-covered Southern Ocean during austral winter. The initial acoustic identification of sounds that had been recorded since the 1960s throughout the southern hemisphere came from a study by Risch et al. (2014) that succeeded in obtaining acoustic records from an AMW using an acoustic tag attached to the animal. The acoustic records obtained during this study revealed that the -until then- mysterious signature, referred to as the 'bio-duck' (Schevill & Watkins, 1972), was produced by AMWs. The bio-duck signature had been found present in various acoustic records collected throughout the Southern Ocean and as far north as off the coast of Australia, in the waters surrounding the Antarctic Peninsula, Chile, South Africa and Namibia (Mccauley et al., 2004; Dominello and Širović, 2016; Thomisch et al., 2019; Buchan et al., 2020; Shabangu et al., 2020). The bio-duck signal is characterized by its repetitive nature, consisting of regular down-sweep pulses, with most energy located in the 50-300 Hz band, although for signals with higher intensity, harmonics can occur up to 1 kHz (Dominello and Širović, 2016). The name bio-duck originates from sonar operators on board old Oberon class submarines who also often detected the signal and associated it with the sound of a duck (e.g., Van Opzeeland, 2010). This recent finding now makes it possible to also retrospectively analyse long-term passive acoustic data sets that have been collected in the Southern Ocean to explore the spatio-temporal patterns in the vocal behaviour and distribution of AMWs.

Antarctic minke whale

Until the 1990s, only one species of minke whale was recognized, the Antarctic minke whale (*Balaenoptera bonaerensis)* being regarded as conspecific with the common minke whale (*Balaenoptera acutorostrata*) (Figure 3). Most of the scientific literature prior to the late

1990s uses the name *B. acutorostrata* for all minke whales including Antarctic minke whales (Williamson, 1975; Best, 1982) . Since 2000, the International Whaling Commission (IWC) Scientific Committee has recognized Antarctic minke whales as the separate species *Balaenoptera bonaerensis*, while all Northern Hemisphere minke whales and all Southern Hemisphere "dwarf" minke whales are regarded as *Balaenoptera acutorostrata* (IWC, 2001). This decision was based on genetic and morphological evidence that indicated that the two minke whale species, which are partially sympatric in the Southern Hemisphere, are distinct species (Wada et al., 1991; Pastene et al., 1991; Rice et al., 1998; Pastene et al. 2007).

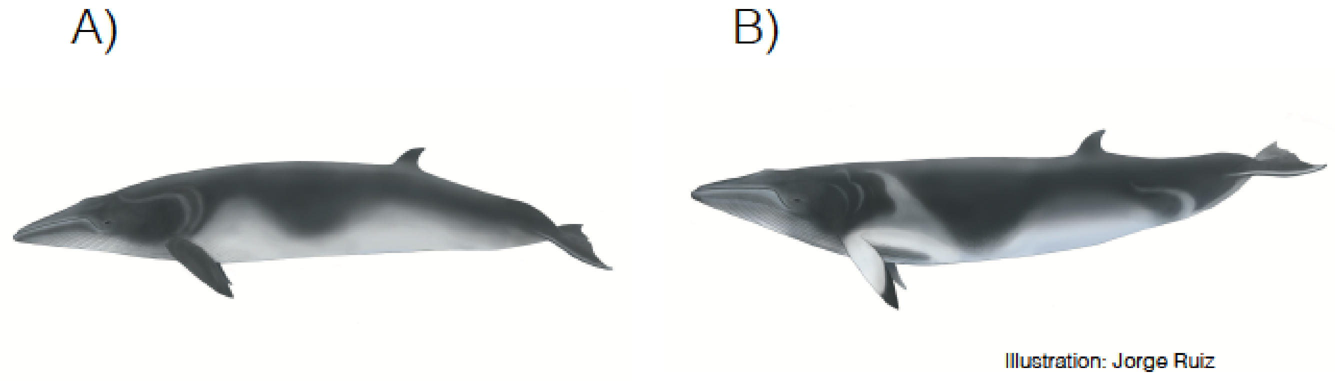

Illustration: Jorge Ruiz

Figure 3. A) Antarctic minke whale *(Balaenoptera bonaerensis*), B) Dwarf minke whale *(Balaenoptera acutorostrata)*

The AMW abundance and population structure is poorly known. Overall abundance estimates for AMWs are currently around 500 000, whereas earlier assessments estimated 720 000 animals, representing a 31% decline (Williams et al., 2014). Despite logistical challenges and ongoing discussions on how to best survey AMWs, current population estimates and their trajectory give reason for concern and accordingly have resulted in the recent classification of AMWs as Near Threatened under the IUCN Red List and under Appendix I of CITES (Cooke et al., 2018b). Recent analyses suggest a genetic distinction between whales in the Indian Ocean and the Pacific Ocean sector, although both populations overlap and lack a sharp geographical boundary between them (IWC, 2013). AMWs have a circumpolar distribution south of 60°S during summer, with high densities reported in parts of the Weddell and Ross Seas (Kasamatsu et al., 1995), (Figure 4). They are a pagophilic (ice-loving) species and are regularly observed in heavily sea-ice covered areas (Ainley et al., 2007; Scheidat et al., 2011). AMWs in polar waters are generally highly associated with sea ice, while less AMWs are observed in ice-free waters (Herr et al., 2019). Their relatively small body size provides increased maneuverability required to navigate in and around sea-ice in search of Antarctic krill, their primary prey (but also *E. crystallorophias*, *E. frigida* and *Thysanoessa macrura*) (Murase et al., 2002). AMWs and humpback whales (*Megaptera novaeangliae*) are thought to partition prey resources in the SO by feeding in different habitats (sea ice versus open water, respectively) but when the two species do overlap in time and space, they have been found to partition prey vertically (Friedlaender et al., 2009).

Figure 4. Geographic distribution of Common minke whale and Antarctic minke whale (Extracted from Cooke et al., 2018).

As most baleen whale species, AMWs are known to undertake annual migrations between high latitude feeding areas and low latitude breeding areas (Best 1982). However, recent passive acoustic data suggest migratory behaviour may be much more complex and variable in this species compared to other baleen whales (e.g., Geijer et al., 2016). Recent studies, including the chapters included in this thesis show detections of the species in association with sea ice for most of the year. However, this species has also been observed and recorded in sub-tropical waters of the South Atlantic, South Pacific, and Indian Ocean during winter (McCauley et al., 2004; Cerchio et al., 2018). A bi-modal temporal distribution pattern of Antarctic minke whales has been visually observed off South Africa, peaking in fall and spring, suggesting migratory movements by parts of the population to lower latitude habitats during winter (Best, 1982). There is also some evidence that AMWs occasionally occur north of the equator (Glover et al., 2010; De Boer, 2015). Overall, AMW migrations seem more protracted and complex than in other baleen whale species, with regular observations of individuals remaining in temperate waters throughout the year, whereas others have been observed in the pack-ice during the austral winter period (Aguayo-Lobo, 1994; Dominello and Širović, 2016; Filun et al., 2020).

Threats

AMWs provide a good example of a baleen whale species that are at risk from multiple environmental pressures driven by climate change. Antarctic minke whales are the largest ice-dependent krill predators in the Southern Ocean. As their distribution and ecology are thought to be tied directly to sea ice (Herr et al., 2019) and foraging on krill, any changes that affect the quantity and quality of their habitat and food availability could be significant. The marine ecosystem around the Antarctic Peninsula is experiencing dramatic warming (Morris and Vaughan, 2003) and significant reductions in the extent and duration of seasonal sea ice cover (Stammerjohn et al., 2008). These changes affect every component of the ecosystem (Schofield et al., 2010; Ducklow et al., 2012), but particularly the demography, behaviors and ecology of predators that rely on sea ice for foraging habitat and prey, such as Antarctic krill. With continued sea ice decline, the potential for overlap, and thus competition for prey with other krill-feeding species (e.g. humpback whales, crabeater seals (*Lobodon carcinophaga*), Antarctic fur seals (*Arctocephalus gazella*), seabirds, and some fish species), increases as does the likelihood that krill abundance will decrease due to poor recruitment (Atkinson et al., 2004). All of these processes occurring in cascade could cause AMWs to move to regions further south e.g., into the Weddell Sea that is still reliably ice-covered, increasing energetic costs of migration to lower latitudes as well as inter-specific competition for resources if suitable habitat is reduced. Furthermore, inter-specific predation risk from killer whales may be a further force driving AMWs from areas with increasing open water (Higdon and Ferguson, 2018).

The implementation of an acoustic monitoring network in the Weddell Sea has generated new information and knowledge about AMW population in the area, providing new insights about the behavior, and spatial and temporal distribution of the species. The findings of this study provide fundamental information for the conservation of this species and how PAM can be used for monitoring purposes.

Objectives

This PhD dissertation comprises the longest temporal PAM effort for Antarctic minke whales in the Southern Ocean. It is based on state-of-the-art passive acoustic recording technology and presents new insights on Antarctic minke whale vocal behavior. This dissertation maps distribution patterns on an unprecedented spatio-temporal scale within the Weddell Sea and is complemented by two studies on AMW vocal behaviour in lower latitudes of the Atlantic Ocean. Specifically, the aims of this thesis were to:

1) Investigate the spatial occurrence of the bio-duck signature throughout the Weddell Sea and correlate call occurrence with local sea ice conditions. Can we draw conclusions on habitat preferences with respect to sea-ice conditions?

2) Investigate the temporal variation in the occurrence of the bio-duck signal; i.e., how does it vary on a diel, seasonal and annual time scale? Can we draw conclusions on the potential function of this sound?

3) Examine the acoustic properties of this signal; do calls differ in space or over time? Do similar differences that have been reported in the signals at the Antarctic Peninsula occur in this data set? Could these be indicators for geographically separated groups?

4) Create a reliable automated detector that can be readily used to process future data for the presence of Antarctic minke whale acoustic signatures.

List of Chapters

This thesis is based on the following research articles:

Chapter I: Filun, D., Thomisch, K., Boebel, O., Brey, T., Širović, A., Spiesecke, S., & Van Opzeeland, I. (2020). Frozen verses: Antarctic minke whales (*Balaenoptera bonaerensis*) call predominantly during austral winter. Published in *Royal Society open science*, *7*(10), 192112. **https://doi.org/10.1098/rsos.192112**

> **Content**: In this paper, I used a nine-year passive acoustic data set recorded across the Weddell Sea. Including 21 locations, my study shows that Antarctic minke whales (AMWs) are acoustically present at all sites between May-Dec, exhibit vocal activity that is highest at sites and during periods with dense ice conditions and are acoustically present throughout austral winter. The primary calling period (Sep-Oct) coincides with the timing of the breeding season of AMW in lower latitudes.

Chapter II: Filun, D. & Van Opzeeland, I. The latest local tune: the calling behavior of Antarctic minke whales (*Balaenoptera bonaerensis*) differs in space and time. Planned to be submitted to *Nature Scientific Reports*.

> **Content**: In this paper we describe and classify the different bio-duck calls produced by AMWs detected in the Weddell Sea. We detected 11 different bio-duck call types. The comparative analyses of the AMW bio-duck call repertoire throughout the WS showed that these 11 call types can be attributed to four call type groups. Furthermore, multi-year data from PALAOA on AMW repertoire composition showed an inter-annual difference in bio-duck call type usage. The observed patterns in AMW vocal behaviour show that AMW vocal behaviour matches the definition of song, exhibiting regional differences and highly dynamic revolutions over time.

Chapter III: Rossi-Santos, MR*., Filun, D.*, Soares-Filho W., Paro A., Wedekin, L. Playing the beat: occurrence of Bio-duck calls in Brazil reveals a complex acoustic behaviour for the Antarctic minke whale (*Balaenoptera bonaerensis*). Revised version in preparation for *PlosOne.*
**Shared first authorship*

> **Content**: In this paper using data recorded with a SeaGlider, in 27 encounters we detected and classified 9 different bio-ducks in Brazilian water. We describe for the first time the acoustic occurrence of AMWs in Brazil previously described as a breeding area for the species. These findings demonstrate that the use of PAM is an efficient tool for monitoring cetaceans in offshore waters.

Chapter IV: Thomisch, K., Boebel, O., Bachmann, J., Filun., D., Neumann, S., Spiesecke, S., Van Opzeeland, I. (2019). Temporal patterns in the acoustic presence of baleen whale species in a presumed breeding area off Namibia. Published in *Marine Ecology Progress Series*, *620*, 201-214. https://doi.org/10.3354/meps12952

> **Content**: In this paper we describe the importance of the oceanic area off Namibia, providing (part of) a suitable cetacean wintering and, possibly, breeding range or

migratory corridor. The occurrence of Antarctic blue and minke whales, concurrent with their reported acoustic presence in high-latitude feeding areas, adds to growing evidence that baleen whale migration is not obligate but much more dynamic than has long been assumed.

Chapter contribution

Chapter I: Filun, D., Thomisch, K., Boebel, O., Brey, T., Širović, A., Spiesecke, S., & Van Opzeeland, I. Frozen verses: Antarctic minke whales (*Balaenoptera bonaerensis*) call predominantly during austral winter.

DF analysed all the data, conducted statistical analyses and wrote the manuscript. KT participated in some data collection and helped draft the manuscript. OB participated in collecting data and coordinated the study. TB helped guide some statistical analyses and with the previous version of the manuscript. SS collected the data. AŠ helped with the draft manuscript and with guidance for the analyses. IVO coordinated the study, collected part of the data and helped draft the manuscript.

The chapter was published in *Royal Society Open Science*,
https://doi.org/10.1098/rsos.192112; published online 07. October 2020

Chapter II: Filun, D. & Van Opzeeland, I. The latest local tune: the calling behavior of Antarctic minke whales (*Balaenoptera bonaerensis*) differs in space and time.

D.F and I.V.O conceived and designed the study. IVO collected part of the data. D.F analyzed all the data and wrote the paper with substantial contributions from I.V.O.

The Chapter is in preparation for submission to *Scientific Reports*

Chapter III: Rossi-Santos, MR*., Filun, D.*, Soares-Filho W., Paro A., Wedekin, L. Playing the beat: occurrence of Bio-duck calls in Brazil reveals a complex acoustic behaviour for the Antarctic minke whale (*Balaenoptera bonaerensis*). **Shared first authorship*

DF and MRRS have equal contributions as leading authors of this study. MRRS, WSF, ADP, LLW collected the data. The analyses were realized by WSF and DF. DF wrote the manuscript with substantial contribution from MRRS.

The Chapter was submitted to the journal *PLOS ONE* in September 2021 and a revised version is currently in preparation.

Chapter IV: Thomisch, K., Boebel, O., Bachmann, J., Filun., D., Neumann, S., Spiesecke, S., Van Opzeeland, I. Temporal patterns in the acoustic presence of baleen whale species in a presumed breeding area off Namibia.

KT designed analyzed and wrote the manuscript. OB and SS collected the data. DF and SN analyzed the data and contributed with the manuscript redaction. IVO supervised and helped writing the manuscript.

The Chapter was published in the *Marine Ecology Progress*
Series, https://doi.org/10.3354/meps12952 ; published online 18. June 2019.

Chapters

Chapter I: Frozen verses: Antarctic minke whales (Balaenoptera bonaerensis) call predominantly during austral winter.

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Research

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Frozen verses: Antarctic minke whales (*Balaenoptera bonaerensis*) call predominantly during austral winter

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The recent identification of the bio-duck call as Antarctic minke whale (AMW) vocalization allows the use of passive acoustic monitoring to retrospectively investigate year-round spatial-temporal patterns in minke whale occurrence in ice-covered areas. Here, we present an analysis of AMW occurrence patterns based on a 9-year passive acoustic dataset (2008–2016) from 21 locations throughout the Atlantic sector of the Southern Ocean (Weddell Sea). AMWs were detected acoustically at all mooring locations from May to December, with the highest presence between August and November (bio-duck calls present at more than 80% of days). At the southernmost recording locations, the bio-duck call was present up to 10 months of the year. Substantial inter-annual variation in the seasonality of vocal activity correlated to variation in local ice concentration. Our analysis indicates that part of the AMW population stays in the Weddell Sea during austral winter. The period with the highest acoustic presence in the Weddell Sea (September–October) coincides with the timing of the breeding season of AMW in lower latitudes. The bio-duck call could therefore play a role in mating, although other behavioural functions of the call cannot be excluded to date.

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1. Introduction

The Antarctic sea-ice environment constitutes a productive and dynamic habitat for many unique migratory and resident species, ranging from zooplankton, fish and birds to marine mammals [1]. During austral summer when the retreating sea-ice exposes large quantities of patchily distributed krill, high densities of various krill consumers aggregate in the ice edge region to feed [2–7]. However, there is increasing evidence that many species remain in Antarctic waters during winter in spite of heavy sea-ice cover, exploiting food resources under the ice and in open water patches [8–13]. Our knowledge on the ecology of these species in their sea-ice habitat is hampered severely by the logistic restrictions imposed on scientific work in such environments. For Antarctic krill (*Euphausia superba*), one of the world's most abundant species and foundation of the Southern Ocean food web, information on winter distribution and sea-ice habitat preferences is virtually lacking because survey ships are typically insufficiently ice-strengthened [7,14–17]. The distribution of Antarctic minke whales (*Balaenoptera bonaearensis*) (AMW) is another striking knowledge gap. AMWs have a circum-Antarctic distribution and are known to occur within the marginal ice zone (MIZ) and the interior sea-ice pack [18–20]. Most detailed information on the species stems from ship-based observations, i.e. data are limited to the austral summer period and regions that are (seasonally) ice-free. Visual sightings from the region indicate that the species' behaviour and appearance often result in low sightability, making visual data collection on this species challenging [7,21]. As a consequence, AMW abundance estimates based on visual survey data are in many cases spatially and temporally biased [7,22]. Only very sparse information exists on the winter distribution of AMW in the Southern Ocean and how the species is associated with different sea-ice concentrations throughout the year [23–25].

The recent identification of the bio-duck calls as vocalizations produced by AMWs [26] allows to use passive acoustic data to study their occurrence patterns and behaviour of this species. Passive acoustic monitoring offers a versatile technology with which long-term archival data can be collected on sound-producing species using autonomous recording units [27]. This makes passive acoustic recording techniques a suitable tool to remotely monitor the acoustic presence and study marine mammal behaviour. This particularly accounts for polar species given that large parts of their habitats are (seasonally) inaccessible for research vessels (e.g. [4,12,13,28]).

The identification of AMW sounds marked the end of a long-standing riddle as the bio-duck calls had been recorded at numerous locations across the Southern Ocean as well as off the Australian and Namibian coasts [26,29–31]. With the confirmation that the sound stems from AMWs, it is now possible to retrospectively process passive acoustic time series to explore this species' year-round distribution and relation to sea-ice conditions to improve our understanding of this species also across years detecting trends in behaviour and distribution. Improving our knowledge of AMW ecology and behaviour is central to our understanding of the effects of ongoing climatic change on the Antarctic pelagic ecosystem. During the last decades, (sub)surface warming has been shown to drastically affect the marine environment around the Antarctic Peninsula in various ways [32]. Elevated temperatures trigger reductions in the seasonal period and extension of sea-ice-covered areas, leading to a chain of reactions by which also zooplankton assemblages are impacted with anticipated negative feedbacks to the ecology of higher trophic level consumers [33,34]. AMWs are krill consumers, preferring areas with substantial ice cover [7,20,35]. The forecasted changes in sea-ice conditions therefore have the potential to drastically affect AMWs [20]. To understand and predict how the cascading effects of climate change impact higher trophic level species, such as AMWs, baseline information on species' distribution and habitat preferences is crucial to identify and interpret potential climate-mediated shifts in range boundaries. Information on AMW spatial-temporal distribution patterns is furthermore of direct relevance for Southern Ocean ecosystem management in the context of the conservation and management mandate of the International Whaling Commission (IWC) and the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR). Recently, AMWs were classified as Near Threatened under the Internal Union for Conservation of Nature (IUCN) Red List and under Appendix I of CITES [36]. Given the current uncertainty regarding AMW abundance estimates (IWC 2013) [37], better insights into spatial-temporal movements of this population or its subpopulations may in part be key to improving methods for abundance estimations.

Here, we use multi-year passive acoustic data from a recording network in the Weddell Sea and along the Greenwich meridian to investigate spatial-temporal patterns in the daily acoustic presence of AMWs.

Table 1. Locations and recordings parameters of acoustic recorders deployed within the Hybrid Antarctic Float Observation System (HAFOS) array in the Weddell Sea. Recorders sorted by deployment period.

recording site ID	recorder ID	latitude	longitude	deployment depth (m)	sampling frequency (kHz)	sampling scheme (min/min)
GW1	AURAL	68 59.74 S	000 00.17 E	189	32.77	5/240
GW2	AURAL	66 01.13 S	000 04.77 E	206	32.77	5/240
GW3	SonoVaults	59 03.02 S	000 06.63 E	1007	5.33	continuous
GW4	SonoVaults	63 59.56 S	000 02.65 W	969	5.33	continuous
GW1	SonoVaults	66 01.90 S	000 03.25 E	934	5.33	continuous
EI1	AURAL	61 00.88 S	055 58.53 W	204	32.77	5/60
WA1	SonoVaults	63 28.84 S	052 05.77 W	945	5.33	continuous
GW1	SonoVaults	68 59.86 S	000 06.51 W	934	5.33	continuous
WA2	SonoVaults	69 03.48 S	017 23.32 W	678	5.33	continuous
WA7	SonoVaults	65 58.09 S	012 15.12 W	734	5.33	continuous
WA6	AU0086	66 36.70 S	027 07.31 W	207	32.77	5/240
WA5	SonoVaults	64 22.94 S	045 52.12 W	678	5.33	continuous
GW5	SonoVaults	59 02.63 S	000 04.92 E	1020	5.33	continuous
WA4	SonoVaults	66 36.45 S	027 07.26 W	423	5.33	continuous
WA4	SonoVaults	66 36.45 S	027 07.26 W	678	5.33	continuous
WA4	SonoVaults	65 37.23 S	036 25.32 W	956	5.33	continuous
WA3	SonoVaults	63 42.09 S	050 49.61 W	487	5.33	continuous
WA3	SonoVaults	63 42.09 S	050 49.61 W	723	5.33	continuous
GW4	SonoVaults	64 00.32 S	000 00.22 W	812	5.33	continuous
GW2	SonoVaults	66 30.71 S	000 01.51 W	943	5.33	continuous
GW1	SonoVaults	68 58.89 S	000 05.00 W	869	5.33	continuous
WA9	SonoVaults	66 30.71 S	000 06.51 W	1083	5.33	continuous
WA8	SonoVaults	70 53.55 S	028 53.47 W	330	5.33	continuous

2. Materials and methods

2.1. Data collection

Passive acoustic data were collected between 2008 and 2016 (9 years) from 21 mooring positions (with varying recording periods, see table 1 for details) throughout the Weddell Sea (WA) and along the Greenwich meridian (GW), covering the area between 59 and 69° S and from 0 to 56° W [13].

Passive autonomous acoustic recorders were attached to oceanographic deep sea moorings of the Hybrid Antarctic Float Observation System (HAFOS) [38]. For this study, two types of autonomous acoustic recorders were used: Autonomous Underwater Recorder for Acoustic Listening, model 2 (AURALs; Multi-Electronique, Quebec) and SonoVaults (Develogic GmbH, Hamburg). All four AURALs recorded with a sampling rate of 32 768 Hz. Three of the AURAL recorders were programmed to collect data 5 min every 4 h (2% duty cycle) and one AURAL was set to record 5 min every hour (8% duty cycle). SonoVaults were programmed to record continuously with a sampling rate of 5333 Hz for data collected during years 2010–2014 and with a sampling rate of 6857 Hz during years 2014–2016 (table 1). Although additional analyses showed that the duty cycles applied underestimated daily AMW acoustic presence during the shoulder seasons, overall presence patterns did not show anomalies compared to nearby recorders collecting data continuously (see electronic supplementary material, appendix S1).

The positions located in the Weddell Sea were sub-divided in four different sectors: Elephant Island (EI), Weddell Sea North (WSN), Weddell Sea South (WSS) and Greenwich Meridian (GW) (figure 1). This sub-division was based on the differences in ice growth patterns across the region [39].

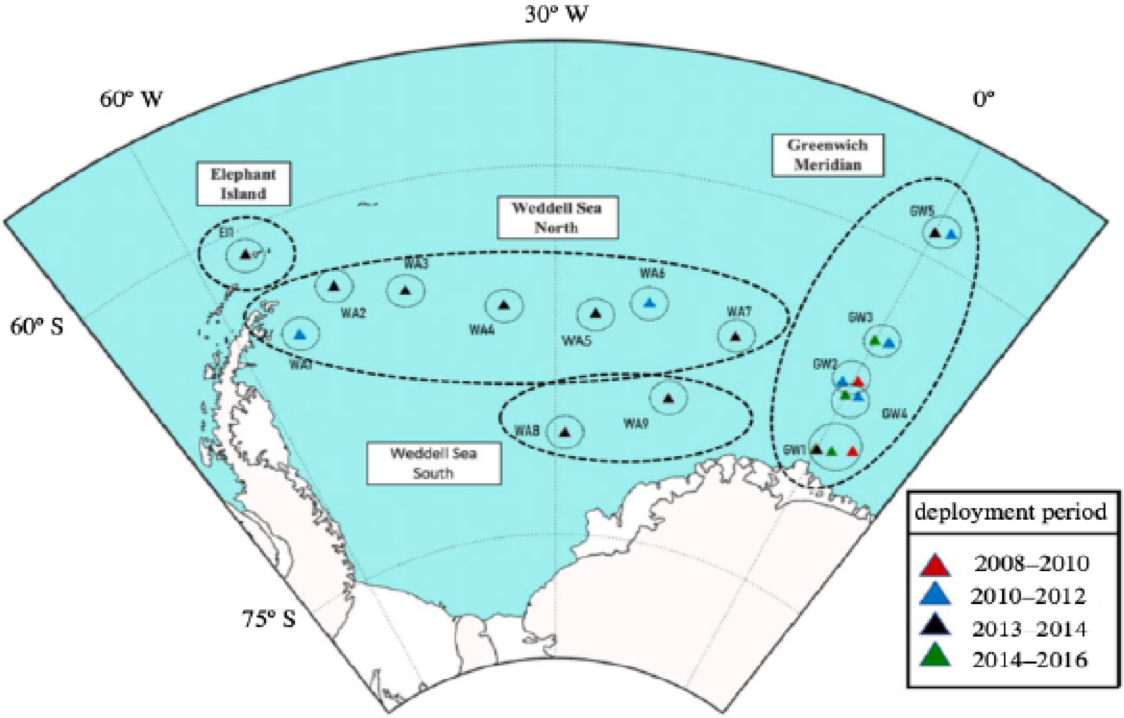


Figure 1. Map of the study area in the Weddell Sea. The triangles denote the positions of the passive acoustic recorders and circles represent their detection range (40 km radius). Triangle colour encodes the different deployment periods. Recording sites names are assigned by geographic location (with 'GW', 'WA' and 'EI' indicating the Greenwich meridian, the Weddell Sea and Elephant Island, respectively) and number for distinct recording sites.

2.2. Acoustic analyses

The acoustic recordings were processed using the Matlab-based (Mathworks, Natick, MA) custom software program *Triton* [40] to create long-term spectral averages (LTSAs) plots. LTSAs visually represent a time series of averaged spectra [40]. For all data successive spectra, with 1 Hz frequency resolution, were calculated by averaging 60 s of acoustic data. These LTSAs were used for all acoustic data to manually log AMW daily acoustic presence. For the continuous SonoVault recordings, a window size of 1 day of data was inspected to identify AMW signatures. For the duty-cycled AURAL recorders, a four-day window size was used to identify the daily presence of AMWs. When presumed AMW signatures were observed in the LTSAs, a 20 s spectrogram window (overlap = 90%, FFT = 1050) of that time section was inspected visually and aurally to verify the presence of AMW signatures.

We used the bio-duck call as proxy for AMW acoustic presence (see for a description of bio-duck call: [25,26,29,30,41]). The bio-duck is characterized by its repetitive nature, consisting of regular downsweeps or pulses in series, with most energy located in the 50–300 Hz band (figure 2), although for signals with higher intensity, harmonics occur up to 1 kHz. In this study, a bio-duck call refers to a cluster of down-swept pulses separated by less than 1 s. Different bio-duck sub-types have been described in the literature, mainly basing on the number of pulses within clusters [25,41,42]. Here, no distinction was made between bio-duck sub-types, and all bio-duck calls were pooled to determine daily AMW acoustic presence. Bio-duck calls never occurred alone (i.e. one cluster of calls or one phrase). The minimum sequence duration that we observed was 20 s. All days with AMW acoustic presence therefore at least had a series of 20 s with bio-duck calls over a 24 h period.

Monthly acoustic presence was calculated for all sites from the number of days with AMW acoustic presence per day divided by the number of days with recording effort. To explore inter-annual variability, two positions with 3 years of deployment (GW1 and GW2) were used.

2.3. Sea-ice data

The sea-ice concentration data used for this study were extracted from satellite images with a resolution of 6.25 × 6.25 km from the Advanced Microwave Scanning Radiometer for EOS (AMSR-E) satellite sensor

To explore how AMW acoustic presence related to sea-ice concentration, ice concentration and acoustic presence data were correlated for every location using a Pearson's correlation. The variability of this relationship with the temporal resolution was explored by correlating AMW presence and sea-ice concentration within moving windows of varying temporal width, i.e. 1, 3, 7, 15, 21, 30 days, to select the best temporal resolution to correlate the acoustic presences with the ice concentration values. Monthly sea-ice concentration data showed highest correlation values ($r = 0.89$)

3. Results

Passive acoustic recordings from 21 mooring positions collected between 2008 and 2016 totalling 8176 days were analysed for AMW acoustic presence. AMWs bio-duck signatures were detected on 2777 days (34% of the total number of recording days). AMWs were found to be present at all except the northernmost position (GW5) in this study (table 2).

For two positions (WA3 and WA4), the moorings each contained three recording devices (SonoVaults), which all were programmed to record simultaneously at different depths. Due to the fact that at these positions, all recorders dropped out for some part of the year and we compiled the data from all three recorders for each mooring to obtain one effective year for data analyses on AMW daily presence.

3.1. Seasonal and spatial acoustic presence

AMW acoustic presence differed by sectors; at the southernmost positions, AMWs were generally acoustically present longer (i.e. over more months) than at the northern positions (figure 3). At the southern recording positions (i.e. between 70° S and 66° S), acoustic presence (i.e. relative AMW acoustic presence/month) was also higher compared to the northern sites.

AMW bio-duck occurrence exhibited in general a strong seasonal pattern, although AMW acoustic detections varied with location (figure 3). In January and February, AMW acoustic presence was low at all sites, generally increasing from April to July, peaking during August, September and October and decreasing again in November to the sporadic presence in December. At the southernmost position along with GW, AMWs were acoustically present virtually year-round. At the more northern positions along the GW meridian, the onset and increase of AMW acoustic presence was delayed by one month with decreasing recording latitude (figure 3). In July, the percentage of days with AMW presence at all positions along the GW exceeded 60% of days with acoustic recording, peaking in September and October with up to 100% of recording days with the acoustic presence at multiple sites. From the second half of December through March, bio-duck signatures occurred only sporadically in the majority of the recordings from the GW.

In the central Weddell Sea (WSN and WSS), the seasonality of the AMW acoustic presence did not exhibit a clear latitudinal gradient as in the GW sector. At some sites, the onset of acoustic presence was in June whereas at others, AMWs were acoustically present throughout 11 months. For all positions in the Weddell Sea, August, September and October generally exhibited the highest percentage of acoustic presence (greater than 80%) over the recording period (the only exception was position WA1 in August with 42% of days with acoustic presence). The positions WA1, WA3, WA4, WA5, WA6 and WA7 located between 63° S and 66° S (WSN) exhibited more days with acoustic presence compared to the positions located in lower latitudes, WA8 and WA9 (WSS). The positions WA1 and WA3 were the only positions located in the Weddell Sea sector that exhibited AMW acoustic presence during January (figure 3). The positions in WSN had more than 23% of days with acoustic activity in April with the exception of the positions WA3 and WA7 (figure 3). The recorders located in position WA3 stopped collecting data between the months of February and April with only 7 days of effort during May. Position WA7 located closer to the GW sector had the first bio-duck detections during the last days of April.

The position at Elephant Island (EI) had a similar seasonal pattern of AMW, but with fewer days with detections. The first calls were detected during the last days of July (only 2% of days with acoustic detections). August and September were the peak (28% and 29% of days with acoustic activity, respectively). In November, the acoustic presence decreased to just 1% presence.

AMWs were acoustically detected over 9 months (GW4), 11 months (GW2) and 12 months along with the GW sector. The overall percentage of monthly acoustic presence at the northern positions was substantially lower compared to the southern positions (figure 3).

In the sector WSN, one position had an acoustic activity for 11 months (WA1), four positions had between six and seven months of acoustic presence and two positions (WA2 & WA5) had two to four

Table 2. Summary table of AMW acoustic presence for all positions. The percentage of days of AMW presence was calculated for every position per year.

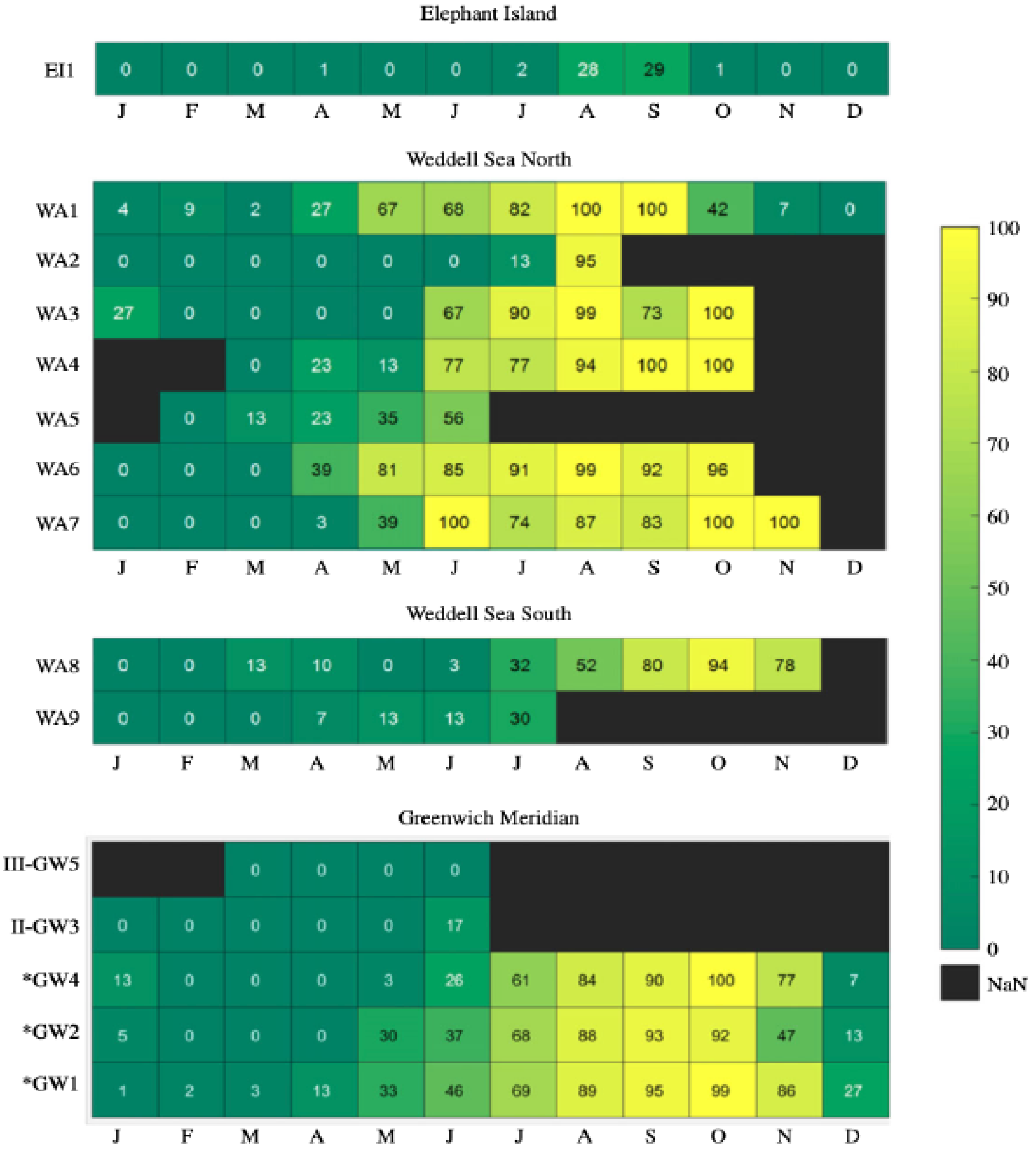
year	position	effort days	days with detections	days excluded	% days AMW presence
2008	GW1	301	164	0	54
	GW2	296	133	0	44
2009	GW1	366	218	0	59
	GW2	366	151	0	41
2010	GW1	353	131	0	37
	GW2	353	152	0	43
	GW3	21	0	0	0
2011	GW3	213	55	0	25
	GW4	169	10	0	5
	GW2	321	155	0	48
	WA1	268	93	0	34
2012	WA2	211	133	0	63
	WA1	225	21	0	9
2013	WA9	233	77	0	33
	WA3	271	33	0	12
	WA1	212	136	0	64
	WA8	288	157	6	54
	WA4	295	174	0	58
	WA5	116	32	0	27
	WA6	292	94	0	32
	WA7	300	140	21	46
	EI1	350	26	0	7
	WA2	221	76	0	34
	GW1	295	189	0	64
	GW5	107	77	0	0
2014	EI1	365	12	0	33
	GW4	161	2	0	1
2015	EI1	365	12	0	33
	GW4	161	2	0	1
	GW1	228	59	0	25
2016	GW2	360	140	0	37
	EI1	93	0	0	0

months with acoustic activity. However, recorders moored in these two positions collected data for only eight and five months. In the WSS sector, AMWs were detected eight months in WA8 and four months in the position WA9, where data collection occurred only during seven months. For the mooring positions located in the middle of the Weddell Sea area, there was no apparent north–south gradient in AMW acoustic presence (figure 3).

In the EI position, AMW were detected during only four months and at a low rate in contrast with the other sectors (figure 3).

3.2. Inter-annual variability

Two sites with multi-year data, GW1 and GW2, had similar trends in AMW acoustic presence across years (figure 4). It gradually increased from April to austral winter, peaking in spring (August,



Elephant Island

	J	F	M	A	M	J	J	A	S	O	N	D
EI1	0	0	0	1	0	0	2	28	29	1	0	0

Weddell Sea North

	J	F	M	A	M	J	J	A	S	O	N	D
WA1	4	9	2	27	67	68	82	100	100	42	7	0
WA2	0	0	0	0	0	0	13	95				
WA3	27	0	0	0	0	67	90	99	73	100		
WA4			0	23	13	77	77	94	100	100		
WA5		0	13	23	35	56						
WA6	0	0	0	39	81	85	91	99	92	96		
WA7	0	0	0	3	39	100	74	87	83	100	100	

Weddell Sea South

	J	F	M	A	M	J	J	A	S	O	N	D
WA8	0	0	13	10	0	3	32	52	80	94	78	
WA9	0	0	0	7	13	13	30					

Greenwich Meridian

	J	F	M	A	M	J	J	A	S	O	N	D
III-GW5			0	0	0	0						
II-GW3	0	0	0	0	0	17						
*GW4	13	0	0	0	3	26	61	84	90	100	77	7
*GW2	5	0	0	0	30	37	68	88	93	92	47	13
*GW1	1	2	3	13	33	46	69	89	95	99	86	27

Figure 3. Percentage of days with AMW bio-duck presence. Positions sorted by latitude (north to south) in separate sectors: Elephant Island (EI), Weddell Sea North (WSN), Weddell Sea South (WSS) and Greenwich Meridian (GW). For positions for which multi-year data was available (indicated with *), the heatmap displays the average monthly acoustic presence.

September, October and November), exhibiting a consistent pattern between years. Most variability between years occurred at the onset of vocal activity.

3.3. Relation to sea-ice concentration

The acoustic presence of AMW was strongly positively correlated with the sea-ice concentration in the Weddell Sea ($r = 0.7$). Days with few detections generally corresponded to days with lower (less than 20%) ice concentration. In general, the acoustic presence of AMW in the Weddell Sea increased with local sea-ice concentration. The positive correlation explains the higher number of days with the acoustic presence with increasing latitude, given that sea-ice is more persistent in the southern recording positions (figure 3). The months with more than 75% of days with acoustic presence typically exhibited local sea-ice concentrations between 75% and 100% in a radius of 40 km around the recording position.

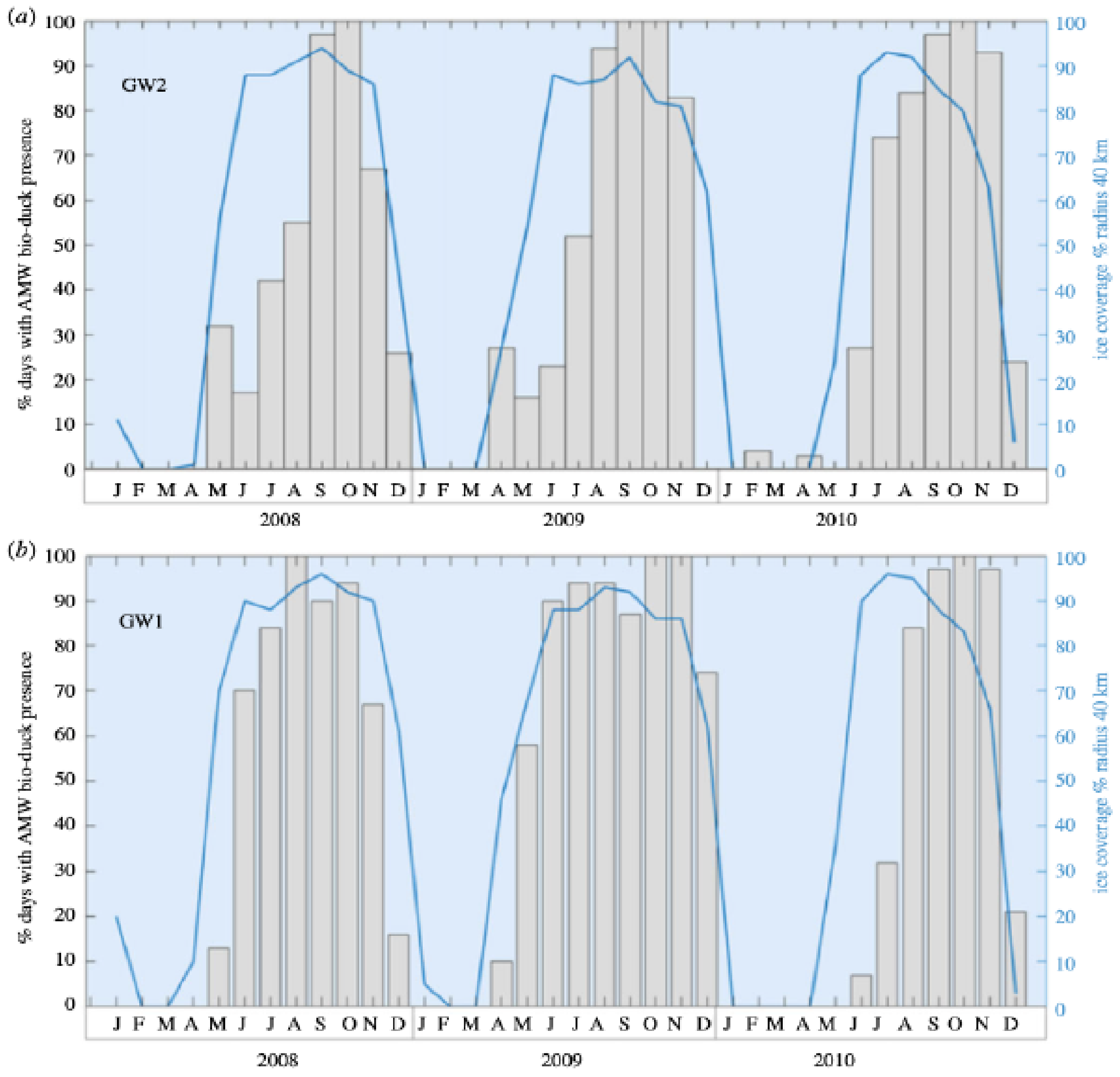


Figure 4. Multi-year acoustic presence of AMW in two different positions (GW2 and GW1) correlated with sea-ice coverage in a radius of 40 km. Per cent of days with AMW acoustic presence between 2008 until 2010.

4. Discussion

4.1. Role of sea-ice

These year-round acoustic observations show that vocally active AMWs exhibit strong affinity with areas featuring dense sea-ice cover. The acoustic observations from winter in the Weddell Sea are consistent with the year-round study west of the Antarctic Peninsula [25], but contrast with what is known about AMW habitat use based on summer sighting data [7,20]. When using icebreaker-supported helicopters for aerial surveys in austral summer, most AMWs were found at the sea-ice edge boundary (defined as the 15% ice concentration contour) during December and January [7]. Herr *et al.* [20] found that during austral summer AMWs occurred close to the sea-ice edge in the Weddell Sea area, and that AMW densities decreased in areas with higher sea-ice concentration values [20]. Contrastingly, the results of our study show none to very little acoustic activity at the recorder locations near the ice edge boundary during December and January. The highest acoustic activity typically occurred in areas and periods of the year with high sea-ice concentrations (greater than 20%). Along the Greenwich meridian, AMW acoustic presence exhibited a latitudinal gradient: at the southernmost positions, AMWs were acoustically present over a longer period (9 to 12 months) compared to the more northern positions. This latitudinal pattern also reflects the strong association between AMW acoustic presence and sea-ice; positions GW1 and GW2 located further south generally are ice covered early (April and May), whereas recording sites III-GW5 and II-GW3 further north along the Greenwich meridian are generally still ice-free during these months. The anomaly between 66° S and 64° S in the latitudinal distribution can be explained due to the presence of a large opening in the sea-ice cover of the Weddell Sea, also known as the Weddell Polynya [47]. AMW acoustic absence in the position GW5 is probably explained by the fact that the recorder only collected acoustic data during the time of the year when all other sites had low acoustic presence of AMW (March until June).

The overall pattern of high AMW acoustic presence associated with high local sea-ice concentrations is the same for the inner Weddell Sea area. The absence of a latitudinal trend in the inner Weddell Sea area may in part be explained by the distribution of the recorders in the Weddell Sea; at the eastern and western edges of the Weddell Sea, data collection was biased towards lower latitudes, where fewer AMW calls were recorded compared to the higher latitude recording sites, probably due to the differences in ice cover period. Furthermore, differences in ice growth processes in the Weddell Sea may affect how areas with higher sea-ice concentrations (to which AMWs are often associated) are distributed. In the central Weddell Sea, cycles of pancake-ice formation developing into consolidated floes are thought to be the dominant processes by which the sea-ice forms, starting from the centre [39]. By contrast, along the Greenwich meridian, the growing sea-ice cover largely consists of ice platelets, which are formed in the underlying water column in front of the ice-shelf edge, causing sea-ice growth to extend northwards from the continent [39]. The differences in ice growth processes between the GW and WS areas possibly lead to locally denser ice cover in the Weddell Sea, potentially explaining the generally earlier onset of AMW acoustic presence in the WS area compared to most of the GW sites.

The acoustic observations of AMWs overall show a strong association between their acoustic presence and sea-ice concentration during austral winter. Our findings on AMW distribution thereby contrast with the information from visual surveys indicating that AMWs occur primarily within the ice at the sea-ice edge. Visual data collection is, however, by and large limited to the austral summer period and areas with low ice cover. Furthermore, differences in AMW behaviour (e.g. surfacing patterns) when in ice-covered areas may also affect their detectability by visual observers and hence skew distribution information. To further insights on potential seasonal differences in AMW habitat usage, further investigations, e.g. employing animal-borne satellite tags, are clearly needed.

4.2. Function of Antarctic minke whale calling

To date little is known on the function of AMW calling behaviour. Across all locations where AMWs have been recorded, acoustic activity is strongly seasonal, albeit with regional differences in the timing of peak calling. Off the Western Antarctic Peninsula, most AMW calls were detected between April and November with peak calling during July [25]. In our study, the peak in AMW acoustic presence throughout the Weddell Sea area occurs from August to October, with few calls occurring throughout the year at the northernmost sites. Recordings of AMWs from lower latitudes on the other hand show that acoustic activity is not restricted to ice-dominated areas and occur during the same period [48,49]. Thomisch *et al.* [31] reported AMW acoustic presence off Namibia with a double peak: the first peak occurring from June to August and a second peak in November and December. In Perth Canyon (Australia), peak calling also occurred in July–August and again in December [29]. As also concluded by Dominello and Širović [25], these observations clearly falsify previous hypotheses that the bio-duck calls exclusively serve navigational purposes in ice-covered areas [30].

AMW acoustic detections are virtually absent during the summer period when most AMW sightings occur in or close to the marginal sea-ice zone where high density patches of Antarctic krill aggregations are known to occur regularly [50]. Risch *et al.* [26] recorded bio-duck calls from tagged AMWs that were in large single-species groups of 5 to approximately 40 animals that were feeding almost continuously. Nevertheless, vocalization rates were low; only 32 clear calls of which 6 were bio-duck calls were recorded in this entire dataset. Visual observations from lower latitudes report that AMW breeding behaviour was observed between August and October [51,52]. Catch data furthermore show that most AMW conceptions occur in September [53]. Information collected during winter surveys mentions the presence of AMWs in Antarctic waters but only mature and large juvenile individuals [23,54]. If the assumption that calling behaviour is related to the reproductive activity is correct, our data could suggest that part of AMW breeding may take place in both high-latitude waters with dense ice cover as well as at lower latitude waters. Kasamatsu *et al.* [55] noted that AMW breeding areas in lower latitude waters may be less concentrated compared to humpback whales (*Megaptera novaeangliae*) and grey whales (*Eschrichtius robustus*), which prefer near shore waters for breeding. They hypothesized this may result in differences in meeting probability between mature males and females compared to species that concentrate in traditional breeding areas in coastal waters. The AMW long calling bouts consisting of repetitive pulses could therefore serve to attract and find mating partners over longer distances. Nevertheless, further work e.g. employing animal-borne tags is needed and underway to further investigate the behavioural contexts in which AMW calls are produced (e.g. [42]).

To date it is unknown how AMW sound production is related to sex, age and reproductive status. Information on staggered and sex-segregated migration in AMWs, presents patchy and partly contrasting information; Kasamatsu *et al.* [55] reported young whales to migrate southbound first, followed by mature and pregnant individuals in October–November. The northbound migration of young animals is thought to start around February, followed by the mature animals in March continuing into early austral winter. Other studies reported female AMWs to prefer higher latitudes during summer [56,57]. Lactating females and calves were rarely observed in Antarctic waters during the summer, whereas pregnant females were found absent from lower latitude waters. Immatures are also thought to avoid high-latitude areas. Laidre *et al.* [58] suggested that off Greenland, in common minke whales (*Balaenoptera acutorostrata*), pregnant females may separate socially to avoid niche overlap or to avoid males by migrating to other areas. Furthermore, occasional sightings of young unweaned common minke whale calves strongly suggest some females calve in more northerly waters outside the breeding areas, possibly skipping migration to low latitudes to calve [59,60].

How these patterns relate to the austral winter situation in Antarctic waters and how calling behaviour relates to sex, age and reproductive status in Antarctic minke whales is not known. However, based on existing evidence, it is possible that the reproductive and conditional status of females determines their migratory strategy.

Although not further quantified here, different bio-duck type calls were observed in our dataset, in accordance to the findings of previous studies that collected similar data in other areas [25,26,29,31,41]. Differences in the acoustic characteristics of bio-duck calls comprised e.g. the duration of the calls, the inter-pulse interval and the number of pulses. Mapping these acoustic differences in the bio-duck calls may shed further light on the function of calling, e.g. whether specific call types are used in different behavioural contexts or if call usage differs in space and time.

4.3. Migratory movement

Our data show that, as for many baleen whale populations (i.e. fin (*Balaenoptera physalus*), humpback and Antarctic blue whales (*B. musculus intermedia*); see Geijer *et al.* [61] for a review), AMWs exhibit complex migration patterns. Sightings and passive acoustic recordings show that AMWs are simultaneously present in both low- and high-latitude waters during austral winter [29,31,48]. Off the Western Antarctic Peninsula, visual sightings confirm AMW winter presence with the highest occurrence close to shore and between islands [22,23]. Meanwhile evidence has been accumulating that alternative migration strategies are more the rule than the exception in baleen whales [61]. Both common and Antarctic minke whales remain among the species for which knowledge on migration patterns and wintering habitats is still scarce. Carretta *et al.* [62] indicated the existence of a non-migratory common minke whale population off the west coast of North America, although Risch *et al.* [63] found evidence for a traditional migration pattern in common minke whales. Migration strategies are likely to depend on sex, age and reproductive status as well as ecological factors, and many species are therefore likely to exhibit a repertoire of migratory behaviours [61]. Recent studies using satellite tags on AMWs off the Antarctic Peninsula also suggest movement strategies may differ dramatically between individuals [64]. Tagged AMWs were found to all remain south of the southern boundary of the ACC. One individual travelled along the sea-ice edge and the others remained in the shallower waters of the continental shelf, but all were closely associated with areas with substantial sea-ice coverage [64]. Off South Africa, a bi-modal temporal distribution of AMWs peaking in fall and spring has been observed, suggesting parts of the population migrate to lower latitudes during austral winter [65].

Adaptations to inhabiting heavy sea-ice environments may enable AMWs to exploit this habitat on a year-round basis, potentially limiting the need for migration to low latitude waters to the period when calves are born [66]. The dense sea-ice environment may offer AMWs a refuge from killer whales (*Orcinus orca*), which are known to prey on the species [67]. Their small size enables them to navigate between ice floes, and their strong rostrum allows them to break the ice creating their own breathing holes [22,24]. These adaptations probably enable AMWs to fill a niche and avoid interspecific competition by exploiting krill resources that may not be accessible to other species that also depend on krill as their main food resource [68,69]. Our data, as well, indicate that the traditional migration model of mysticete migration (e.g. [70,71]) is too simplified to describe their life history. However, given that

AMWs seem to produce calls only seasonally, further investigations on their migratory behaviour will need to integrate different methods (i.e. visual and passive acoustic surveys as well as animal-borne tags) to improve our understanding of their migratory repertoire (see [72] for a review).

5. Conclusion

The strong relation between AMWs and sea-ice suggests that this species is likely to be sensitive to climate-induced changes to its sea-ice habitat over time. Passive acoustics provide a highly effective tool for monitoring this species during austral winter. Data presented here suggest that the migratory behaviour of this species is more complex than previously thought. Part of the population may undertake seasonal migrations while another part may remain in the ice, with a continuous presence in the Antarctic Southern Ocean during the year. Overall abundance estimates for AMWs are currently around 500 000, whereas earlier assessments estimated 720 000 animals [37] representing a 31% decline. Despite uncertainties and lack of confidence in parts of the assessment, this trend gives reason for concern and recently has led to the classification of AMWs as Near Threatened under the IUCN Red List and under Appendix I of CITES [36]. Japan's decision to leave the IWC could contribute to the recovery of the AMW population in the Southern Ocean. The major difficulties in generating reliable abundance estimates for AMWs are the environment they inhabit [7,20,72]. Clearly, multi-disciplinary approaches are therefore needed to improve our understanding and conserve this elusive species.

Ethics. For this study, we used data deployed and collected from several expeditions, with the *RV Polarstern*. Permission was granted to the Alfred Wegener Institute, Helmholtz-Zentrum für Polar- und Meeresforschung by the Federal Environment Office (Umweltbundesamt UBA). Expedition ANT - XXIV/3 UBA permit no. I 2.4 - 94003-3/207, Expedition ANT - XXV/2 UBA permit no. I 2.4 - 94003-3/217, Expedition ANT - XXVII/2 UBA permit no. I 3.5 -94003-3/255, Expedition ANT - XXVIII/2 UBA permit no. I 3.5 - 94003-3/271, Expedition ANT - XXIX/2 UBA permit no. I 3.5 - 94003-3/286, Expedition ANT- XXX/2 UBA permit no. II 2.8 - 94003-3/324, Expedition PS103 UBA permit no. II 2.8 - 94003-3/38

Data accessibility. Our data are deposited at Dryad: doi:10.5061/dryad.7sqv9s4pd [73].

Authors' contributions. D.F. analysed all the data, conducted statistical analyses and wrote the manuscript. K.T. participated in some data collection and helped draft the manuscript. O.B. participated in collecting data and coordinated the study. T.B. helped guide some statistical analyses and with the previous version of the manuscript. S.S. collected the data. A.Š. helped with the draft manuscript and with guidance for the analyses. I.V.O. coordinated the study, collected part of the data and helped draft the manuscript. All the authors reviewed and contributed to the final document edits. All the authors gave the final approval for publication.

Competing interests. We have no competing interest.

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Chapter II: The latest local tune: the calling behavior of Antarctic minke whales (Balaenoptera bonaerensis) differs in space and time.

The latest local tune: Antarctic minke whale (*Balaenoptera bonaerensis*) calling behaviour differs over space and time

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Abstract

The acoustic behavior in baleen whales has several functions, such as social and mating related calling behaviour. Since the attribution of the bio-duck call to Antarctic minke whales (*Balaenoptera bonaerensis*), different studies have retrospectively identified several bio-duck call types at different sites throughout the Southern Hemisphere. The function of their vocal behaviour however, remains largely unknown. Further insights into their vocal behaviour can reveal the function of the calling. Here, we use passive acoustic monitoring (PAM) data from 6 positions located along the Weddell Sea (WS) during 2013 as well as three consecutive years of PAM data (2015-2016-2017) recorded at the PALAOA Observatory to study inter-annual variability in the acoustic behavior of AMWs. This is the first study to show that like other whales, AMWs produce songs. During 2013, throughout the WS we detected 11 different types of bio-duck calls.

The different bio-ducks were detected between May and December. Only one position located at the western side of the WS, presented acoustic activity during February. The comparative analyses of bio-duck calls diversity show a differentiation of four call type groups in the area. Furthermore, the inter-annual acoustic data show that there exists a difference in the acoustic repertoire among years. This study provides new information to identify different populations of AMWs using passive acoustic methods. It also describes and classifies the acoustic repertoire of this species for future comparison of vocalizations recorded at other sites in the Southern Hemisphere. Furthermore, there is a change in the acoustic repertoire between years.

Introduction

Knowledge that baleen whales produce sound is relatively recent; only since the 1940's, the scientific community has become aware that baleen whales are not mute, but produce a large variety of sounds (e.g., Schevill and Watkins 1962). Insights into repertoire and repertoire usage are fundamental for PAM (passive acoustic monitoring)-based remote sensing studies on behaviour and distribution. Baseline knowledge on vocal behaviour can nevertheless be difficult to obtain due to the logistic constraints to accessing the remote habitats that some species occupy during the time they are vocally active. Although the repertoire of the majority of baleen whale species has at least to some extent been described in literature, new studies attributing previously unknown acoustic signatures to certain species still continue to be published (Risch, Gales, et al. 2014; Cerchio et al. 2017).

The origin of the bio-duck sound also was long an unsolved mystery. First described and named by submarine personnel in the 1960s, the bio-duck had since been recorded at various locations in the Southern Hemisphere from lower to higher latitudes. Based on data derived from acoustic tags deployed on AMWs, the bio-duck sound could finally be attributed to AMWs (Risch et al. 2014) and recordings from the Southern Ocean (SO) retrospectively explored for AMW acoustic presence (Dominello & Sirovic 2016; Filun et al. 2020). Bio-duck calls occur simultaneously in lower, middle and higher latitudes and have been found present in these areas exclusively during austral winter and spring (Matthews et al. 2004; Thomisch et al. 2019; Filun et al. 2020; Shabangu et al. 2020). These aspects clearly distinguish AMW calling behavior from the calling patterns of other baleen whale species, that for the larger part migrate between lower latitude breeding and higher latitude feeding areas (Stern 2009; Horton et al. 2011). In the SO, these other baleen whale species generally peak in calling during the austral summer season during which they are believed to mainly be present and use the area for feeding (Širović et al. 2004; Širović et al. 2009; Garland et al. 2013; Thomisch et al. 2016) - although year-round acoustic presence has been reported for multiple species as well. Across all locations where AMWs have been recorded to date, acoustic activity has been found strongly seasonal, peaking during the austral winter period. Based on its coinciding timing with AMW female receptivity, acoustic behavior has been suggested to potentially play a role in the context of reproduction (Dominello and Širović 2016; Filun et al. 2020), but hypotheses on its behavioral function remain highly speculative. Although the number of studies on AMW vocal behavior is still limited to date, all report the existence of different types of bio-duck calls (Matthews and McCauley 2004; Risch et al. 2014; Shabangu et al. 2020; Dominello and Širović 2016). However, in absence of a systematically sampled data set, it remains unclear how this call diversity relates to geographic and temporal distance in data collection. Insights into the spatio-temporal patterns of bio-duck call type usage could provide further knowledge on the behavioral context in which these calls are used and what drives this call type diversity.

To systematically explore the spatio-temporal patterns in AMW bio-duck call occurrence, we here use two different passive acoustic data sets (1) six moored positions deployed across the Weddell Sea collected continuous data during 2013 and (2) three years of acoustic data collected from the PerenniAL Acoustic Observatory in the Antarctic Ocean, PALAOA, (Boebel et al. 2008).

Methods

HAFOS data collection

The HAFOS (Hybrid Antarctic Float Observation System) PAM data set was collected using hydrophones attached to a network of oceanographic deep-sea moorings deployed throughout the Weddell Sea (Rettig et al. 2013). For this study data were used from 2013 from 6 different mooring positions distributed between 59° and 69° S and from 0° to 56° W across the Weddell Sea, Antarctica (Figure 1). Passive autonomous acoustic recorders (SonoVaults developed by Develogic GmbH, Hamburg) were programmed to record continuously with a sampling rate of 5,333 Hz (Rettig et al. 2013; Filun et al. 2020).

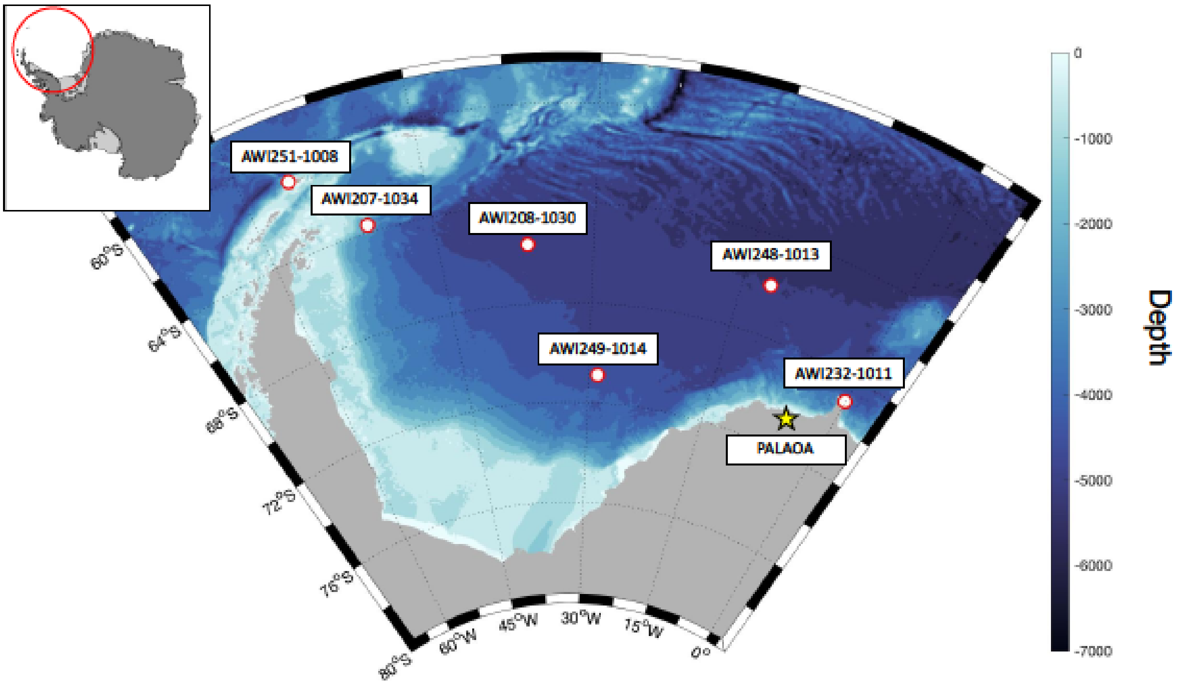

Figure 1. Map of the Weddell Sea area showing the locations where passive acoustic recordings were collected. Red-white dots represent the offshore mooring positions across the Weddell Sea from which one year of recordings was used. The yellow star represents the location of the PALAOA observatory on the edge of the Ekström ice-shelf from which three years of consecutive recordings were used.

PALAOA data collection

The PerenniAL Acoustic Observatory in the Antarctic Ocean (PALAOA) collects continuous underwater recordings from a coastal Antarctic environment and is located on the Ekström Ice

Shelf at 70° 30.717' S, 008° 13.178' W (Figure 1). During 2014, the observatory switched from multiple-hydrophone, live streaming mode (Boebel et al. 2008), to archival data collection with a single hydrophone. Here, we used data from 2015 to 2018 which were collected using the archival set up. Recordings are made continuously year-round with a RESON TC4032 hydrophone (5 Hz to 120 kHz, sens. –170 dB re 1 V µPa–1) deployed underneath the 100 m thick floating Antarctic ice shelf (Boebel et al. 2008). Water depth below the floating ice shelf is approximately 160 m. The hydrophone is at a depth of 80 m below the floating ice shelf. The hydrophone is connected to a Sonovault-OEM unit that is positioned on the ice in a protective case. It records the data (sensitivity -133.4 dB ±1 dB, sampling rate 96 kHz, 24-bit resolution) and stores it on SD cards. For the subsequent analysis process, the PALAOA data were decimated to 6,000 Hertz.

Manual data preprocessing

To detect the occurrence of AMW bio-duck calls in the recordings, both acoustic data sets were processed using the Matlab-based (Mathworks, Natick, MA) custom-written software program Triton (Wiggins et al. 2010) to create long-term spectral averages (LTSAs) spectrograms. LTSAs visually represent time series of averaged spectra (Appendix Figure 1). Figure 2. shows an overview of how the PAM data were processed. The successive spectra for all the data were calculated by averaging 60 s of acoustic data with a frequency resolution of 1 Hz. These LTSAs were used to manually log AMW hourly acoustic presence for all acoustic data. The LTSAs were analyzed with a window length of 12 hours to identify AMW signatures. When presumed AMW bio-duck calls were observed in the LTSAs, a 30 s spectrogram window (overlap = 90%, FFT = 1050) of that time section was inspected visually and aurally to verify the presence of AMW bio-duck calls (Filun et al. 2020). Here, a bio-duck call was defined as a series of clustered downswept pulses, with single pulses separated by <1 s (Dominello and Širović 2016; Shabangu et al. 2020). Generally, bio-duck calls never occurred alone, but always occurred in sequences of clusters (Filun et al. 2020) (Appendix Figure 1). AMW acoustic presence (i.e., AMW positive hours) was assessed on an hourly basis for the full acoustic data set. Hours during which a sequence of at least 1 min of consecutive bio-duck vocalizations was present were considered AMW positive. For all AMW sequences, a 10-second audio fragment was extracted for further subsequent analyses and classification according to bio-duck call type.

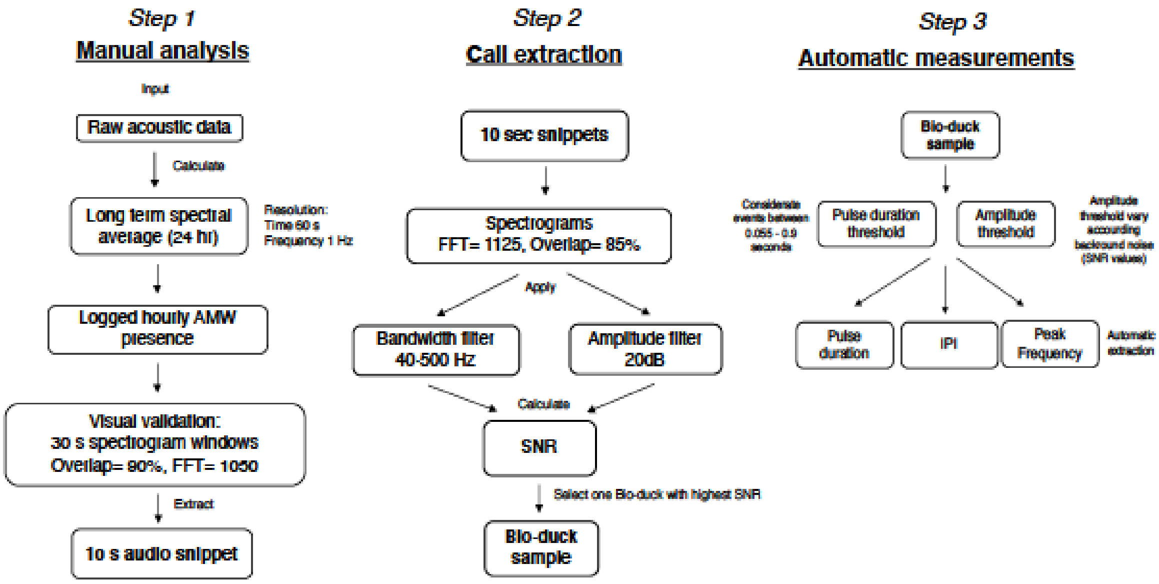

Figure 2. Flow chart showing the description of the different steps of the acoustic data processing.

Automated extraction of AMW bio-duck call acoustic features

To allow automated feature extraction for call type classification, individual bio-duck pulses were automatically detected in the 10-second audio fragments. Spectrograms (1125 point FFT, 85% overlap, Hanning window) of the audio fragments that were extracted from the LTSAs were manually checked in RStudio Version 1.2.5042 with the 'Seewave' package (Sueur et al. 2020). Furthermore, the 10-seconds audio files were frequency filtered between 40-500 Hz.

For every 10-second audio fragment, the signal-to-noise ratio (SNR) of bio-duck calls in the snippet was calculated. In some cases, more bio-duck pulses were detected in the 10-second fragments, then, the one with the highest SNR was selected for further processing. To define SNR, for each call, background noise was measured during 0.6 seconds prior to the detected call event in the frequency bands between 40 – 500 Hz. The signal value was measured during 1.1 seconds after the time point of background noise measurement. Then, an amplitude filter of 20 dB was applied to increase the SNR of the bio-duck pulse train spectrum. Only bio-duck calls with a resulting SNR that was sufficiently high, were selected for further processing using the pulse detector. The pulse detector was used to automatically extract call characteristics from each bio-duck call for the classification. The automated pulse detector was designed to work using the low frequency downswept component present in all bio-duck calls. Bio-duck pulse detection thresholds were custom-defined based on the individual bio-duck call SNR (SNR = 20*log10(rms(signal)/rms(noise)). For acoustic detections with a SNR<5 dB we applied a detector threshold=50, for detection with SNR>5 dB and SNR<10 dB a threshold=30, with SNR>10 dB and SNR<15 dB threshold=20, with SNR>15 dB and SNR<20 dB threshold=15 and with an SNR>20 dB a threshold=12 (Appendix Figure 2). To reduce false positives of other pulsed signals, only detections of pulses with a duration within the range of 0.055 - 0.9 seconds (which were the known minimal and maximal durations of AMW pulses) were included as part of the bio-duck pulse sequence (Appendix Table 1).

Table 1. Location, sampling rate, duty-cycle and recording data of passive acoustic recorders.

Mooring ID	Latitude	Longitude	Sampling Rate (KHz)	Duty-Cycle	Effort (days)	Acoustic detections Days	Acoustic detections Hours
AWI251-1008	-61.0146667	-55.826833	5.333	continuous	291	30	201
AWI207-1034	-63.7013889	-50.826667	5.333	continuous	281	84	749
AWI208-1030	-65.6205	-36.422	5.333	continuous	289	101	978
AWI249-1014	-70.8925	-28.891167	5.333	continuous	305	75	531
AWI248-1013	-65.6205	-36.422	5.333	continuous	316	96	748
AWI232-1011	-65.9976417	-0.108925	5.333	continuous	269	96	718
PALAOA2015	-70.5	-8.21666667	96	continuous	365	97	736
PALAOA2016	-70.5	-8.21666667	96	continuous	365	105	893
PALAOA2017	-70.5	-8.21666667	96	continuous	270	112	977

For the final classification of the different AMW calls detected in our data set, we used the detections to extract different variables with a custom-built algorithm in RStudio Version 1.2.5042, using the R packages 'Seewave' (Sueur et al. 2008) and 'warbleR' (Araya Salas and Smith Vidaurre 2017).

Parameters that were automatically extracted by the algorithm included the number of pulses (NP), total duration (TD), average inter-pulse interval (AvIPI), duration first pulse (DFP), duration last pulse (DLP) and peak frequency (PF) (Table 2 & Appendix Figure 2). The algorithm is based on an amplitude detector capable to automatically extract and calculate different measurements from the waveform of AMW bio-duck calls between 40-500 Hz. Although the different types of bio-duck can have harmonics up to 2,000 Hz, these are not a reliable feature as their presence and quality depends on different factors such as, for example, proximity of the animal to the hydrophone, ambient noise levels and call directionality. Only the fundamental frequency of the downswept pulses was included in the measurements as robust frequency parameter.

We separated the different bio-duck calls using cluster analysis based on the calculated acoustic parameters in order to optimize the classification. The different parameters extracted from each bio-duck call type were used to perform a hierarchical agglomerative cluster analysis to generate unsupervised call type groups. A Euclidean method was used to calculate the distances between the different clusters. To determine the number of clusters (*k*) we used the 'NbClust' package (Charrad et al. 2014). This automatically calculates and provides 30 different indices for determining an appropriate number of *k* from the different results obtained by varying all combinations for number of clusters, distance measures and clustering methods.

Table 2. Description of the variables automatically measured to classify the different Bio-duck call types

NP	Number of pulses	N° of pulses that form a Bio-duck call
TD	Total duration	Time length between the start time of the first pulse detected in the Bio-duck sequence until the time when finish the last pulse detected in the sequence who compone a call
DFP	Duration first pulse	Time duration of the first pulse that forms a Bio-duck call
DLP	Duration last pulse	Time duration of the last pulse that forms a Bio-duck call
AvIPI	Average inter-pulse interval	Average of the time duration af all the inter-pulse intervals in a Bio-duck call
PF	Peak frequency	Frequency of maximum power value obtained measuring the down sweep componen of the Bio-duck calls

Sea ice concentration

The values of sea ice concentration for this study were extracted from: a combination of satellite sensor data from the Nimbus-7 Scanning Multichannel Microwave Radiometer (SMMR), the Defense Meteorological Satellite Program (DMSP) -F8, -F11 and -F13 Special Sensor Microwave/Im rs (SSM/Is), and the DMSP-F17 Special Sensor Microwave

Imager/Sounder (SSMIS), with a grid size of 25 km and the satellite images from the Advanced Microwave Scanning Radiometer for EOS (AMSR-E) satellite sensor with a grid size of 6.25 km. The data were used to calculate the daily sea-ice concentration of the area within 40 km radius around each recording location deployed throughout the Weddell Sea (Peng et al. 2013; Spreen, Kaleschke, and Heygster 2008).

Calculation sunset-sunrise diel pattern

To calculate the hours of light and darkness in a day during our study, we used the Sunrise/Sunset tool in *MATLAB* (Mahooti 2020). We calculated the equation of time and sun angle to estimate the periods of sunrise and sunset in the UTC time zone according the specific latitude and longitude for every recording position. The calculations were based on data available from NOAA's Earth System Research Laboratory.

Monthly acoustic variability

The percentage of occurrence of the different AMW signals was calculated based on the sum of the number of hours of each type of signal divided by the total number of hours with detections for each month.

Results

HAFOS network

To explore the spatial patterns in call type usage for 2013, a total of 1,751 days from 6 different anchoring positions located throughout the Weddell Sea were analyzed to detect and classify AMW bio-duck signatures. The number of days with AMW acoustic presence varied between sites with lowest AMW presence at site AWI251-1008 (30 days, corresponding 201 hours, see

Table 1) and most AMW acoustic presence at AWI208-1030 (101 days, corresponding 978 hours, see Table 1). AMW bio-duck calls had a seasonal occurrence between May and October. In addition, at position AWI207-1034, AMWs were present during 4 days in January 2013.

PALAOA

To see how the AMW acoustic repertoire varied among years, we used the PALAOA data and analyzed a total of 937 days from the 3-year period spanning 2015 until 2018 (Table 1). In 2015, we detected AMWs during 97 days corresponding to 736 hours with bio-ducks. In 2016, the number of days with AMW acoustic presence was 105 with a total of 893 hours. In 2017, AMWs were detected during 112 days, corresponding to 977 hours of bio-duck calls.

Bio-duck call type classification

Bio-duck calls typically consisted of sequences of 1-9 pulses with an IPI between 0.03-0.4 s. The duration of the detected single bio-duck pulses ranged from 1.02 – 1.9 seconds (Appendix Table 1). The durations of the first and last pulse of a bio-duck sequence were included as variable in the classification and measured between 0.095 to 0.718s and 0.058 to 0.428s, respectively. The peak frequency of the downswept bio-duck element varied substantially between the different bio-duck call types, ranging from 114.5 to 197.9 Hz (Appendix Table 1).

Based on the extracted measurements (Appendix Table 1), the cluster analysis classified the 16 different bio-duck call types into 4 groups (Groups A-D) (Figure 3). Group A has two calls "A1" and "A2." Group B is composed of 6 calls; "B4","B5","B6","B7","B8 "and "B9." Group C has 5 calls; "C2","C3","C4","C5" and "C6". The last group D is composed of 3 calls; "D3","D4" and "D5" (Figure 3).

HAFOS data set: Spatial variability in AMW call repertoire

The occurrence of the different bio-duck call types varied between the HAFOS recording positions. Position AWI251-1008 exhibited least variability in recorded AMW vocalizations and only 6 types of calls were recorded at this location (Figure 4). At position AWI232-1011, 11 different types of bio-ducks were recorded, showing the richest AMW repertoire of all recording sites. At positions AWI207-1034 and AWI208-1030, 9 different types of bio-duck were detected, whereas at positions AWI 249-1014 and AWI 246-1013, 8 and 7 call types were detected, respectively (Figure 4).

Bio-duck type "A2" and "D4" were detected at all HAFOS positions in 2013 (Figure 4). In addition, the "D4" call was detected during January (three days) at position AWI201-1034. This position was the only one to record acoustic activity during the summer period in the Weddell Sea area. Bio-duck types "C4", "D5", "C3" and "B9" were recorded at all positions, except for AWI251-1008. Call type "B8" was found at all positions, except at AWI20-1014.

Table 3. Location, sampling rate, duty-cycle and recording data of passive acoustic recorders.

Mooring ID	Latitude	Longitude	Sampling Rate (KHz)	Duty-Cycle	Effort (days)	Acoustic detections Days	Hours
AWI251-1008	-61.0146667	-55.826833	5.333	continuous	291	30	201
AWI207-1034	-63.7013889	-50.826667	5.333	continuous	281	84	749
AWI208-1030	-65.6205	-36.422	5.333	continuous	289	101	978
AWI249-1014	-70.8925	-28.891167	5.333	continuous	305	75	531
AWI248-1013	-65.6205	-36.422	5.333	continuous	316	96	748
AWI232-1011	-65.9976417	-0.108925	5.333	continuous	269	96	718
PALAOA2015	-70.5	-8.216	96	continuous	365	127	974
PALAOA2016	-70.5	-8.216	96	continuous	365	152	1223
PALAOA2017	-70.5	-8.216	96	continuous	270	77	695

At positions AWI251-1008 and AWI207-1034, “D4“ was the most dominant call type and the call “A2” the second most occurring type (Figure 4). For the remaining positions, the most dominant call was type “A2” with “D4” being the second most frequent occurrence at positions AWI20-1034, AWI208-1030 and AWI20-1014 and “D5” the second most common call at positions AWI248-1013 and AWI232-1011 (Figure 4). We detected only 4 hours in our dataset with presence of more than one bio-duck call type.

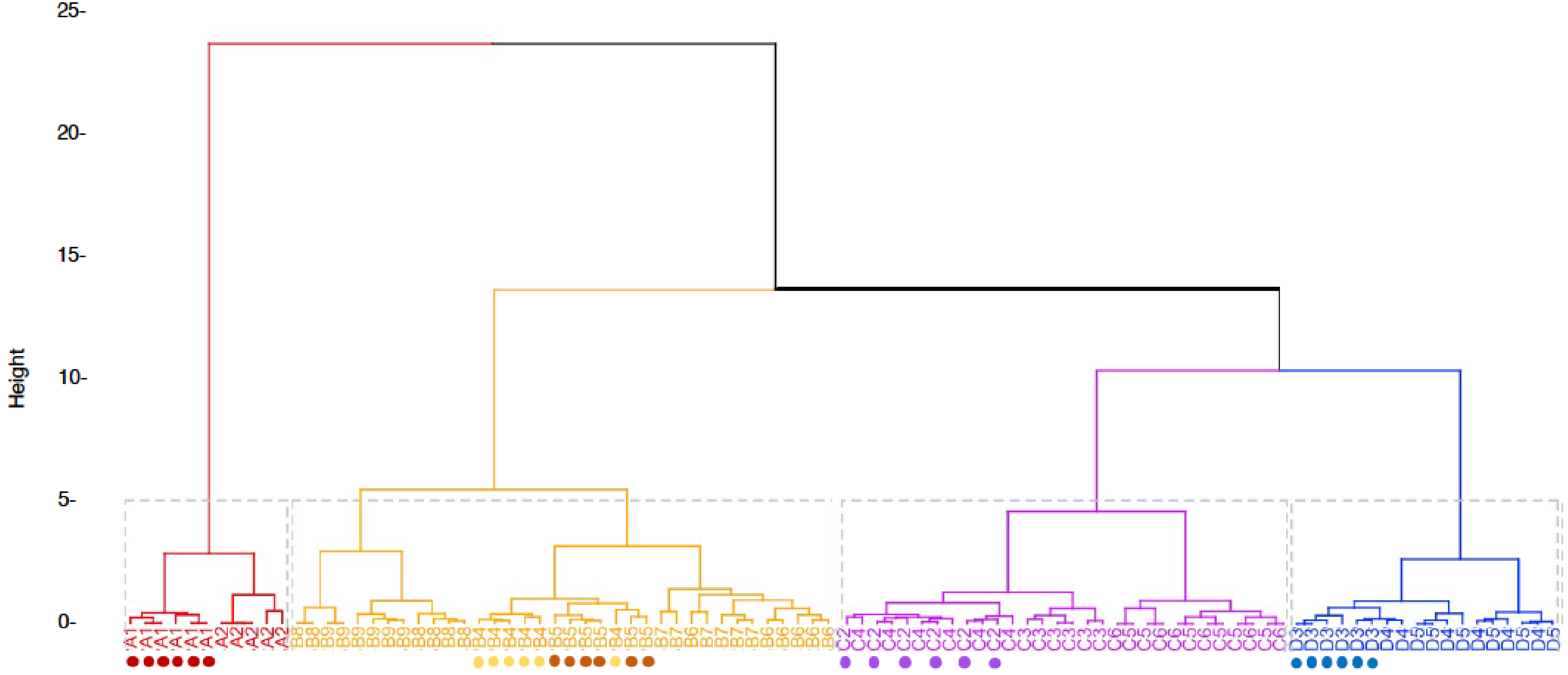

Figure 3. Hierarchical dendrogram. Visualization of the different bio-duck calls classification groups detected in the HAFOS network (Weddell Sea) and PALAOA (dots). NP, TD, DFP, DLP, AvIPI and PF variables used to split.

Seasonal variability in AMW call repertoire

In both data sets, bio-duck calls occurred from May to November. The duration of the period during which bio-duck calls are recorded however varied between positions lasting from 4 to 6 months according to latitude; with longer acoustic presence occurring at higher latitudes (Filun et al., 2020). AWI207-1034 was the only position that showed AMW acoustic activity during January and February (Figure 5).

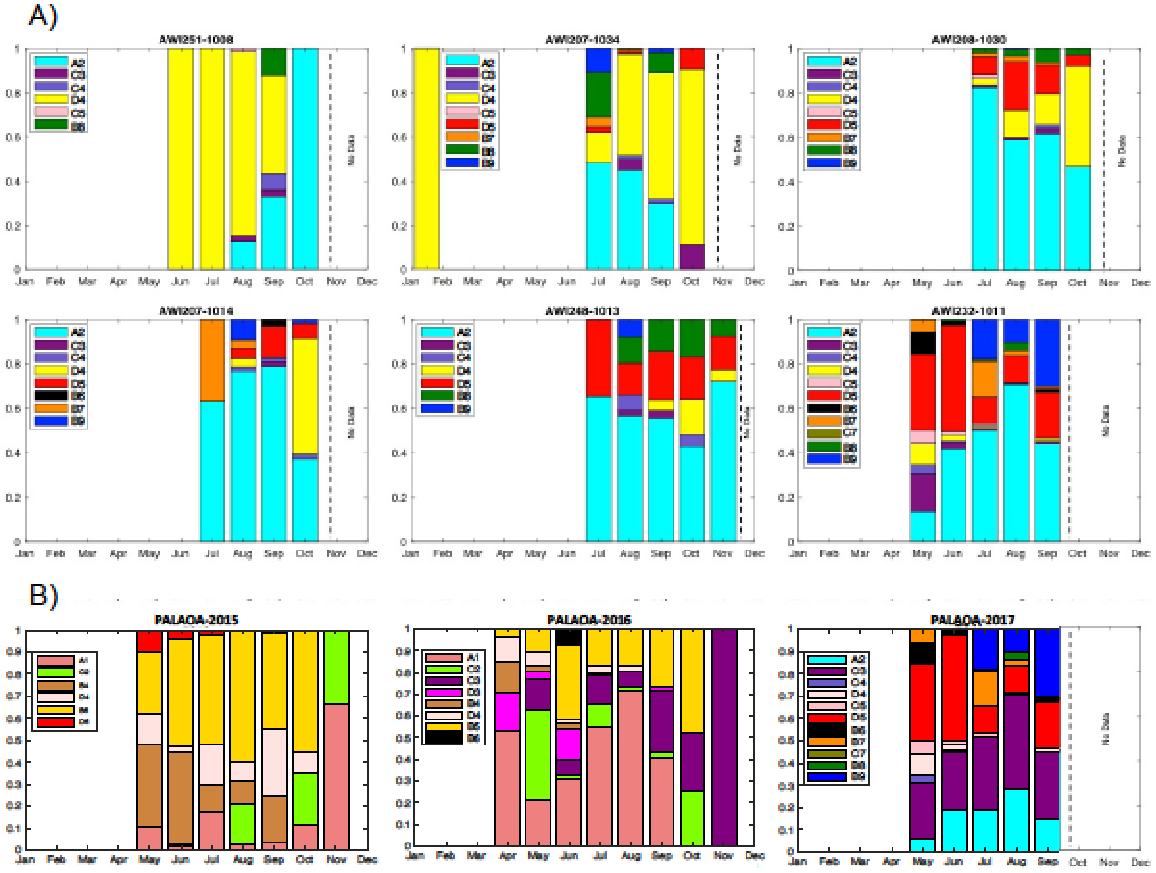

Figure 4. Proportion of occurrence of the different bio-duck call types per month identified for (A) 2013 from the 6 HAFOS sites and (B) from the multi-year PALAOA data. The dotted line indicates periods during which no data were collected.

Diel AMW calling pattern

For both data sets, we did not find a daily pattern in AMW call activity or call type usage when call occurrence was explored in relation to local light regimes across months (Figure 5).

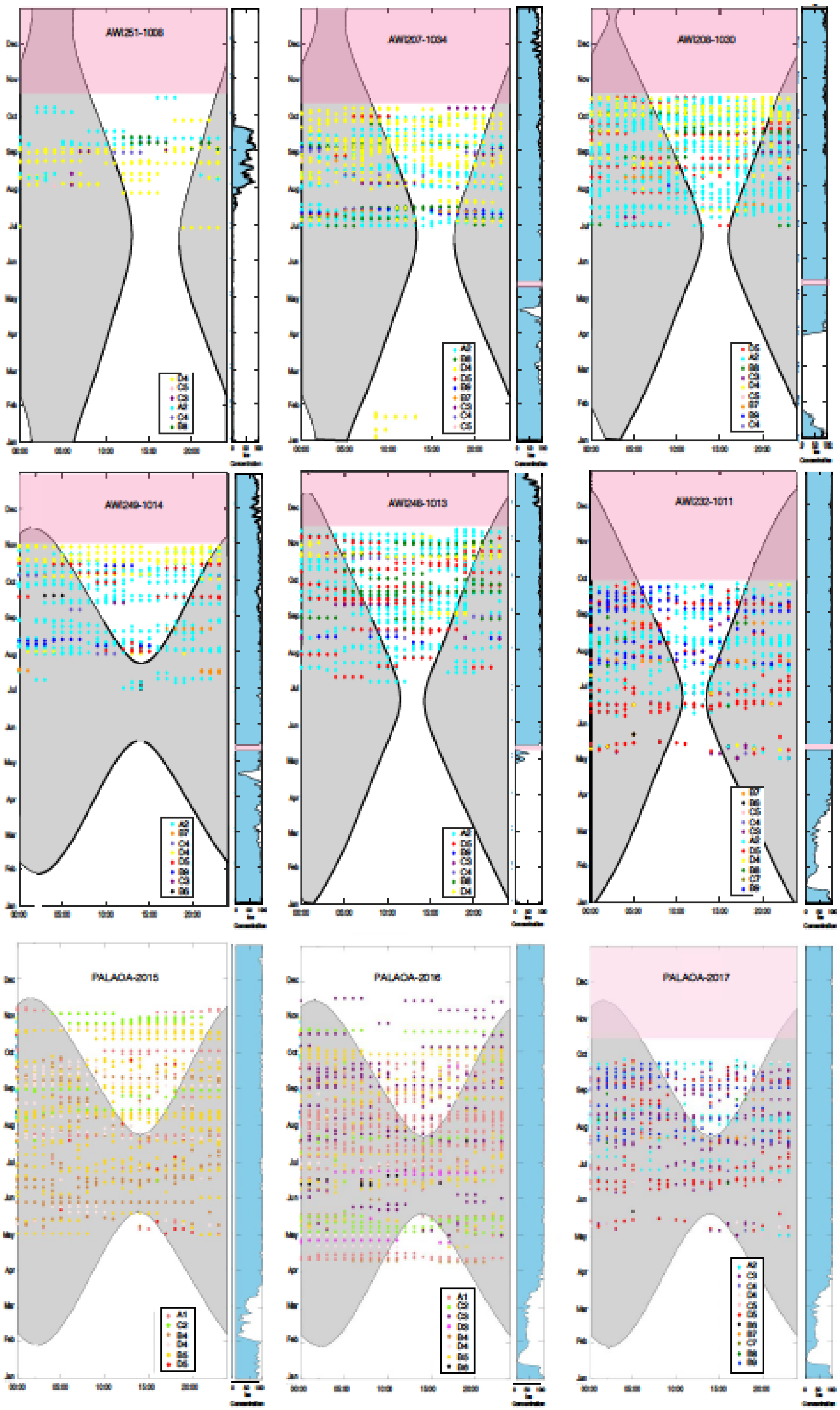

Figure 5. Seasonal and diel distribution of the different bio-duck call types from the HAFOS data set during 2013 and the multi-year PALAOA data. Every dot represents an hour with AMW acoustic detection. The dot coloring represents the different AMW bio-duck call types detected in every monitoring position. *Y-axes* shows date; left *X-axis* time of the day (hours); right *X-axis* ice concentration in a 50 km radius. Grey shading represents the periods between sunset and sunrise. Light pink shading represents periods during which no data were collected.

Multi-year patterns in AMWs calling behavior

The PALAOA data allowed to also compare AMW presence, repertoire composition and usage over a time span of three years. During 2015 we detected the occurrence of AMW calls between May and November and six different bio-duck calls were identified, being “A1”, ”B4”, “B5”, “C2”, “C4” and “D5”. In 2016, AMWs were acoustically present between April and November and eight different bio-duck calls “A1”, “B4”, “B5”, “C2”, “C3”, “D3” and “D4” were found to be present (Figure 4). During 2017, AMWs were found acoustically present between May and September and 11 different types of bio-ducks were identified, being “A2”, “B6”, “B7”, “B8”, “B9”, “C3”, “C4”, “C5”, “C7”, “D4” and “D5” (Figure 5). Due to electronic noise, it was not possible to analyze the 2017 data from October to December.

During the 3 years of continuous monitoring, the proportion in which the different calls were found present was not constant. In 2015, the predominant call was “B5” (47.4% of all detections). The secondary call was “B4” with 18.7% of all detections. In 2016 the predominant call was “A1” corresponding a 42.8% of all detections that year. The secondary bio-duck was "B5” with a 21.1 %. Finally in 2017, the most frequently detected call was “C3” composing 32.7% of all detections. The second most detected call was “D5” with a 22.3% but the call “A2” was 18.8% (see Appendix Table 2).

Discussion

This study provides the first quantitative description and classification of the acoustic repertoire of AMWs in the Weddell Sea. Our classification method distinguished 4 clear groups of bio-duck types, each consisting of different subtypes of bio-duck calls that all have a similar acoustic structure, but differ in the number of pulses and the duration of the inter-pulse interval. The classification and nomenclature method applied in this study forms a critical step forward in understanding more about the acoustic behavior of AMWs. With an automatic classifier we can now systematically and objectively analyze how the acoustic repertoire of these whales is composed and how it varies over space and time, also including further data from other Antarctic regions.

Several of the bio-duck call types that we identified from the Weddell Sea data have also been described by studies conducted at other locations, e.g. the West Antarctic Peninsula bio-duck 'A1' and 'A2' (Dominello and Širović 2016), seems to be C4 and category B in our study, as well 'B' and 'C' (Risch, Gales, et al. 2014) present similar shape as C3 and C6 in the Weddell Sea. In South Africa bio-ducks 'A1' and 'A2' (Shabangu et al.,2020) seems to match our C4 and A2 and Australia type '2B' (Matthews et al., 2004) looks similar as our A2. AMW sounds described in earlier studies match our overall classification groups A-D, but partly represent additional bio-duck call subtypes that differ from the subtypes that were identified in this study (i.e., in terms of variability in the number of pulses). An in-depth comparison of the AMW calls recorded by other studies and ours is in progress, but was beyond the scope of this study. Although systematic comparisons are pending, the similarity in the classification groups with studies conducted in other latitudes and sectors of the Southern Ocean already demonstrates that the AMW acoustic repertoire has an overall consistent structure as to how calls are composed. However, the fact that the bio-duck subtypes that compose the groups are not the same, could reflect differences in the acoustic behavior between AMW stocks, cohorts, sexes or behavioral contexts when calls are produced. Furthermore, the observed temporal variability in bio-duck subtypes, shown by the PALAOA data, suggests that AMW calling behavior may change over the course of seasons, reminiscent of humpback whale song evolutions (K. Payne 2000).

Do Antarctic minke whales sing?

In this study we postulate that similar to the majority of other large whale species e.g. humpback whales (*Megaptera novaeangliae*) (Payne & McVay 1971), Northern Pacific, North

Atlantic and Southern right whales (*Eubalaena japonica, E. glacialis* and *E. australis)* (Crance et al. 2019; Mussoline et al. 2012; Webster et al. 2016; Clark 1982), fin whales (*Balaenoptera physalus*) (Croll et al. 2002) and blue whales *(B. musculus*) (McDonald et al. 2006), AMW bio-duck calls suit the definition of song (e.g., Cholewiak et al. 2013) . AMW bio-duck calls can

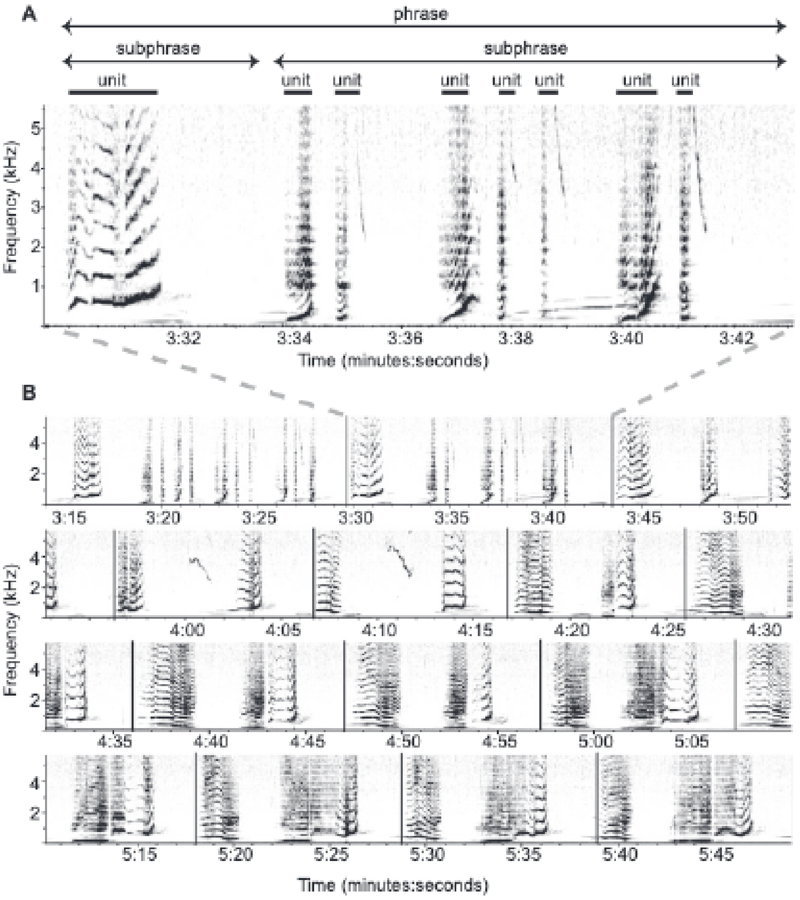

Figure 6. Spectrographic representation of humpback whale song sequence, recorded at IslaSocorro, Mexico, on 27 March 2006 (1,024 pt FFT, Hann window,50% overlap). Time on the x-axis is in minutes:seconds, while frequency on the y-axis is in kHz. (A) One phrase consisting of two subphrases. The first subphrase is composed of one unit,while the second subphrase is composed of a repeating pattern of 2–3 individual units. Notethat units 3, 5, 6, and 8 within the example phrase are continuous, although their full frequency range exceeds that chosen for display in this figure. (B) 155 s sequence of song, in which multiple phrases types can be observed. Phrases have been delineated by vertical lines (extracted from Cholewiak et al. 2013).

be broken down into “units” and “phrases” that are repeated in a regular pattern. Similar as in NPRWs and NARWs, AMWs seem to produce the same call type (bio-duck unit) in higher rate forming song bouts (Parks et al. 2012; Crance et al. 2019). Those bouts can be described as phrases and those phrases can be produced during hours conforming a song (Appendix Figure 1), as has been described for other mysticete species (Cummings and Thompson 1971; McDonald et al. 2001; Clark and Clapham 2004).

Furthermore, the existence of themes cannot be excluded, but was beyond the scope of the current study and should be explored in follow up work.

For marine mammals, song is best-studied in humpback whales (Payne and McVay 1971). It is typically unique for each population, evolving from year to year, but can also be transmitted between populations (Garland et al., 2011). Song is documented to be produced only by males, occurring primarily on the breeding grounds (Frankel et al. 1995) and less frequently on feeding grounds (Clark and Clapham 2004; Schall et al. 2021). Less complex songs are also common among other mysticete species. Blue and fin whales produce relatively simple songs that can be used to acoustically distinguish among different populations (McDonald et al. 2006; Delarue et al. 2009). In these species, the overall structure of songs remains constant over many years[1], even decades (Širović et al., 2007; Gavrilov., 2012) Our study postulates that AMWs produce songs of less complexity than described for humpback whales (Payne and McVay, 1971). Its structure is more similar to blue and fin whale song with several relatively simple repetitive sequences forming a song (Watkins et al., 1987; Croll et al., 2002; Delarue et al., 2009b), although the rate of change over time and between regions seems to be similar as what occurred with fin whales in the Northern Pacific (Širović et al., 2017).

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[1] Although the overall structure of songs remains stable, the frequency of fin and blue whales has been reported to decrease over time. The origin and reason of this decrease are to date unknown (Leroy et al. 2018).

Males or females?

PAM data do not provide information on the identity of the caller and therefore in many species it still is debated if both males and females are equally vocal and what sounds are produced by which sex. In species such as humpback, blue and fin whales, the evidence to date indicates that only males sing (Darling and Berube 2001; McDonald et al. 2001; Croll et al. 2002; Olseon et al. 2007). Much of the prevailing speculation on the function of song in these species has evolved around if, and how, singing functions as a mating display (Payne and McVay, 1971; Darling and Berube, 2001; Croll et al., 2002; Darling, 2002). However, recent data indicate that males also sing during migration and on feeding grounds (Norris et al., 1999; Clark and Clapham, 2004). It has been suggested that such 'off-season' singing may represent low-cost opportunistic intrasexual display or advertising by potentially younger or subdominant males to court females that failed to conceive during the winter (Clapham & Clark 2004). For AMWs, it remains unknown if the sounds are produced by only one or both sexes. However, comparative evidence from other mysticete species suggests that the more elaborate vocal displays most often stem from males (Watkins, 1981; Darling and Berube, 2001; Croll et al., 2002). For AMWs, the limited studies available are consistent with the hypothesis that the observed complex acoustic behaviour appears to coincide with the breeding season from May to November (G. R. Williamson 1975; Best 1982). These aspects seem to further support the existing hypothesis that the AMW calling activity forms part of male vocal display.

Geographic characterization and population identity

Different studies have long noted and applied the potential utility of whale songs as an indicator of biologically meaningful stocks for blue whales (*Balaenoptera musculus*) (Cummings and Thompson, 1971; Edds, 1982; McDonald et al., 2006), humpback whales (Payne and Guinee, 1983; Cerchio et al., 2001), fin whales (*Balaenoptera physalus*) (Thompson et al., 1992; Hatch and Clark, 2004) and Bryde's whales (*Balaenoptera borealis*) (Oleson et al., 2003). These data and those from other recent studies provide a growing body of evidence that geographic differences in whale songs can provide useful information for discovering and determining population boundaries. As noted above, a study on the acoustics of fin whales (Hatch and Clark, 2004) showed that fin whale song varied significantly among regions in two ocean basins, although the differences were not reflected in genetic differentiation, therefore potentially representing more recent discontinuities in movement and/or behaviour (Hatch and Clark, 2004).

Studies of the acoustics of minke whales suggest a simple downswept call is used across geographic regions (Edds-Walton, 2000; Schevill and Watkins, 1972), but more complex vocalizations often referred to as the 'star-wars', 'thump-train' or 'boing' sound are regionally distinctive (Gedamke et al., 2001; Mellinger et al., 2000; (Risch et al., 2014). Here, we show that bio-duck calls are also regionally distinctive and can potentially be used to identify different populations or stocks of AMWs in the Southern Hemisphere.

Previous studies implementing different genetic techniques provide strong evidence to retain the hypothesis of multiple AMW stocks in the Southern Ocean. The results suggest that there are at least two stocks present in the SO: an eastern Indian (I) and a western South Pacific (P) stock (Pastene et al., 2006). These stocks are thought to mix across a soft boundary, which would probably best be placed near 165ºE . These stocks could be related to the breeding areas proposed for the eastern Indian Ocean and western South Pacific. Although our acoustic data come from the Atlantic sector of the South Sea, they also indicate the presence of multiple clusters in the Weddell Sea sector. There is one group in the west (Antarctic Peninsula region) and another in the east, closer to the Greenwich meridian area. In addition, there is a third group that could be in between these two groups and that could be where the interaction between individuals takes place. This presence of different groups may be similar to that already described for humpback whales in the area (Schall et al. 2021). Furthermore, we cannot rule out that the occurrence of different groups could be connected with possible breeding grounds in Brazil or Namibia and South Africa.

The bio-duck call as AMW stock indicator?

In the Weddell Sea we recorded bio-duck calls at all our monitoring sites but not all positions recorded the same call types. Overall sites, only one bio-duck call type "A2" was recorded at all monitoring sites. This call exhibited the highest occurrence of detections (>49% hours with acoustic detections (Appendix Table 2) at almost all monitoring locations with the exception of the two most westerly sites near the Antarctic Peninsula (AP) (AWI251-1008 and AWI207-1034). The D4 is the dominant one in the west of our study area occurring most frequently at positions AWI251-1008 and AWI207-1034 near the AP. D5 is another frequently occurring call type, but occurred at the positions located on the east side of the Weddell Sea, e.g., AWI248-1013 and AWI232-1011 (Greenwich) and not at all at the most western recording site (AWI251-1008).

I postulate two possible hypotheses regarding the acoustic behavior of AMWs in the Weddell Sea. The first is that the predominant call types are associated with specific behavior performed by the animals in the respective area. If certain calls are linked to behavior that is area-specific, the observed differences in repertoire usage could reflect spatial variation in AMW habitat usage across the Weddell Sea. However, in this case it might be more likely that the time span over which the calls occur differs between recording locations as presence and behavior are linked to f.e. different habitat features (El-Gabbas et al., 2021b). Our second hypothesis therefore, is that these calls indicate the existence of different groups or subpopulations of AMWs that occur simultaneously during the winter and spring season in different parts of the Weddell Sea (Appendix Figure 3). If the second hypothesis holds true, our findings could indicate that three possible groups of AMWs coexist in the Weddell Sea: the group near the Antarctic Peninsula (sites AWI251-1008 and AWI207-1034) using the “D4” call as a distinctive call type. Second, the group present in the center of the Weddell Sea using the “A2” call as a distinctive call type (Appendix Table 2 and Appendix Figure 3). And finally, the third group that would use the “D5” call as distinctive and that would correspond to the area east of the Greenwich Meridian. Call type “D5” is not very present in our study area, possibly because our Greenwich recorders are at the western limit of its distribution.

However, the multi-year data from PALAOA show that the AMW repertoire composition changes from year to year. Therefore, single bio-duck call types may not be reliable indicators of stocks, but should be interpreted in the context of larger scale patterns in AMW vocal behaviour.

Differences in multi-year AMWs acoustic repertoire

In addition to the spatial variability in AMW repertoire, the data from PALAOA show that the acoustic repertoire of AMWs varies from year to year. Each year there is a "predominant" call, which is detected throughout the entire acoustic season. This call is present in >40% of the total hours with bio-ducks records. This "predominant" call change every year. In general, the new dominant call corresponds to a bio-duck call type that was already increasing in presence in the repertoire towards the end of the previous year. For the time frame analyzed, this ‘replacement’ call in our data proved to be the third most frequent call detected during 2015 and 2016. In addition, the dominant call of one year does not disappear the following year, but its occurrence decreases, being the second-third most frequent. The composition of the acoustic repertoire also changes from year to year. Vocalizations that disappear from one year to the next, or those that appear and were not recorded before, are generally detected at very low frequencies of occurrence. These calls individually constitute <10% of the total acoustic repertoire of the season.

This information strongly suggests that, like humpback whales, AMWs change their repertoire from year to year (Garland and McGregor 2020). This inter-annual change in AMWs acoustic repertoire, matches the pattern of song "revolutions" in humpback whales, where the single population-wide shared song type is rapidly replaced by a new, novel song type introduced from a neighboring population (Noad et al., 2000; Garland et al., 2011). We speculate that it cannot be excluded that the dynamic of the AMW vocal behaviour potentially reflects a similar mechanism through which the simultaneous presence of different groups or populations of AMWs mutually affects the composition of the annual repertoire.

Conclusions

The function of the bio-duck call is still unknown. It has been suggested that bio-duck calls are related to mating behaviour since the calls occur mostly in a period that is thought to represent their breeding season. Since there are many similarities in the change of AMW bio-duck call type patterns to mating related songs of other whale species, this would further support our previous suggestion that bio-duck calls are associated with mating behaviour (Filun et al. 2020). Also, the observation that there is no diel pattern in calling activity, matches observations in other species where mating-related calling behaviour did not exhibit any light-regime related fluctuations (e.g., Van Opzeeland et al. 2010; Thomisch et al. 2016; Burkhardt et al., 2021). The Weddell Sea (or any region of the Southern Ocean south of 60°) is however not a known breeding ground for AMWs. However, in other cetacean species, mating related vocal behaviour was also found to occur on the feeding grounds. According to the description of whale songs, our study shows that AMWs are capable of producing complex songs, which in some cases were found to be broadcasted for hours. We systematically documented a wide diversity of bio-duck calls, which can be classified into groups according to the structure of the pulses that constitute them. These groups are made up of different bio-duck call types that coincide in overall structure but differ in their number of pulses. Our methods have proved to be robust for multi-site, multi-year data and can therefore be applied to further data sets to enable consistent comparisons of additional data, covering larger spatial and temporal scales. Finally, we postulated the potential distinction of groups or populations of AMWs based on the acoustic signals they emit, as has been shown for other whale species (McDonald et al. 2006; Oleson et al. 2014; Širović et al. 2017; Garland et al. 2015). Future studies integrating more acoustic data, covering more spatial and even circumpolar coverage in the Southern Ocean are needed to test the hypothesis about the identification of different populations of AMWs based on their vocal behaviour. Nevertheless, the combined spatial and temporal dynamicity of the AMW vocal behaviour is likely to complicate identification based on single recordings. Along these lines, implementing and extending the area and timing of AMW monitoring effort in low latitude areas would help to better understand their distribution and identify potential migration routes. Lastly, further research needs to focus on the larger scale pattern of occurrence of bio-duck call types to unravel if phrases occur in repeating patterns that can be identified as themes. We hope that this study has contributed a small piece to the AMW riddle which needs prompt answers to understand how we can effectively conserve this species in its critical habitat.

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Chapter III: Playing the beat: occurrence of Bio-duck calls in Brazil reveals a complex acoustic behaviour for the Antarctic minke whale (Balaenoptera bonaerensis).

"Playing the Beat ": occurrence of Bio-duck calls in Brazil reveals a complex acoustic behaviour for the Antarctic minke whale (*Balaenoptera bonaerensis*)

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Abstract

The Antarctic minke whale (*Balaenoptera bonaerensis*) (AMW) is one of the smallest species among the baleen whales, occurring in the southern hemisphere from Antarctica to near the equator, and performing seasonal migration from polar to tropical waters. Information about (AMW) occurrence in the winter breeding grounds is scarce, mostly regarded to old records from whaling stations before the 1960's international moratorium, such as Costinha Station in Northeastern Brazil (6° S / 34° W) and some sightings from a few dedicated visual surveys. Acoustic methods can provide important data on the occurrence and distribution of migratory species. This work describes the occurrence of the Antarctic minke whale through Bio-duck acoustic detections in the Santos Basin, South-Southeastern Brazil (22° and 28° S / 42° and 48° W), utilizing highly technological passive acoustic methods, such as autonomous underwater vehicle (SeaGlider) sampling. Data was recorded between November 12 and December 19, 2015. AMW calls were detected during 12 days. We detected and classified 9 different Bio-duck calls in Brazilian coastal waters, evidencing a highly diverse acoustic behaviour for the minke whale breeding ground. This is the first study to describe the acoustic diversity of AMW vocalizations in lower latitudes, constituting important information to the conservation and management of AMWs and their habitat. Therefore, our study presents the foremost acoustic evidence of the Antarctic minke whale in Brazililian coastal waters.

Keywords: Antarctic Minke Whale, *Balaenoptera bonaerensis*, Bio-duck calls, acoustic ecology, Brazilian breeding ground.

Introduction

Marine mammals are important species in the marine ecosystem, generally belonging to higher trophic levels in the food chain, controlling natural populations, cycling nutrients, and providing food when decomposing at the oceanic bottom [1]. For some cetaceans, such as the baleen whales, acoustic behaviour plays an important role during foraging and breeding and has been extensively studied for species such as humpback whales (*Megaptera novaeangliae*) [2, 3], fin whales (*Balaenoptera physalus*) [4, 5], and blue whales (*Balaenoptera musculus*) [6, 7]. For some whale species the acoustic ecology remains scarcely understood. Furthermore, whale vocalisations can show patterns of occurrence, breeding behaviour, movement, and seasonality of a species within a certain area [8-11] and even geographic differences in acoustic repertoire between different areas [12-15].

The Antarctic minke whale (*Balaenoptera bonaerensis*) (AMW) occurs in the southern hemisphere from Antarctica to near the equator (10º S), performing seasonal offshore migration from polar to tropical waters, like other whale species [16, 17]. The seasonal occurrence, distribution, migration patterns and population structure of AMWs are poorly understood [18].

Notwithstanding, information on AMWs distribution in the South Atlantic Ocean are scarce, restricted to the whaling station reports along the 20th century, such as Durban, South Africa (29º 53' S, 31º 03' E) from 1968 to 1982 [19] and Costinha, Paraiba state, Northeastern Brazilian coast (6° 53′ S, 34° 52′ W), from 1904 to 1985 [20-23]. More recent information, collected during visual surveys, describe the presence of AMWs during autumn-spring, being sighted only in offshore waters [17, 24-26].

With great technological advances in recent decades, passive acoustic methods have been considered an efficient non-intrusive method to study and monitor cetacean ecology and occurrence across an ocean basin [18, 27-29]. This study presents the first acoustic evidence of AMW Bio-duck calls in Brazil, utilizing high technological passive acoustic methods

(SeaGlider).The Bio-duck sound was attributed to AMWs in 2014 [30], after more than five decades of unknown "mysterious" recordings in the Southern Ocean. AMW calls have been recorded at high and low latitudes with similar seasonal patterns of occurrence.They are detected during autumn to late spring. [28,29].

Species-specific whale sounds have been utilized to describe occurrence and distribution patterns for migratory species, highlighting the annual cycle that results in different acoustic environments [2, 27, 31, 32]. The study and implementation of monitoring programmes to understand the ecology and acoustic behaviour of AMWs are important steps to help generate conservation and management policies for the protection of the species and the ecosystem.

The goal of this work is to describe the AMW Bio-duck calls detected in a potential breeding ground area, contributing information about occurrence of this species in the western South Atlantic Ocean.

Methods

Study area

The Santos Basin is situated off the south and southeast Brazilian coast, between 22° and 28° S and 42° and 48° W, in the western South Atlantic Ocean (Fig 1). This basin presents a wide continental shelf, extending almost 200 km offshore in some locations, crossing a diverse depth gradient, and hosts large oil deposits and fisheries resources [33, 34].

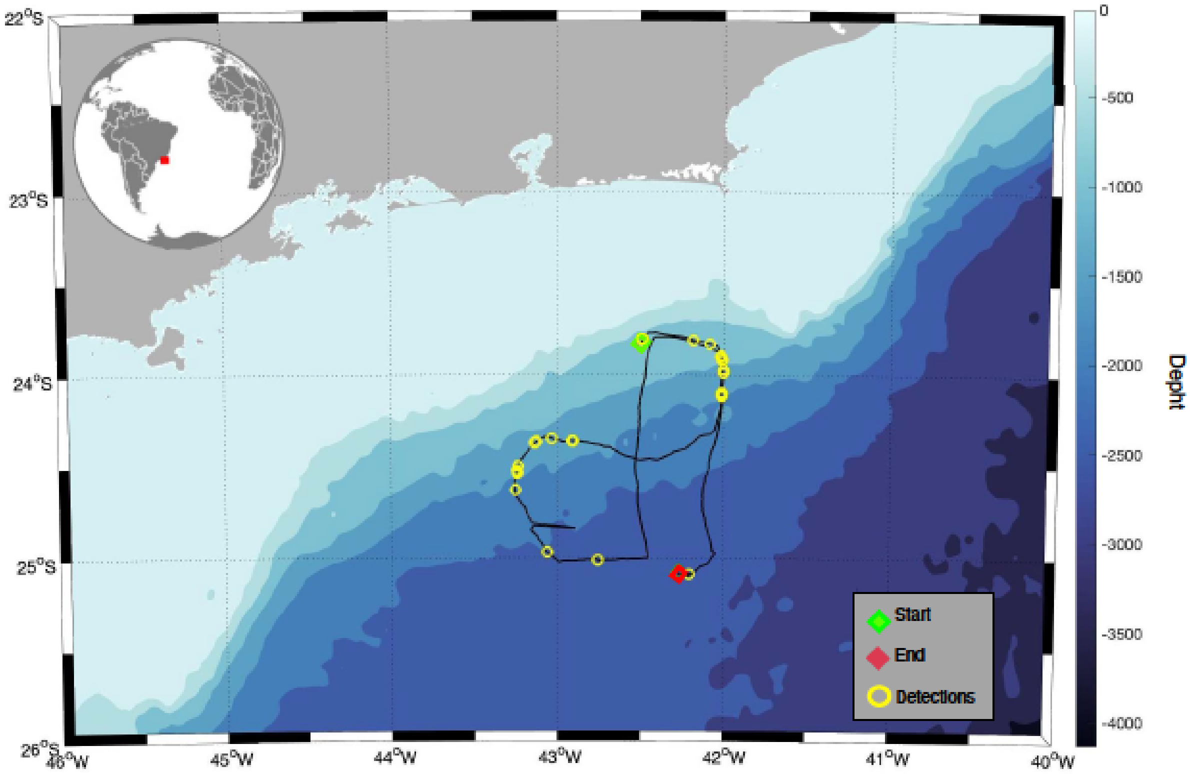

Fig 1. Map of the study area, the Santos Basin, showing the Glider track on Brazilian offshore waters between November 12, 2015 (green marker) until December 19, 2015 (red marker). Yellow dots show the positions where Antarctic minke whales Bio-duck calls were detected.

Data collection

Since November 2015, the Underwater Acoustic Soundscape Monitoring Project (PMPAS-BS, in the Portuguese acronym) has been collecting data in the Santos Basin using different types of methodologies, including a glider, equipped with a custom-designed and built-in passive acoustic recording system. The SeaGlider® (Kongsberg Maritime) is designed for continuous, long-term measurements of oceanographic parameters. The SeaGlider used in this study was equipped with a recording system, composed of a hydrophone HT-92-WB, from High Tech Inc., sensitivity: -165 dB re 1V/ µPa, amplified by 25 dB, and recording at 125 kHz sample rate and 16-bit resolution. It was programmed to record one hour data every one hour (1/2 duty cycle). Acoustic data is stored on SD cards (up to 500 hours per survey) in the glider and recovered after each survey. The SeaGlider was deployed between 12 November until 19 December 2015. It was programmed to execute a previous programmed trajectory (Supplement Fig.2) and perform dives down to 1000 m depth (Supplement Fig. 3) with a speed of 25 cm/s (0.5 knot).

AMW acoustic detection and classification

In this study, a Bio-duck call was defined as multiple series of downsweep pulses clustered, separated by <1 second. The call is characterized by its repetitive nature, consisting of regular down-sweeps or pulses in a series, with most energy located in the 50–300 Hz band, although for signals with higher intensity, harmonics occur up to 1 kHz [30, 32, 35]. The Bio-duck call never occurred alone and it always occurred in repetitive sequences [36].

To detect the occurrence of AMW Bio-duck calls in Brazilian waters, the PAMGuard whistle and moan detector [37, 38] was applied to the acoustic files, as a pre-processing to obtain information on whale signals up to 3 kHz. For this reason, the acoustic data was decimated to 6 kHz and the spectrograms were generated with 1024 FFT points (leading to a window size of 171 milliseconds) and an overlap of 95%. An audio file of 1 minute length was generated when the PAMGuard whistle and moan detector identified Bio-duck calls presence. To allow automated feature extraction for call type classification, individual Bio-duck pulses were automatically detected in the 1-minute audio fragments. Spectrograms (1125 point FFT, 85% overlap, Hanning window) of the audio fragments that were extracted from the PAMGuard whistle and moan detector were manually checked in RStudio Version 1.2.5042 with the 'Seewave' package (Sueur et al. 2020). Furthermore, the 1-minute audio files were frequency filtered between 40-500 Hz. For every 1-minute audio fragment, the signal-to-noise ratio (SNR) of Bio-duck calls in the snippet was calculated. In some cases, more Bio-duck pulses were detected in the 1-minute fragments, then, the one with the highest SNR was selected for further processing. To define SNR, for each call, background noise was measured during 0.6 seconds prior to the detected call event in the frequency bands between 40 – 500 Hz. The signal value was measured during 1.1 seconds after the time point of background noise measurement. The beginning and end of each Bio-duck call in the 1-minute fragment was designated manually. Then, an amplitude filter of 20 dB was applied to increase the SNR of the Bio-duck pulse train spectrum. Only Bio-duck calls with a resulting SNR that was sufficiently high, were selected for further processing using the pulse detector. The pulse detector was used to automatically extract call characteristics from each Bio-duck call for the classification. The automated pulse detector was designed to work using the low frequency downswept component present in all Bio-duck calls. Bio-duck pulse detection thresholds were custom-defined based on the individual Bio-duck call SNR (SNR = 20*log10(rms(signal)/rms(noise)). For acoustic detections with a SNR<5 dB we applied a detector threshold=50, for detection with SNR>5 dB and SNR<10 dB a threshold=30, with SNR>10 dB and SNR<15 dB threshold=20, with SNR>15 dB and SNR<20 dB threshold=15 and with an SNR>20 dB a threshold=12 (Fig. 2). To reduce false positives of other pulsed signals, only detections of pulses with a duration within the range of 0.05 - 0.33 seconds (which were the known minimal and maximal durations of AMW pulses) were included as part of the Bio-duck pulse sequence (values measured in this study (Table2)).

For the final classification of the different AMW calls detected in our data set, we used the detections to extract different variables with a custom-built algorithm in RStudio Version 1.2.5042, using the R packages 'Seewave' and 'warbleR'[3].

Parameters that were automatically extracted by the algorithm included the number of pulses (NP), total duration (TD), average pulse duration (average duration of all the pulses that constitute a Bio-duck call) (AvDP), average inter-pulse interval (AvIPI), duration first pulse (DFP), duration last pulse (DLP) and peak frequency (PF) (Table 2). The algorithm was based on an amplitude detector capable to automatically extract and calculate different measurements from the waveform of AMW Bio-duck calls between 40-450 Hz. Although the different types of Bio-duck can have harmonics up to 2,000 Hz (Fig. 3), these are not a reliable feature as their presence and quality depends on different factors such as, for example, proximity of the animal to the hydrophone, ambient noise levels and call directionality. Only the fundamental frequency of the downswept pulses was included in the measurements as robust frequency parameter.

We separated the different Bio-duck calls using cluster analysis based on the calculated acoustic parameters in order to optimize the classification. A Euclidean method was used to calculate the distances between the different clusters. To determine the number of clusters (*k*) we used the 'NbClust' package [4]. This automatically calculates and provides 30 different indices for determining an appropriate number of *k* from the different results obtained by varying all combinations for number of clusters, distance measures and clustering methods.

The different parameters extracted from each Bio-duck call type were used to perform a hierarchical agglomerative cluster analysis to generate unsupervised call type groups. To perform the automatic classification analysis, we used the values extracted from 30 samples for each type of Bio-duck detected. From type B3, due to the small number of samples, we were able to use only 14 calls.

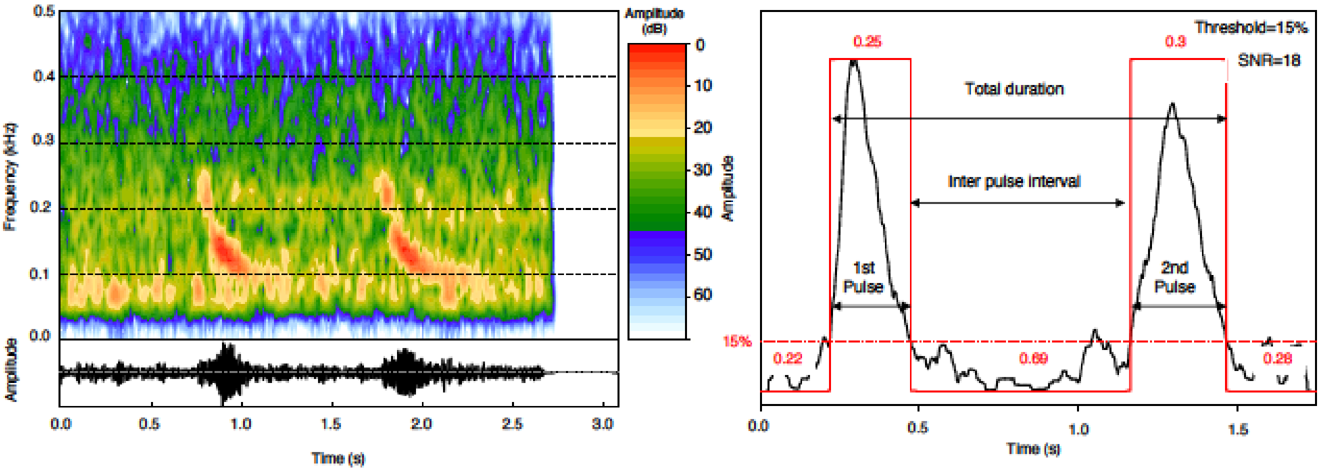

Fig 2. Spectrogram and waveform of the downsweep component of the Antarctic minke whale Bio-duck "A2". Waveform of the Bio-duck "A2" showing the 15% threshold to identify and measure the different pulse durations and inter-pulse-intervals (IPIs) in seconds.

We separated the different Bio-duck calls using clustering analysis based on the calculated acoustic parameters. An Euclidean method was used to calculate the distances between the different clusters. To determinate the number of *k* we used the 'NbClust' R package [42], which automatically calculates and provides 30 different indices for determining an appropriate number of *k* from the different results obtained by varying all combinations of number of clusters, distance measures and clustering methods.

The different parameters extracted from each Bio-duck call type were used in a hierarchical agglomerative cluster analysis to generate unsupervised call type groups. The information from the matrix of distances calculated a dendrogram to identify the dissimilarities and connections between the different Bio-duck call types detected in Brazilian waters.

Results

Between November 12 and December 19, 2015, the SeaGlider covered approximately 725 km of distance and collected 262 hours of acoustic data during 187 glider dives. AMW calls were detected along the transect for 12 days Table 1. Manual analyses confirmed the detections were AMW Bio-duck calls, based on the literature description [30, 32, 35, 43].

Table 1. Antarctic minke whale Bio-duck call encounters in Brazilian offshore waters.

Date	Hour start	Hour end	Latitude S°	Longitude W°	Glider depth (m)	Bio-duck types
12.11.2015	13:49:00	13:54:41	-23.80815506	-42.48846817	112.98	D6
14.11.2015	08:26:00	08:43:40	-23.80920029	-42.18441772	1.30	D6
14.11.2015	15:47:00	16:04:40	-23.82978058	-42.08476257	279.75	D6
15.11.2015	03:16:00	03:49:47	-23.89512062	-42.02005386	130.18	D6
15.11.2015	03:50:47	04:14:46	-23.89885521	-42.01930618	52.63	C11
15.11.2015	05:46:00	06:21:21	-23.9147644	-42.01307678	345.10	D6
15.11.2015	06:23:21	06:57:20	-23.91983223	-42.01108932	118.74	A4
15.11.2015	11:50:00	12:21:07	-23.97163963	-42.00485611	876.99	A4
15.11.2015	13:31:05	13:41:05	-23.98914909	-42.0019455	108.62	A4
16.11.2015	00:12:00	00:43:19	-24.09622574	-42.01313782	947.00	B3
16.11.2015	00:45:19	01:17:18	-24.10261917	-42.01353836	874.85	D6
16.11.2015	01:19:18	01:51:17	-24.10923958	-42.01395416	645.67	B4
16.11.2015	01:53:17	02:17:16	-24.11581612	-42.01436615	435.60	B3
22.11.2015	07:37:27	08:09:26	-24.35966492	-42.90554047	129.98	B3
22.11.2015	08:11:26	08:23:26	-24.35882759	-42.90994263	177.80	D6
23.11.2015	09:39:00	10:08:33	-24.34605026	-43.03238297	761.20	D6
24.11.2015	13:26:00	13:38:07	-24.36293983	-43.12480164	150.02	B5
24.11.2015	15:16:16	15:44:15	-24.37080193	-43.13537979	121.74	D7
25.11.2015	17:30:52	17:52:51	-24.49822235	-43.2351265	525.01	D6
25.11.2015	21:12:00	21:43:14	-24.52141762	-43.24263382	1.28	D6
25.11.2015	23:13:16	23:43:15	-24.53253174	-43.2402153	589.22	A2
25.11.2015	23:45:15	23:50:15	-24.5354538	-43.23957825	198.02	A2
26.11.2015	00:01:15	00:11:14	-24.53692055	-43.23926163	6.73	A4
26.11.2015	15:11:26	02:39:00	-24.63012505	-43.2525177	133.27	A4
29.11.2015	22:37:30	23:44:49	-24.96931648	-43.05936813	409.64	A3
01.12.2015	19:34:00	19:41:03	-25.01185799	-42.75591278	546.45	A4
17.12.2015	14:27:00	14:44:00	-25.08859062	-42.20511627	4.25	A4

Description of vocalizations

The vocal classes or groups were named according to acoustic properties extracted from Bio-duck calls detected in Brazilian waters based on automatic classification (Table 2) and indicated in capital letters followed by a number. This number value corresponds to the number of down swept pulses present in a classified Bio-duck call (Fig 2). Call types were qualitatively named, to maintain consistency between naming schemes and sound structure. For the automatic measurements we did not consider the harmonics because they varied in relation to the proximity of the animals to the SeaGlider. We do show, however, spectrograms with the full frequency range to illustrate the harmonics in the Bio-duck calls detected up to 2000 Hz.

Table 2. Antarctic Minke Whale Bio-duck call extracted measurements with the amplitude detector. All time variables measured in seconds *(s)*, *(n)* =n° of samples, Peak Frequency measured in Hertz.

Cluster	NP	TD (s)	Av DP (s)	Av IPI (s)	DFP (s)	DLP (s)	PF (Hz)	(n)
A	2	1.26±0.3	0.28±0.4	0.7±0.3	0.28±0.2	0.29±0.4	131.8±15	30
A	3	1.3±0.2	0.31±0.3	0.19±0.2	0.32±0.3	0.3±0.2	182.9± 12	30
A	4	1.61±0.2	0.28±0.3	0.17±0.1	0.33±0.1	0.1±0.3	177.4±9	30
B	3	1.04±0.2	0.09±0.2	0.38±0.0	0.08±0.2	0.09±0.2	162.9±16	14
B	4	1.45±0.3	0.19±0.2	0.23±0.0	0.18±0.2	0.09±0.2	181.6±16	30
B	5	1.7±0.3	0.23±0.5	0.14±0.1	0.27±0.2	0.1±0.1	159.8±8	30
C	10	1.45±0.2	0.08±0.3	0.05±0.0	0.07±0.1	0.08±0.3	245.6±10	30
D	6	1.39±0.3	0.14±0.4	0.11±0.2	0.11±0.2	0.11±0.2	116.3±18	30
D	7	1.62±0.3	0.16±0.2	0.08±0.2	0.18±0.1	0.06±0.2	86.3± 10	30

Bio-duck calls classification

Nine different Bio-duck calls (Fig 3) were detected and classified with a hierarchical agglomerative cluster analysis (Fig 4). Every call analyzed contained between 2 and 11 pulses. The duration of a Bio-duck sound was between 1.04 – 1.70 seconds and the average pulse duration was between 0.08 – 0.31 seconds. The AvIPI was 0.05-0.38 seconds. For all

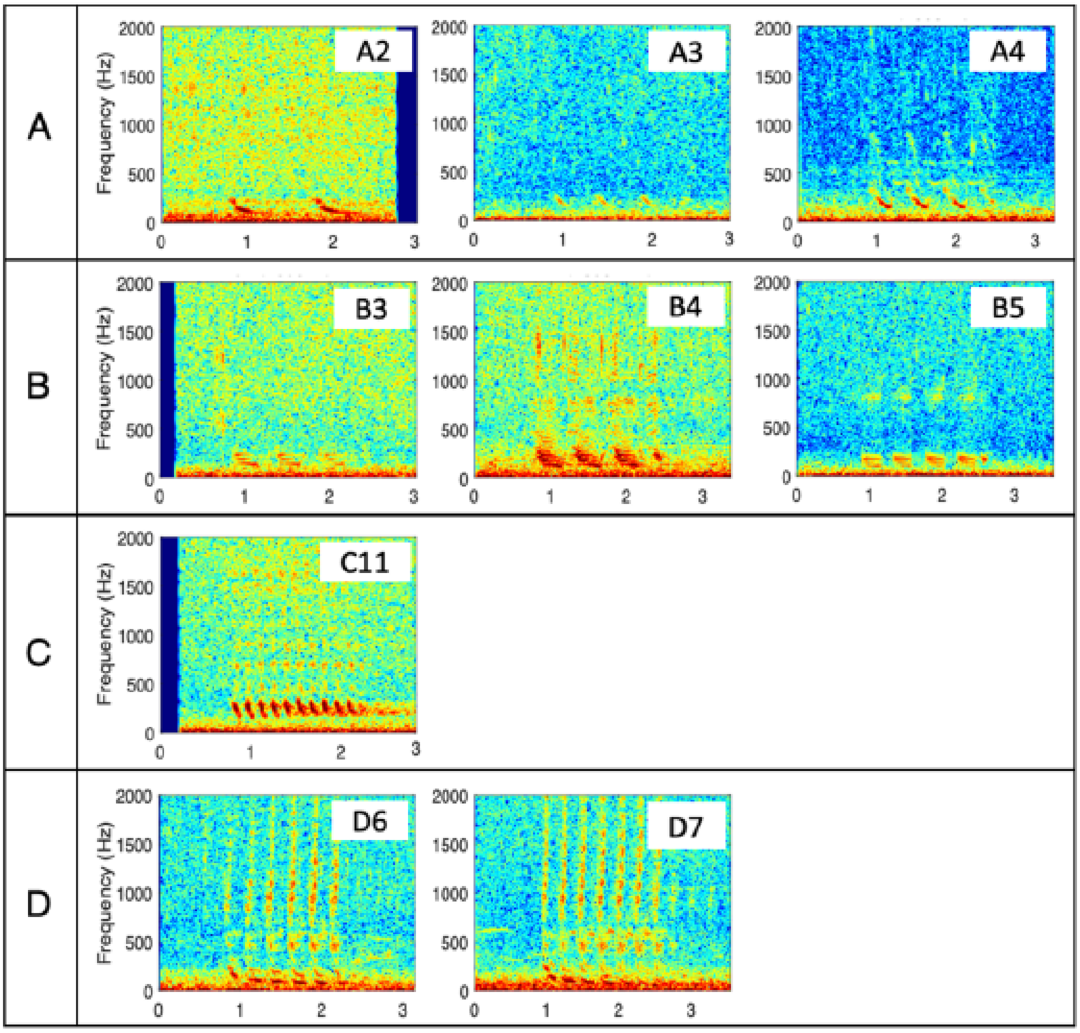

Fig 3. Spectrograms of the different Bio-duck calls of the Antarctic Minke Whale detected in the Santos Basin, Brazilian offshore waters. FFT=512, overlap= 95%, Time expressed in seconds and frequency scale in Hz.

categories, whenever a Bio-duck call increased the number of pulses, the AvIPI decreased while the total duration increased. The DFP varied from 0.07 – 0.33 seconds and the DLP was between 0.06 – 0.3 seconds. The peak frequency of the down swept component was 86.3-245.6 Hz Table 2. The analysis identified 4 different clusters (73%), grouping the "A2", "A3" and "A4" calls in the cluster A, Bio-ducks "B3", "B4" and "B5" in the cluster B, and only one call, "C10", in the cluster C. Finally, the cluster D was composed by two calls: "D6" and "D7".

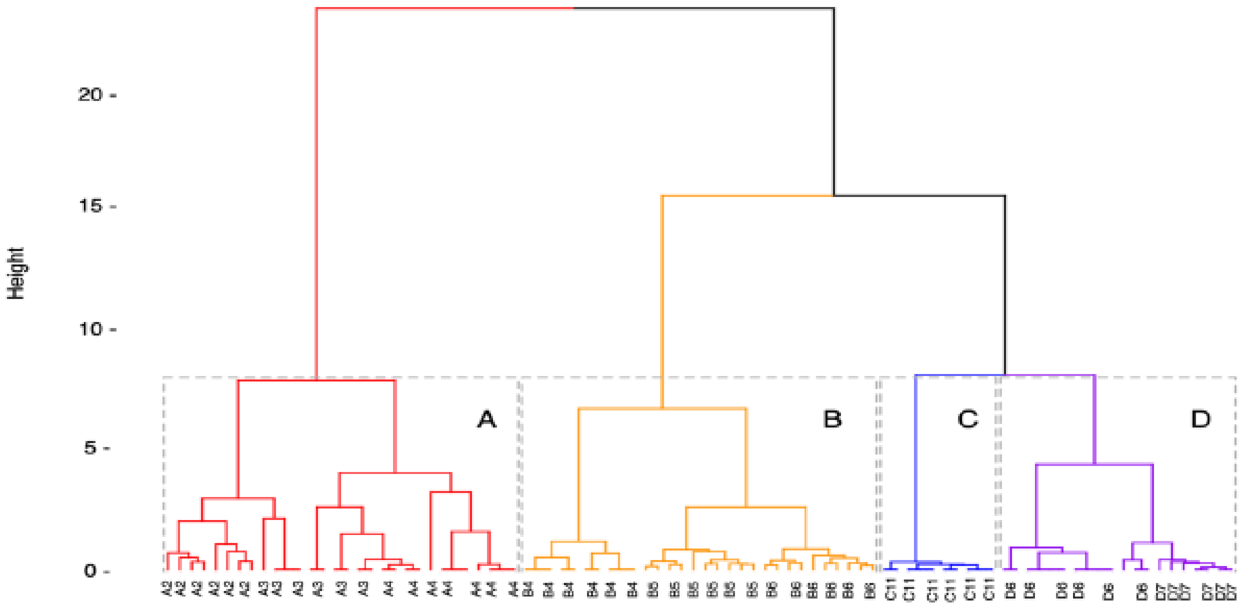

Fig 4. Dendrogram showing results of a hierarchical cluster analysis. Clusters representing the four classes of Antarctic minke whale Bio-duck calls. Cluster A corresponds A2, A3 and A4; Cluster B with the B3, B4 and B5 sounds; Cluster C with the C11; Cluster D with D6 and D7 calls.

Bio-duck call occurrence

The Bio-duck call "D6" was the most common call detected in the data, being present during 7 different days. The second most common call detected was the Bio-duck "A4" present on 4 days. The Bio-duck "B4" was detected on 3 different days. The other Bio-duck calls were detected only one day along the glider deployment period analyzed. On 15 November 2015, three different Bio-duck calls were detected. It was the day with most acoustic diversity of Bio-duck call occurrence, from 3:16 am until 1:41 pm. During that day, the Bio-duck calls "D6", "A4" and "C11" were detected. The second day with most acoustic variability was 25 November 2015 with the presence of two different call types ("D6" and "A2"). During the rest of the days with acoustic presence, the type of call detected was repeated throughout the day, and was the only call type detected Table 1.

Discussion

This work presented 9 different Bio-duck calls found off the Brazilian coast, a low latitude presumed breeding ground for migratory baleen whales in the western South Atlantic Ocean. This constitutes the highest diversity of acoustic behaviour reported for the species so far. The diversity of calls found suggests that the AMWs may produce organized and repetitive sounds, which suits the description of songs for other whale species, such as the humpback whale [2], southern right whales [44] and north Atlantic right whales [45](Parks and Tyack 2005). In addition to the variability of sounds produced by AMWs, their vocalizations are produced in repetitive sequences just like those of, for example, Antarctic blue whales [46] or fin whales [47-49].

Bio-duck calls comparison

Regarding acoustic structure, the Bio-duck has been considered a very conspicuous signature call [18, 30, 36, 43]. The most obvious characteristic is that energy is in a frequency band from 50 to 500 Hz [30, 32, 35, 43], although more intense signal harmonics have been observed up to 2 kHz.

The first study attributing the Bio-duck sounds to AMWs described the calls in series between 5-12 pulses, produced in regular sequences with an inter-sequence interval of 3.1 s. The data were collected from a tagged AMW in Wilhelmina Bay, in the Antarctic Peninsula, and they described 3 different Bio-ducks composed between 3-7 pulses and 3 types of low-frequency downsweep [30](Risch, Gales, et al. 2014). Another study in the Antarctic Peninsula region [32], using year round acoustic data from a mooring position, described 4 distinct Bio-duck call variants, with one variant having two sub-types. The calls were described with sequences between 4-13 pulses. In addition, this study also indicate the presence of a call type of low-frequency downsweep. Recently, [35] described the occurrence of AMW calls in South African waters and Maud Rise, Antarctica. The vocalisations detected in the study presented harmonics up to 2000 Hz and were classified in 3 categories with one category presenting 2 sub-types. The Bio-ducks presented sequences between 4-10 pulses. In Perth Canyon, western Australia, were distinguish two different types of call. One with a low repetition rate (T=1.6 seconds) and one with approximately doubled period (T=3.1 seconds) [43].

Based on a simple visual comparison of spectrograms of Bio-ducks detected in other studies, the calls described in our study match some of the Bio-ducks previously described in Perth Canyon [43], Western Antarctic Peninsula [30, 32], South Africa and Maud Rise, Antarctica [35]. Similarly, 7 of 9 calls detected in Brazil, classified in different categories, presented harmonics up to 2000 Hz. At first glance, comparing the spectrograms of our study and that of Shabangu. 2020, the shape and structure of the South African Bio-duck C-type resembles the category C of our study. The difference at first glance would be that the South African Bio-duck is composed of 4 pulses and in this study our category C is composed of two Bio-ducks with 6 and 7 pulses. This information highlights the complex structure of the vocal behaviour produced by AMWs. The new classification postulated in this study shows that based on different acoustic parameters extracted from the Bio-duck calls, these can be classified into different categories. Furthermore, these categories are composed of different calls which are called subtypes and are differentiated according to the number of pulses that make up each call. With the information that AMW Bio-duck calls can be classified into categories, studying the subtypes of sounds could help to better understand the acoustic behaviour of this species and possible populations identity.

Acoustic occurence and similarity with other regions

Comparing the present data with other regions, the acoustic occurrence seems to match. In Brazil (24 and 25° S), we recorded Bio-duck calls during November and December. Likewise, Bio-duck calls were recorded in the Perth Canyon during November (32° S) [43]. In Namibia (20° S), a double peak was recorded between June-August and November-December [50](K Thomisch et al. 2019). In South African waters (34°S) a peak of acoustic activity was described between September-October [35] and in the Juan Fernandez Archipelago, off Chile, (33°S) a year-round acoustic presence was recorded with a peak between May-August [51].

When comparing low and high latitude areas, there appear to be similarities in the acoustic seasonality of AMWs. In the Southern Ocean, specifically in the western Antarctic Peninsula, periods of acoustic activity have been described for AMWs between the months of May-November with peaks during July-October [32](Dominello and Širović 2016). A similar situation occurs in the Weddell Sea, where the acoustic presence has been described between May-December, with a peak during June-November [28, 32, 36](Van Opzeeland 2010; Shabangu, Findlay, and Stafford 2020; Filun et al. 2020). The similarity in the seasonality of the acoustic behaviour of AMWs between low and high latitudes indicates that not all the individuals migrate to the breeding ground. Part of the population possibly stays in Southern Ocean waters for a longer time than in lower latitudes. The fact that AMWs exhibit simultaneous acoustic behaviors in different regions also shows that there are probably distinct populations. Moreover, the fact that the acoustic behaviour occurs simultaneously in high and low latitudes infers that the sound emission is related to animal behaviour rather than to environmental conditions.

Antarctic minke whales in Brazil

Little is known about the distribution and ecological relations of baleen whales from the genus *Balaenoptera* in their breeding grounds (IWC, 2021). For the Antarctic feeding ground, it is known that despite an evident habitat segregation between minkes and humpbacks they can overlap in their distribution close to the ice-edge [52, 53]. Regarding the AMW distribution, our recordings in Santos Basin were made between 24 and 25° S, while the Perth Canyon lies at 32° S. This geographic area could represent a different temporal niche choice, comparing to other frequent whale species such as the humpback whale. Similarly, the presence of AMWs, through the Bio-duck calls, indicates that this species is occurring on the Brazilian continental slope and oceanic waters, as suggested by other recent observations [17, 24-26], possibly in a search for an emptier acoustic habitat, similar to the case in the Western Antarctic Peninsula where MWs and Humpback whales differ in foraging areas [14]. Our area of study represent the southern boundary described for breeding area of humpback whales on Brazilian coast, the Abrolhos Banks [15] . This area is distributed from Rio de Janeiro to Rio Grande do Norte (24° to 5°S) [16,17] were humpback whale songs dominate the soundscape of the continental shelf during breeding seasons.

We registered the presence of AMW in November and December in a low latitude area, the Brazilian coast. The species also occurs in their feeding areas in high latitudes of Antarctica in this period [36]. This information raises consideration that is possible that part of the AMW does no migrate, staying in the low latitude areas, where they could find enough resources to live year-round, as occur with other species/populations, such as the humpback whale from the Arabian sea population [54, 55].

Conclusions

In summary, our results show that Antarctic minke whales perform a diverse repertoire of Bio-duck calls in oceanic waters off Brazil. The distinctiveness of these call types in Santos Basin reinforces the occurrence of this species in the region, that is further south than the main areas of whaling, where their presence is well documented through historical accounts. Further studies using passive acoustics to detect Bio-duck calls may provide important information about this species seasonality, migratory timing and connections with other feeding and breeding regions of the southern hemisphere.

Once the Bio-duck calls were registered in deeper waters, it seems that minke whale distribution does not completely overlap with the distribution of humpback whales in the western South Atlantic breeding ground. This pattern could be related to a certain spatial acoustic niche, as the humpback whale sounds dominate in the soundscape during their breeding season [56].

This study also highlights the importance of further implementation of passive acoustic monitoring in Brazil, nowadays limited to a few initiatives as requirements for oil and gas seismic and exploitation activities. We suggest the use of passive acoustic monitoring should be a mandatory routine to study cetacean occurrence, behaviour, and potential noise impacts on them, in many other marine exploitation activities, such as port constructions and cargo ship traffic, considered to impact Brazilian coast without any previous assessment [57]. Further investigation with a broader acoustic dataset can elucidate important questions about the minke whale annual cycle, such as the migration timing, if they are breeding, foraging or doing both vital activities while in their tropical breeding grounds.

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Author Contributions

MRRS and DF have equal contributions as leading authors of this study. Conceptualization: MRRS DF. Data curation: WSF ADP MRRS LLW. Investigation: MRRS DF WSF ADP LLW. Methodology: WSF MRRS DF. Formal analysis: WSF ADP MRRS DF. Data Validation: WSF ADP MRRS DF. Contributed analysis tools/software: WSF DF. Project Management: LLW. Writing – original draft: MRRS DF. Writing – review & editing: MRRS DF WSF LLW.

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Chapter IV: Temporal patterns in the acoustic presence of baleen whale species in a presumed breeding area off Namibia.

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Temporal patterns in the acoustic presence of baleen whale species in a presumed breeding area off Namibia

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ABSTRACT: The eastern Atlantic Ocean is considered to provide important breeding and wintering habitats for several migratory cetacean species. The spatio-temporal distributions and migratory behaviors of cetaceans off southern Africa are nevertheless still poorly understood. This study investigated the temporal patterns of acoustic occurrence of baleen whales in a presumed baleen whale breeding area off Namibia using passive acoustic recordings collected between November 2011 and May 2013. Our results show seasonal acoustic presence of humpback whales *Megaptera novaeangliae*, fin whales *Balaenoptera physalus* and Antarctic minke whales *B. bonaerensis* from November to January and from June to August. Their acoustic absence from February to May possibly indicates that most animals migrated to other areas (presumably in higher latitudes) in austral summer to feed. By contrast, Antarctic blue whales *B. musculus intermedia* were acoustically present throughout the recording period, indicating that part of the population remains at lower latitudes year-round. Our findings support the presumed ecological importance of the oceanic area off Namibia, providing (part of) a suitable cetacean wintering and, possibly, breeding range or migratory corridor. Furthermore, the occurrence of Antarctic blue and minke whales off Namibia, concurrent with their reported acoustic presence in high-latitude feeding areas, adds to growing evidence that baleen whale migration is not obligate but much more dynamic than has long been assumed.

KEY WORDS: Antarctic blue whales · Antarctic minke whales · Baleen whale breeding grounds · Fin whales · Humpback whales · Migratory behavior · Passive acoustic monitoring · South Atlantic Ocean

1. INTRODUCTION

Technological advances in the study of animal behavior have led to an increased understanding of animal migration, revealing that migratory patterns are far from uniform for species, populations and even individuals across many animal taxa (see e.g. Chapman et al. 2011, Avgar et al. 2014, Geijer et al. 2016 for reviews). For marine mammals, passive acoustic monitoring provides an important tool to investigate large-scale spatio-temporal patterns in (acoustic) presence and distribution (e.g. Mellinger et al. 2007, Van Parijs et al. 2009, Au & Lammers 2016). Evidence is accumulating that the migratory behavior of marine mammals is more dynamic than previously thought (e.g. Brown et al. 1995, Geijer et al. 2016, Thomisch 2017). The paradigm of a complete baleen whale migration arose from earlier studies that were primarily based on whaling data (e.g. from Kellogg 1929, Mackintosh & Wheeler 1929). However, in many cases these data

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already implied a diverse migratory behavior in baleen whales, e.g. by reporting year-round presence of blue and fin whales on Southern Ocean whaling grounds but also in low-latitude waters (e.g. Hinton 1915, Risting 1928, Kellogg 1929, Mackintosh & Wheeler 1929, Harmer 1931, Hjort et al. 1932, Branch et al. 2007). In accordance with these early findings, recent passive acoustic data from the Southern Ocean show that fin whales *Balaenoptera physalus* (Meister 2017), Antarctic blue whales *B. musculus intermedia* (Širović et al. 2004, Thomisch et al. 2016) and humpback whales *Megaptera novaeangliae* (Van Opzeeland et al. 2013) are present in the feeding areas year-round. As the extent of the Antarctic ice sheet in mid-winter is likely to periodically exclude large-scale meridional migratory movements, these findings indicate that at least parts of the blue and humpback whale populations are likely to overwinter in high-latitude waters of the Southern Ocean (Van Opzeeland et al. 2013, Thomisch et al. 2016). Such partial migration, i.e. a population composed of migratory and (intermittently or permanently) non-migratory individuals, has been suggested to be advantageous in the context of increasing fecundity (Brown et al. 1995, Shaw & Levin 2011). In baleen whales, females, and to a lesser extent individual immature males, may benefit from skipping migration to remain at the feeding grounds to maximize growth and body mass (Brown et al. 1995). Body condition and size are thought to primarily determine the attainment of sexual maturity in baleen whales (Lockyer 1984). Information on baleen whale migratory behavior from breeding areas is sparse to date and mainly based on historic catch data and the Discovery tagging program (Mackintosh & Wheeler 1929, Best 2007, Cooke 2008). In fact, the locations of baleen whale breeding and wintering areas in the South Atlantic Ocean are still largely unknown (Best 2007). Within the eastern South Atlantic Ocean, different parts of the Angola Basin, and in particular the waters off Namibia, are thought to represent important winter habitats and potential breeding grounds for several species, particularly Antarctic blue whales, fin whales, Antarctic minke whales *B. bonaerensis* and sei whales *B. borealis* (Mackintosh & Wheeler 1929, Best 1998, 2007, Weir 2010).

Despite the presumed importance of the eastern South Atlantic Ocean as baleen whale habitat, few studies on baleen whales have been conducted in this area, and in the waters off Namibia in particular (Elwen et al. 2011). Much of our knowledge on baleen whale occurrence in the eastern South Atlantic Ocean is based on whaling records: substantial numbers of blue, fin and humpback whales were caught at shore whaling sites off Angola, Congo, Namibia (Walvis Bay) and South Africa (Saldanha Bay) (Risting 1928, Mackintosh & Wheeler 1929, Harmer 1931, Dawbin 1997, Best 1998, Findlay 2001, Branch et al. 2007). Soviet whaling was conducted relatively far offshore in the South Atlantic Ocean, but no blue whale catches were reported off Namibia (Branch et al. 2007). Antarctic minke whales have rarely been caught on the west coast of southern Africa; however, a single stranding is considered to confirm the occurrence of Antarctic minke whales off southern Angola (Best 1994, 2007, Weir 2010). Visual or acoustic data on baleen whale occurrence in Namibian waters are sparse (Elwen et al. 2011). No sightings of Antarctic blue, fin or Antarctic minke whales have been reported from off Namibia to our knowledge. Nevertheless, blue whales have been observed off Angola at distances of <200 km from shore (Figueiredo & Weir 2014). Humpback whales have been observed in coastal waters close to Walvis Bay, Namibia (Weir 2008, Elwen et al. 2014). Furthermore, sounds of humpback whales and (presumably pygmy) blue whales have been recorded off northern Angola (Cerchio et al. 2010). Antarctic blue and fin whales have been acoustically present south-west of South Africa (Shabangu et al. 2019). No multi-year passive acoustic monitoring has been conducted to date in the eastern South Atlantic Ocean off Namibia, despite its suggested potential importance as a breeding area for many species (Best 2007).

In this study, we investigated temporal patterns in cetacean acoustic presence using passive acoustic data collected in the waters off northern Namibia to better understand the ecological importance of the Angola Basin as a potential wintering and breeding habitat for baleen whales.

2. MATERIALS AND METHODS

2.1. Passive acoustic data

Between November 2011 and May 2013, passive acoustic data were collected using 2 SonoVault recorders (hereinafter referred to as 'SV'; manufactured by Develogic). The recorders were deployed at a depth of about 740 m in the Atlantic Ocean off Namibia, north-west of Walvis ridge (20° 58' S, 5° 59' E), at a distance of about 730 km to shore (Table 1, Fig. 1).

The recorders were deployed between November 2011 and November 2014. Devices were configured to record continuously at a sample rate of 5333 Hz, with an effective bandwidth of 0.3 to 2666 Hz. Both recorders stopped operating prior to their recovery due to battery exhaustion. The duration of the utilizable recordings was 274 and 189 d for SV1008 and SV1019, respectively (Table 1). Overall, passive acoustic data were collected between November 2011 and May 2013 (i.e. from 17 months), with no data available between 25 August and 22 November 2012.

2.2. Manual data analysis

All passive acoustic recordings were visually and aurally analyzed using XBAT (Extensible Bioacoustic Tool; Figueroa & Robbins 2008) (spectrogram settings: fast Fourier transform [FFT] between 512 and 2048 points, Hanning window, resulting in a frequency resolution of ca. 3 to 9 Hz and time resolution of ca. 0.1 to 0.4 s). Detected vocalizations were classified to species level wherever possible based on spectrograms and signature descriptions from literature (e.g. Ljungblad et al. 1998, Dunlop et al. 2007, Širović et al. 2009, Risch et al. 2014b, Dominello & Širović 2016). Data analysis was performed qualitatively on a daily scale, i.e. a species was considered acoustically present on a particular day if at least one sound attributed to this species was detected during that day. Apart from baleen whale vocalizations, the presence of anthropogenic noise originating from seismic sounds ('airguns') was assessed the same way. To inspect low frequency (i.e. <125 Hz) acoustic

Table 1. Locations and recording parameters of passive acoustic SonoVault recorders deployed off Namibia. Dates are given as mo/yr

Latitude	Longitude	Recorder ID	Deployment period	Recording period	Deployment depth (m)	Sampling freq. (Hz)	Sampling scheme	Operational period (d)
20° 57.90' S	5° 58.82' E	SV1008	11/2011–11/2012	11/2011–08/2012	741	5333	Continuous	274
20° 58.54' S	5° 59.07' E	SV1019	11/2012–11/2014	11/2012–05/2013	736	5333	Continuous	189

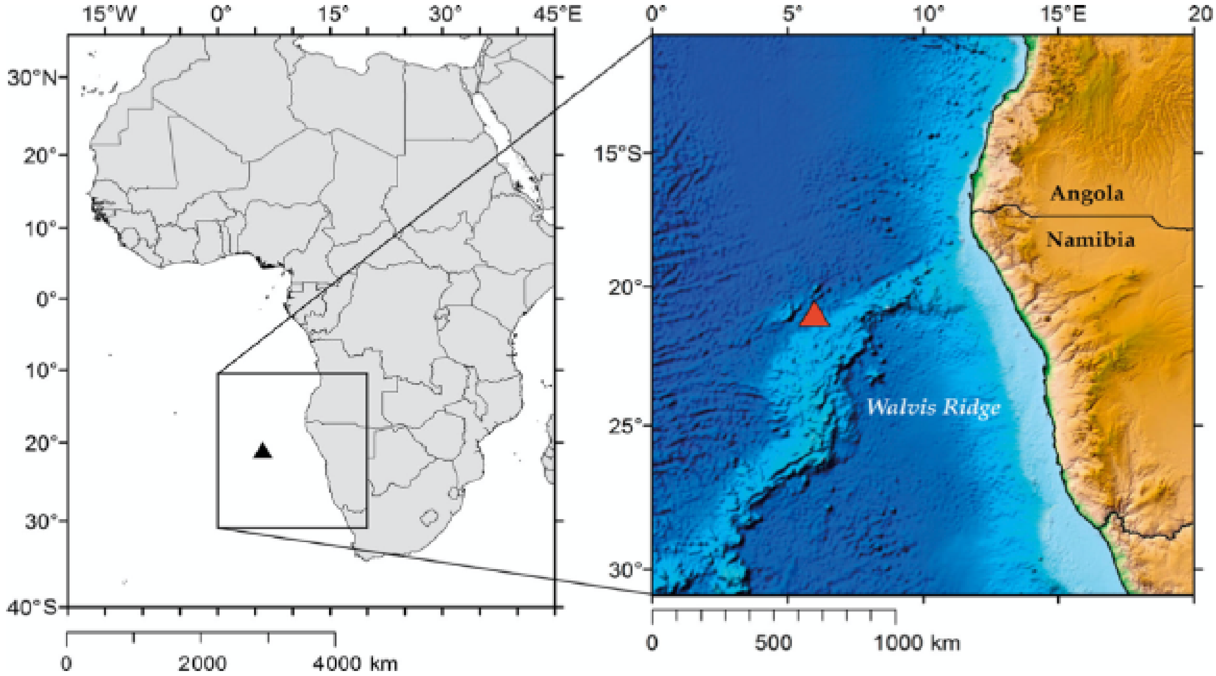

Fig. 1. Recorder position (▲) in the Atlantic Ocean (left panel) and bathymetry map showing recorder position (▲) off Namibia, north-west of Walvis Ridge (right panel). Maps were created using the ETOPO1 global relief model map provided by the NOAA National Centers for Environmental Information, NCEI (based on dataset of Amante & Eakins 2009), and the World Countries Basemap by Esri, Garmin International (formerly DeLorme Publishing Company), US Central Intelligence Agency (The World Factbook)

signatures, data were additionally downsampled to a sample rate of 250 Hz and inspected visually (spectrogram settings of FFT 256 points, Hanning window, frequency resolution of ca. 1 Hz). For each identified species, the percentage of days per month featuring acoustic presence was calculated to allow comparison of results from different months and recorders.

2.3. Automated analysis of Antarctic blue whale Z-calls

Antarctic blue whale Z-calls are highly stereotypic, low-frequency vocalizations, typically consisting of 3 units within the frequency range of 18 to 28 Hz (Ljungblad et al. 1998, Rankin et al. 2005), and are produced by Antarctic blue whales year-round (e.g. Širović et al. 2004, Stafford et al. 2004, Samaran et al. 2013, Thomisch et al. 2016). Vocalizations produced by distant Antarctic blue whale individuals are only partly received by a recording device as the 2nd and 3rd unit of the call increasingly vanish with distance. This results in the formation of a tonal 'chorus' within the 26 to 28 Hz frequency band (Gedamke et al. 2007), which complicates the detection of single Z-calls.

The outcome of manual analyses of passive acoustic data for Antarctic blue whale Z-calls can be subject to high variability that depends on both inter- and intra-analyst effects and has been found to be strongly affected by the presence of Antarctic blue whale chorus in the data (Leroy et al. 2017b). Hence, to reproducibly analyze the acoustic presence and activity of Antarctic blue whales, Z-calls were automatically detected using spectrogram-correlation (e.g. Mellinger & Clark 2000). The passive acoustic recordings were downsampled to 250 Hz prior to automated processing. The spectrogram-correlation had an estimated average false detection rate of 1% (see Thomisch et al. 2016 for more detailed method description). Both the percentage of days per month with acoustic presence of Antarctic blue whales and weekly sums of Z-call detections were calculated.

Previously, a blue whale index (BWI) was developed as a further measure to capture Antarctic blue whale acoustic presence relating to the occurrence of the tonal chorus (see Thomisch et al. 2016 for details). The BWI quantifies the time during which the acoustic energy in the Antarctic blue whale chorus (26–28 Hz band) dominated over the ambient noise (23–24 Hz and 29–30 Hz bands). BWI values were averaged for each day and smoothed using Savitzky-Golay filtering to reduce variability in BWI between days to extract the long-term patterns in acoustic activity (window length = 31 d, step size = 1 d, regression based on polynomial order 2).

Both measures applied in the present study differ in the spatial range over which they represent Antarctic blue whale presence. While individual Antarctic blue whale Z-calls are likely to originate from individuals within a (comparatively) small distance of a recording site (Samaran et al. 2010, Thomisch et al. 2016), the propagation range of Antarctic blue whale chorus (represented by the BWI in the present study) is not clear to date, but might cover large distances, e.g. across ocean basins.

Sound propagation modeling using the BELLHOP ray tracing model (Porter 2011) was applied to understand the range over which calls were detected by our receivers. Based on information on the Antarctic blue whale Z-call detection range (Širović et al. 2007, Thomisch et al. 2016), this call was assumed to exhibit the maximum propagation range for baleen whale vocalizations and therefore used for sound propagation modeling (see the Supplement at www.int-res.com/articles/suppl/m620p201_supp.pdf for a detailed explanation of the sound propagation modeling approach applied here). Sound propagation was modeled for 3 north–south directed transects between the actual receiver position (20° 58′ S, 5° 59′ E, receiver moored at 740 m depth) and fictive sender positions at a distance of 200, 500 and 3229 km south of the receiver. The sender was assumed to produce sounds at a frequency of 27 Hz at 20 m depth. The BELLHOP beam tracing model exhibits a useful frequency range lower than standard ray trace programs; however, ray tracing models in general should be applied only for scenarios with water depths substantially lower than the wave length of the sound of interest (Jensen et al. 2000). Although a frequency of 27 Hz is comparatively low for ray-tracing models such as BELLHOP (assuming an average sound speed of 1500 m s^{-1}, the resulting wavelength is 56 m), water depths exceeded 700 m for all 3 transects modeled. Therefore, in the present study, the BELLHOP ray-tracing model was considered a suitable method to assess the maximum propagation range of baleen whale calls off Namibia.

3. RESULTS

3.1. Acoustic biodiversity

Four baleen whale species were identified based on their species-specific acoustic signatures: Antarctic blue whales, fin whales, Antarctic minke

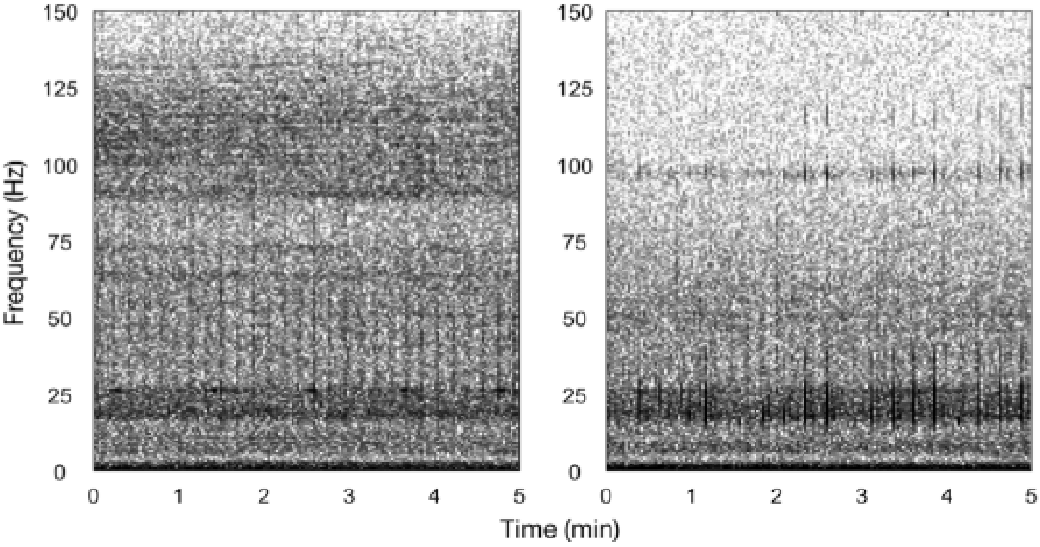

Fig. 2. Sequence of unit A of Antarctic blue whale Z-calls (left panel, 8 June 2012) and sequence of fin whale 20 Hz pulses (right panel, 9 July 2012) recorded by SV1008 (spectrogram settings: FFT size of 20 000 points, Hanning window, 90 % overlap)

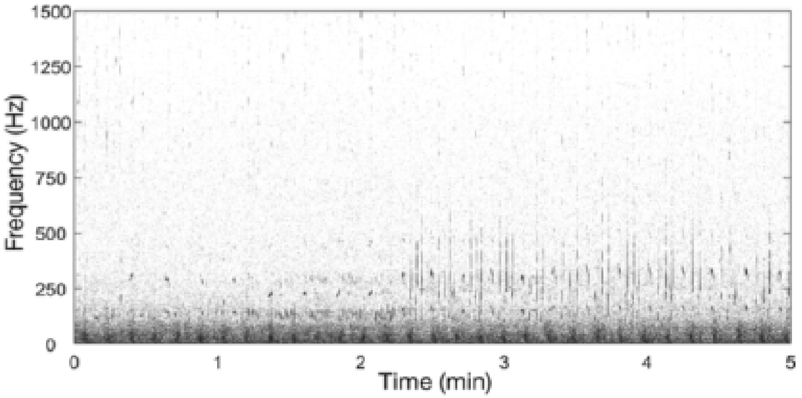

Fig. 3. Humpback whale song recorded by SV1008 on 7 August 2012 (spectrogram settings: FFT size of 5000 points, Hanning window, 90 % overlap)

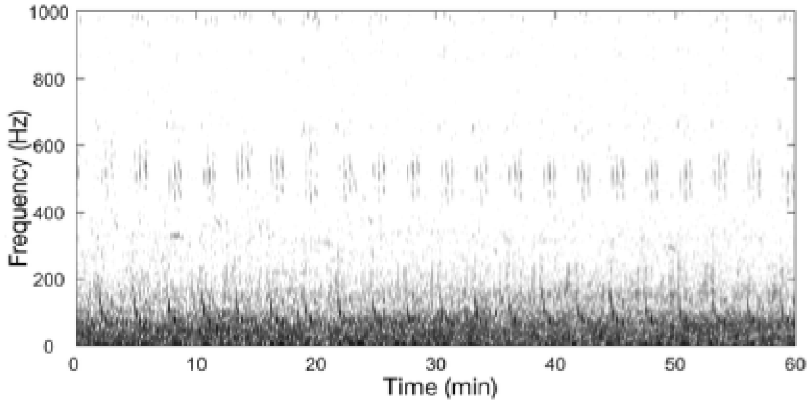

Fig. 4. Antarctic minke whale 'bio-duck' calls recorded by SV1008 on 22 August 2012 (spectrogram settings: FFT size of 5000 points, Hanning window, 90 % overlap)

whales and humpback whales (Figs. 2, 3 & 4). The Antarctic minke whale signatures recorded off Namibia are consistent with those frequently recorded in the Southern Ocean, previously referred to as 'bio-duck' (Risch et al. 2014b). Click trains, often exhibiting regular inter-click intervals of about 1 s, were present throughout our recording period, possibly representing sperm whale *Physeter macrocephalus* clicks. Whistles were detected on several days, presumably originating from small odontocetes. However, it was not possible to assign these clicks and whistles to specific species with certainty, as the sampling rate of the recordings was too low to allow reliable analysis of these high-frequency sounds.

During the 17 months from which passive acoustic data were available, Antarctic blue whales (in terms of both single Z-calls and the BWI metric) were acoustically present throughout the recording period (Figs. 5 & 6). Humpback whale sounds were recorded during 9 months, while both fin and Antarctic minke whales were acoustically present during 5 months (Fig. 5).

Furthermore, sounds of unknown, but presumably biological, origin were recorded. One sound frequently recorded throughout the recording periods, and

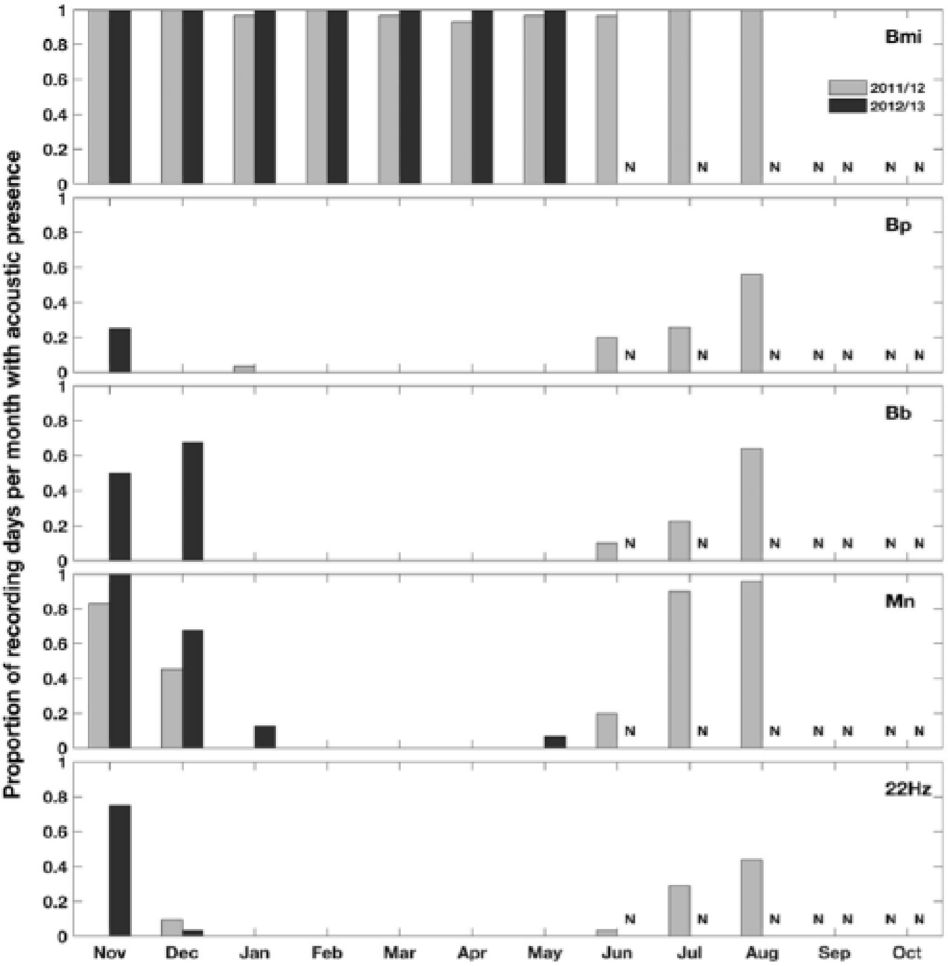

Fig. 5. Acoustic presence of baleen whale species off Namibia from November 2011 to August 2012 (recorded by SV008) and from November 2012 to May 2013 (recorded by SV1019). N: months when no passive acoustic data were available; Bmi: *Balaenoptera musculus intermedia*, Antarctic blue whale; Bp: *B. physalus*, fin whale; Bb: *B. bonaerensis*, Antarctic minke whale; Mn: *Megaptera novaeangliae*, humpback whale; 22Hz: the 22 Hz sound of unknown origin. Note that Antarctic blue whale acoustic presence was evaluated based on automated analysis (via spectrogram-correlation), while acoustic presence of all other species was assessed via manual analysis (see Section 2)

hereinafter referred to as '22 Hz sound', featured a frequency of about 22.5 Hz, lasted about 8 to 10 s and occurred in long sequences, repeated at intervals of approximately 2.5 min (Fig. 7). In 2012, frequency-modulated sounds of about 1 s duration were occasionally recorded, sweeping downwards from 130 to 40 Hz (with harmonics between 260 and 120 Hz) and occurring in pairs or triplets (Fig. 8). These sounds were present in June (1 day), July (3 days) and August (1 day).

Apart from cetacean vocalizations, low-frequency sounds (< 200 Hz), originating from seismic airguns, significantly shaped the acoustic environment throughout the recording period, with seismic noise being present on more than 90 % of recording days during all months (Fig. 9, Table 2).

3.2. Temporal patterns in acoustic presence

The acoustic presence of most baleen whale species identified in the recordings exhibited clear temporal patterns. Antarctic blue whales were acoustically present during the entire recording periods (Figs. 5 & 6). During the recording period in 2011/2012, the BWI and the number of detected Antarctic blue whale calls were low from November until April and peaked in mid-June (Fig. 6). In 2012/2013, the acoustic activity

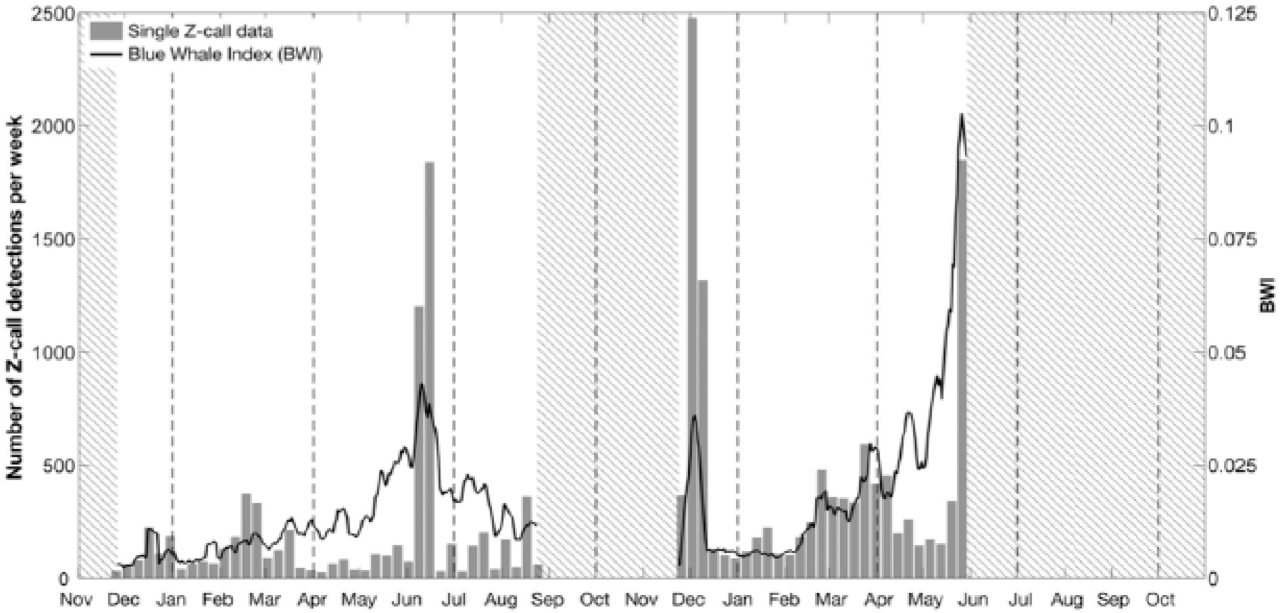

Fig. 6. Acoustic presence of Antarctic blue whales off Namibia from November 2011 until October 2013, showing the numbers of Z-call detections per week (in 7 d bins) and the daily mean BWI (smoothed using Savitzky-Golay filter; window length = 31 d, polynomial order = 2). Hatched areas: periods without recordings; dashed lines: beginnings of quarters of the years

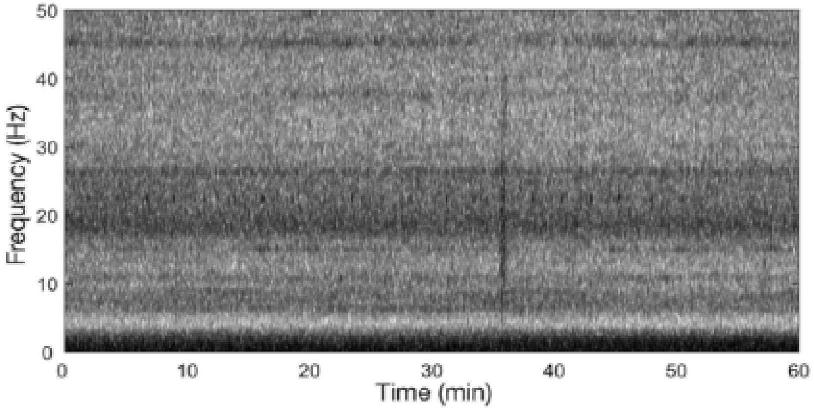

Fig. 7. Sequence of the unknown '22 Hz sound' (frequency of ca. 22.5 Hz, duration of 8–10 s, intervals of ca. 2.5 min between single sounds), recorded by SV1008 on 1 July 2012 (spectrogram settings: FFT size of 5000 points, Hanning window, 90% overlap)

peaked first in early December, and thereafter decreased from mid-December to early February when it started to increase again. The acoustic activity then increased considerably towards late May 2013. Fin whales were recorded in January and from June to August in 2012 and acoustically absent from November to December and from February to March during recording period 2011/2012. In 2012/2013, they were acoustically present only in November and absent from December to May. Antarctic minke whales were acoustically absent from November 2011 to May 2012 and present from June to August 2012 as well as in November and December 2012, after which they were acoustically absent until the end of the recording period in May 2013 (Fig. 5). Humpback whales were acoustically present from November to December 2011 and from June to August 2012 as well as from November 2012 to February 2013 and in May 2013. In both recording periods, humpback whales were acoustically absent from February to April.

The 22 Hz sound was recorded in December 2011, from June to August 2012 and in November and December 2012. In both recording periods, the 22 Hz sound was absent from January through May (Fig. 5).

For humpback and Antarctic blue whales, the intra-annual patterns in acoustic presence were similar for both recording periods, likely reflecting the local seasonality of the species' (acoustic) presence (Figs. 5 & 6). Inter-annual variation in the acoustic presence was evident for fin and Antarctic minke whales (as well as for the 22 Hz sound). While little to no acoustic presence of either species was recorded in austral spring and summer during 2011/2012, there was (at least some) acoustic presence of these species during spring and summer in 2012/2013 (Fig. 5).

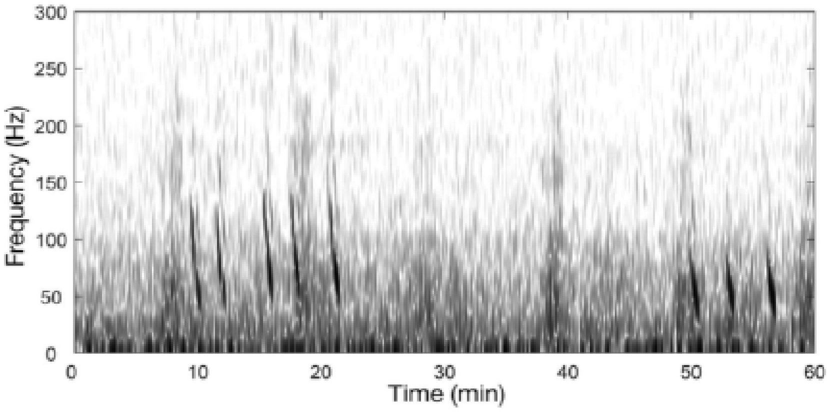

Fig. 8. Sequence of an unknown sound (frequency range ca. 40–130 Hz, duration about 1 s), recorded by SV1008 on 7 June 2012 (spectrogram settings: FFT size of 5000 points, Hanning window, 90% overlap)

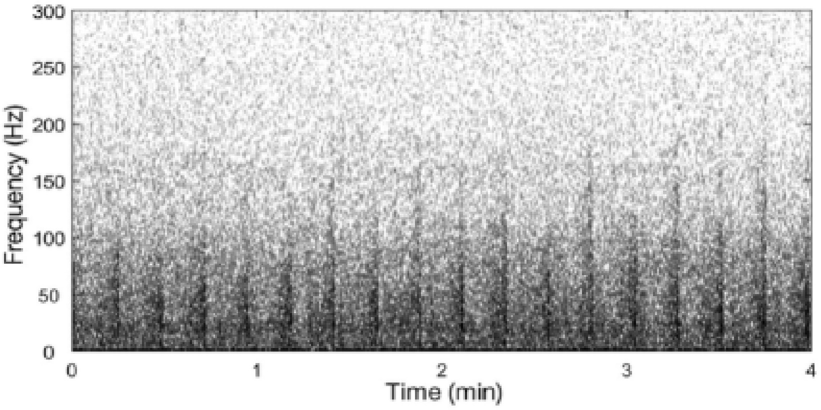

Fig. 9. Low-frequency sounds (<200 Hz) produced by seismic airguns recorded by SV1008 on 7 August 2012 (spectrogram settings: FFT size of 10000 points, Hanning window, 90% overlap)

Table 2. Acoustic presence (in percentage of recording days per month) of seismic sounds in passive acoustic recordings collected off Namibia between November 2011 and May 2013

Month	Acoustic presence of seismic sounds	
	2011/12	2012/13
November	100%	100%
December	100%	100%
January	100%	100%
February	100%	100%
March	100%	100%
April	97%	100%
May	100%	100%
June	100%	No data
July	100%	No data
August	97%	No data

4. DISCUSSION

Conclusions on the importance of the study area as a baleen whale habitat are strongly dependent on the actual location of calling whales in this study. Here, we used Antarctic blue whale Z-calls to estimate the maximum propagation range of baleen whale vocalizations in the study area. The results of the propagation range estimation imply that the majority of Antarctic blue whale Z-calls were produced by whales that were within a 200 km radius of the recording site (Tables S1, S2 & S3 in the Supplement). Only during austral spring (November and December) 2011, part of the recorded Antarctic blue whale Z-calls originated from a larger radius of (at maximum) 500 km of the recording site. This however applies to a relatively small proportion of Antarctic blue whale calls recorded, as the number of Z-call detections was comparatively low with a total of <700 during these months.

4.1. Acoustic presence of baleen whales

Based on the absence of a bimodal pattern in historic catch data, the waters off Namibia have been hypothesized to represent the northern limit of migration in the South Atlantic Ocean for some baleen whale species, e.g. for Antarctic blue whales (Best 1998, 2007). However, the absence of a bimodal pattern for a given area does not necessarily reflect a distribution range limit for a given species. For humpback whales, sighting data clearly exhibited a bimodal pattern off Namibia, with a secondary peak in September presumably representing individuals migrating southwards (Elwen et al. 2014). Off Durban, aerial sighting data from the 1970s showed a bimodal pattern in the presence of blue, sei and humpback whales, while a unimodal seasonality was observed for fin whales and minke whales (*Balaenoptera bonaerensis* or *B. acutorostrata*) (Findlay & Best 2016). Best (1982) reported that there was no clear temporal pattern in the movement direction of minke whales off Durban from March to September, as both northward- and southward-moving animals were sighted during each month, except for March, where no individuals moving southward were recorded. Similarly, a bimodal pattern in the seasonal acoustic presence of Antarctic blue whales off the west coast of South Africa between May and August implies this coastal area serves as an overwintering ground and migratory corridor for Antarctic blue whales (Shabangu et al. 2019). However, in the present study, no passive acoustic data from September and October were available, which prohibits conclusions on a potential presence or absence of a bimodal pattern in the acoustic winter presence of the 4 baleen whale species recorded. Nevertheless, blue whale catches reported from off Angola indicate that the distribution range of Antarctic blue whales extents further north to (at least) the waters off Angola (Branch et al. 2007). Accordingly, Figueiredo & Weir (2014) reported visual sightings of blue whales off Angola, although information on the subspecies is lacking.

The mismatch between our acoustic observations and the available information from sighting data on baleen whale distribution may further be explained by the fact that baleen whale migratory routes and timing are known to differ both within and between age- and sex-classes of a population (e.g. Kellogg 1929, Mackintosh & Wheeler 1929, Bannister & Gambell 1965, Williamson 1975, Brown et al. 1995, Kasamatsu et al. 1995, Dawbin 1997, Best & Lockyer 2002, Craig et al. 2003, Rosenbaum et al. 2014). It therefore has to be kept in mind that local, single sensor acoustic data only represent the (acoustically active) part of the population that occurs or passes in relative proximity of the recorder. Lastly, inferences on whether our data represent significant parts of baleen whale (breeding) populations or rather cohorts of the populations are not possible. Estimating the number of acoustically active individuals in recordings from single, fixed sensors requires knowledge of the detection function, i.e. the probability of detecting calls as a function of distance (e.g. Küsel et al. 2011, Marques et al. 2013), which was beyond the scope of this study. However, the fact that the seasonal pattern is consistent between years for many species, suggests these observations do not reflect incidental presences, but that the area is a structurally significant habitat for these species for overwintering and, possibly, breeding.

4.2. Unknown signatures

The resemblance between the temporal pattern in the acoustic presence of the 22 Hz sound and that of most other baleen whales recorded indicates that this sound is potentially produced by a mysticete species. The 22 Hz sound recorded off Namibia closely resembles the 'M-call', recently described in the southern Indian Ocean (Leroy et al. 2017a). The M-call has been hypothesized to be produced by a blue whale subspecies, possibly by pygmy blue whales (Leroy et al. 2017a). Similar blue whales calls have also been recorded in the central North Pacific Ocean (Stafford et al. 2001), supporting the hypothesis that 22 Hz sounds could be produced by a blue whale subspecies. Calls attributed to the northern Indian Ocean pygmy blue whale population ('Sri Lanka' type) have been recorded off northern Angola (Cerchio et al. 2010). Since this was a single observation, it could not be concluded whether this observation represented an accidental migrant or an unknown migratory strategy of pygmy blue whales (Cerchio et al. 2010). In this context, the seasonal occurrence of 22 Hz sounds off Namibia could indicate that at least part of a pygmy blue whale population occurring in the Indian Ocean migrates to the South Eastern Atlantic Ocean on a regular basis.

Alternatively, a similar signature, recorded off New Zealand, was previously attributed to Bryde's whales *B. brydei* (McDonald 2006, his Fig. 4e). However, given the similarity of these calls to the M-calls described by Leroy et al. (2017a), it is not unlikely that M-calls, the calls recorded by McDonald (2006) and the 22 Hz sounds reported in this study are produced by the same species. Nevertheless, a pelagic Bryde's whale population occurs in the Southeast Atlantic Ocean and seems to exhibit north–south directed migrations within their distribution range between the equatorial region in the north and the area of 34° S (Best 2001). Hence, the observed temporal pattern in the presence of the 22 Hz sound could potentially also be caused by migrating Bryde's whales.

The frequency-modulated downsweeps recorded in the present study are similar to vocalizations of sei whales recorded off Hawaii (Rankin & Barlow 2007), but also to a presumed variant of the Antarctic minke whale 'bio-duck' call, recently reported from off the western Antarctic Peninsula ('bio-duck call D', Dominello & Širović 2016) and to frequency-modulated calls of Antarctic blue whales and pygmy blue whales recorded in the Southern Ocean (Rankin et al. 2005) and the eastern Indian Ocean (Gavrilov et al. 2011), respectively. All these species, i.e. Antarctic blue, minke and sei whales, may winter in the waters off Namibia (Best 2007). However, without concurrent visual information, it is not possible to attribute this sound to any specific source with certainty.

4.3. Temporal patterns in acoustic presence off Namibia: Evidence for (partial) migration?

Off Namibia, intra-annual variability in the acoustic presence most likely reflects decreased spring and summer presence of the 4 baleen whale species, as (at least parts of) the populations leave the area to feed in higher latitude waters. During winter, acoustic presence increased as whales return to the South Atlantic Ocean for overwintering and, potentially, to breed. However, we also found that Antarctic blue and minke whales were (intermittently) acoustically present throughout the year. This adds to existing evidence for partial migration occurring more widely than previously assumed. For Antarctic blue and minke whales, our data indicate that the populations are composed of migratory and non-migratory individuals. Along with findings from the Indian Ocean (see Samaran et al. 2013), the continuous acoustic presence of Antarctic blue whales off Namibia during the recording period possibly indicates that some individuals skip migration to high latitudes to remain in the warmer waters of the study area during summer. Such skipped migrations may to some extent be fueled by the year-round availability of prey in high-productivity waters of the Benguela region and the associated high-turbulence eddy regime. In accordance, presumed feeding-associated calls of Antarctic blue whales have been recorded off the west coast of South Africa during austral winter, possibly indicating (opportunistic) feeding of Antarctic blue whales in the Benguela ecosystem (Shabangu et al. 2019). Based on catch data, non-migratory or 'resident' whales have been suggested to be juvenile individuals (Mackintosh & Wheeler 1929). Juvenile whales with a poor body condition predominated in winter catches off Namibia, implying that these whales may not have migrated to high-latitude feeding grounds during the previous summer but remained at low latitudes (Mackintosh & Wheeler 1929). Another part of the population, presumably adult whales, is thought to remain at the feeding grounds during austral winter, as indicated by year-round catches and acoustic presence of Antarctic blue whales in the Southern Ocean (Risting 1928, Harmer 1931, Hjort et al. 1932, Širović et al. 2004, Branch et al. 2007, Širović et al. 2009, Thomisch et al. 2016). However, behavioral features other than partial migration may have caused a continuous acoustic presence of baleen whales off Namibia. Baleen whales exhibit a wide spectrum of migratory strategies, including differential migratory behavior with intra-specific differences in migratory timing (e.g. Mackintosh & Wheeler 1929, Brown et al. 1995, Geijer et al. 2016). This migratory pattern may result in a continuous, procession-like movement of individuals to and from their feeding and breeding areas, and hence continuous (acoustic) presence in these areas, although no individual is pervasively present (see e.g. Mackintosh & Wheeler 1929, Brown et al. 1995, Kasamatsu et al. 1996, Craig et al. 2003, Geijer et al. 2016, Thomisch 2017).

Similar to Antarctic blue whales, Antarctic minke whales have been reported to be simultaneously present in both polar waters of the Southern Ocean (e.g. Thiele et al. 2004, Van Dam & Kooyman 2004) and temperate waters of the Indian Ocean (e.g. Best 1982, McCauley et al. 2004), particularly during austral winter. Off Namibia, Antarctic minke whales were acoustically present from June to August (this study), when they have also been reported to exhibit highest acoustic presence in the Southern Ocean (Van Opzeeland 2010, Dominello & Širović 2016). Catch data from low-latitude waters off Brazil indicate that the first minke whale individuals arrive off Brazil in late June and July, with the number of whales present in the area increasing from September to November (Williamson 1975). Data from off Durban, South Africa, match the trend described by Williamson (1975), although minke whales have been reported to arrive already earlier (i.e. in April and May) in South African waters than off Brazilian coasts (Best 1982). Furthermore, Williamson (1975) observed that a few juvenile individuals were present off Brazil at the beginning of the season and that mature minke whales started to arrive in July. These results were derived from whaling data, sightings and passive acoustic recording and jointly provide evidence for a partial or a differential (temporally segregated) migration in Antarctic minke whales.

Partial migration of Antarctic blue and minke whales may represent a variant of a 'low-frequency breeding migration' (Shaw & Levin 2011), where non-migratory individuals forego reproduction. Skipping migration and hence foregoing a mating opportunity may increase an individual's life time fecundity (Shaw & Levin 2011). Mainly female individuals are thought to benefit from skipping migration (Lockyer 1984, Brown et al. 1995), by improving their energy budget, which is strongly influenced by the high energetic costs of reproduction (Lockyer 1978, Lockyer 1984), and hence, their long-term reproductive success. However, our recordings partially contained song sequences of Antarctic blue whales, fin whales and humpback whales, with song generally considered a male reproductive display (e.g. Winn & Winn 1978, Croll et al. 2002, Oleson et al. 2007). The functionality of Antarctic minke whale ('bio-duck') vocalizations is not yet understood, but potentially also involves reproduction (Van Opzeeland 2010, Dominello & Širović 2016). Hence, simultaneous acoustic presence of Antarctic minke whale ('bio-duck') calls and Antarctic blue whale songs at both high and mid-latitudes potentially indicates that (opportunistic) baleen whale mating may also take place outside the presumed breeding areas and seasons (e.g. Norris et al. 1999, Clark & Ellison 2004, Širović et al. 2013, Risch et al. 2014a, Thomisch et al. 2016). Catch data strengthen this hypothesis as 90% of the minke whale adult females caught in Antarctic waters during southern summer were pregnant (Bando & Hakamada 2014). Differences in the size of the embryos may indicate an extended mating season from August until probably November (Williamson 1975, Best 1982). Future in-depth analyses of baleen whale vocal behaviors, e.g. unraveling acoustic characteristics and patterns in sound production, are essential to provide further insights into the (acoustic) ecology of the species in temperate waters off Namibia.

4.4. Ecological importance of the eastern South Atlantic Ocean

The waters off south-west Africa are greatly influenced by the Benguela ecosystem, which exhibits a coastal upwelling system at its eastern side and transports cold, nutrient-rich water along the Namibian and Angolan coast (Shannon 1985). Furthermore, these waters are characterized by an oceanic high-turbulence regime comprising cyclonic eddies that cause local upwelling of nutrient-rich waters and likely feature local high productivity in our study area (Boebel et al. 2003, Matano & Beier 2003). In turn, this area may not only represent an overwintering and breeding ground, but also offer potential for summer and winter foraging for many cetacean species (Best 2007, Shabangu et al. 2019). In particular, the Angola Basin in the South Atlantic Ocean has been hypothesized to represent part of the winter range of Antarctic blue whales, fin whales and Antarctic minke whales based on historic whaling data (Harmer 1931, Best 2007). Furthermore, the area also provides foraging opportunities for cetaceans during summer, driven by the highly productive Benguela upwelling system (Best 2007, Barendse et al. 2011, Findlay et al. 2017).

Our results highlight the importance of the eastern South Atlantic Ocean off Namibia, i.e. the area within a 200 km radius of the recording site north-west of Walvis Ridge, as a seasonal or year-round habitat for Antarctic blue whales and other baleen whale species. In particular, the results of the present study provide further evidence for a potential breeding area for Antarctic minke whales, Antarctic blue whales and humpback whales in the Atlantic Ocean off southern Africa. The timing of the acoustic presence of these species in this study coincides with the period during which most of their conceptions are thought to occur in the southern African subregion, i.e. from August through November for Antarctic minke whales, May through June for Antarctic blue whales and July through August for humpback whales (Lockyer & Brown 1981, Best 2007).

Despite the ecological importance of the eastern Atlantic Ocean for several cetacean species, local threats to marine life from anthropogenic activities are manifold and include fisheries, habitat loss, marine tourism, shipping, and gas and oil exploration (Weir & Pierce 2013). A more precise localization of crucial wintering and breeding habitats of cetacean species in the eastern South Atlantic Ocean is essential to inform present and future conservation and management strategies, and can promote the identification and designation of potential marine protected areas. In this context, the omnipresence of low-frequency sounds produced by seismic airguns in this potentially crucial baleen whale habitat urgently calls for further investigation of temporal patterns in anthropogenic noise levels to assess potential (short- and long-term) effects of the quasi-continuous presence of anthropogenic noise on animals off Namibia (see also Gordon et al. 2003, Di Iorio & Clark 2010, Cerchio et al. 2014).

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Synthesis

In this PhD thesis, I studied the distribution and acoustic occurrence of Antarctic minke whales on a spatial and temporal scale using data from recording sites at high and low latitudes of the Atlantic Ocean. This allowed me to cover a large spatial scale investigating the ecology of AMWs in their feeding and breeding areas. This thesis presents new findings and hypotheses about their acoustic behavior, seasonal occurrence, distribution and migration patterns.

The results of this thesis have been discussed in detail across the presented chapters (Chapter I-IV). In the following synthesis I will therefore discuss general aspects and open questions of the most important findings of this PhD thesis i.e., why do AMWs vocalize, can we biogeographically characterize different AMW populations based on PAM data, how are AMWs distributed over space and time, what are the effects of climate change on the species' ecology and finally, a discussion of the species' conservation status and management approaches.

Lastly, I discuss potential future directions and perspectives of AMW research.

Acoustic behavior of AMWs

In this PhD thesis, I provide evidence that similar to other large whale species e.g. Humpback whales, North Pacific (NPRW), North Atlantic (NARW) and Southern right whales (SRW) (*Eubalaena japonica, Eubalaena glacialis* and *Eubalaena australis,* respectively*)* (Crance et al., 2019; Mussoline et al., 2012; Webster et al., 2016; Clark, 1982), fin whales (*Balaenoptera physalus*) (Croll et al., 2002) and blue whales *(Balaenoptera musculus*) (McDonald et al., 2006), AMW bio-duck calls suit the definition of song since the bio-duck call can be broken down into "units" and "phrases" that are repeated in a regular pattern (in anology to humpback whale songs, see Cholewiak et al., 2013) (*Chapter II*).

Singing is the behavior during which a limited number of stereotypic sound types are produced in regular succession and form a recognizable pattern in time. Calling, on the other hand, is the behavior in which individual, transient sounds are produced at irregular intervals or as call and counter-call between two or more individuals. Songs can be divided into units, which are continuous segments of sound, and phrases, which are repeated combinations of units (e.g., Payne and McVay, 1971; Mellinger and Clark, 2003). Song in marine mammals is most complex and best-studied in humpback whales (see Cholewiak et al., 2013 for a review). It is typically unique for each population, evolving from year to year, but can also be transmitted between populations (Garland et al., 2011). Humpback whale song is documented to be produced only by males, occurring primarily on breeding grounds (Payne, 1978; Frankel et al., 1995) and less frequently on feeding grounds (Clark and Clapham, 2004). Less complex songs are more common among mysticetes; blue and fin whales produce relatively simple songs that also can be used to distinguish among different populations (McDonald et al.,2006). For example, blue whale songs are composed of a series of phrases, with each phrase containing one to five call units (Cummings and Thompson, 1971; McDonald et al., 2006). In contrast to humpback whales, blue whale songs remain constant over many years, even decades (Thomisch et al., 2016)[2]. Singing behavior in mysticete whales may continue for many hours or even days (Cummings and Thompson, 1971; McDonald et al., 2001; Clark and Ellison, 2004).

For mysticetes, the available evidence to date indicates that only males sing (Watkins, 1981; Darling and Berube, 2001; Croll et al., 2002). Much of the prevailing speculation on the function of song in these species has revolved around if, and how, singing functions as a mating display (Payne and McVay, 1971; Tyack, 2000; Darling and Berube, 2001; Croll et al., 2002;

2Although the overall structure of songs remains stable, the frequency of fin and blue whales has been reported to decrease over time. The origin and reason of this decrease are to date unknown. (McDonald et al. 2009; Gavrilov et al. 2012; Leroy et al. 2018)

Darling, 2002) but recent data indicate that males also sing during migration and on feeding grounds (Norris et al., 1999; Thomisch et al., 2016; Schall et al., 2021), potentially serving opportunistic mating behavior (e.g., Clark and Clapham, 2004).

Our study postulates that AMWs produce songs with less signal complexity than described for humpback whales (Payne and McVay, 1971) but potentially comparable flexibility in their temporal changes. The relatively simple structure of AMW songs seems to be comparable to blue and fin whale song with several repetitive sequences together forming the song (Watkins et al., 1987; Croll et al., 2002; Delarue et al., 2009b). In AMWs, the same call type (bio-duck unit) is produced at a high rate in bouts (Chapter II) similar to songs in NPRW and NARW (Parks et al. 2012; Crance et al. 2019). Those bouts can be described as phrases and those phrases can be repeated over hours, then forming a song (*Chapter II*; Figure 6 & Appendix Figure 1).

Future research needs to focus on the larger scale pattern of occurrence of bio-duck call types to unravel if phrases occur in repeating patterns that can be identified as themes. Integrating more acoustic data, covering more spatial and even circumpolar coverage in the Southern Ocean are needed to investigate the potential for the identification of different populations of AMWs based on their vocal behaviour or songs, as will be further discussed in the next section. Nevertheless, the combined spatial and temporal dynamicity of the AMW vocal behaviour, as observed in the PALAOA data, is likely to complicate identification based on single recordings. Along these lines, implementing and extending the area and timing of AMW monitoring effort in low latitude areas would help to better understand how vocal behaviour is connected, potentially revealing aspects of their distribution and migration routes. Obtaining information about the behaviour, distribution and migratory routes of AMWs is essential to develop and implement management and conservation programs for the species and its habitat.

Biogeographic characterization of different populations

Different studies have noted and exploited the utility of whale songs to provide useful information for discovering and determining population boundaries and as an indicator of biologically meaningful stocks for mysticetes (blue whales: Cummings and Thompson, 1971; Edds, 1982; McDonald et al., 2006), humpback whales: Payne and Guinee, 1983; Cerchio et al., 2001, fin whales: Thompson et al., 1992; Hatch and Clark, 2004; Archer et al., 2020, and Bryde's whales: Oleson et al., 2003). In humpback whales, differences in songs among different populations have been well documented (Helweg et al., 1998), though sharing of song elements among neighboring populations can complicate attempts at acoustically identify populations based solely on song (Cerchio et al., 2001).

Studies on the acoustics of minke whales suggest a simple downswept call is used across different geographic regions (e.g., Edds-Walton, 2000; Schevill and Watkins, 1972), but that more complex vocalizations also referred to as the 'star- wars', 'thump-train' or 'boing' sounds are regionally distinctive (Gedamke et al., 2001; Mellinger et al., 2000) (Figure 1). AMWs have been attributed the bio-duck vocalization as a regionally characteristic call (Risch et al., 2014). However, studies at different sites in the Southern Hemisphere using the detection of this call as an indicator of occurrence have described not only one type of bio-duck, but several types (Matthews and McCauley, 2004; Shabangu et al., 2020; Dominello and Širović, 2016, *Chapter II* this thesis).

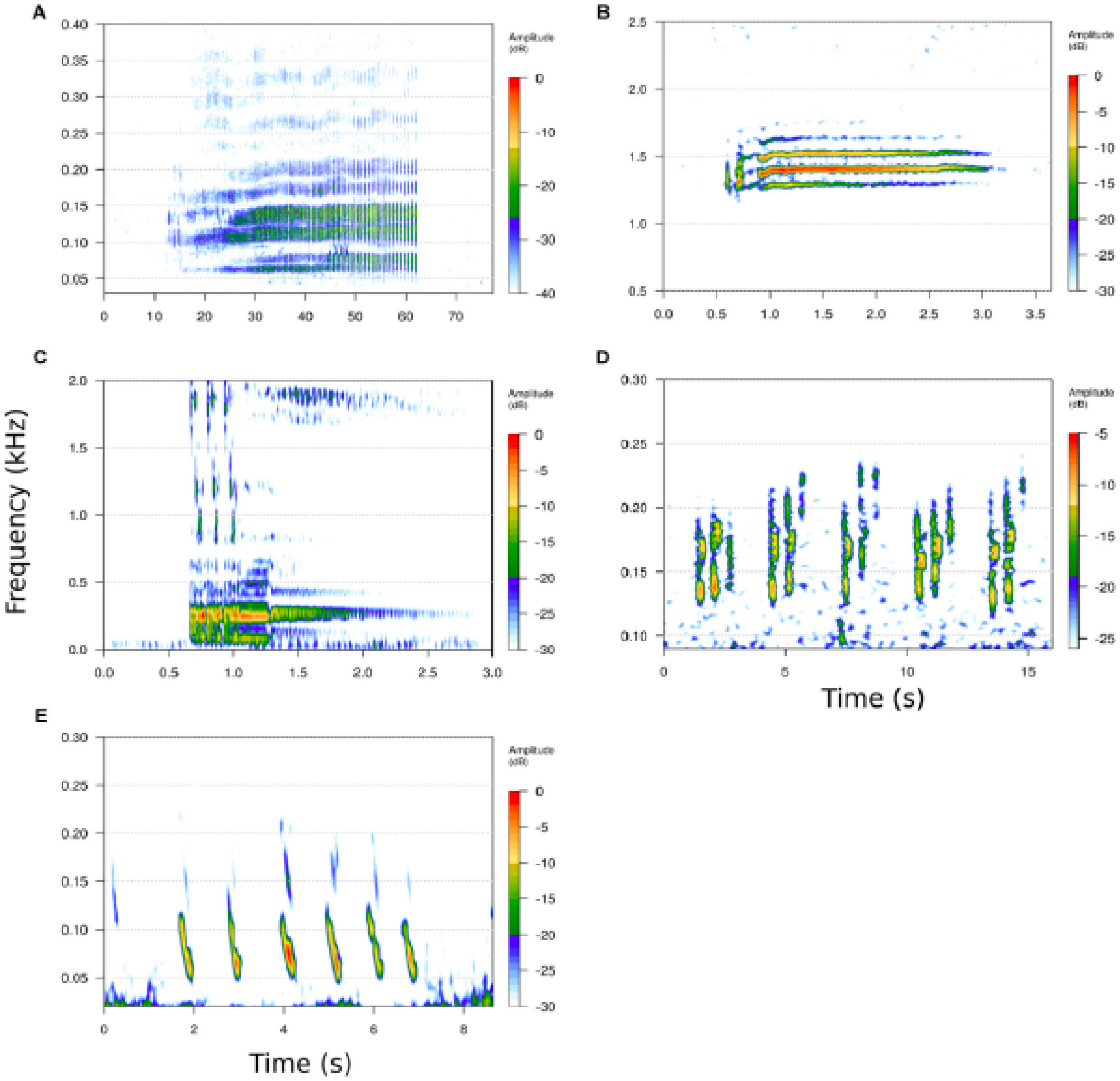

Figure 1. Spectrograms of known minke whale vocalizations from different ocean basins. (A) North Atlantic slow-down pulse trains, (B) North Pacific "boing" vocalization, (C) Australian dwarf minke whale "starwars" vocalization, (D) Antarctic "bio-duck," (E) Antarctic downsweeps. Note different time and frequency scales. Spectrogram parameters: (A) Fast Fourier Transform (FFT) = 1024 pt, overlap (ovlp) = 75%,samplerate (SR) = 2000 Hz: frequency resolution (FR) = 1.9 Hz, time resolution (TR) = 128 ms; (B) FFT = 512 pt, ovlp = 75%, SR = 8000 Hz: FR = 15.6 Hz, TR = 16 ms; (C) FFT = 512 pt, ovlp = 75%, SR = 16,000 Hz: FR = 31.5 Hz, TR = 8 ms; (D) FFT = 1024pt, ovlp = 75%, SR = 4000 Hz: FR = 3.9 Hz, TR = 64 ms; (E) FFT = 4096 pt, ovlp = 75%, SR = 25,811 Hz: FR = 6.3 Hz, TR = 39 ms. Extracted from (Risch et al. 2019).

I was able to use a unique data set to structurally investigate how the occurrence of different bio-duck call types varies over space and time. In the Weddell Sea, we recorded bio-ducks at all our recording sites, but not all positions recorded the same call types. Overall, there was one dominant bio-duck (type A2) which was recorded at all monitoring sites (*Chapter I and II*). This call was also the one with the highest occurrence of presence (>49% hours with acoustic detections at almost all monitoring locations with the exception of the two most westerly sites near the Western Antarctic Peninsula (WAP) (i.e., AWI251-1008 and AWI207-1034)) (*Chapter II*). The D4 call was the dominant one in the west of our study area occurring most frequently at positions AWI251-1008 and AWI207-1034 near the WAP. D5 is another frequently occurring call type, but it occurred at positions located on the east side of the Weddell Sea, e.g., AWI248-1013 and AWI232-1011 (Greenwich) and not at all at the most western recording site (AWI251-1008; *Chapter II*). There are also two types of secondary bio-ducks, the D4 and D5. According to our classification, both calls are classified in group D.

Our study postulates two possible hypotheses regarding the acoustic behavior of AMWs in the Weddell Sea. The first is that this predominant A2 call could be associated with some specific behavior performed by the animals in the area. In contrast, the group D calls could not only be associated with different habitat uses of AMWs throughout the Weddell Sea, but could also be a distinctive call of groups or subpopulations of animals that coexist simultaneously during the winter and spring season in the Southern Ocean. The second hypothesis regarding this variability in the occurrence of bio-ducks could be due to the fact that three possible groups of AMWs coexist in the Weddell Sea, which would be the group near the WAP using the D4 call as distinctive. This would explain the predominance of the D4 call at sites AWI251-1008 and AWI207-1034 and its reduced frequency of occurrence as it approaches the center of the Weddell Sea. The group present in the center of the Weddell Sea using the A2 call as distinctive which reduces in frequency of detection as we compare sites at the far edges away from our area of study. Finally, the third group that would use the D5 call as distinctive and that would correspond to the area east of the Greenwich Meridian (GM). This last one is not very present in our study area, possibly because it is the western limit of its distribution.

First indications of "revolution" in the acoustic behaviour of AMWs.

In addition to the results previously described, it is important to keep in mind the results obtained in *Chapter II* on the inter-annual acoustic variability of AMW calls. I postulate that, like humpback whales, AMWs change their repertoire from year to year (Garland and McGregor, 2020). This inter-annual change in AMWs acoustic repertoire, matches the pattern of song "revolutions" in humpback whales, where the single population-wide shared song type is rapidly replaced by a new, novel song type introduced from a neighboring population (Noad et al., 2000; Garland et al., 2011). It cannot be excluded that the observed dynamics of the AMW vocal behaviour potentially reflect a similar mechanism through which the simultaneous presence of different groups or populations of AMWs mutually affect the composition of the annual repertoire. It is known, that male humpback whales produce a long, stereotyped and constantly evolving vocal breeding display, termed 'song' (Payne and McVay, 1971). The conformity to a single song type within a population is thought to occur via vocal learning from surrounding males and, when song transmission is examined at the ocean basin scale, is considered one of the best examples of horizontal cultural transmission (Garland et al., 2011). Payne (1983) hypothesized three possible mechanisms to allow acoustic contact and subsequent song transmission among populations in any ocean basin. The first possibility is movement of individuals from one breeding population to another between seasons (a phenomenon which has been observed repeatedly; see Calambokidis et al., 2001; Garrigue et al., 2002). The second is within-season movement of individuals between two breeding populations (rarely observed; see Garrigue et al., 2020). The third is song exchange on shared migration routes and/or on summer feeding grounds in high latitudes (see Schall et al., 2021). This last statement could explain the results regarding the inter-annual acoustic variability found in the Weddell Sea. This hypothesis of acoustic evolution based on cultural transmission in AMWs could be supported by the results of the study in *Chapter II*. There, I mentioned the existence of possible three regional dialects (predominant call occurrence) detected throughout the Weddell Sea. Due to the simultaneous presence of these three groups in a common feeding area, a possible cultural transmission of AMW calls may potentially occur as individuals interact with each other.

These new findings and hypotheses on the acoustic behaviour of AMWs mentioned in this PhD thesis help to improve our understanding of the ecology and behaviour of these whales. However, further research is still needed to explore individuals produce the calls e.g., females, males, adults, juveniles, etc. To date it is also unclear if the different acoustic groups identified in the Weddell Sea interact with populations of AMWs vocalizing during the same period at lower latitudes, or if they are distinct groups. To advance research and answer the above-mentioned questions, a broadening of the temporal scale of acoustic monitoring for AMWs is necessary. Furthermore, complementing and comparing different acoustic databases collected at different sites may help to better understand more about the distribution patterns, cultural transmission and ecology of the species.

Population distribution and migration patterns

I have shown that AMWs are vocally present simultaneously in lower and higher latitude waters (*Chapter, III* and *IV*). In the polar waters we observed acoustic presence of individuals remaining in the pack-ice waters throughout the year, whereas we also recorded abundantly AMWs in temperate waters during the austral winter period (Table 1). The acoustic seasonality of AMWs therefore generally covers the same time period independent of location. For AMWs, migratory behaviour therefore seems more complex than in other baleen whale species.

Table 1. Comparative table of AMW acoustic seasonality in different areas in the Southern Hemisphere. The (-) represent periods with no data.

	Acoustic Seasonality												
Area of study	J	F	M	A	M	J	J	A	S	O	N	D	Reference
Chile					🟦	🟦	🟦	🟦					Buchan et al.,2020
Brazil	-	-	-	-	-	-	-	-	-	-	🟧	🟧	This PhD thesis
Namibia						🟩	🟩	🟩			🟩	🟩	This PhD thesis
South Africa								🟩	🟩	🟩	🟩	🟩	Shabangu et al.,2020
Australia							🟨	🟨		🟨	🟨	🟨	Matthews et al.,2004
W. Antarctic Peninsula				▨	▨	▨	▨	▨	▨	▨			Dominello & Širović 2016
Weddell Sea					▨	▨	▨	▨	▨	▨	▨	▨	This PhD thesis

In high and low latitude areas where AMWs have been recorded (Figure 2), the seasonality in acoustic presence is similar, with the winter-spring period (i.e., June until December) being the most important in terms of AMW vocal activity. In some places, such as off Chile (Juan Fernández) and the Antarctic Peninsula, the acoustic seasonality starts a little earlier (April). Moreover, at these two sites, this time shift is also reflected at the end of the acoustic season. In Chile singing ends around the beginning of September and off the Antarctic Peninsula beginning of October. In contrast, at recording sites off Brazil, Namibia, South Africa, Australia and the Weddell Sea, the AMW acoustic seasonality extends into December.

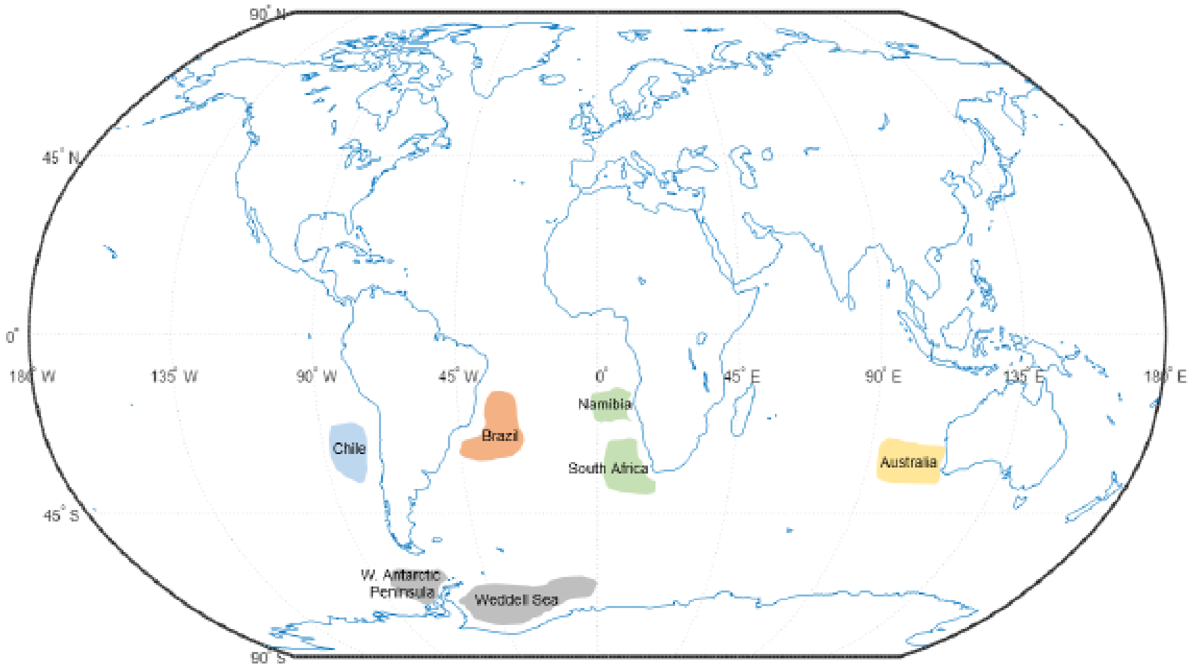

Figure 2. Map of the world with the different areas where Antarctic minke whales have been acoustically detected. Blue= Chile (Juan Fernandez), Orange= Brazil (Santos Basin), Green= Namibia and South Africa coast, Yellow= Australia (Perth Canyon) and Grey= Western Antarctic Peninsula and Weddell Sea (Southern Ocean).

These findings of simultaneous acoustic presence in different locations in the Southern Hemisphere can be explained by several reasons. Migratory behavior of baleen whales is not obligate for all individuals, which results in further diversification of the migratory strategies between, but also within populations. An individuals' migratory status and behavior is likely determined by a variety of, most likely interdependent, factors. Environmental conditions, and in particular food availability and foraging opportunities, may influence the migratory status. Prey distribution is considered to be a fundamental driver of movement patterns in marine megafauna (Hays et al., 2016) and the poleward migration of baleen whales is assumed to be driven by profitable foraging opportunities in high latitude waters (Avgar et al., 2014). Another important fact is that whale individuals of different age classes and sexes differ in their migratory behavior according to their strategies for improving their life-time fitness. These sex- and age-specific strategies are reflected in various observations of sex-related differences in the migratory behavior of baleen whales, including differences in the migratory routes (Kellogg, 1929; Valsecchi et al., 2010) or timing (Dawbin, 1997; Craig et al., 2003). Female baleen whale decisions on migratory strategies are presumed to be strongly mediated by the energetic costs of reproduction, i.e., gestation, parturition and lactation (Lockyer, 1978; Lockyer, 1984). In addition, their reproductive status, which includes resting, pregnant and lactating individuals accompanied by a calf, also plays a role (e.g., Dawbin, 1997). Additionally, female baleen whales have a higher tendency to skip migration e.g., remaining in high latitude waters in some years, whereas other individuals migrate northbound again to lower latitudes. This hypothesis is supported by observations of a sex-bias in migrating humpback whales towards male individuals, both on migration towards the breeding sites and on the breeding grounds (Brown et al., 1995; Craig & Herman, 1997; Pomilla & Rosenbaum, 2006). Furthermore, a female-biased sex-ratio of humpback whales was observed off the west coast of South Africa, indicating that females (rather than males) may not complete the full migration towards the breeding grounds located further north off the African coast (Barendse et al., 2010). These findings potentially indicate that some females skip migration and overwinter on the high-latitude feeding grounds to save the cost of migrating, while extending their time on the feeding grounds. For males, exhibiting a longer residency time on the breeding grounds to optimize mating opportunities may be more effective in terms of fitness and reproduction (Brown et al., 1995; Craig & Herman, 1997; Valsecchi et al., 2010). In humpback whales, male migration towards the breeding grounds has been shown to succeed the migration of females with a calf and to take place simultaneous to the migration of resting females (Dawbin, 1997). The migratory timing of males may therefore represent a strategy to maximize their reproductive success (Craig et al., 2003).

For humpback whales, previous studies suggested that there are also age-related differences in movement patterns between juveniles and adults, indicating that the age and sexual maturity of an individual influences its migratory status and behaviour. (Dawbin, 1997; Craig et al., 2003). The migratory routes have been suggested to differ between juvenile and adult individuals (Brown, 1981). Juveniles are thought not to penetrate as far into high-latitude waters on the feeding grounds as adult whales and to more often inhabit shallow coastal waters than adults (Lockyer & Brown, 1981; Swartz, 1986). This is possibly explained by the fact that juvenile individuals are more vulnerable compared to adults, e.g. in terms of predation and harsh or dangerous oceanographic conditions (Geijer et al., 2016). Also, for juveniles a longer residency time on the feeding grounds may benefit as this enables them to maximize their growth and hence, body size which is considered a major factor in determining sexual maturity of baleen whales (Geijer et al., 2016).

Finally, the cultural knowledge of baleen whale populations transmitted by social learning is also considered to influence the migratory behavior of individual baleen. Migration has been described as being not only a movement behavior but also an information usage strategy, with historical information (i.e., preexisting knowledge on migration, either genetically inherited or acquired during previous migrations) being a crucial factor in directing the movements of migrants (Glover et al., 2010; Shaw & Couzin, 2013). Hence, the accumulation and transmission of migratory experiences and knowledge within a population is considered to improve the overall migratory performance of migrants (e.g., Mueller et al., 2013; Geijer et al., 2016).

The results of this PhD thesis on the acoustic seasonality of AMWs at different sites in the Southern Hemisphere and their simultaneity of acoustic occurrence among sites at high and low latitudes can possibly be explained by the complex distribution and migration patterns of these whales. The current data complicate formulating clear hypotheses on what could explain the simultaneous (substantial) acoustic presence of AMWs at high and low latitudes. However, one possibility could be that the ability of this species to move in and cope with dense ice cover, puts less restrictions on their movements, allowing for more flexible and differential migratory behaviour. This could then result in year-round presence of AMWs in both high and low latitude areas (e.g. in analogy to the observations on humpback whales by Straley (1990). To understand more about the migratory decisions of this species, it is necessary to identify the feeding and breeding sites of these animals and understand how they connect and if continuous movements genuinely occur. The identification of these key areas and further population studies will help us to decipher how the populations are connected and which, how and in which directions they migrate.

Following the line of this doctoral thesis study, it is necessary in the future to develop and implement an acoustic monitoring system, capable of simultaneously covering different sites to compare acoustic data at high and low latitudes. In this study, I developed a methodology for the classification of AMW sounds. The use of this tool allows us to standardize the databases with respect to the classification of different bio-duck sounds recorded in different regions and to be able to compare them with each other. Furthermore, a circumpolar study would provide novel information about the dynamic and the number of possible groups that co-exist in the Southern Ocean and in which way they interact with each other. In addition, long-term monitoring of these sites will help to identify how cultural transmission between populations takes place in space and time, and also to identify potential migration routes. In order to make these comparisons of sounds from different regions, it is important to take into account the inter-annual variability in the acoustic repertoire of AMWs. That is why in order to compare different databases it is necessary to take into account to perform this analysis by comparing similar years.

Effect of climate change on AMWs

Attempts to predict climate-change impacts on biodiversity have often relied on the species–climate 'envelope' modelling, whereby present day distributions of species are combined with environmental variables to project distributions of species under future climates (Pearson & Dawson, 2003). Species ranges are shifting, contracting, expanding and fragmenting in response to global environmental change (Chen et al., 2011). Information on marine species' spatio-temporal distribution and their relationship to the environment is pivotal for well-informed, proactive management strategies and conservation actions (Becker et al., 2016; Guisan et al., 2013). Critical habitats are typically defined as habitats necessary for the persistence, or long-term recovery, of threatened species (Greenwald et al., 2012). Many threatened species have restricted distributions and specific habitat requirements, so decisions to protect critical habitat may need to be made with some urgency to avoid critical population status potentially followed by extinction (Martin & Maron, 2012). However, records of observed species occurrence typically provide information on only a subset of sites occupied by a species (Rondinini et al., 2006). Even dedicated surveys typically provide only a snapshot of species distribution and represent only a limited time and space range (Kaschner et al., 2006). The snapshot nature along with the often limited sighting effort over time and space for high latitude areas, compromise future predictions in areas that have not been surveyed, or that may be colonised in the future following climate change (Hoegh-Guldberg et al. 2008). Information of the spatial distribution of AMWs, is crucial for assessing the species' vulnerability with regard to predicted, climate-related changes in sea ice conditions (Silber et al., 2017). High-latitude marine systems are among the regions responding most rapidly to changing climatic conditions, with ice-obligate species facing some of the largest changes in their habitat (Nicol, 2008; Silber et al., 2017). The nature and magnitude of future responses of AMWs as an ice-dependent species are uncertain in novel environments as projected under climate change. An overall decrease of sea-ice cover would narrow available habitat for AMWs. These results suggest that the forecast sea ice changes (Böning et al., 2008; Rignot, 2008; Silber et al., 2017) have the potential of heavily impacting AMWs populations and distribution.

Such information is important for making robust conservation management decisions. Given that PAM can collect data autonomously over large spatial and temporal scales (covering austral winter), crucial insights and data on AMWs in a changing environment can potentially (at least partially) be provided by e.g., PAM-based predictions of species occurrences derived from environmental suitability models that combine biological records with spatial environmental data.

Conservation and management

Under the scope of this PhD thesis, I presented evidence that PAM can be a powerful tool to study AMWs populations in a range-wide scale monitoring effort inclusive of remote regions and combined with multiple environmental variables, it can be a helpful tool to define critical habitats to conserve.

Information on AMW spatio-temporal distribution patterns is furthermore of direct relevance for Southern Ocean ecosystem management in the context of the conservation and management mandate of the International Whaling Commission (IWC) and the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR). Recently, AMWs were classified as Near Threatened under the Internal Union for Conservation of Nature (IUCN) Red List and under Appendix I of CITES. At the same time, information on stock distributions while on the feeding grounds is lacking, but is crucial to management decisions on ecosystem and population conservation. Providing further investigations of AMW vocal behaviour are able to develop more robust measures of determining stock identity based on song or repertoire, PAM data could play a crucial role to improve our understanding of AMW stock structures.

Future Research

In this thesis, I aimed to achieve a better understanding of aspects of the acoustic ecology of AMWs, to improve the feasibility of using passive acoustic monitoring to obtain data on their seasonal distribution in remote areas. Such data are of major importance for conservation and management of this mysterious species, that has proven difficult to survey with other means (e.g., Williams et al., 2014). In addition, acoustic monitoring can also help to investigate migration or corridor routes between high and low latitudes. Despite all the information described in this thesis, there are still gaps in information that would help us better understand the ecology of this species. The following is a list of the next steps to be taken:

i. Increase sampling effort in regions potentially or already described as low latitude breeding grounds for the species.
ii. Implement circumpolar acoustic monitoring, in order to identify the presence of AMWs around the Southern Ocean.
iii. Compare with genetic information, if there is coincidence between acoustic groups on different stocks.
iv. Identify migration corridors for this species to enhance conservation policies and observe potential threats.

It is my hope that with this thesis, I have been able to contribute to improving our understanding of this wonderful species, so that we can protect its habitat and conserve its existence for the future.

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Bremen, 16.March 2022

Diego Filún

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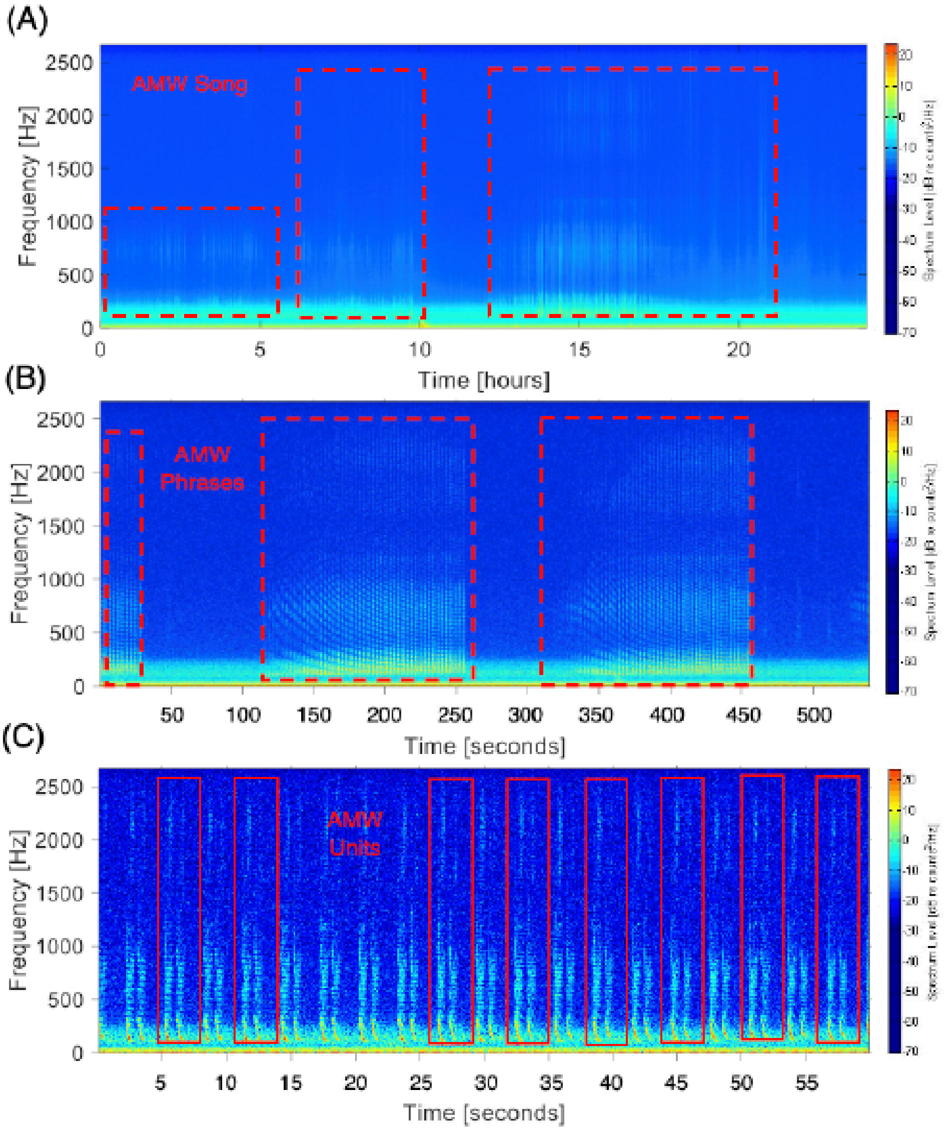
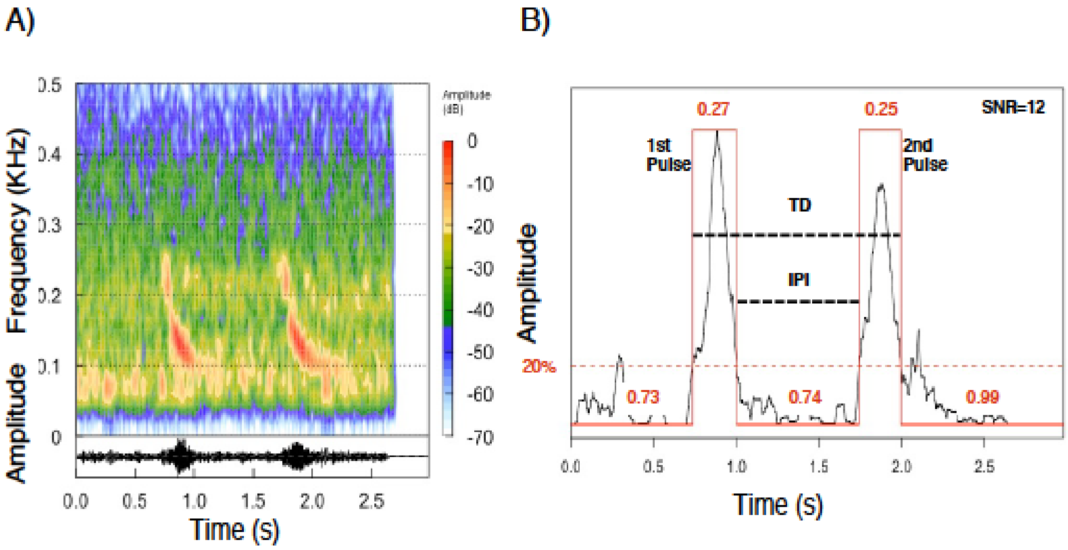
Appendix

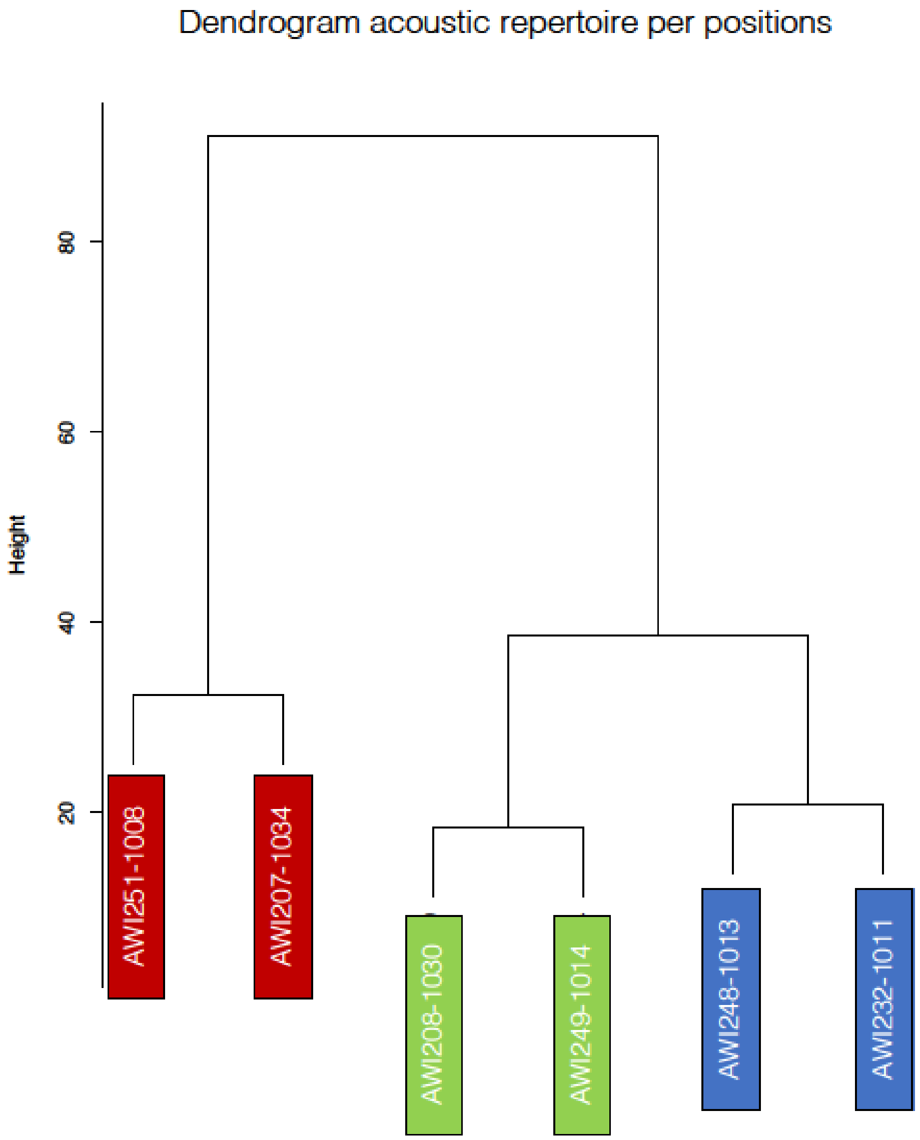
Appendix Chapter II: Filun, D. & Van Opzeeland, I. The latest local tune: the calling behavior of Antarctic minke whales (*Balaenoptera bonaerensis*) differs in space and time. Planned to be submitted to *Nature Scientific Reports*.



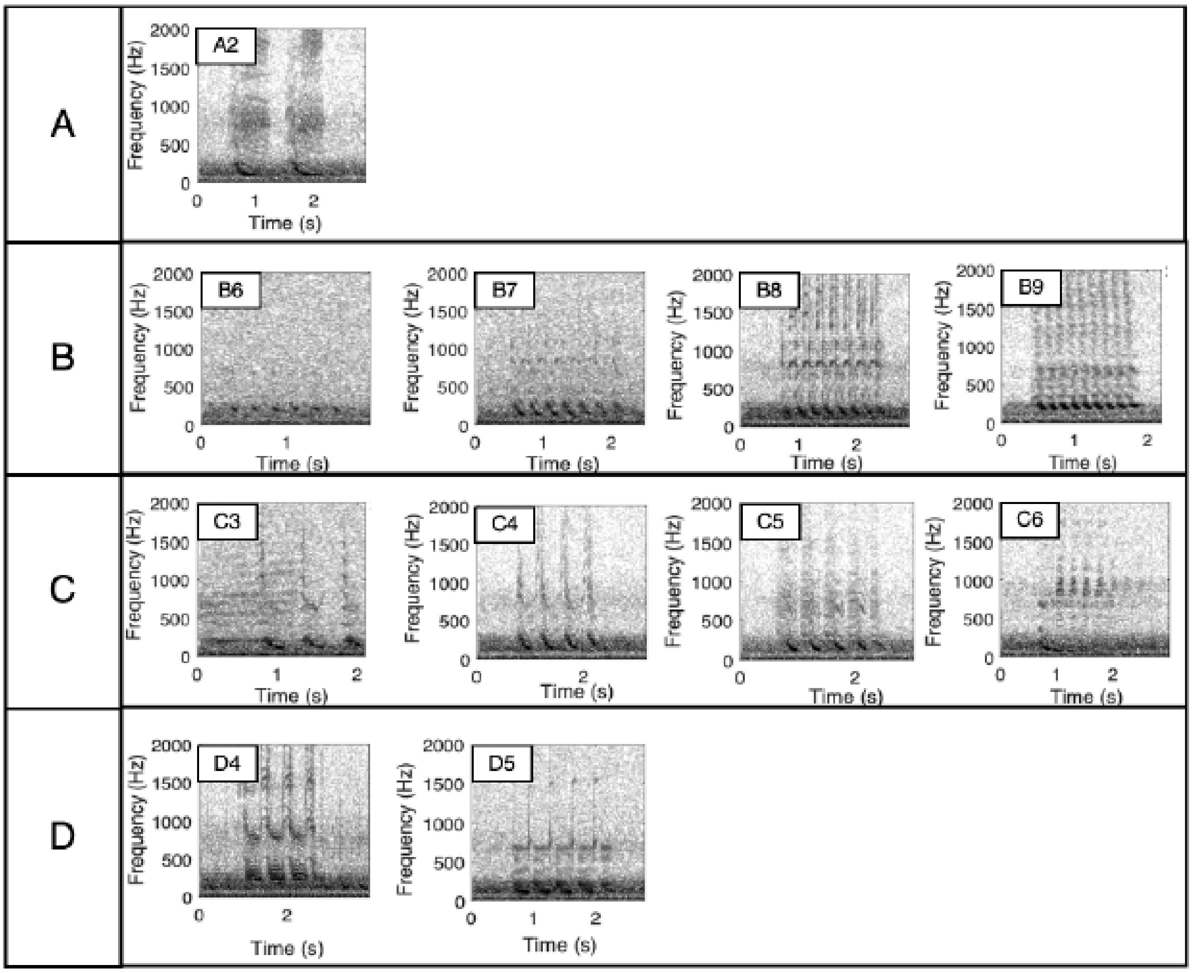
Appendix Figure 1. Spectrograms with examples of AMW (A) Song bouts, (B) phrases and (C) units. Spectrogram (B) exhibits a Lloyd Mirror effect in the AMWs phrases. The visualized data are from the position AWI208-1030 during the 15/07/2013.



Appendix Figure 2. Left figure (A) showing a spectrogram and waveform of bio-duck call type A2. Right spectrogram (B) shows the different measurements that were automatically extracted. Numbers in red correspond to the length in seconds of the different measurements (Table. 2). The example represents an SNR= 12 dB and a threshold = 20.



Appendix Figure 3. Dendrogram based on the acoustic repertoire per mooring position across the Weddell Sea.



Appendix Figure 4. Spectrograms of the different AMW call types detected and classified from the HAFOS (2013) and PALAOA data (2015-2017) . Spectrogram settings HAFOS data: Fast Fourier Transform (FFT) length of 1,125 samples, 95% overlap and Hanning window

Appendix Table 1. Classification and measured values obtained of the different Bio-duck calls identified (*n*=60 for every Bio-duck call type). Calls with * were detected only in PALAOA.

Group	N° Pulses	Avg Total Duration (seconds)	Avg 1st Pulse (seconds)	Avg Last Pulse (seconds)	Avg Inter-pulse interval (seconds)	Avg Peak Frequency (Hertz)
A*	1	1.2	1.2			115
A	2	1.7	0.718	0.428	0.478	114.5
B*	4	1.43	0.13	0.089	0.034	194.3
B	5	1.51	0.12	0.11	0.039	191.2
B	6	1.403	0.145	0.058	0.047	197.9
B	7	1.525	0.138	0.123	0.038	185.82
B	8	1.73	0.12	0.123	0.035	177.07
B	9	1.985	0.135	0.08	0.025	184.16
C*	2	1.47	0.26	0.123	0.094	134.45
C	3	1.08	0.25	0.173	0.21	137.56
C	4	1.418	0.325	0.165	0.118	145.82
C	5	1.61	0.23	0.118	0.085	135.408
C	6	1.86	0.095	0.078	0.044	138.16
D*	3	1.221	0.197	0.23	0.193	145.34
D	4	1.273	0.198	0.1	0.177	142.56
D	5	1.533	0.202	0.073	0.118	151.57

Appendix Table 2. Percentage of occurrence of the different Bio-duck types for every location. Monitoring sites HAFOS and PALAOA

Area	Data	A1	A2	B4	B5	B6	B7	B8	B9	C2	C3	C4	C5	C7	D3	D4	D5
HAFOS	AWI251-1008	-	27.36	-	-	-	-	6.47	-	-	2.49	3.98	0.5	-	-	59.2	-
	AWI207-1034	-	37.3	-	-	-	1.47	8.96	3.61	-	2.27	1.2	0.13	-	-	43.45	1.6
	AWI208-1030	-	61.86	-	-	-	1.33	3.68	0.1	-	1.12	0.51	0.41	-	-	19.22	11.76
	AWI249-1014	-	59.32	-	-	0.56	3.2	-	3.77	-	0.38	1.51	-	-	-	24.11	7.16
	AWI248-1013	-	54.81	-	-	-	-	12.69	1.39	-	1.53	2.79	-	-	-	7.11	19.67
	AWI232-1011	-	49.06	-	-	1.44	4.75	1.15	15.4	-	2.45	0.58	1.01	0.14	-	1.73	22.3
PALAOA	2015	8.7	-	18.7	47.4	-	-	-	-	8	-	14.8	-	-	-	-	2.4
	2016	42.8	-	2	21.1	1	-	-	-	10.7	15.6	-	-	-	3.7	3.1	-
	2017	-	18.8	-	-	1.4	4.7	1.2	15.4	-	32.7	0.6	1	0.1	-	1.7	22.3

Appendix Chapter III: Rossi-Santos, MR*., Filun, D.*, Soares-Filho W., Paro A., Wedekin, L. Playing the beat: occurrence of Bio-duck calls in Brazil reveals a complex acoustic behaviour for the Antarctic minke whale (*Balaenoptera bonaerensis*). Revised version in preparation for *Journal PlosOne.*

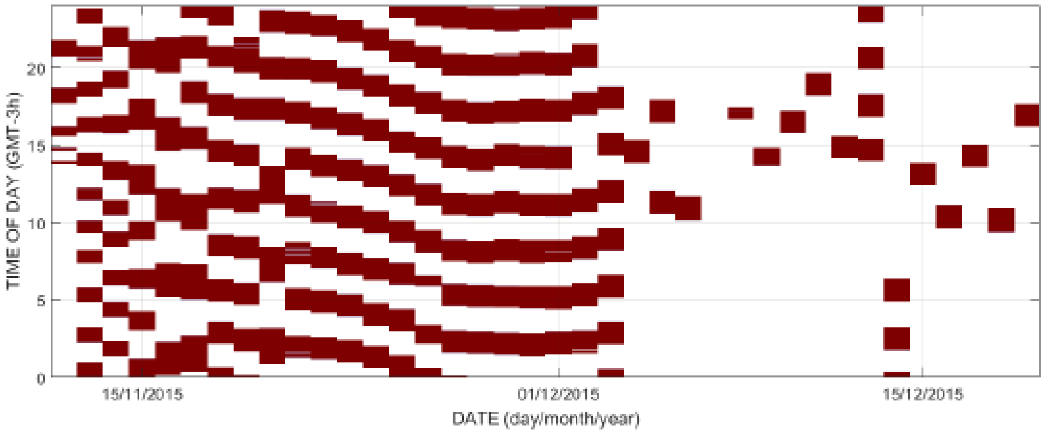


Figure 1. Scheduled recording scheme for the glider monitoring period (12 November - 19 December 2015). Recording periods for each monitoring day (red squares). The glider was programmed to record one hour every one hour (1/2 duty cycle). From 03 December the glider started to have problems to continue with the scheduled duty cycle due to technical problems.

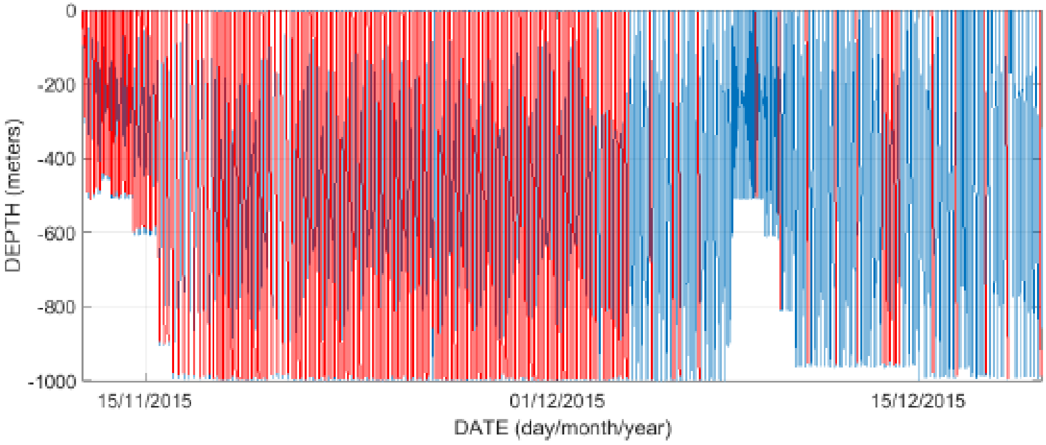


Figure 2. Profile of depth and time of the recordings periods. Section with recordings as a function of depth during the monitoring period.

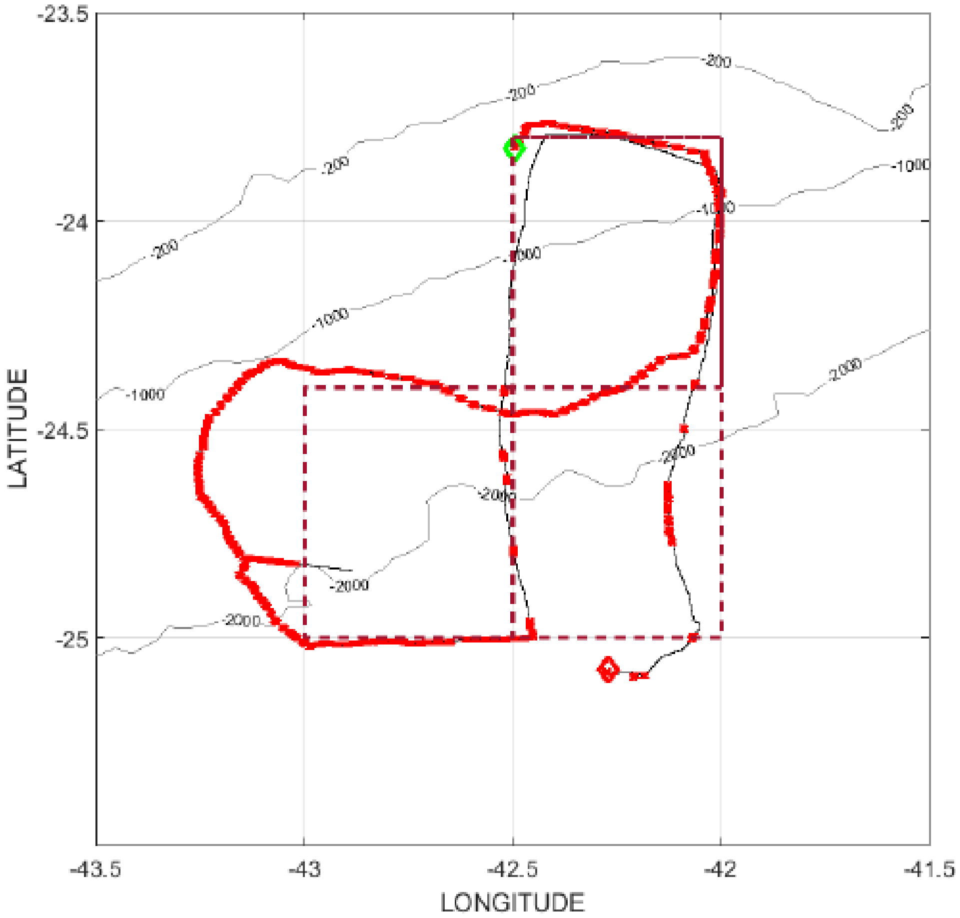


Figure 3. Glider trajectory, highlighting the sections with recording. Includes a dashed line indicating the programmed trajectory. Green and Red squares shown the start and end position of the SeaGlider deployment trajectory.