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Distribution patterns and migratory behavior of Antarctic blue whales

Karolin Thomisch

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"The feeling is now abroad that if we can’t save the largest animals in the world
we have little chance of saving the biosphere itself
and therefore of saving our own species.”

Sir Peter Scott, 1972

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Die vorliegende Arbeit ist die im wesentlichen inhaltlich unveränderte Fassung einer Dissertation, die am Fachbereich Biowissenschaften in der Sektion Physikalische Ozeanographie des Alfred-Wegener-Instituts Helmholtz-Zentrum für Polar- und Meeresforschung entstand und im Oktober 2016 dem Fachbereich Biologie/Chemie der Universität Bremen vorgelegt wurde.

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SUMMARY

The development of effective management and conservation strategies for extant baleen whale populations bases on a solid understanding of the large-scale and long-term spatio-temporal patterns in their distribution and migratory behavior. A generalized migration paradigm has long been considered representative of the migratory behavior for most baleen whale species. This concept assumes that the majority of individuals of a baleen whale population undertakes a regular, seasonal migration between high-latitude feeding grounds where the whales spend the summer feeding and low-latitude overwintering and breeding grounds in warmer waters where mating and parturition take place. However, this paradigm likely oversimplifies the observed patterns in the distribution and migration of many baleen whale species. The occurrence of divergent migratory behaviors was already noted in early whaling reports, but the (relative) importance of such behaviors in baleen whale migration has long been overlooked. Thanks to advancing marine mammal monitoring technologies, an increasing body of evidence now strengthens the hypothesis that the migratory behavior of baleen whales is not complete, obligate and uniform, but comprises partial, facultative and differential migration.

After having been one of the primary targets of commercial whaling during the 20th century, Antarctic blue whales (*Balaenoptera musculus intermedia*) are still listed as critically endangered by the IUCN (International Union for Conservation of Nature) to date. Many aspects of Antarctic blue whale distribution and migration patterns remain poorly understood to date, not least because of their low abundances and the remoteness and seasonal inaccessibility of their polar habitats and the high financial and logistic costs associated to long-term research projects in these habitats.

This dissertation investigates spatio-temporal patterns in the (acoustic) presence of Antarctic blue whales in the Atlantic sector of the Southern Ocean and in the South Atlantic Ocean in order to contribute to a better understanding of their distribution patterns and migratory behavior. The results are presented in six independent scientific publications (comprising both published papers and manuscripts).

Publication I represents a methodological evaluation and investigates the effects of subsampling on passive acoustic data collected to infer patterns in baleen whale acoustic presence and vocal behavior. It reveals that unsuitable sampling schemes have the potential to negatively affect the accuracy of assessments of both daily acoustic presence and call rates of baleen whales. This publication thereby highlights the importance of informed decisions on subsampling schemes for passive acoustic data collection and analyses to avoid biasing inferences on a focal species' presence and hence distribution.

Publications II, III, IV and V provide insights into the spatio-temporal distribution patterns and partially, the migratory behavior of Antarctic blue whales.

Publication II reports blue whale sightings in the Weddell Sea in January 2015 and implies that the eastern Weddell Sea forms part of a blue whale hot spot in the Southern Ocean.

Publications III and IV explore spatio-temporal patterns in the acoustic presence of Antarctic blue whales in the Atlantic sector of the Southern Ocean based on two different call types and interpret findings in the context of Antarctic blue whale distribution and migratory behavior. Antarctic blue whales were acoustically present throughout the study area during austral summer, indicating a wide distribution range and possibly a differential migration with different migratory destinations or timing of Antarctic blue whale individuals. Furthermore, acoustic presence of Antarctic blue whales was recorded both close to the ice edge and in heavily ice-covered areas during austral winter months. These findings imply that Antarctic

blue whales exhibit partial migration, with a fraction of the population overwintering in high-latitude waters, and highlight the importance of the Weddell Sea as a year-round Antarctic blue whale habitat.

Publication V explores temporal patterns in the acoustic presence of large cetacean species in the South Atlantic Ocean off Namibia and indicates that the area serves as an overwintering habitat for baleen whales. Intra-annual patterns in the acoustic presence of Antarctic minke whales (*Balaenoptera bonaerensis*), fin whales (*Balaenoptera physalus*) and humpback whales (*Megaptera novaeangliae*) likely reflect migratory movements of the animals towards higher latitudes during austral summer. Antarctic blue whales were acoustically present throughout the study period, possibly reflecting partial or differential migration of the population.

Finally, publication VI investigates long-term temporal shifts in the vocalization frequency of Antarctic blue whales and discusses potential reasons for the observed inter- and intra-annual patterns. An understanding of temporal changes in the vocal characteristics of Antarctic blue whales is crucial, because such changes may considerably affect the performance of automated call detection algorithms over time. Consequently, such changes may impact the reliability of further inferences based on the call detections, including (acoustic) presence, distribution and migratory behavior.

This dissertation sheds further light on spatio-temporal patterns in the distribution and migration of Antarctic blue whales. It adds to increasing evidence that Antarctic blue whales inhabit both high- and low-latitude areas in the Southern Hemisphere year-round and thereby indicates that a diverse migratory repertoire is rather the rule than the exception in Antarctic blue whales. An improved understanding of the distribution and migration of Antarctic blue whales can aid the development of effective conservation strategies for this critically endangered species, such as the designation of marine protected areas in Antarctic blue whale key habitats.

ZUSAMMENFASSUNG

Die Erarbeitung effizienter Management- und Schutzstrategien für rezente Bartenwalpopulationen basiert auf einem fundierten Verständnis der Verbreitungsmuster und Wanderungsbewegungen dieser Populationen in Raum und Zeit. Ein allgemeines „Migrationsleitbild" wurde lange als repräsentativ für das Wanderungsverhalten der meisten Bartenwalarten angesehen. Dieses Leitbild beruht auf der Annahme, dass die Mehrzahl der Individuen einer Bartenwalpopulation regelmäßige jahreszeitliche Wanderungen zwischen Fressgebieten in höheren geografischen Breiten, wo die Wale den Sommer über fressen, und Überwinterungs- und Fortpflanzungsgebieten in wärmeren Gewässern niedrigerer Breiten, in denen die Paarung stattfindet und die Wale ihre Kälber gebären, unternimmt. Diese Annahme stellt allerdings eine zu starke Vereinfachung der beobachteten Verbreitungs- und Migrationsmuster vieler Bartenwale dar. Abweichende Muster im Wanderungsverhalten wurden bereits in frühen Walfangberichten erwähnt, die tatsächliche (relative) Bedeutung dieser Verhaltensmuster in der Migration von Bartenwalen wurde dennoch lange Zeit übersehen. Doch dank des technologischen Fortschrittes hinsichtlich des Monitorings von Meeressäugetieren wächst die Anzahl an Hinweisen darauf, dass das Wanderungsverhalten von Bartenwalen anstelle von allgemeingültigen, obligaten und einheitlichen Verhaltensweisen auch partielle, fakultative und differenzielle Komponenten aufweist.

Während des 20. Jahrhunderts war der Antarktische Blauwal (*Balaenoptera musculus intermedia*) eines der primären Ziele des kommerziellen Walfangs. Aktuell wird die Art durch die IUCN (‘International Union for Conservation of Nature’) als vom Aussterben bedroht eingestuft. Zahlreiche Aspekte der Verteilungs- und Migrationsmuster Antarktischer Blauwale sind allerdings noch wenig erforscht. Dies beruht nicht zuletzt auf der geringen Abundanz der Antarktischen Blauwale, der Abgeschiedenheit und Unzugänglichkeit ihrer polaren Lebensräume, sowie dem hohen logistischen und finanziellen Aufwand, den die Durchführung langfristiger Forschungsprojekte in diesen Gebieten erfordert.

Die vorliegende Dissertation erforscht räumliche und zeitliche Muster in der (akustischen) Präsenz von Antarktischen Blauwalen im Atlantischen Sektor des Südozeans und im Südatlantik, um zu einem besseren Verständnis ihrer Verteilungsmuster sowie ihres Migrationsverhaltens beizutragen. Die Ergebnisse dieser Studien werden in sechs unabhängigen Publikationen bzw. Manuskripten dargelegt.

Publikation I untersucht die Effekte von ‘Subsampling‘, d.h. einer Stichprobennahme aus kontinuierlichen akustischen Aufnahmen nach einem vordefinierten System, auf passiv akustische Daten aus denen Muster in der akustischen Präsenz und dem Vokalverhalten von Bartenwalen abgeleitet werden sollen. Diese Studie zeigt auf, dass ungeeignete Stichprobensysteme die Genauigkeit von Abschätzungen hinsichtlich der akustischen Tagespräsenz und Rufrate von Bartenwalen negativ beeinflussen können. Die Studie stellt dadurch heraus, dass fundierte Entscheidungen bezüglich geeigneter Stichprobensysteme eine wichtige Rolle für die Erhebung und Analyse von passiv akustischen Daten spielen, um letztlich eine Verfälschung der Rückschlüsse auf die akustische Präsenz und Verbreitung einer Zielart zu vermeiden.

Publikationen II, III, IV und V bieten neue Einblicke in die räumlichen und zeitlichen Verteilungsmuster und (teilweise) in das Wanderungsverhalten Antarktischer Blauwale.

Publikation II schildert visuelle Sichtungen von Blauwalen im Weddellmeer im Januar 2015 und deutet darauf hin, dass das östliche Weddellmeer Teil eines Schlüsselhabitats für Blauwale im Südozean ist.

Die Publikationen III und IV erforschen räumliche sowie zeitliche Muster in der akustischen Präsenz von Antarktischen Blauwalen im Atlantischen Sektor des Südozeans anhand von zwei verschiedenen Ruftypen und interpretieren die Ergebnisse im Kontext der Verbreitung und des Migrationsverhaltens der Art. Im Südsommer waren Antarktische Blauwale im gesamten Untersuchungsgebiet akustisch präsent. Dies deutet auf ein ausgedehntes Verbreitungsgebiet der Art und möglicherweise auf ein differenzielles Wanderungsverhalten hin, bei dem sich die Tiere innerhalb der Population hinsichtlich der Ziel- und Zeitpunkte ihrer Wanderung unterschieden. Im Südwinter waren Antarktische Blauwale sowohl nahe der Meereisgrenze als auch in stark eisbedeckten Gebieten akustisch präsent. Diese Ergebnisse lassen eine partielle Migration bei Antarktischen Blauwalen vermuten, wobei ein Teil der Population in hohen Breiten überwintert, und heben die Bedeutung des Weddellmeeres als ganzjähriges Habitat für Antarktische Blauwale hervor.

Publikation V untersucht zeitliche Muster in der akustischen Präsenz verschiedener Großwalarten im Südatlantik vor Namibia und deutet darauf hin, dass das Gebiet Bartenwalen als Überwinterungshabitat dient. Saisonale Veränderungen in der akustischen Präsenz von Antarktischen Zwergwalen (*Balaenoptera bonaerensis*), Finnwalen (*Balaenoptera physalus*) und Buckelwalen (*Megaptera novaeangliae*) spiegeln vermutlich Wanderungsbewegungen der Tiere in Richtung höherer Breiten während des Südsommers wieder. Antarktische Blauwale waren den gesamten Aufnahmezeitraum über akustisch präsent, was möglicherweise auf eine partielle oder differenzielle Migration der Population hinweist.

Publikation VI analysiert langfristige Veränderungen in der Vokalisationsfrequenz Antarktischer Blauwale und diskutiert mögliche Gründe für die beobachteten zwischen- und innerjährlichen Muster. Veränderungen der vokalen Eigenschaften von Antarktischen Blauwalen können die Ergebnisse und Leistungsfähigkeit von automatischen Detektionsalgorithmen maßgeblich beeinflussen. Daher ist eine umfassende Kenntnis solcher zeitlichen Veränderungen von grundlegender Bedeutung um die Verlässlichkeit weiterer Schlussfolgerungen, z.B. hinsichtlich der (akustischen) Präsenz, der Verbreitung und des Migrationsverhaltens, zu gewährleisten.

Die vorliegende Dissertation gibt Aufschluss über die räumlichen und zeitlichen Muster in der Verbreitung und Migration Antarktischer Blauwale und liefert weitere Hinweise auf ein ganzjähriges Vorkommen der Art in sowohl hohen als auch niedrigen geografischen Breiten der Südhemisphäre. Die Ergebnisse dieser Dissertation legen damit nahe, dass ein vielfältiges Repertoire an Verhaltensweisen die Migration Antarktischer Blauwale auszeichnet. Ein vertieftes Verständnis der Verbreitung und des Wanderungsverhaltens von Antarktischen Blauwalen kann die Erarbeitung effizienter Schutzstrategien für diese vom Aussterben bedrohte Art fördern, beispielsweise die Ausweisung von marinen Schutzgebieten in den Kernhabitaten Antarktischer Blauwale.

1. MOTIVATION: MIGRATION AS A FUNDAMENTAL LIFE HISTORY TRAIT IN BALEEN WHALES

The impressive long-distance movements of animals have been fascinating both laymen and scientists throughout human history (e.g. Aristotle, 350 BCE; Alerstam *et al.*, 2003; Dingle, 2014). Baleen whales are considered to undertake the most extensive migrations of all mammals, with their seasonal migration covering distances of several thousand kilometers (Alerstam *et al.*, 2003; Rasmussen *et al.*, 2007; Stevick *et al.*, 2011). Despite the iconic status of baleen whales in nature conservation, our knowledge on long-term spatio-temporal distribution patterns and migratory behavior is still scarce for many baleen whale species. This scarcity of knowledge is not least due to the mobile and elusive life style of baleen whales, their often remote or seasonally inaccessible habitats, and the comparatively low abundances of many species due to heavy exploitation of their populations during commercial whaling. Although commercial whaling activities have largely ceased since the commercial whaling moratorium took effect in 1986 (Clapham & Baker, 2008), some baleen whale species, such as the Antarctic blue whale (*Balaenoptera musculus intermedia*), are still listed as critically endangered by the IUCN (International Union for Conservation of Nature). Their current abundance and status of recovery are uncertain to date (Reilly *et al.*, 2008c; Thomas *et al.*, 2016).

Current threats to baleen whale populations are nevertheless manifold, including climate change and ocean acidification but also the increasing extent of anthropogenic activities (such as ship traffic, fishing activities, oil and gas exploration or anthropogenic noise) in the worlds' oceans (Thomas *et al.*, 2016). Baleen whales play a crucial ecological role in marine food webs (e.g. Bowen, 1997; Lavery *et al.*, 2014; Ratnarajah *et al.*, 2014). However, short- and long-term effects of these threats on baleen whales and potential consequences on the structure, dynamics and stability of entire ecosystems remain yet to be investigated (Thomas *et al.*, 2016). Reliable assessment of the potential impacts of the various threats on baleen whales requires a solid understanding of the *status quo* of baleen whale populations, e.g. in terms of their abundance, distribution patterns, and (migratory) behavior. Such insights are also indispensable in the light of developing effective conservation and management strategies (e.g. Costa *et al.*, 2012).

The present study focuses on Antarctic blue whales and aims at contributing to a deeper understanding of their distribution patterns and migratory behavior, which will aid future conservation efforts for this critically endangered species. For this purpose, I investigated spatial and temporal patterns in the acoustic presence of Antarctic blue whales based on passive acoustic monitoring data collected over multiple years by a large-scale network of passive acoustic recorders in the Atlantic sector of the Southern Ocean and in the South Atlantic Ocean[a]. In the following, I will first provide general background information on migration and will then elaborate on existing hypotheses on the driving factors of baleen whale migration.

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[a] The respective studies are presented as independent publications, see chapter 'Publications'.

1.1. What is migration?

In animal movement ecology, different (and partially overlapping) definitions of the term ‘migration’ exist, which differ in their dimensions, ecological perspectives and spatial or temporal scales (e.g. Dingle & Drake, 2007; Fryxell *et al.*, 2011; Dingle, 2014; Hansson & Åkesson, 2014). For the purpose of this thesis, I follow the definition developed by Kennedy (1985) and summarized by Dingle (2014). This definition considers migration as an individual movement that is straightened out or persistent, undertaken actively (by an animals’ locomotion) or passively (e.g. via air or water currents) and involves temporary suppression of (behavioral) responses to certain stimuli, such as resources or suitable habitats.

In general, migration represents a behavioral adaptation to variations in the quality of resources in space and time in order to optimize long-term survival and reproductive success (Dingle & Drake, 2007; Avgar *et al.*, 2014). Migratory behavior is most likely to occur in seasonal habitats and is expected to be evolutionary stable as long as different habitats exhibit seasonal variation in the conditions determining long-term fitness of the migratory animals (Avgar *et al.*, 2014). It is considered to have evolved independently in various (unrelated) taxa across the animal kingdom (Alerstam *et al.*, 2003; Dingle, 2006; Avgar *et al.*, 2014).

Animal migration is known to occur in a variety of forms, which can be classified based on whether the differences in migratory behaviors concern the spatial or temporal scales of migration (Table 1), or the organism itself (Table 2) (see also Dingle & Drake, 2007). Examples of spatial and temporal patterns in migration include the diel vertical migration of zooplankton, the one-way migration of insects undertaken once in a lifetime as well as the long-distance seasonal to-and-fro migration of birds, ungulates and baleen whales (e.g. Chapman *et al.*, 2014; Dingle, 2014).

Table 1: Overview of patterns in the migratory behavior of animals in space and time, modified after Dingle & Drake (2007).

Migratory patterns	Description
Spatial patterns	
one-way	migration between locations of birth & reproduction undertaken once in a life time
to-and-fro	migration between habitats varying in environmental conditions & suitability
round-trip	variant of to-and-fro migration where individuals head for several destinations
vertical/altitudinal	migration between different water depths / heights
nomadic	migration not exhibiting a regular pattern or route
Temporal patterns	
daily	migration undertaken on a daily basis
seasonal	migration undertaken on a seasonal basis
irruptive	migratory movements that are occasional and irregular

The patterns in the migratory behavior on organism level can be divided into three major categories, distinguishing between i) patterns that concern intra-individual differences in migratory behavior, ii) patterns that concern the migratory status of individuals within a population, and iii) migratory patterns that concern the migrating individuals of a population or species (see also Table 2). On an intra-individual level, migratory behavior can either be *obligate* or *facultative*, depending on whether migratory behavior remains stable or changes throughout the individual’s life. On a population-level, migration can be either *complete* or *partial*, depending on whether the population comprises only migratory individuals or both resident and migratory individuals. Furthermore, the migratory behavior of migratory individuals can be *uniform* or *differential* within a population, depending on whether the individuals exhibit the same migratory behavior or differ in their migratory patterns, e.g. in space or time. It is important to bear in mind that the different categories of migration are not necessarily exclusive, e.g. a *facultative* or an *obligate partial* migration may occur in a population. Furthermore, these categories of migration are not clearly distinct in all cases. The term *differential* migration for instance, has been used restricted to populations in which all individuals migrate, but can also be used as a modifier for migratory behavior in general (see Terrill & Able, 1988). In the present study, I have adopted the latter approach, since this allows taking into account that spatial or temporal differences in the migratory behavior may also occur in partially migrating populations.

Table 2: Basic framework of categories of migratory behavior applied in the present study. All categories concern the migratory species at organism level, i.e. represent patterns in the migratory behavior within or between individual animals of a population or species (see also e.g. Terrill & Able, 1988).

Category of migration	Definition
Intra-individual patterns in the migratory behavior	
Obligate migration	Migratory behavior of an individual remains stable throughout its entire life
Facultative migration	Migratory behavior of an individual may change depending on local conditions
Intra-population patterns in the migratory status between individuals	
Complete migration	All individuals of a population are migratory
Partial migration	Within-population dimorphism with population comprising both migrating and & resident individuals
Intra-population patterns in the migratory behavior between migrating individuals	
Uniform migration	Migratory patterns are equal among all individuals in a population or species
Differential migration	Migratory patterns differ among classes (e.g. sex, age) of migrating individuals in a population in time or space, or both

1.2. Why do baleen whales migrate?

Understanding the driving forces of long-distance migration has recently been identified as one of the key challenges in the movement ecology of marine megafauna (Hays *et al.*, 2016). A profound understanding of long-distance migration can provide crucial information on the cues that determine the migratory timing or the selection of specific migratory routes and destinations. Such insights can hence favor the development of much more effective conservation strategies for migratory species. Marine species often encounter seasonal fluctuations in environmental conditions that cause suitable habitats for foraging and breeding to occur in different, often distant locations, favoring migration between these habitats (Shaw & Couzin, 2013; Avgar *et al.*, 2014). In baleen whales, most species are generally considered to undertake long-distance migrations on a seasonal basis. They commute between their high-latitude feeding grounds, where they spend the summer foraging, and their breeding grounds located at lower latitudes, where the animals are thought to overwinter, mate and give birth to their calves (Fig. 1) (e.g. Lockyer & Brown, 1981). Nevertheless, the migratory behavior of baleen whales is most likely not obligate, uniform and complete, but is known to differ between individuals, populations and species, including facultative, partial and differential migration (see chapter 4).

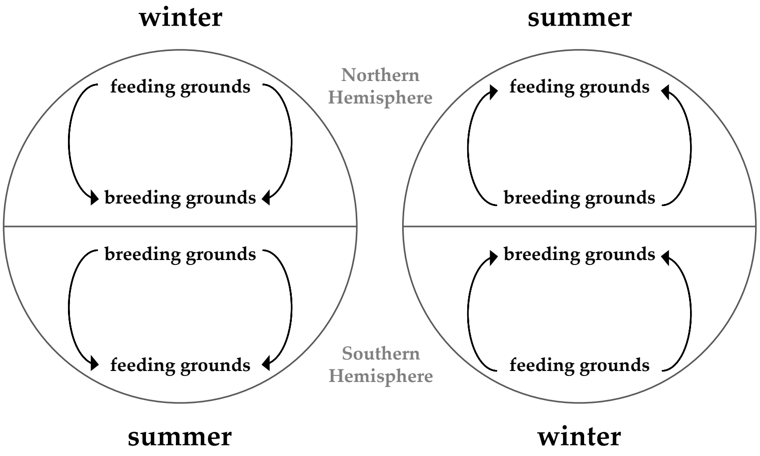

Fig. 1: *Generalized scheme of traditionally assumed migration patterns of baleen whales on the Northern and Southern Hemispheres in different seasons (after Mackintosh, 1966; Stern, 2009).*

The evolutionary drivers and reasons of baleen whale migration are still debated to date, and factors driving migration are also likely to differ between migratory directions: the poleward migration to cold, high-latitude waters is likely primarily driven by feeding opportunities, whereas the equatorward migration is likely mainly driven by an enhanced calf survival and development in warm(er), low-latitude waters (Corkeron & Connor, 1999; Clapham, 2001; Connor & Corkeron, 2001). In this context, it is mainly the equatorward migration of baleen whales out of the (seasonally) highly productive high-latitude waters that is the most remarkable and enigmatic. It is likely that an interplay of different factors has shaped the evolution and maintenance of migratory behavior in baleen whales, while the composition and importance of these factors likely largely differs between species. In the following, the most prominent hypotheses on the drivers of baleen whale migration are summarized (see also Fig. 2).

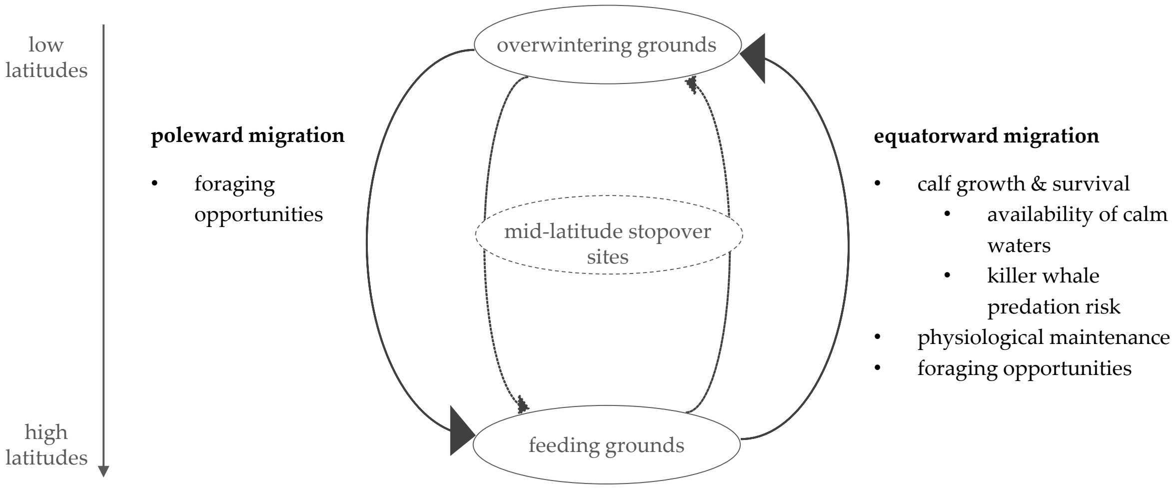

Fig. 2: *Overview of the most prominent hypothesis on factors driving (Southern Hemisphere) baleen whale migration between high-latitude feeding grounds and low-latitude breeding areas.*

Killer whale predation hypothesis: Corkeron & Connor (1999) stated the most likely selective advantage of the baleen whale equatorward migration to be the reduced predation pressure by killer whales (*Orcinus orca*) on the newborn calves and hence increased calf survival and female fitness in low-latitude waters. The distribution of mammal-eating killer whales is considered to be mainly determined by their primary dependence on pinniped prey (Baird *et al.*, 1992), which frequently occurs in polar and subpolar areas, but is comparatively sparse in tropical waters (Forney & Wade, 2006; Berta, 2009; Ropert-Coudert *et al.*, 2014). Accordingly, killer whale predation on neonate baleen whales is rarely observed in low-latitude waters and likely to make seasonal migration an evolutionary successful strategy (Corkeron & Connor, 1999; Connor & Corkeron, 2001). However, Clapham (2001) challenged this hypothesis by arguing that the occurrence of lethal attacks by killer whales on baleen whales represents rather occasional phenomena instead of a selective force shaping baleen whale behavior. Clapham (2001) argued that, instead of predation pressure being the evolutionary driver of baleen whale migration, a more favorable energy budget of calves born in warm waters may lead to an increased growth and, subsequently, future reproductive success of these calves and hence may represent the major selective force for the evolution of migratory behavior in baleen whales.

Calm water hypothesis: Environmental conditions in low-latitude areas offer calmer waters which likely contribute to a decreased energy expenditure by the calves and hence, enhance calf survivorship and fitness compared to the stormy waters of high-latitude areas (Corkeron & Connor, 1999). However, the ‘calm water hypothesis’ is likely mainly advantageous for calf survival in species that breed in shallow, coastal waters, e.g. humpback whales (*Megaptera novaeangliae*), southern right whales (*Eubalaena australis*) or gray whales (*Eschrichtius robustus*) (Reilly *et al.*, 2008b; Reilly *et al.*, 2008a; Reilly *et al.*, 2013). It may not necessarily apply to species such as Antarctic blue whales, which may breed in oceanic low-latitude areas farther from land (Mackintosh & Wheeler, 1929).

Resource tracking hypothesis: Exploration of seasonally available resources in mid latitudes has been suggested to be a driving factor of baleen whale migration towards lower latitude water during winter months by reducing the fasting period of baleen whales (Payne, 1995). Corkeron & Connor (1999) argued that this hypothesis is weakened by the observed presence of Antarctic minke whales (*Balaenoptera bonaerensis*) and humpback whales in polar waters during winter months and is unlikely to hold true at least for gray whales and humpback whales, which were rarely observed feeding in low-latitude waters. However, thanks to advancing tagging and tracking technology, feeding activities at mid-latitude ‘stopover sites’ have been observed during migration in several baleen whales, including blue whales, fin whales (*Balaenoptera physalus*) as well as humpback whales (e.g. Mate *et al.*, 1999; Bailey *et al.*, 2010; Silva *et al.*, 2013; Owen *et al.*, 2016). Hence, foraging opportunities may indeed lower the energetic costs associated with long-distance migrations in baleen whales.

Physiological maintenance hypothesis: Durban & Pitman (2011) suggested that periodical migration to warm waters serves the function of ‘physiological maintenance’, improving an individuals’ energy budget by allowing skin regeneration at lower metabolic costs in low-latitude waters. Although this hypothesis was developed based on observations of killer whales, the functionality of migration in physiological maintenance may possibly also hold true for baleen whales (Durban & Pitman, 2011).

Most likely, an interplay of several factors is driving baleen whale migration between high- and low-latitude waters and furthermore also mediates individual variations in migratory behavior (Fig. 2). Before further elaborating on baleen whale migration (chapter 4 and following), I will first provide background information on the methods with which baleen whale migration can be studied in the chapters 2 and 3, since such information is essential for further interpretation and discussion of my work.

2. STUDYING MIGRATORY BEHAVIOR OF BALEEN WHALES

A variety of methods has been applied to study movement patterns and migratory behavior of marine species, ranging from direct observations, identification based on natural or artificial markings and movement tracking approaches to passive acoustic monitoring. In a broader sense, research techniques to capture animal movement can be classified into Eulerian and Lagrangian approaches (Turchin, 1998). Eulerian approaches are based on observations from a specific, spatially confined location which the individuals of interest pass, while in Lagrangian approaches the observer follows a moving individual through time and space (Fig. 3) (Turchin, 1998). Lagrangian methods are used to quantify movements of individuals and can provide movement information at great detail, while Eulerian approaches quantify and characterize the redistribution and movements of populations or species over much larger temporal and spatial scales (e.g. Turchin, 1998; Chetkiewicz *et al.*, 2006; Nathan *et al.*, 2008).

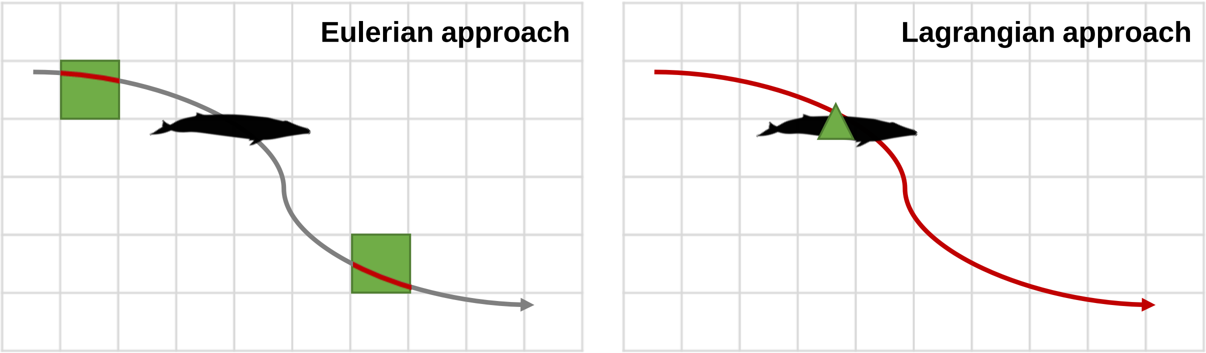

Fig. 3: *Exemplary generalized scheme of an Eulerian (left panel) and a Lagrangian (right panel) approach to study animal movements. In Eulerian approaches, the observer or receiver is restricted to a spatially confined location and is passed by moving individuals. In Lagrangian approaches, the observer or receiver follows the moving individual through space and time. Arrows indicate the movement of an exemplary individual with red parts indicating the portion of the individual movement that is captured by the respective receiver.*
(Whale icon made by Freepik from www.flaticon.com)

In the following, I will discuss the various methods used to investigate distribution and movement patterns of baleen whales, along with their respective advantages and disadvantages for studying a focal species' migratory behavior.

2.1. Lagrangian approaches

In the marine realm, several Lagrangian methods have been applied to obtain detailed information on the movements of individuals of the focal species, such as distance, speed, acceleration and directionality of movement. All of these methods are based on determining the positions of moving individuals in time and hence, are summarized as 'tracking' approaches in the following.

2.1.1. Tracking

Tracking bases on equipping individual animals with devices, which (directly or indirectly) locate the position of the individual at predefined time intervals and store the positional data until the device is retrieved (archival tags) or until transmission is possible (e.g. in satellite tags or telemetry approaches (see e.g. Wilson *et al.*, 2007; Costa *et al.*, 2012). Tagging and tracking approaches have been successfully used to study long-term patterns in the movements of marine animals, e.g. during the ‘Tagging of Pacific Predators’ (TOPP) project which was conducted under the auspices of the Census of Marine Life Program (‘COML’). This project involved different tagging approaches to investigate the movement behavior of marine megafauna, including cetaceans, pinnipeds, fishes and turtles (Block *et al.*, 2011; see also Costa *et al.*, 2012). With regard to baleen whales, satellite tracking in particular has become a common tool to track movements of individuals, locate migratory pathways and assess an individuals’ behavior during migration (e.g. Mate *et al.*, 1999; Bailey *et al.*, 2010; Double *et al.*, 2014; Prieto *et al.*, 2014; Garrigue *et al.*, 2015).

When studying marine species, tracking approaches face the challenge of determining the position of animals that spend most of their lives underwater (Wilson *et al.*, 2007; Dingle, 2014). Some methods (e.g. acoustic telemetry) are suitable to operate underwater, while other methods require the tagged individual to be at the surface for some time to obtain and transmit positional data, e.g. via satellite (Wilson *et al.*, 2007). Besides the need of transmitting positional data, tracking approaches are to a certain degree constraint by the necessity to attach the tags to the focal animals. In some cases also recovery of the device is necessary to obtain the archived data. Hence, tag deployment or recovery requires direct and close encounters with individuals of the focal species which can be particularly challenging in the case of baleen whales as they are highly mobile, spend most of their life under water, and their abundances are low. Tracking approaches are further complicated for focal species inhabiting areas that are remote or (seasonally) inaccessible or exhibit harsh environmental conditions, such as the seasonally ice-covered polar oceans.

2.2. Eulerian methods

Eulerian methods provide insights into population-level movement behavior by observing the redistribution of a large number of (marked or unmarked) individuals. These methods comprise visual observations, natural and artificial markings and passive acoustic monitoring.

2.2.1. Visual observations

Much of our current knowledge on baleen whales is based on visual sighting surveys, particularly on large-scale, long-term monitoring programs such as the International Decade of Cetacean Research (IDCR) and the Southern Ocean Whale Ecosystem Research (SOWER) programs, which were conducted from 1978 to 2010 (e.g. Branch & Butterworth, 2001b; Matsuoka *et al.*, 2003). These (and other) visual surveys provided valuable information on presence and distribution, potential breeding and feeding ground locations as well as migration and abundances of cetaceans (e.g. Kasamatsu *et al.*, 1995; Kasamatsu *et al.*, 1996; Branch & Butterworth, 2001b; Matsuoka *et al.*, 2006; Branch, 2007; Murase, 2014). Furthermore, visual surveys allow collecting additional critical data on the focal species that can hardly be collected otherwise, such as photographs for identification, health assessments as well as vital biological (biopsy or fecal samples) or behavioral information (e.g. Double *et al.*, 2015).

However, visual surveys are subject to several limitations, e.g. are only able to detect a fraction of the individuals present in an area (Mellinger *et al.*, 2007). In baleen whales, the frequently low abundances due to heavy exploitation by commercial whaling as well as their elusive and mobile life style generally lead to a low detection probability during visual surveys. Furthermore, visual observations are restricted by factors limiting visibility, such as rough seas, fog, rain and snow, and are strongly dependent on daylight conditions (e.g. Mellinger *et al.*, 2007). In species that inhabit remote or seasonally ice-covered waters, the logistic and financial efforts of accessing these areas constrain or impede data collection even further.

2.2.2. Natural and artificial markers

Studies using markers to investigate animal movements can be based on natural (biological or biogeochemical) markers or artificial markers (e.g. Rubenstein & Hobson, 2004).

In baleen whales, natural markings of individuals, e.g. color patterns or shape of flukes, fins or body parts, allow the identification and recognition of individuals (Samuels & Tyack, 2000) and have led to the establishment of comprehensive catalogues of individual identification photographs for several cetacean species (e.g. Allen *et al.*, 2006; Olson, 2012). Photo identification data have been successfully used to study movement patterns of cetaceans, including both baleen whales (e.g. Calambokidis *et al.*, 2001; Stevick *et al.*, 2013; Olson *et al.*, 2015) and toothed whales (e.g. Dahlheim *et al.*, 2008; Mizroch & Rice, 2013).

Apart from morphological markings, stable isotope signatures, which can be obtained from samples of muscle or, in case of mysticetes, baleen plate tissue, represent a natural biogeochemical marker (e.g. Best & Schell, 1996; Hobson & Schell, 1998; Lee *et al.*, 2005; Witteveen *et al.*, 2009). Stable isotope signatures of an animals' prey species exhibit spatial variations between different food webs (Hobson, 1999; West *et al.*, 2006). Differences in the isotopic signatures that are stored in the tissue of the animal can therefore be linked to geographical regions. Such differences can provide insights into the movements of an individual over different temporal scales, depending on the turnover rate of the storage tissue (Hobson, 1999; Rubenstein & Hobson, 2004).

Besides using natural markings to study distribution and migration of cetaceans, artificial markings were intensively applied under the framework of the Discovery marking program. Within this program, metal tubes (each equipped with a unique serial number) were fired into the muscles of whales. During commercial whaling, these tubes were recovered once a (marked) whale was taken, thus providing insights into the movement behavior of different baleen whale species (e.g. Brown, 1954; Branch *et al.*, 2007; Mizroch *et al.*, 2009).

Studies based on natural and artificial markers can provide valuable information on the distribution of baleen whales, minimum travel distances, migratory links between distinct habitats or connectivity between populations (e.g. Branch *et al.*, 2007; Mizroch *et al.*, 2009; Witteveen *et al.*, 2009; Olson *et al.*, 2015; Torres-Florez *et al.*, 2015; Stevick *et al.*, 2016). However, reliable information on population-level distribution patterns requires relatively large numbers of recaptured or re-sighted individuals.

Another caveat of marking approaches with regard to studying the migratory behavior of a species is the limited amount or coarse resolution of the data obtained. The actual trajectory of an individual cannot be inferred based on its positions during marking and recapture (or sighting and re-sighting). Thus, depending on the time span between marking and recapture, observations based on markings provide comparatively coarse data on movement patterns of a focal species. This applies particularly to data of the Discovery marking program, which only provided two positional data points for each recaptured whale, i.e. the position of marking deployment, and the position of recapture, i.e. catch of the marked individual (see e.g. Brown, 1954). Stable isotope data can provide information on the areas where a whale foraged and hence, on movements between areas, however, the resolution of these information strongly depends on the spatial scale of variation between the isotopic signatures of different local food webs (e.g. Hobson, 1999; Dingle, 2014). Furthermore, similar to visual sighting surveys, marking approaches require (repeated) direct encounters with the focal individuals and can hence be considerably affected by environmental conditions determining an area's accessibility or the visibility conditions during the study.

2.2.3. Passive acoustic monitoring

Passive acoustic monitoring ('PAM') provides an important, non-invasive method to study baleen whale species. The range of PAM applications comprises e.g. the monitoring of fine-scale behavior (e.g. Goldbogen *et al.*, 2013) and behavioral responses to human activities (e.g. Di Iorio & Clark, 2010; Parks *et al.*, 2011; Hatch *et al.*, 2012; Risch *et al.*, 2012), the investigation of large-scale spatio-temporal patterns in occurrence, distribution and migration (e.g., Mellinger et al., 2007; Van Parijs et al., 2009, Au & Lammers 2016), as well as the estimation of density and abundance of marine mammal species in an area (e.g. Küsel *et al.*, 2011; Thomas & Marques, 2012; Marques *et al.*, 2013). By applying autonomous passive acoustic recording devices, PAM is highly amenable for long-term data collection. Seasonally unbiased multi-year data are particularly important to investigate long-term and large-scale spatio-temporal patterns in a focal species' presence, distribution and habitat use in remote areas, such as the polar oceans (e.g. Van Opzeeland *et al.*, 2013b; Clark *et al.*, 2015; Nowacek *et al.*, 2016; Publications III and IV). PAM is therefore suitable to study patterns in the distribution and migration of vocalizing, potentially rare, marine mammal species inhabiting remote areas, such as the Antarctic blue whale. The advantages and limitations of PAM techniques in this respect will be discussed in the next chapter.

3. PASSIVE ACOUSTIC MONITORING TO STUDY ANTARCTIC BLUE WHALE DISTRIBUTION AND MIGRATION

PAM provides valuable insights into patterns in the (acoustic) presence and distribution of vocalizing marine mammal species over large spatial and temporal scales. Particularly in remote, seasonally inaccessible areas where research is hampered by high logistic and financial costs that impede year-round visual data collection, PAM can provide a versatile alternative to traditional methods (Mellinger *et al.*, 2007).

PAM is particularly well suited to study Antarctic blue whales based on the species' unique vocal behavior, characterized by the production of stereotyped, subspecies-specific vocalizations, which are presumably produced year-round (e.g. Ljungblad *et al.*, 1998; Širović *et al.*, 2004). Antarctic blue whales are widely distributed across high-, mid- and low-latitude waters of the Southern Hemisphere (Reilly *et al.*, 2008c). The species is hard to study based on visual sightings or immediate encounters alone because of its highly mobile, elusive life style and the often remote, and in part seasonally ice-covered habitats. Furthermore, the abundance of Antarctic blue whales is low as a result of heavy exploitation during the commercial whaling era in the 20th century (Tønnessen & Johnsen, 1982; Branch *et al.*, 2004). Their relative scarcity further constrains the probability of detecting Antarctic blue whales using visual sighting methods. Hence, knowledge of their abundance and population recovery, as well as of distribution patterns and migratory behavior is still scarce to date. PAM provides a relatively cost-effective method to collect data on patterns in the acoustic presence of Antarctic blue whales at large temporal and spatial scales.

3.1. Acoustic behavior of Antarctic blue whales

Blue whale subspecies worldwide are known to produce specific, often stereotyped, low-frequency vocalizations (McDonald *et al.*, 2006). These vocalizations exhibit geographic variations and at least 9 acoustically distinct blue whale populations have been described to date (Fig. 4) (McDonald *et al.*, 2006; Širović *et al.*, 2016).

Antarctic blue whales produce several types of low-frequency vocalizations, with the 'Z-call' (named after its spectrographic shape) being the most prominent vocalization (Fig. 5). Z-calls are highly stereotypic in frequency and time and are composed of three units (in the following named as units A, B and C). A Z-call starts with a tonal signal in the 26 – 28 Hz range lasting for about 8 – 10 s (unit A), which is followed by a downsweep of about 1 – 2 s to ca. 19 Hz (unit B) and a slightly frequency-modulated signal (decreasing from 19 to 18 Hz) of about 8 – 12 s duration (unit C) (Ljungblad *et al.*, 1998). Nevertheless, also calls consisting of 1 (unit A) or 2 units (units A and B) are recorded (Rankin *et al.*, 2005), yet it remains unclear whether this is an artefact of the respective environmental acoustic conditions. Vocalizations that are produced by distant Antarctic blue whales deteriorate with increasing distance, resulting in a tonal 'chorus' within the 26 – 28 Hz frequency band (Gedamke *et al.*, 2007). This chorus can be used as an alternative measure of Antarctic blue whale (acoustic) presence throughout a broader area (Fig. 5) (see Publications III and V).

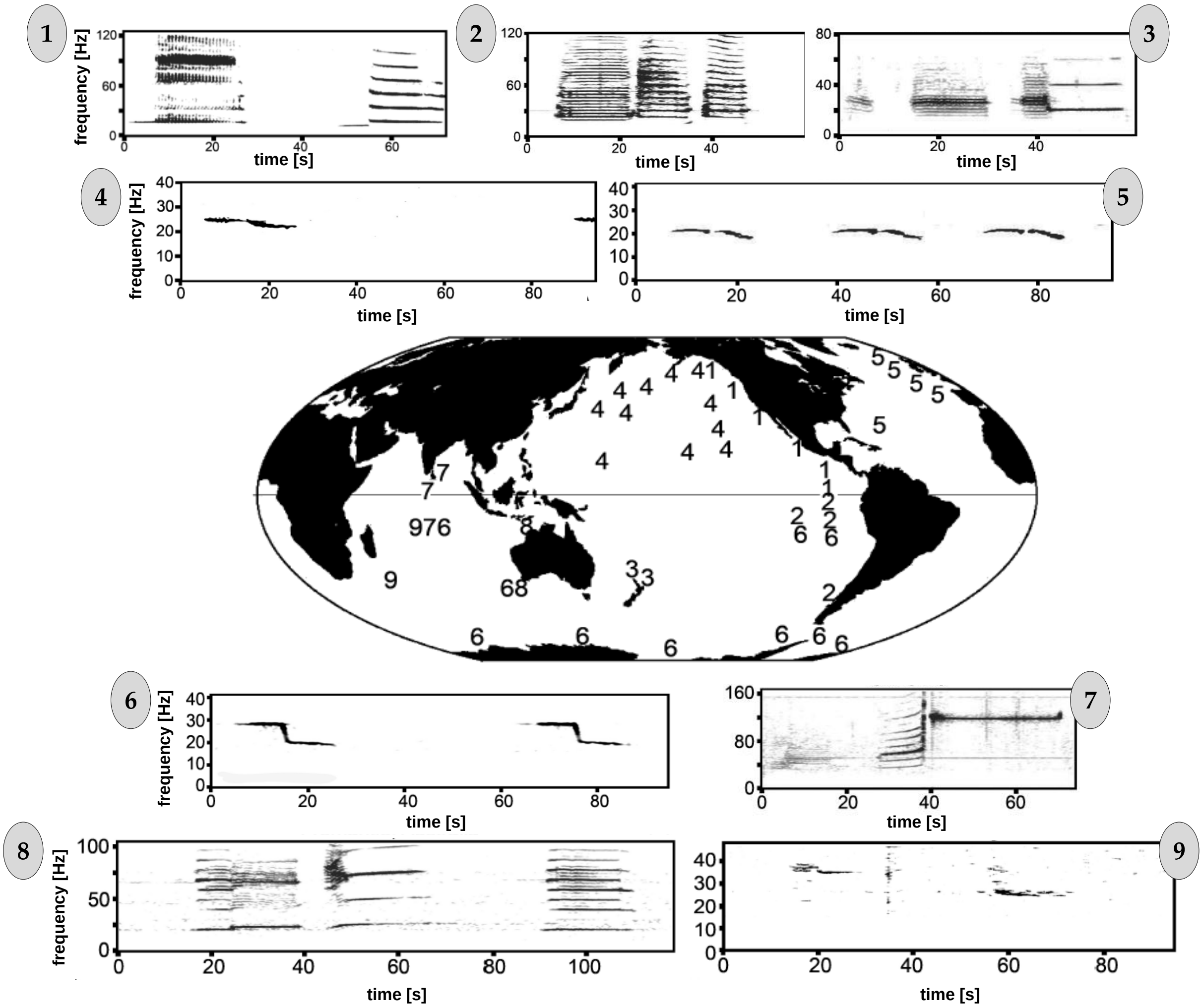

Fig. 4: Worldwide distribution of different blue whale song types with exemplary spectrogram views of song types from different regions. Numbers refer to regional designations of acoustically distinct song types as defined in McDonald et al. (2006, Table 1): 1 - Northeast Pacific, 2 - Southeast Pacific, 3 - Southwest Pacific, 4 - North Pacific, 5 - North Atlantic, 6 - Southern Ocean, 7 - North Indian, 8 - Southeast Indian, 9 - Southwest Indian. Figures taken from McDonald et al. (2006), with permission of the authors.

Antarctic blue whale Z-calls are often produced in long, repetitive patterns, with inter-call intervals of about 62 s (Širović *et al.*, 2004). These repetitive calling patterns of Antarctic blue whales are considered song, in accordance with Broughton (1963) who defined song as "[…] a series of notes, generally of more than one type, uttered in succession and so related as to form a recognizable sequence or pattern in time". In analogy to other baleen whales' song, Antarctic blue whale song is presumed to represent a male reproductive display (e.g. Tyack, 1981; Croll *et al.*, 2002; Oleson *et al.*, 2007). Nevertheless, Z-call production is not restricted to (presumed) low-latitude breeding grounds or breeding seasons, but has been reported year-round in high-, mid- and low-latitude waters (Širović *et al.*, 2004; Samaran *et al.*, 2013; Leroy *et al.*, 2016; Publications III and V). These findings potentially indicate that (acoustic) behaviors related to reproduction are not restricted to specific seasons or habitats (see also Clark & Clapham, 2004; Vu *et al.*, 2011).

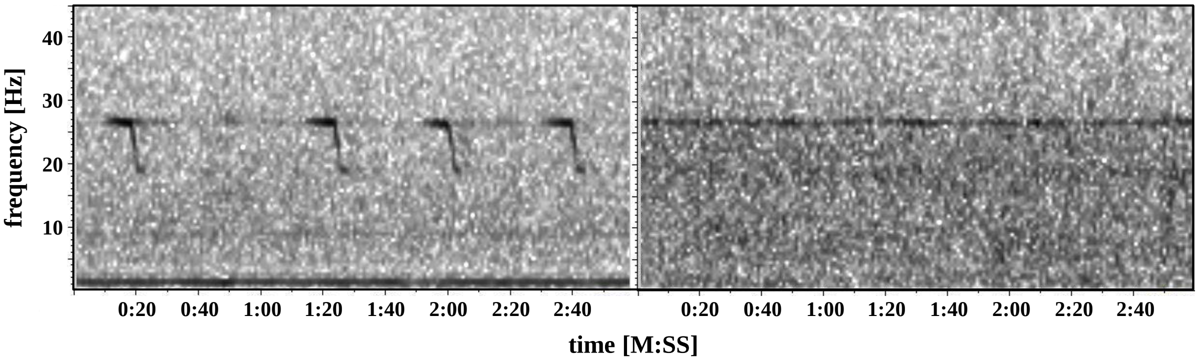

Fig. 5: *Spectrogram view of Antarctic blue whale song sequence composed of Z-calls (left panel) and Antarctic blue whale chorus (right panel) recorded on 12 December 2010 at 59° 03' S, 0° 07' E and 10 March 2011 at 66° 37' S, 27° 08'W, respectively (sample rate 250 Hz [after downsampling]; spectrogram settings: FFT 512 points, Hanning window, 50% overlap). Figure taken from Thomisch et al. (2016) (Publication III).*

The peak frequency of vocalizations of Antarctic blue whales (and other blue whale populations) is subject to shifts both within and between years (McDonald *et al.*, 2009; Gavrilov *et al.*, 2011; Miller *et al.*, 2014a; Miller *et al.*, 2014b; Publication VI). A long-term decrease in the calling frequency has been reported in blue whale populations worldwide (McDonald *et al.*, 2009; Gavrilov *et al.*, 2011; Gavrilov *et al.*, 2012; Miller *et al.*, 2014a). In Antarctic blue whales, the frequency of Z-call unit A has been found to decrease by about 0.1 Hz per year (Gavrilov *et al.*, 2012; Publication VI). In the Weddell Sea, the general decreasing trend was evident in both unit A und unit C of single Z-calls and the Antarctic blue whale chorus (Publication VI). Publication VI further indicates that between 2008 and 2013 the inter-annual decrease in the peak vocalization frequency occurred at a slower rate than in previous records. This may indicate spatial differences between recording sites or a deceleration in the inter-annual decline of the Antarctic blue whale vocalization frequency over time (Publication VI). Besides the inter-annual trend, the peak frequency of Z-calls also varies over the course of a season, with maximum peak frequencies in austral summer and minimum values during austral autumn and winter months (Gavrilov *et al.*, 2012; Miller *et al.*, 2014b; Publication VI). The reasons for the observed inter- and intra-annual patterns in the vocalization frequency remain poorly understood, with potential explanations including variations in population size, sexual selection, body condition, vocalization depth, as well as Doppler shift, migratory patterns and global change (McDonald *et al.*, 2009; Gavrilov *et al.*, 2012; Miller *et al.*, 2014b).

Alongside Z-calls, Antarctic blue whales and other blue whale populations produce frequency-modulated downsweep calls (further referred to as ‘FM-calls’, Fig. 6), which are highly variable in duration, frequency range and, hence, spectrographic shape (Rankin *et al.*, 2005; Oleson *et al.*, 2007; Samaran *et al.*, 2010; Double *et al.*, 2015). Blue whale FM-calls range between 22 and 107 Hz with bandwidths of 12 to 66 Hz, lasting from 0.8 to 7.5 s (McDonald *et al.*, 2001; Rankin *et al.*, 2005; Gavrilov *et al.*, 2011).

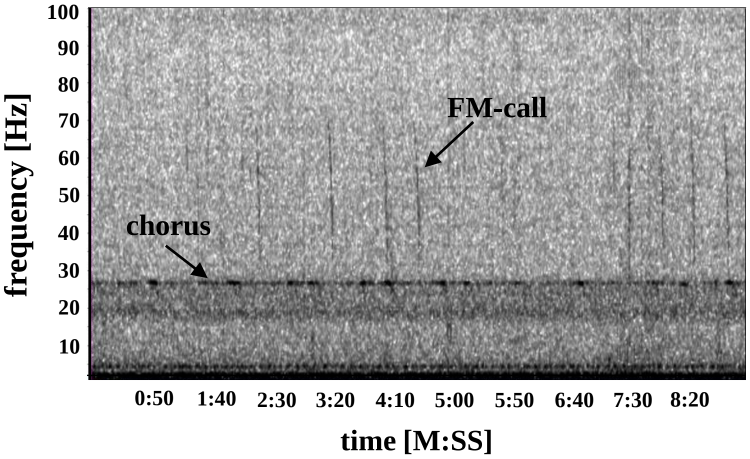

Fig. 6: *Spectrogram view of Antarctic blue whale frequency-modulated (FM) calls (in the frequency range 35-70 Hz) recorded on 24 March 2011 at 66° 02'S, 0° 03'E (sample rate 250 Hz [after downsampling]; spectrogram settings: FFT 512 points, Hanning window, 50% overlap).*

In the Northern Hemisphere, FM-calls are produced by both sexes within groups of foraging blue whales (Oleson *et al.*, 2007). FM-calls are therefore thought to be related to social interactions of blue whales, potentially functioning as contact calls, rather than being related to reproduction (McDonald *et al.*, 2001; Oleson *et al.*, 2007). Downsweep calls that resemble blue whale FM-calls in frequency range, duration and spectrographic shape are also produced by other baleen whale species, e.g. Antarctic minke whales, fin or sei whales (*Balaenoptera borealis*) (see Publication IV for further details). The functionality of baleen whale downsweep calls is not well understood to date and they have been hypothesized to function in maintaining spacing between individual whales and might contribute to a reduced competition for food (Edds-Walton, 1997; 2000). In this context, the similarity of downsweep calls among several baleen whale species might indicate a both intra- and inter-specific importance and functionality of downsweep calls (see Publication IV).

3.2. Opportunities and constraints of PAM for studying distribution and migration patterns

3.2.1. Opportunities

PAM features several advantages over visual observations, for example allowing data collection under adverse weather conditions and during darkness. PAM can be implemented using autonomous recorders, which are increasingly able to collect continuous data over multiple years, further extending the advantages of this method to application in remote or seasonally inaccessible areas (e.g., Mellinger *et al.*, 2007; Rettig *et al.*, 2013; Sousa-Lima *et al.*, 2013; Van Opzeeland *et al.*, 2013b; Publications III, IV and VI). PAM further enables distinction and identification of blue whales on subspecies- and population-level based on their acoustic behavior (McDonald *et al.*, 2006). This is of particular relevance for distinguishing the two subspecies of blue whales inhabiting the Southern Hemisphere, Antarctic blue whales and pygmy blue whales (*Balaenoptera musculus brevicauda*). These two subspecies are morphologically similar and hence at-sea subspecies identification can be difficult (Branch *et al.*, 2009), but they differ in their vocal behavior (McDonald *et al.*, 2006; Širović *et al.*, 2016).

PAM can provide insights into the distribution patterns and migratory behavior of Antarctic blue whales and other baleen whales, which would be hard or impossible to acquire based on visual surveys alone. For instance, simultaneous recordings of the acoustic presence of Antarctic blue whales in the Pacific and Indian Ocean during austral winter revealed the existence of several migratory destinations for Antarctic blue whales at low latitudes (Stafford *et al.*, 2004). Furthermore, PAM data collected in polar waters during winter have confirmed observations from whaling data, showing that at least a fraction of the population of some baleen whales is most likely to overwinter in polar waters on a regular basis (Van Opzeeland *et al.*, 2013b; Publication III) (see also chapter 4.2). Recently, PAM has successfully been used to localize and track Antarctic blue whales in the Southern Ocean (Miller *et al.*, 2015). Thereby, PAM did not only provide detailed knowledge on the Antarctic blue whale fine-scale distribution in the Southern Ocean, but at the same time enabled additional, direct observations and data collection (e.g. photo-identification, biopsies and satellite-tagging of individuals) (e.g. Double *et al.*, 2013; Double *et al.*, 2015; Miller *et al.*, 2015).

Information on the acoustic presence of a focal species in an area can directly benefit conservation applications, such as the designation of marine protected areas or the mitigation of human impacts on marine species (e.g. Van Parijs *et al.*, 2009; Clark *et al.*, 2010; Mussoline *et al.*, 2012; Parks *et al.*, 2014). In the North Atlantic Ocean, (near)real-time passive acoustic data are being used to mitigate ship strikes of large baleen whales (e.g. Van Parijs *et al.*, 2009). More recently, the Northeast Passive Acoustic Network (‘NEPAN’) project combines stationary and mobile, archival and real-time passive acoustic devices and will provide large-scale, long-term year-round data on acoustic presence and distribution of vocal cetaceans and fish (Van Parijs *et al.*, 2015). Such insights can subsequently considerably benefit conservation and mitigation applications (Van Parijs *et al.*, 2009; Van Parijs *et al.*, 2015).

3.2.2. Constraints

Despite its many advantages, PAM is nevertheless subject to several biological, physical and methodological constraints. These constraints need to be taken into account when interpreting PAM data, particularly in terms of estimating local animal densities and abundances, but also with respect to a species’ distribution or migratory behavior.

First of all, PAM techniques provide ‘presence-only’ data as they essentially depend on the presence and vocalizations of the target species, while acoustic absence could represent either physical absence or acoustic inactivity. In this context, knowledge of the species-specific vocal signatures is mandatory to be able to reliably attribute a sound to its respective source (e.g. Risch *et al.*, 2014). The acoustic ecology of a species is a function of a variety of factors, which all influence the species’ acoustic behavior. These factors include a species’ behavioral ecology (such as the mating system or the distribution of the species), biotic factors (in terms of prey and predators), abiotic factors (such as the site-specific acoustic environment of the study area) as well as anthropogenic factors (e.g. underwater noise) (Van Opzeeland, 2010). PAM data therefore need to be interpreted in the context of the acoustic ecology of the focal species in a regionally and seasonally appropriate context.

Second, PAM is subject to a variety of site-specific and (partly) seasonally fluctuating physical factors that influence the signal detection range. The area monitored by a passive acoustic device can vary substantially, based on variations in, e.g. sound speed profile, bathymetry, sediment type, ice coverage or ocean noise levels in space and time (e.g. Urick, 1983; Helble *et al.*, 2013). An understanding of the monitored area is however essential to be able to estimate the spatial scale covered by PAM, e.g. to assess whether the passive acoustic data are reflective of larger parts of a population inhabiting an area or of single individuals residing near a respective recorder. Additionally, when comparing data from different recorders, locations or study periods, knowledge of the respective detection ranges is crucial.

Finally, recorder settings also affect the representativeness of passive acoustic data. Subsampling of passive acoustic data for instance can result in false representation of the acoustic behavior of a focal species and hence can cause misinterpretations of the species' presence or distribution in an area, as discussed in detail in Publication I (see also Riera *et al.*, 2013; Stanistreet *et al.*, 2016).

Overall, a variety of factors might (directly or indirectly) affect PAM data collection and interpretation. Hence, a thorough consideration of these factors and their potential impact on PAM data collection or interpretation is crucial to avoid biasing inferences on the (acoustic) ecology of a focal species.

4. BALEEN WHALE MIGRATION: SEASONAL DISTRIBUTION AND MIGRATORY BEHAVIOR OF ANTARCTIC BLUE WHALES IN CONTEXT

4.1. The baleen whale migration paradigm

Early work on baleen whale migration, e.g. by Kellogg (1929) or Mackintosh & Wheeler (1929), has often been interpreted to imply that in both hemispheres most baleen whale species share a general tendency to undertake a to-and-fro migration between feeding grounds at higher latitudes and breeding habitats at lower latitudes on an annual basis. This generalized ‘migration paradigm’ is based on several observations. First, the seasonal variations in whale abundance on Southern Ocean whaling grounds, with peak whale abundances during austral summer and few whales present during winter, were considered indicative of migratory movements (e.g. Mackintosh & Brown, 1956). Second, direct observations of baleen whale species migrating nearshore showed a bimodal, strongly directional pattern shifting between northward and southward movements during the course of the year (e.g. Lockyer & Brown, 1981). Finally, examinations of whales caught off South Georgia showed large quantities of food contained in their stomachs, while stomachs of whales caught in the Atlantic Ocean off Saldanha Bay (South Africa) during winter contained little or no food (Mackintosh & Wheeler, 1929). These observations suggested that baleen whales primarily forage in high latitudes during summer and fast in low-latitude areas during winter (Mackintosh & Wheeler, 1929; Dawbin, 1966).

However, to date evidence is increasing that a generalized migration model assuming a complete, obligate and uniform annual migration in baleen whales is overly simplistic and unlikely to hold true for most baleen whale species (see e.g. Geijer *et al.*, 2016). Early whaling data already implied baleen whale migratory behavior to be more diverse, potentially including partial and differential migration (e.g. Ingebrigsten, 1929; Kellogg, 1929; Mackintosh & Wheeler, 1929; Harmer, 1931; Hjort *et al.*, 1932; Branch *et al.*, 2007). Recently, Geijer *et al.* (2016) reviewed existing data on migration patterns of fin and other baleen whales and suggested that the migratory behavior of baleen whales should be considered a continuum of different strategies. In this context, a complete migration likely represents only one end of the spectrum of baleen whale migratory behavior, while complete residency represents the other end (Geijer *et al.*, 2016).

4.2. Distribution and migratory behavior of Antarctic blue whales

4.2.1. High-latitude feeding areas

In the Southern Ocean, Antarctic blue whales have been reported to exhibit a circumpolar distribution during austral summer, including the waters off the Western Antarctic Peninsula, in the Lazarev Sea off Queen Maud Land, off eastern Antarctica and in the Ross and Weddell Sea (e.g. Širović *et al.*, 2004; Rankin *et al.*, 2005; Gedamke *et al.*, 2007; Širović *et al.*, 2009; Gedamke & Robinson, 2010; Findlay *et al.*, 2014; Miller *et al.*, 2015; Publication II). They are thought to occur close to the ice edge on their Southern Ocean feeding grounds, with their movements likely being determined by the formation and retreat of sea ice (Kasamatsu *et al.*, 2000; Širović *et al.*, 2004).

Data on Antarctic blue whale occurrence obtained during the commercial whaling era already implied that their migratory behavior includes partial and differential migration instead of being complete and uniform for all individuals (Mackintosh & Wheeler, 1929; Harmer, 1931; Hjort *et al.*, 1932). Discovery marks[b] indicated that large-scale, longitudinal movements between feeding areas in the Southern Ocean regularly occurred both intra- and inter-annually, implying a circumpolar connectivity of Antarctic blue whales (Brown, 1962; Branch *et al.*, 2007). Year-round catches of blue whales off South Georgia (site 1 in Fig. 7) indicated that some individuals were present on the Southern Ocean feeding grounds during austral winter as well (Harmer, 1931; Hjort *et al.*, 1932; Branch *et al.*, 2007), potentially indicating a partial migration in Antarctic blue whales (Table 3). Furthermore, the composition of the blue whale population on the Antarctic whaling grounds changed during austral summer, with adult whales predominating the population early in the season, while juvenile individuals and lactating females with dependent calves arrived on the feeding grounds not until February (Mackintosh & Wheeler, 1929). These observations implied a differential migration in Antarctic blue whales, resulting in a continuous, temporally staggered movement of Antarctic blue whales to and from the Southern Ocean (Table 3). Besides differences in migratory timing, different age- and sex-classes of Antarctic blue whales have also been suggested to differ in their migratory routes and destinations (Mackintosh & Wheeler, 1929; Harmer, 1931; Hjort *et al.*, 1932).

Post-whaling studies provided further insights into the spatio-temporal patterns in Antarctic blue whale occurrence and distribution, supporting earlier observations of a versatile migratory repertoire in Antarctic blue whales (see also Table 3). Findings based on photo-identification and satellite tagging are in line with the Discovery mark data, implying that Antarctic blue whales undertake longitudinal movements between different feeding areas within seasons (Andrews-Goff *et al.*, 2013; Olson *et al.*, 2016). Further evidence for a diverse migratory repertoire in Antarctic blue whales stems from passive acoustic studies. Seasonal patterns in the acoustic presence of Antarctic blue whales in the Southern Ocean often exhibited a peak in the detected call numbers during austral summer (Širović *et al.*, 2004; Gedamke *et al.*, 2007; Širović *et al.*, 2009; Publication III). This could indicate seasonal variation in the abundance of (calling) whales related to migration. Off the Western Antarctic Peninsula (site 2 in Fig. 7), however, Antarctic blue whales were found acoustically present year-round as indicated by the presence of Z-calls (Širović *et al.*, 2004; Dziak *et al.*, 2015), potentially reflecting a differential, temporally segregated migration of Antarctic blue whales (see also Kasamatsu *et al.*, 1996). Alternatively, some (presumably adult) individuals may forego migration and overwinter on their feeding grounds off the Western Antarctic Peninsula (Širović *et al.*, 2004; see also Harmer, 1931; Hjort et al. 1932). In the Weddell Sea and along the Greenwich meridian (sites 3-4 in Fig. 7), passive acoustic data indicate a wide distribution of Antarctic blue whales both during summer and winter (Publications III and IV). A clear seasonality in the acoustic presence of Antarctic blue whale Z-calls (Publication III) and FM-calls (Publication IV) was evident at all recording sites. Acoustically, Antarctic blue whales were most frequently present between December and April, while their acoustic presence decreased between May and October, consistent with previous studies in the Southern Ocean (Širović *et al.*, 2004; Gedamke *et al.*, 2007; Širović *et al.*, 2009) (see also sites 5-7 in Fig. 7). Nevertheless, Antarctic blue whale Z-calls were present during austral winter at latitudes as high as 69°S, where the sea ice cover exceeded 90%, hence, Publication III provides the southernmost record of Antarctic blue whales in the Southern Ocean during winter. Since such high ice concentrations likely inhibit large-scale, latitudinal movements of Antarctic blue whales to and from the Southern Ocean, the acoustic winter presence is presumably indicative of a partial migration of Antarctic blue whales, with part of

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[b] See also chapter 2.2.2. For Antarctic blue whales, a total of only 104 out of 2295 deployed marks (i.e. metal tubes fired into the muscles of the whales) has been recovered within the Discovery mark program (Branch *et al.*, 2007).

the population skipping migration to lower latitudes during austral winter (Publications III and IV). In making these inferences, it has to be kept in mind that Z-calls are presumed to be a male reproductive display, hence Z-call presence most likely only indicates the presence of (possibly only reproductively active) male Antarctic blue whales, while FM-calls are thought to be produced by both sexes (Oleson *et al.*, 2007).

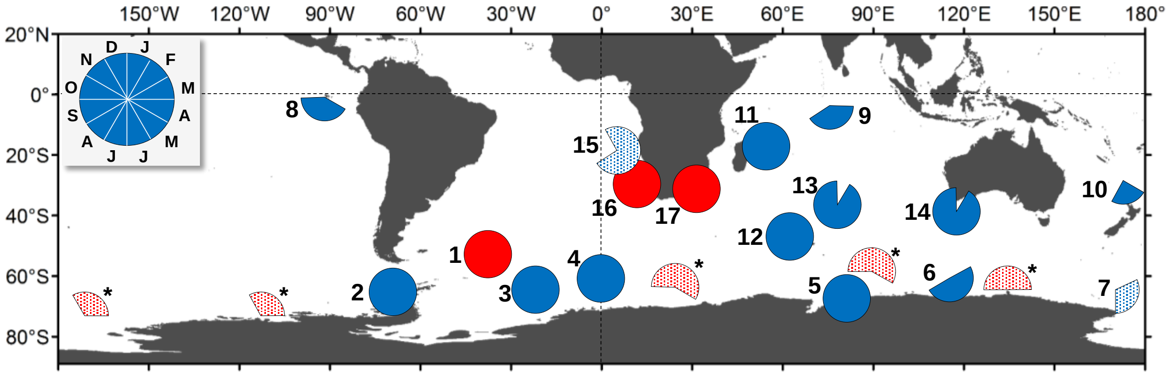


Fig. 7: *Overview of spatial and temporal patterns in the presence of Antarctic blue whales in the Southern Hemisphere based on PAM data (circles and sectors colored in blue) and whaling (circles colored in red; largely based on information reviewed by Branch et al. (2007)). Appearance of circles indicates period of Antarctic blue whale (acoustic) presence in an area, with colored parts indicating months with Antarctic blue whale presence (see legend in upper left corner). Full circles imply year-round presence, while colored sectors indicate that Antarctic blue whales were not present year-round. Numbers indicate different study sites (see also main text and Table 3). Circles with blue hatching indicate sites where PAM data did not cover an entire year. Circles with red hatching indicate whaling grounds close to the Antarctic continent that were inaccessible during austral winter due to heavy ice coverage. See also Branch et al. (2007) for further information on spatial and seasonal distribution of blue whale catches in the Southern Ocean.*

Publication IV provides the first study of seasonal patterns in the presence of Antarctic blue whale FM-calls over large temporal and spatial scales in the Southern Ocean. FM-calls were present at 59°S during austral winter, but largely absent south of 60°S between May and November (Publication IV). Given that the sea ice edge was located close to 59°S during winter months, the winter presence of FM-calls may represent individuals that overwinter in or near the sea ice edge area (Publication IV). Alternatively, the observed acoustic winter presence at 59° may be explained by a time-lagged, differential migration, e.g. causing overlap in the timing of departure and arrival of Antarctic blue whales to and from the sea ice edge. Given the persistent presence of Z-calls indicates Antarctic blue whale year-round presence in the Southern Ocean, the (near-)absence of FM-calls south of 60°S during austral winter may reflect differences in the spatial scale at which Z-calls and FM-calls are representative of Antarctic blue whale acoustic presence. Alternatively, the observed pattern might indicate a change in the species' (vocal) behavior with regard to FM-calls (Publication IV).

Overall, Antarctic blue whales occur on their high-latitude feeding grounds year-round (sites 1-5 in Fig. 7), possibly inhabiting areas near the sea ice edge or open water areas during winter. There is increasing evidence of a partial migration in Antarctic blue whales, with a fraction of the population skipping migration to lower latitudes during winter months. However, it is not understood to date which individuals may remain on the feeding grounds and whether (and to which extent) facultative residency on the feeding grounds forms a common trait in an individuals' life.

4.2.2. Overwintering areas in mid- and low-latitude waters

Knowledge on the location of wintering areas of Antarctic blue whales is still scarce to date, but several migratory destinations of Antarctic blue whales are likely to be located in low-latitude waters (Stafford *et al.*, 2004). Migratory links have been proposed between the Southern Ocean and several temperate or tropical locations, including the eastern Indian Ocean off Southern Australia (Gedamke *et al.*, 2007; Tripovich *et al.*, 2015), the central and southern Indian Ocean (Stafford *et al.*, 2004; Samaran *et al.*, 2013; Leroy *et al.*, 2016), the Eastern Tropical Pacific Ocean (Stafford *et al.*, 2004), the western South Pacific Ocean (McDonald, 2006) and the South Atlantic Ocean (Best, 2007; Publication V) (see also Table 3). In the Pacific and Indian Oceans (sites 8-10 in Fig. 7), seasonal patterns in the acoustic presence may be indicative of Antarctic blue whales seasonally inhabiting or passing these regions en route to their feeding and wintering areas, respectively (Stafford *et al.*, 2004; McDonald, 2006; Tripovich *et al.*, 2015; Leroy *et al.*, 2016). Nevertheless, Antarctic blue whales were acoustically present year-round or almost year-round in the central, eastern and southern Indian Ocean (sites 11-14 in Fig. 7), as indicated by Z-calls (Samaran *et al.*, 2013; Tripovich *et al.*, 2015; Leroy *et al.*, 2016). Year-round presence of Antarctic blue whales in mid- and low-latitude waters may either be caused by individuals skipping the poleward migration or by a temporally staggered, continuous movement of whales to and from these areas. Hence, these findings provide further confirmation that the migratory behavior of Antarctic blue whales includes partial or differential migration, or a combination of both (Table 3). In the eastern Atlantic Ocean, and in particular the Angola Basin, the absence of a bimodal pattern in blue whale catches indicates that the waters off Namibia may represent the northern limit of Antarctic blue whale migration in the eastern Atlantic Ocean (Best, 2007). Recently, passive acoustic data indicated that Antarctic blue whales are acoustically present from November to at least August in the waters off Namibia (site 15 in Fig. 7), with peak acoustic presence during June, i.e., austral winter (Publication V). Hence, the eastern Atlantic Ocean, particularly the Angola Basin area, may serve as an important wintering and breeding area for Antarctic blue whales, and other baleen whale species (Stafford *et al.*, 2004; Best, 2007). Historic winter catch data reported year-round presence of Antarctic blue whales off eastern and western southern Africa (site 16-17 in Fig. 7) (Mackintosh & Wheeler, 1929; Branch *et al.*, 2007). In line with these whaling data, the continuous (acoustic) presence of Antarctic blue whales in low-latitude waters off southern Africa during both summer and winter indicates that some individuals skip migration to higher latitudes (site 15-17 in Fig. 7). Alternatively, a differential, temporally staggered migration may cause continuous presence of Antarctic blue whales in these waters (Publication V) (Table 3). Based on the observation that juvenile individuals with poor body conditions predominated the winter catches off Namibia, Mackintosh & Wheeler (1929) suggested that these juveniles may not have migrated to higher latitudes but remained on the breeding grounds during their first summer, i.e. implying (facultative) partial migration of Antarctic blue whales off Namibia.

In conclusion, there is currently increasing evidence of a diverse migratory behavior featuring different migratory strategies in Antarctic blue whales, similar to the migratory behavior of fin whales and other baleen whales (Geijer *et al.*, 2016). PAM has been particularly insightful for obtaining information on the distribution of Antarctic blue whales, by showing their concurrent (acoustic) presence in high, mid, and low latitudes both seasonally and year-round (Širović *et al.*, 2004; Samaran *et al.*, 2013; Leroy *et al.*, 2016; Publications III, IV and V). These findings indicate that, instead of undertaking a complete and uniform seasonal migration between high-latitude summer feeding grounds and low-latitude overwintering and breeding habitats, Antarctic blue whales are likely to exhibit a migratory behavior that includes partial and differential migration. There is currently no evidence for (truly) resident Antarctic blue whale populations in the Southern Ocean or elsewhere, although a resident population may exist (or may have existed) in the Southern Ocean (Attard *et al.*, 2016) (Table 3). The year-round acoustic presence recorded in the Weddell Sea (Publications III and IV), off the Western Antarctic Peninsula (Širović *et al.*, 2004), off eastern Antarctica (Širović *et al.*, 2009) and in the Indian Ocean (Leroy *et al.*, 2016) is likely to reflect facultative residents that occasionally skip migration to lower latitudes. However, it should not be excluded that these observations possibly also represent remainders of former resident Antarctic blue whale populations that were drastically depleted during commercial whaling, in analogy to observations in other baleen whale species (see chapter 4.3.1 below).

Table 3: Overview of Antarctic blue whale distribution and presumed migratory behavior in the Southern Hemisphere. Numbers in brackets refer to different study sites, as indicated in Fig. 7.

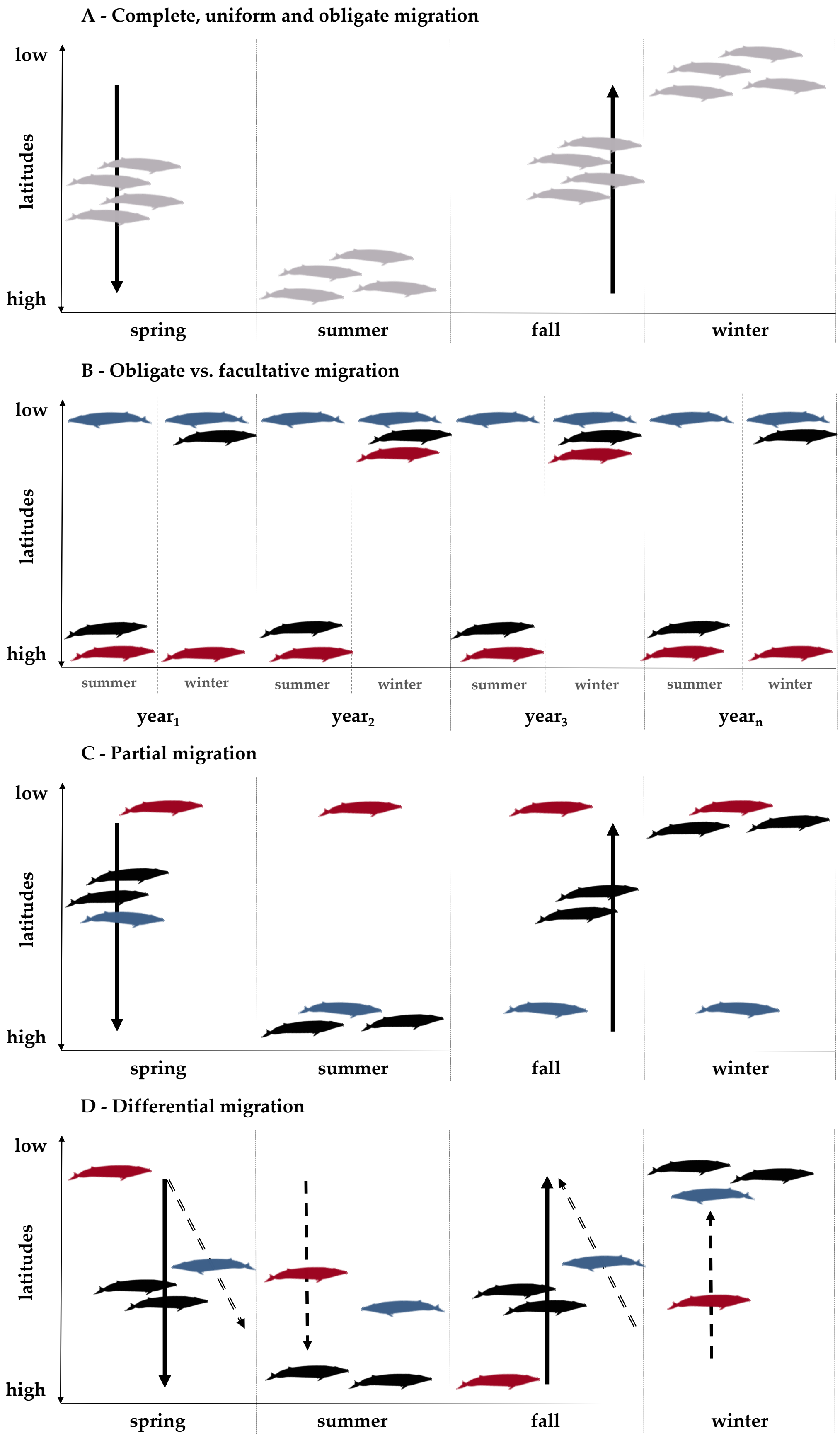
Migratory behavior	**Observations**	**Study area**	**Method**	**References (exemplary)**
migratory	seasonal pattern in the number of whales caught	South Georgia (1)	whaling	Mackintosh & Wheeler (1929), Harmer (1931), Hjort *et al.* (1932), Mackintosh & Brown (1956), Mackintosh (1966)
	seasonal pattern in the acoustic presence or the number of detected calls	Western Antarctic Peninsula (2)	PAM	Širović *et al.* (2004), Dziak *et al.* (2015)
		Weddell Sea (3, 4)	PAM	Publications III and IV
		Southern Ocean, Indian Ocean sector (5, 6, 7)	PAM	Gedamke *et al.* (2007), Širović *et al.* (2009)
		Indian Ocean (9, 11, 12, 13, 14)	PAM	Stafford *et al.* (2004), Gedamke *et al.* (2007), Tripovich *et al.* (2015), Leroy *et al.* (2016)
		eastern tropical Pacific Ocean (8)	PAM	Stafford *et al.* (2004)
		South Pacific Ocean, off New Zealand (10)	PAM	McDonald (2006)
	seasonal pattern in the number of whales caught	South Atlantic Ocean, south-west coast of Africa (16)	whaling	Best (2007)
differential	seasonal patterns in encounter rates considered indicative of gradual movement	Southern Ocean, circumpolar	visual	Kasamatsu *et al.* (1996)
	composition of population changed over the whaling season potentially reflecting differential migration	South Georgia (1)	whaling	Mackintosh & Wheeler (1929)
partial	year-round presence juveniles with poor body condition predominated winter catches (possibly skipped migration to feeding areas in previous summer)	South Atlantic Ocean, south-west coast of Africa (15)	whaling	Mackintosh & Wheeler (1929)
partial or differential	year-round presence	South Georgia (1)	whaling	Mackintosh & Wheeler (1929), Harmer (1931), Hjort *et al.* (1932),
	year-round acoustic presence	Western Antarctic Peninsula (2)	PAM	Širović *et al.* (2004), Dziak *et al.* (2015)
		Weddell Sea (3, 4)	PAM	Publications III and IV
		Southern Ocean, Indian Ocean sector (5)	PAM	Širović *et al.* (2009)
		South Atlantic Ocean, off Namibia (15)	PAM	Publication V
		Indian Ocean (11, 12, 13, 14)	PAM	Samaran *et al.* (2013), Tripovich *et al.* (2015), Leroy *et al.* (2016)
resident	possible existence of a resident population in the Southern Ocean	Southern Ocean	genetics	Attard *et al.* (2016)

4.3. The migratory repertoire of baleen whales

Recently, Geijer *et al.* (2016) comprehensively reviewed existing literature on migratory behavior in baleen whales. By combining evidence from multiple sources, the authors highlight that a migratory behavior that comprises a wide spectrum of migratory strategies is rather the rule than the exception in many baleen whale species (Geijer *et al.*, 2016). They concluded that although the ‘traditional’ migratory strategy with seasonal migrations between feeding and breeding grounds occurs in most baleen whale species, there is also ample evidence that alternative strategies including residency, partial or differential migration, as well as feeding activities during winter or on migration are not anomalous habits (see Geijer *et al.*, 2016 for a review). Hereinafter, I will refer to the entity of all migratory behaviors, expressed by a baleen whale species or population, as its ‘migratory repertoire’ (see also Fig. 8).

In the following, I will briefly summarize the state of knowledge on the migratory behaviors that comprise the migratory repertoire of the better studied blue whale subspecies, i.e. the pygmy blue whale (*Balaenoptera musculus brevicauda*) and the Northern Hemisphere blue whale (*B. m. musculus,* see also Table 4). Due to their close relationship to Antarctic blue whales, these subspecies can provide valuable comparative evidence of the migratory behavior of Antarctic blue whales. I will also relate to other baleen whale species to put the migratory behavior observed in Antarctic blue whales into a broader context. Although the occurrence of feeding activities during winter or on migration (which I will refer to as ‘off-season foraging’ in the following) does not represent a migratory behavior, it challenges the aspect of the migration paradigm, which assumes that baleen whales fast outside their feeding grounds. Hence, findings on the occurrence of off-season foraging (and, similarly, of off-season breeding activities) in baleen whales will also be briefly outlined in the following.

Fig. 8 (following page): *Generalized scheme of the migratory repertoire of baleen whales. Panel A represents a complete, uniform and obligate migration of a whale population (indicated by gray icons) between high-latitude summer feeding grounds and low-latitude overwintering grounds (here on the Southern Hemisphere). Panel B represents individual whales exhibiting an obligate (black icons) vs. a facultative (red icons) migratory behavior. Whale icons colored in blue indicate obligate residency. Note that the time scale in panel B differs from that of other panels. Panel C indicates partial migration in a population, comprised of migratory individuals (black icons) and resident individuals (colored icons; animals can be obligate or facultative residents). Panel D indicates differential migration in a population, including spatial differences (e.g. different migratory routes or destinations (black vs. blue icons)) and temporal differences (black vs. red icons) in the migratory behavior. In all panels, directions of migratory movements are indicated by black arrows. (Whale icon made by Freepik from www.flaticon.com)*


A - Complete, uniform and obligate migration

B - Obligate vs. facultative migration

C - Partial migration

D - Differential migration

Table 4: Presumed migratory behavior of populations of pygmy blue whales and Northern Hemisphere blue whales.

Population	**Migratory behavior**	**Observations**	**Method**	**References (exemplary)**
Northeast Pacific blue whales	partial migration	migratory movements along the western coast of North and Central America year-round presence on wintering ground in eastern tropical Pacific Ocean feeding throughout the migratory cycle, also on wintering grounds	visual, tagging, PAM	Calambokidis *et al.* (1990), Reilly & Thayer (1990), Stafford *et al.* (1999a), Mate *et al.* (1999), Stafford (2003), Bailey *et al.* (2010)
Northwest Pacific blue whales	migratory	seasonal acoustic presence at high latitudes presumed migratory movements to lower latitudes during winter, potentially including waters off Hawaii and Japan	visual, PAM	Clapham *et al.* (2008), McDonald *et al.* (2006), Reeves *et al.* (1998), Stafford *et al.* (2001)
Southeast Pacific blue whales	partial or temporally segregated migration	migratory link between southern Chile, Patagonia & Galápagos Islands year-round acoustic presence on presumed breeding grounds off Galápagos Islands	visual, photoID, tagging, PAM	Buchan *et al.* (2014), Hucke-Gaete *et al.* (2004), Hucke-Gaete *et al.* (2016), Stafford *et al.* (1999b), Torres-Florez *et al.* (2015)
New Zealand blue whales	partial migration	year-round presence in coastal waters off New Zealand seasonal acoustic presence possibly indicates seasonal movements (acoustic) link between Tonga & New Zealand and Tonga & Tasman Sea	visual, PAM	Branch *et al.* (2007), Miller *et al.* (2014a), Olson *et al.* (2015), Torres (2013), Balcazar *et al.* (2015)
Australian blue whales	migratory	seasonal acoustic presence off southern and southwestern Australia seasonal acoustic presence in central Indian Ocean	PAM	Balcazar *et al.* (2015), Samaran *et al.* (2013), Stafford *et al.* (2011), Tripovich *et al.* (2015)
Northern Indian Ocean blue whales	non-migratory with seasonal dispersal	year-round (acoustic) presence in northern Indian Ocean seasonal dispersal within the Indian Ocean	visual, PAM	Anderson *et al.* (2012), Anderson (2005), de Vos *et al.* (2014), Samaran *et al.* (2013), Stafford *et al.* (2011)
Southwest Indian Ocean blue whales	uncertain (migratory?)	seasonal acoustic presence unknown winter and spring distribution	PAM	Samaran *et al.* (2013), Stafford *et al.* (2011), Cerchio *et al.* (2016)
North Atlantic blue whales	partial migration	year-round (acoustic) presence in high-latitude waters migratory links between Iceland and Greenland & Iceland and Mauretania forage in mid-latitude waters during presumed northward spring migration	visual, tagging, PAM	Charif & Clark (2009), McDonald *et al.* (2006), Reeves *et al.* (2004), Sears *et al.* (1990), Silva *et al.* (2013)
*South Atlantic blue whales	uncertain	acoustic winter presence on feeding ground off South Georgia	PAM	Pangerc (2010), Širović *et al.* (2016)
*SW Indian Ocean blue whales II	uncertain	seasonal acoustic presence	PAM	Sousa & Harris (2015)
*Western Tropical Pacific blue whales	uncertain	acoustic presence from austral winter to summer (but data availability limited)	PAM	Frank & Ferris (2011)

* Identity of blue whale population is uncertain to date due to lacking visual confirmation of passive acoustic data.

4.3.1. Residency

The only blue whale population considered resident to date is inhabiting the northern Indian Ocean (Anderson, 2005; Anderson *et al.*, 2012; de Vos *et al.*, 2014), potentially representing another blue whale subspecies, *B. m. indica* (Ilangakoon & Sathasivam, 2012). Passive acoustic data indicated year-round presence of this blue whale population in the northern and central Indian Ocean (Stafford *et al.*, 2011; Samaran *et al.*, 2013). Nevertheless, the individuals are thought to undertake seasonal movements within these waters related to monsoonal upwelling events (Anderson, 2005; Anderson *et al.*, 2012; de Vos *et al.*, 2014) (see Table 4).

Among the mysticetes, bowhead whales (*Balaena mysticetus*) form an exception as they remain in arctic and subarctic waters year-round, although some (seasonal) dispersal occurs within the Arctic (Bockstoce *et al.*, 2005; Citta *et al.*, 2012). Besides, residency has been reported or suggested for fin whale populations in the Gulf of California (Bérubé *et al.*, 2002), off Southern California (Campbell *et al.*, 2015) and in the Mediterranean Sea (Notarbartolo di Sciara *et al.*, 2003; Castellote *et al.*, 2012) and for humpback whales in the Arabian Sea (Mikhalev, 1997). Similarly, there is evidence for a non-migratory population of minke whales (*Balaenoptera acutorostrata*) in the North Pacific Ocean (Caretta *et al.*, 2007). In Bryde’s whales, both a non-migratory, coastal subspecies (*Balaenoptera edeni edeni*) and a migratory, pelagic subspecies (*B. e. brydei*) are known to occur off the western South African coast (Best, 2001). Resident baleen whale populations are likely to benefit from local oceanographic conditions, such as currents and upwelling processes, which favor primary productivity and hence, decrease the need to migrate to high latitudes for foraging (e.g. Mikhalev, 1997).

4.3.2. Partial migration

Apart from bowhead whales, all other baleen whale species (including blue whales) exhibit some form of migratory behavior, with at least part of the population(s) commuting between seasonal feeding and breeding habitats. Partial migration is likely to occur in blue whale populations inhabiting the Northeastern Pacific Ocean (e.g. Reilly & Thayer, 1990; Mate *et al.*, 1999; Stafford *et al.*, 1999a), the Southeastern Pacific Ocean (e.g. Hucke-Gaete *et al.*, 2004; Buchan *et al.*, 2014; Torres-Florez *et al.*, 2015), the waters off New Zealand (e.g. Balcazar *et al.*, 2015; Olson *et al.*, 2015) and the North Atlantic Ocean (e.g. Sears *et al.*, 1990; McDonald *et al.*, 2006; Charif & Clark, 2009). These inferences are based on observations showing both year-round presence of blue whales on presumed feeding or breeding grounds and migratory movements or (acoustic) migratory links between distant habitats (see also Table 4). Such observations possibly indicate that part of the populations remains on the feeding or breeding grounds year-round, while another part commutes between these areas.

Furthermore, baleen whale occurrence on high-latitude feeding grounds in polar and sub-polar waters during winter, indicative of partial migration, has been reported for several species, including humpback (Van Opzeeland *et al.*, 2013b; Magnúsdóttir *et al.*, 2014), fin (Moore *et al.*, 2006; Simon *et al.*, 2010), minke (both *Balaenoptera acutorostrata* and *B. bonaerensis* subspecies) (Thiele *et al.*, 2004; Acevedo *et al.*, 2011), and gray whales (Moore *et al.*, 2007; Stafford *et al.*, 2007). Particularly in high latitude waters of the Southern Ocean, seasonally high ice concentrations are likely to restrict large-scale movements of baleen whales during winter, but confine individuals to local open water areas (Taylor, 1957; Ainley *et al.*, 2010b). Hence, baleen whale winter presence in these areas most likely reflects that part of the population foregoes migration and overwinters on the Southern Ocean feeding grounds (Van Opzeeland *et al.*, 2013b; Publication III).

Overall, the migratory behavior of baleen whales seems to represent a variant of a ‘low-frequency breeding migration’, a type of partial migration where non-migrating individuals are thought to forego reproduction in favor of an increased life-time fecundity (e.g., Shaw & Levin, 2011). In literature, partial migration is often considered as representing one of two forms: in ‘non-breeding partial migration’, migrating and resident individuals share a breeding ground but winter apart (Fig. 9). In ‘breeding partial migration’, migrants and residents share a wintering ground but breed apart (Chapman *et al.*, 2011; Shaw & Levin, 2011). In both of these variants of partial migration, all (sexually mature) individuals of a population are thought to reproduce every year, irrespective of whether they are migratory or resident (Shaw & Levin, 2011). However, there exists a third form of partial migration, referred to as ‘low-frequency breeding migration’ (Shaw & Levin, 2011) or ‘skipped breeding partial migration’ (Chapman *et al.*, 2011). This form is known to occur in sea turtles and many fish species (Bull & Shine, 1979; Rideout *et al.*, 2005), but is rarely described or considered in literature concerning partial migration. In this form of partial migration, migration is considered necessary for successful reproduction. Consequently, not all individuals reproduce every year, with non-migrating individuals foregoing reproduction and breeding at longer intervals (Shaw & Levin, 2011) (Fig. 9). The spatial separation between breeding and feeding habitats in many baleen whale species is presumed to be ultimately driven by elevated prey availability in polar areas and increased calf survival in low-latitude waters (as has been outlined in chapter 1.2). Hence, the reason for baleen whales to migrate to low-latitude waters could be concluded to be successful reproduction. Partial migration in baleen whales therefore possibly represents a variant of the skipped breeding partial migration described by Shaw & Levin (2011).

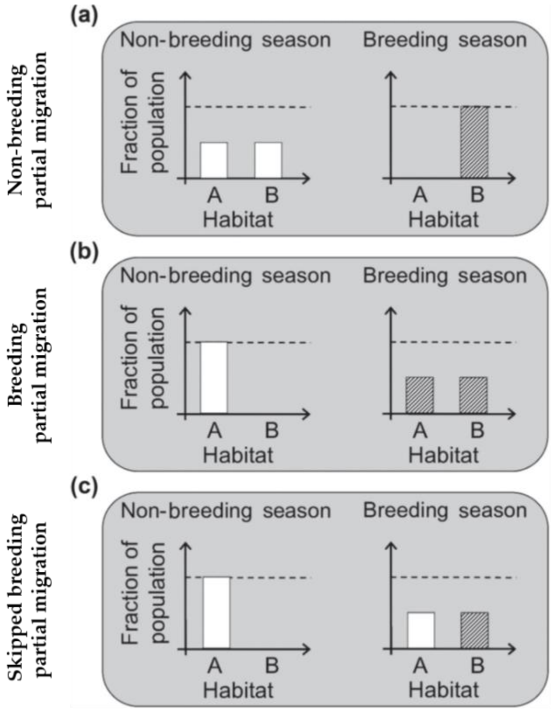


Fig. 9: *Schematic of three types of partial migration. (a) Non-breeding partial migration: Residents and migrants share a breeding habitat but spend the non-breeding season apart. (b) Breeding partial migration: Residents and migrants share a nonbreeding habitat and breed apart. (c) Skipped breeding partial migration: Residents and migrants exhibit different distributions during the breeding season, but since migration is required for reproduction only migrant individuals reproduce. Each panel shows the fraction of the population in each of the two habitats (A and B) during each of two seasons (non-breeding and breeding). Hatched bars indicate individuals that are reproducing. Figure from Shaw & Levin (2011), with permission from the publisher.*

4.3.3. Differential migration

Year-round presence of baleen whales in an area may not (solely) be caused by partial migration, but may also result from differences in the migratory behavior between individuals of the population (e.g. Straley, 1990). Differential (energetic) requirements of individuals within a population can cause a temporally segregated migration to and from the feeding and breeding grounds, with the migratory timing depending on the individuals' sex, age and reproductive state (Brown *et al.*, 1995; Dawbin, 1997; Craig *et al.*, 2003). In humpback whales, pregnant females and immature individuals are the first to migrate towards the feeding grounds during spring, followed by adult males and finally, lactating females with accompanying calves; with the backward migration to the breeding grounds in autumn taking place in reverse order (Dawbin, 1997; Craig *et al.*, 2003). Similarly, sex- and age-related differences in migratory timing occur in Antarctic minke whales, fin whales, sei whales, gray whales and bowhead whales (e.g. Kellogg, 1929; Mackintosh & Wheeler, 1929; Kasamatsu *et al.*, 1995; Best & Lockyer, 2002).

In addition to a temporally staggered migration, differential migratory behavior likely also includes differences in routes and destinations among individuals of a population, causing a spatially segregated migration. On high-latitude feeding grounds, adult baleen whales are thought to penetrate into polar waters farther than juvenile individuals (Lockyer & Brown, 1981). Mackintosh & Wheeler (1929) suggested that starting points and routes of migration may differ between adult and immature blue and fin whale individuals. Furthermore, sex-segregated migratory routes were observed in bowhead whales, with female bowhead whales accompanied by calves migrating along different routes than males (Kellogg, 1929).

4.3.4. Off-season feeding and breeding activities

Both baleen whale feeding and breeding activities are likely not restricted to the presumed feeding and breeding areas and seasons. Foraging has also been observed on migration or during winter months in Northeast Pacific blue whales (Reilly & Thayer, 1990; Mate *et al.*, 1999; Bailey *et al.*, 2010) and North Atlantic blue whales (Silva *et al.*, 2013) (see also Table 4), as well as in fin and sei whales (Silva *et al.*, 2013), humpback whales (Straley, 1990; Bortolotto *et al.*, 2016) and gray whales (Moore *et al.*, 2007). In particular, mid-latitude areas serve as stopover sites during migration towards the feeding grounds. Here, whales may refuel their depleted energy stores after the overwintering period, which is energetically costly due to the reduced availability of food during winter months and the high energy losses during migration and breeding, particularly for female individuals (Lockyer & Brown, 1981; Lockyer, 1984; Silva *et al.*, 2013). Similarly, the aseasonal or year-round occurrence of calls or songs, which likely represent a male reproductive display in baleen whales, at both high and low latitudes indicated that breeding or breeding-related activities are not spatially and temporally restricted to the (presumed) breeding areas and seasons (e.g. Clark & Clapham, 2004; Vu *et al.*, 2011; Oleson *et al.*, 2014). These findings are supported by whaling data on fetal lengths indicating the occurrence of aseasonal conceptions and, in turn, off-season births in baleen whales (e.g. Mackintosh & Wheeler, 1929; see Clark & Clapham, 2004 and references therein). Similarly, the resident inshore Bryde's whale population is considered to breed throughout the year (Best, 1977). Hence, the occurrence of off-season feeding and breeding activities contrasts the assumption of spatially and temporally restricted feeding and breeding areas and seasons. It thus further blurs the picture of baleen whales migration. The frequency with which such events occur as well as the proportion of the whale population involved in these activities is however unknown to date.

4.4. Revisiting the migration paradigm in baleen whales

The observed diverse migratory behavior in most baleen whale species adds new aspects to the 'traditional' migration paradigm. This paradigm assumed most baleen whales to undertake seasonal long-distance migrations between high-latitude feeding areas and low-latitude breeding grounds (see also Fig. 8A). Instead, baleen whale populations are likely to exhibit divergent migratory strategies more regularly than previously assumed, with their migratory repertoire comprising a spectrum of migratory behaviors ranging from complete residency over partial migration to complete migration, as well as differential migratory behavior, depending on the individuals' sex, age or reproductive state (Fig. 8B, C, D) (see also Geijer *et al.*, 2016). The generalized assumption of a (largely) complete, obligate and uniform 'to-and-fro' migration in most baleen whale species is hence likely an oversimplification of the observations of migratory movements, by interpreting these as representing the dominant behavioral trait in all baleen whales. At the same time, existing evidence of divergent migratory behaviors has likely been underestimated for a long time, hence neglecting the importance of such behaviors in contributing to the migration repertoire of baleen whales.

The migration paradigm may to a large degree have been shaped by drawing (in most cases premature) parallels between well-studied species (such as humpback whales) and comparatively poorly studied species (such as blue whales). Observations of coastally migrating species, e.g. humpback, right or gray whales, show a pronounced directionality and timing in their migratory movements (Lockyer & Brown, 1981). By analogy, these have often been considered largely representative for other species, such as blue whales or fin whales (Mackintosh & Wheeler, 1929; see also Branch *et al.*, 2007; Geijer *et al.*, 2016). However, current knowledge suggests that these species are likely to exhibit a mating and migratory behavior different from that of e.g. humpback whales. Mackintosh & Wheeler (1929) had already suggested that the comparatively low number of blue whales caught off south-west Africa may reflect that the species resides (and mates) farther offshore, i.e. outside the operational range of land-based whaling stations[c], and that breeding may not be restricted to distinct periods of the year. In turn, the migratory behavior of Antarctic blue whales may not be analogous to that of humpback whales, but differ in e.g. spatial and temporal dimensions, highlighting the importance of taking into account species-specific behavioral traits in baleen whale movement ecology.

Advancing technology, such as PAM or satellite tracking, has facilitated data collection on baleen whales over large temporal and spatial scales, thus improving our knowledge on the variety of migratory behaviors of baleen whales. Nevertheless, several caveats arise when attempting to understand and interpret the migratory behavior of baleen whales. Residency, partial migration and complete, seasonal migration (or 'traditional' migration according to Geijer *et al.* (2016)) are categories along a continuous behavioral spectrum. Hence, given our comparatively scarce knowledge on the migratory behavior of many baleen whale species, conclusions on whether complete residency or complete migration occurs in a population may in fact not be possible based on the current knowledge basis. Complete residency or complete migration would require the population to be entirely resident or migratory, respectively, while partial migration includes all populations where the percentage of migrants ranges between 1 and 99%, and is more likely to be the dominant strategy in migratory species (Chapman *et al.*, 2011). Furthermore, the currently observed migratory behaviors of baleen whales might not be representative of the migratory repertoire during the pre- or early-whaling era as formerly existing, potentially resident, baleen whales populations may have become extinct (Clapham *et al.*, 2008). Potential caveats hence need to be carefully considered when making inferences on the migration of (past or extant) baleen whale populations in order to avoid over- or underestimating the importance of particular strategies in the migratory repertoire of a focal species.

Moreover, inferences on migratory behavior are likely to have been further complicated by the lack of a common, consistently used terminology regarding animal migration (see also Dingle, 2014). Terrill & Able (1988) already pointed out that e.g. the term 'differential'

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[c] In the whaling area off western Africa, the whaling flee has been reported to operate within a distance of ca. 130 miles of the whaling station at Saldanha Bay, South Africa (Best, 1969).

migration has been used in different ways, either limited to populations in which all individuals migrate or, more broadly, as a modifier for migratory behavior in general. According to the latter approach (as adopted in the present study), differential migration does not exclude partial migration and could occur in populations exhibiting complete migration and those that are partially migrating. In other words, differences in the migratory behavior in terms of timing, routes or destination may exist in any migratory population regardless whether the entire population or only a fraction of the population migrates (see also Terrill & Able, 1988). In future studies on baleen whale migration, it would therefore be worthwhile to clearly define the attributes or categories that are used to characterize the migratory behavior of an individual, a population or a species (see also Table 2, Fig. 8).

5. FACTORS INFLUENCING THE MIGRATORY BEHAVIOR OF BALEEN WHALES

Our knowledge on long-distance migration in marine species is still scarce to date. Improving our understanding of the driving forces and impact factors of migration is considered one of the key challenges in marine megafauna movement ecology (Hays *et al.*, 2016). As summarized in the previous chapter, there is evidence for a diverse repertoire of migratory strategies in Antarctic blue whales and other baleen whale species. A thorough understanding of drivers and influencing factors of baleen whale migratory behavior is crucial not only to develop effective conservation and management strategies, but also to assess potential impacts of past and future threats on baleen whale species. In this chapter, I outline factors that are likely to contribute to the observed diversity in the migratory behavior in Antarctic blue whales and other baleen whale species.

5.1. Why is the migratory behavior of baleen whales so diverse?

The diversity of migratory strategies in Antarctic blue whales and many other baleen whales is likely to arise from an interplay of various factors, which vary in importance between e.g. individuals, age classes or sexes. 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. Based on both previous observations from baleen whale populations and parallel evidence from other migratory species, the following sections will outline some of these factors and how these contribute to the complex migratory behavior of baleen whales.

5.1.1. Food availability & environmental conditions

Environmental conditions, and in particular foraging opportunities and food availability, may influence the migratory status and behavior of baleen whales. Prey distribution is considered a fundamental driver of movement patterns in marine megafauna (e.g. Hays *et al.*, 2016) and the poleward migration of baleen whales is presumed to be driven by profitable foraging opportunities in high-latitude waters (Avgar *et al.*, 2014). In contrast to the traditional 'feast or famine' hypothesis, baleen whales were observed feeding throughout their migratory cycle, i.e. also on migration or at mid- or low latitudes (e.g. Reilly & Thayer, 1990; Moore *et al.*, 2007; Gales *et al.*, 2009; Bailey *et al.*, 2010; Owen *et al.*, 2016). Foraging opportunities can cause deviations or interruptions in the migration of baleen whales (Dawbin, 1956; Barendse *et al.*, 2010). Stopover sites on the migratory pathways presumably provide resting areas and supplemental feeding sites for baleen whales to refuel their energy stores after overwintering at lower latitudes (e.g. Silva *et al.*, 2013; Garrigue *et al.*, 2015; Owen *et al.*, 2016). Prey availability is essentially determining baleen whale distribution patterns (e.g. Reilly & Thayer, 1990; Branch *et al.*, 2007). Therefore, the migratory behavior of baleen whales is likely to be considerably affected by changes in local and regional prey distribution or abundance, such as a decline in krill stocks potentially related to global warming (e.g. Atkinson *et al.*, 2004).

Additionally, between-population differences in baleen whale migratory behavior may relate to local environmental conditions and food availability. Some populations have been reported or suggested to remain resident (see also chapter 4.3), including populations of blue whales, fin whales, humpback whales or Bryde's whales (e.g. Mikhalev, 1997; Best, 2001; Bérubé *et al.*, 2002; Anderson *et al.*, 2012). Baleen whale migrations are proposed to be driven by a spatial trade-off between habitats that supply sufficient foraging opportunities and those that provide suitable conditions improving calf survival and growth (Corkeron & Connor, 1999) (see also chapter 1.2). Therefore, environmental conditions in habitats of resident baleen whale populations are likely to be sufficiently favorable for baleen whales to sustain these populations year-round. Most resident baleen whale populations have been reported to reside in temperate or subtropical waters, such as the Mediterranean Sea, the Gulf of California or the Arabian Sea, which presumably exhibit favorable conditions for parturition and calf rearing (e.g. in terms of the availability of shelter and calm waters or a decreased predation risk). Additionally, local oceanographic conditions (such as upwelling processes) within these habitats are likely to favor primary productivity and thus, enhance prey availability for baleen whales.

5.1.2. Sex and reproductive state of individual baleen whales

Baleen whale individuals of different sexes differ in their migratory behavior according to their strategies for improving their life-time fitness. These sex-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).

Migratory behavior of females

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). Hence, female individuals likely engage in migratory behaviors that improve their energy budget and their long-term reproductive success, e.g. the likelihood of calf survival (e.g. Craig *et al.*, 2003; Valsecchi *et al.*, 2010; Barendse *et al.*, 2013).

The migratory behavior of females is also likely to be influenced by their reproductive state, comprising resting, pregnant and lactating individuals accompanied by a calf (e.g. Dawbin, 1997). In humpback whales and gray whales, pregnant females arrive on the feeding grounds early during the spring or summer months, followed by resting females (although Craig *et al.* (2003) pointed out that those are hard to identify with certainty) and finally, lactating females with dependent calves (Dawbin, 1966; Swartz, 1986; Dawbin, 1997). The migration towards the breeding grounds takes place in reverse order (Dawbin, 1966; 1997). Thereby, pregnant females maximize their residency time on the feeding grounds and enhance their energy stores, while lactating females spend less time on the feeding grounds, potentially to reduce the time calves are exposed to cold waters and the energetic costs of thermoregulation (Dawbin, 1966).

Furthermore, the reproductive state of female baleen whales may also impact (at least to some degree) their choice of migratory routes or destinations, potentially to avoid male harassment (Swartz, 1986; Craig *et al.*, 2014). On their feeding and breeding grounds, mother-calf pairs of humpback and gray whales migrate to shallower waters close to the coast, presumably to avoid the increased energetic costs associated with male harassment for both mothers and calves (Swartz, 1986; Craig *et al.*, 2014). Similarly, female bowhead whales with calves migrate along different routes than males (Kellogg, 1929).

Additionally, female baleen whales have a higher tendency to remain resident at high-latitudes in some years compared to males. 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 (other 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 or, alternatively, that males exhibit a longer residency time on the breeding grounds (Brown *et al.*, 1995; Craig & Herman, 1997). Primarily females may benefit from overwintering on the feeding grounds by an increased energy uptake due to a prolonged foraging period and a decreased energy expenditure by saving the energetically costly migration (see also Shaw & Levin, 2011). Pregnant and lactating females are generally assumed to migrate back to lower latitudes after the feeding season to give birth and wean their calves, respectively (e.g. Lockyer & Brown, 1981). Hence, mainly resting females may benefit from skipping migration (and possibly reproduction) in some years to replenish their energy stores and thus, presumably improve their life-time reproductive success (see also Shaw & Levin, 2011). However, direct observations supporting this hypothesis are lacking to date.

Changes in the reproductive state of individual females can affect their migratory behavior both within and between years (e.g. in terms of migratory timing of pregnant vs. lactating females) (Craig & Herman, 1997; Craig *et al.*, 2003). Females that conceived during migration to or shortly after arrival on the breeding grounds are thought to not complete a full migration or to exhibit a shorter residency time in lower latitudes (Craig & Herman, 1997; Craig *et al.*, 2003; Barendse *et al.*, 2010). Newly pregnant females may migrate back to high(er)-latitude waters after conception, potentially explaining the male-bias in baleen whale populations observed both on migration and breeding grounds (Brown *et al.*, 1995; Craig & Herman, 1997; Craig *et al.*, 2003). Furthermore, the loss of a calf, also representing a change in the reproductive state, might also have the potential to alter the migratory behavior, as has been shown in a terrestrial migratory ungulate species where the females' moving speed slowed down after losing a calf (Singh & Ericsson, 2014).

Migratory behavior of males

The migratory behavior of male baleen whales is likely to aim at optimizing mating opportunities (e.g. Craig *et al.*, 2003; 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). On the breeding grounds, males are thought overlap their residency time with that of resting and lactating females, which both are potential mating partners for the male individuals (Craig *et al.*, 2003). The migratory timing of males may therefore represent a strategy to maximize their reproductive success (Craig *et al.*, 2003).

Furthermore, there is evidence that also males skip migration towards lower latitudes and overwinter on the feeding grounds. Passive acoustic studies reported persistent presence of baleen whale song on the feeding grounds outside the breeding season (e.g. Clark & Clapham, 2004; Širović *et al.*, 2004; Vu *et al.*, 2011; Publication III). Baleen whale song is presumed to represent a male reproductive display (e.g. Tyack, 1981; Croll *et al.*, 2002; Oleson *et al.*, 2007). Therefore, the year-round presence of song likely indicates that reproductively active male individuals are present on the feeding grounds throughout the year, potentially skipping migration to overwinter at high latitudes. In males, facultative residency at high latitudes may be driven by opportunistic mating opportunities on the feeding grounds, possibly with little intra-sexual competition. Accordingly, the occurrence of aseasonal conceptions and aseasonal births indicates that breeding in baleen whales is likely not limited to specific habitats or to distinct periods of the year (Mackintosh & Wheeler, 1929; Clark & Clapham, 2004).

In migrating mammal species, males and females also differ in their dispersal patterns (see also Greenwood, 1980; Ruckstuhl & Neuhaus, 2005). Female philopatry, i.e. a strong site fidelity of females to specific feeding or breeding grounds, has been suggested for e.g.

Antarctic blue whales (e.g. Sremba *et al.*, 2012), fin whales (e.g. Brown, 1954; Clapham & Seipt, 1991), humpback whales (e.g. Rizzo & Schulte, 2009) and southern right whales (Baker *et al.*, 1999). In contrast, male baleen whales have been suggested to disperse more often than females (male dispersal) and migrate between different breeding and feeding grounds, thereby maintaining connectivity between different populations or stocks (Baker *et al.*, 1990; Baker *et al.*, 1993; Baker *et al.*, 1998). Male-biased dispersal likely improves the reproductive success of male individuals by increasing the access to females and avoidance of inbreeding (Greenwood, 1980; Valsecchi *et al.*, 2010).

5.1.3. Age and sexual maturity

Age-related differences in the movement patterns have been suggested to occur between juvenile and adult individuals, indicating that an individuals' age and sexual maturity influences its migratory status and behavior (e.g. Mackintosh & Wheeler, 1929; Dawbin, 1997; Craig *et al.*, 2003).

The origins and destinations of baleen whale migration as well as migratory routes have been suggested to differ between juvenile and adult individuals. 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 (Mackintosh & Wheeler, 1929; 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. Hence, juveniles occur in more sheltered, coastal waters or in greater distance to the ice edge, which may pose the risk of entrapment (Taylor, 1957; see also Loseto *et al.*, 2006).

Furthermore, juvenile individuals are probably more restricted than adults in their capacity to store energy due to their smaller body sizes (Calder, 1984; as cited in Craig *et al.*, 2003). Hence, along with the fact that immature individuals are not capable of reproduction, juveniles may not remain on the low-latitude wintering grounds for prolonged periods of time (Craig *et al.*, 2003). Instead, juvenile baleen whales may benefit from a longer residency time on the feeding grounds as this enables them to maximize their growth and hence, body size which is (rather than age) considered a major factor in determining sexual maturity of baleen whales (Lockyer, 1984).

However, some observations on the migratory timing and behavior of juvenile individuals are contradictory and may indicate age-related or species-specific differences among juvenile baleen whales. Some previous studies on humpback, gray, minke and bowhead whales showed or suggested that juvenile or subadult individuals arrived on the summer feeding grounds earlier than their adult conspecifics (Finley, 1990; Kasamatsu *et al.*, 1995; Perryman & Lynn, 2002). Other findings indicated that a fraction of the adult baleen whales (also depending on sex or reproductive state) migrates earlier towards the feeding grounds than juvenile individuals, including humpback whales (Dawbin, 1966; 1997; Craig *et al.*, 2003), gray whales (Swartz, 1986) and Antarctic blue whales (Mackintosh & Wheeler, 1929). These contrasting results may in part be explained by internal, age-related changes in the migratory behavior within the group of juvenile (i.e. sexually immature) individuals. For example, juvenile humpback whales were observed to arrive early on the low-latitude breeding grounds (Craig *et al.*, 2003) which is in contrast to previous findings (e.g. Dawbin, 1966; 1997). Craig *et al.* (2003) suggested these juvenile whales to be yearlings that were just weaned on or shortly after migration to the breeding grounds and have been traveling with their mothers, which are known to depart from the feeding grounds earlier than other groups of whales (see also chapter 5.1.2).

With increasing age, habitat preferences of cetaceans may differ, e.g. due to changes in nutritional needs or and predation risk (e.g. Loseto *et al.*, 2006). This might not only result in differences in the migratory behavior between juvenile and adult individuals, but also among different age-classes of juvenile and adult whales (see also Whitehead, 2003).

5.1.4. Cultural knowledge and social learning

The cultural knowledge of baleen whale populations transmitted by (maternally mediated) social learning is also considered to influence the migratory behavior of individual baleen whales. 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 (Shaw & Couzin, 2013). Hence, the accumulation and transmission of migratory experiences and knowledge within a population is considered to improve the migratory performance of migrants (e.g. Mueller et al., 2013).

In baleen whales, knowledge on migratory destinations is considered to be culturally transferred, mediated by strong maternal site fidelity to specific habitats (e.g. Baker et al., 1990; Clapham & Seipt, 1991; Stevick et al., 2006; Clapham et al., 2008; Valenzuela et al., 2009; Sremba et al., 2012; Barendse et al., 2013). In particular, an individuals' migratory destination is assumed to depend substantially on early, maternally transferred, migratory experiences during its first year (Baker et al., 1990; Weinrich, 1998; Rizzo & Schulte, 2009; Barendse et al., 2013). Hence, due to social learning of migratory routes or destinations, baleen whale individuals belonging to different breeding or feeding stocks may differ in their migratory behavior, e.g. visit different feeding areas (e.g. Stevick et al., 2003; International Whaling Commission, 2011).

Cultural transmission of migratory behavior is considered particularly beneficial in habitats with highly variable environmental conditions, since it enables a faster adaptation to changed conditions compared to genetically transferred traits (Bauer et al., 2011). Furthermore, sharing of information within groups of individuals increases the individual fitness by facilitating the transmission of ecologically relevant behaviors that help to maximize feeding success or to avoid predators in local environments (Petitgas et al., 2010). However, social learning can also lead to 'entrainment' of an individual in the habits of its stock or population, e.g. in terms of the migratory behavior, and to a certain degree prevent the establishment of new (migratory) behaviors (Petitgas et al., 2010). Furthermore, a decrease in the number of experienced individuals with historical knowledge on migration, e.g. on migratory routes or destinations, may impede the transfer of cultural knowledge in a population (Brown & Laland, 2003). Hence, differences in the population structure might considerably affect the ability of a population or species to migrate in a way that favors long-term fitness (Shaw & Couzin, 2013).

5.1.5. Behavioral plasticity

Phenotypic plasticity is considered an important factor contributing to the diversity of migratory behavior in many species and facilitates the establishment of new or alternative migratory behaviors. In terms of migratory diversity, it thereby represents an opposing factor to culturally transferred behavioral traditions. Migratory routes and destinations of baleen whales are not fixed, but baleen whales also migrate between alternative feeding grounds (or breeding grounds), with male individuals presumably dispersing more than females (e.g. Baker *et al.*, 1990; Baker *et al.*, 1993; Baker *et al.*, 1998; but see Stevick *et al.*, 2013). Besides sex-related differences in spatial baleen whale dispersal patterns, the rate of dispersal likely varies between species. Blue whales, for example, have been shown to disperse more often and over larger distances than fin whales (Brown, 1954). Behavioral plasticity and resulting dispersal behavior in baleen whales (and other migratory species) can facilitate the exploration of new habitats (Carroll *et al.*, 2014). Hence, behavioral plasticity is likely to be essential for establishing connectivity (e.g. in terms of gene-flow) between populations over large spatial scales by immigration of animals into adjacent or distant populations (Clapham *et al.*, 2008; Rizzo & Schulte, 2009; Stevick *et al.*, 2016). Furthermore, it avoids inbreeding and increases access to mating partners (Greenwood, 1980; Valsecchi *et al.*, 2010), which is presumed to be a powerful factor shaping the (migratory) behavior in many migratory species (Avgar *et al.*, 2014). Moreover, behavioral plasticity is an essential feature of facultative migrants such as baleen whales, as it allows individuals to express different migratory strategies (Cresswell *et al.*, 2011), depending on e.g. their energetic requirements and reproductive state.

The contribution of behavioral plasticity to a complex migratory repertoire has also been demonstrated in other taxa. In terrestrial herbivores, young individuals mimic the migratory behavior of their mothers, but are capable of shifting to different strategies, such as residency or partial migration, during the course of their lives (Bauer *et al.*, 2011). In fish species, straying individuals are considered important to maintain the species' phenotypic diversity by connecting populations, exploring new habitats or initiating novel life-cycle patterns (Petitgas *et al.*, 2010). The establishment of alternative behaviors in stabile populations is kept in balance by the process of social learning and hence, mostly occurs when the ratio between experienced and naïve individuals is biased towards the latter (Petitgas *et al.*, 2010), e.g. under situations involving damage of population structures.

5.1.6. Genetic determinism

Despite the assumption that migratory behavior in baleen whales is culturally transmitted via early, maternally determined, experiences in a calf's life, it should not be excluded that genetic imprinting may also influence (and maintain) migratory behavior of baleen whales at least to a certain degree, although evidence is lacking to date. In general, successful migration may depend on both social learning and innate programs in migratory species, although the importance of experience and learned behavior is thought to increase during the course of an individuals' life (Bauer *et al.*, 2011; Mueller *et al.*, 2013). From experiments with naïve birds, there is evidence that the migratory behavior in terms of timing, direction and termination of migration is in part socially transferred and partly genetically inherited (Bauer *et al.*, 2011; Mueller *et al.*, 2013). However, it is currently not well understood how migratory performance is influenced by experience and social learning (mediated through cultural transmission of knowledge) on the one hand and innate, genetically inherited, programs on the other hand (Alerstam *et al.*, 2003). Hence, understanding the effects of learning and memory versus innate behavior is considered another key challenge in animal movement ecology (Alerstam *et al.*, 2003; Hays *et al.*, 2016).

Furthermore, in facultative migrants, to which baleen whales belong due to their flexible migratory behavior, behavioral plasticity is considered to be a result of a plastic genotype and the responses to environmental conditions (Cresswell *et al.*, 2011). Hence, genetic variation may provide individuals with the ability to express different phenotypes under varying environmental conditions, as it defines the potential range of an individuals' behaviors in response to environmental conditions (Cresswell *et al.*, 2011).

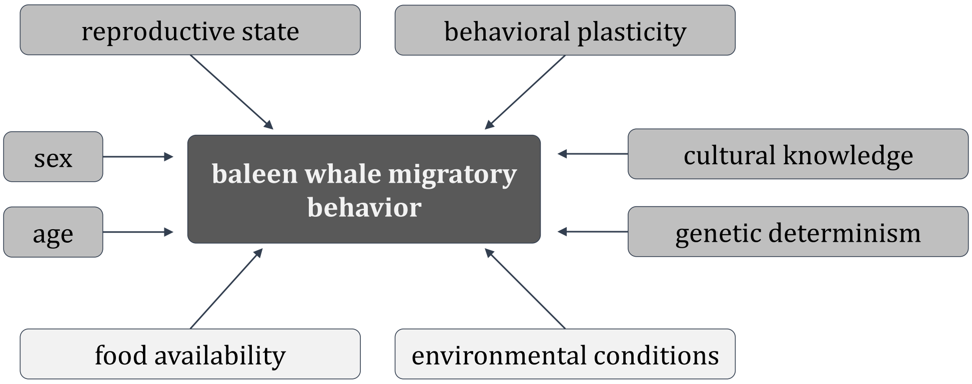

Fig. 10: *Schematic overview of factors influencing the migratory behavior of baleen whales. Boxes colored in light grey indicate external factors, boxes colored in darker gray indicate internal characteristics of individual baleen whales.*

In conclusion, the observed diverse migratory repertoire of baleen whales is likely a result of a combination of several, interrelated factors (Fig. 10), which however are not fully understood to date. Similarly, evidence from migratory fish species indicates that a variety of factors can be important in characterizing the species' migratory behavior. Such factors include the migratory knowledge of an individual (acquired through social learning or migratory experiences), environmental cues, genetic components as well as predation risk (Skov *et al.*, 2010a; Skov *et al.*, 2010b). However, neither the extent to which each of the single factors influence the migratory repertoire of migratory species, nor the interrelations between these factors are well understood to date.

Improving our knowledge on the drivers of migratory behavior is particularly crucial in the light of conservation and management of migratory marine animals (Alerstam *et al.*, 2003; Costa *et al.*, 2012; Hays *et al.*, 2016). However, understanding the factors that influence the migratory repertoire in baleen whales is further complicated by possible effects of large-scale changes in environmental conditions, such as global warming or ocean acidification (e.g. Learmonth *et al.*, 2006; Moore & Huntington, 2008; Ramp *et al.*, 2015), or of anthropogenic threats on their migratory behavior (e.g. Clapham & Baker, 2008; Clapham *et al.*, 2008; Thomas *et al.*, 2016).

6. EFFECTS OF A POPULATION BOTTLENECK ON THE MIGRATORY BEHAVIOR OF BALEEN WHALES

Commercial whaling during the 20th century caused a population bottleneck, i.e. a substantial decrease in population size (e.g. Calow, 2009), in many baleen whale species worldwide (Tønnessen & Johnsen, 1982; Clapham & Baker, 2008; Rocha *et al.*, 2014). Effects of population bottlenecks due to human harvest of wild animal populations are manifold and include genetic effects such as alterations in the genetic subdivision of populations or a loss of genetic diversity, but also behavioral changes, e.g. in migratory patterns (e.g. Allendorf *et al.*, 2008; Petitgas *et al.*, 2010; Holdo *et al.*, 2011). In fishes, drastic declines in stock sizes have been shown to be associated with changes in the migratory behavior, including the disappearance and establishment of former and new migratory patterns, respectively (Petitgas *et al.*, 2010). Furthermore, migratory species are thought to be an essential factor in shaping ecosystem dynamics (e.g. Fryxell & Sinclair, 1988; Brönmark *et al.*, 2010; Holdo *et al.*, 2011). Hence, alterations of a species' migratory behavior have the potential to impact entire ecosystems, including changes in nutrient transports, food web structures as well as ecosystem structure and functioning (e.g. Brönmark *et al.*, 2010; Chapman *et al.*, 2011; Chapman *et al.*, 2012).

In the following sections, I will discuss whether there is evidence that the population bottleneck due to commercial whaling might have affected the migratory behavior of baleen whales, using parallel evidence from other taxa that have undergone a bottleneck situation. I will outline the ecological role of migratory species in general and of baleen whales in particular to highlight the potential large(r)-scale ecosystem effects which changes in the migratory behavior of a species might entail.

6.1. Commercial whaling on Antarctic blue whales

The drastic exploitation of Antarctic blue whales and other baleen whale populations worldwide by commercial whaling has resulted in severe population bottlenecks and has driven several baleen whale species close to extinction (e.g. Tønnessen & Johnsen, 1982; Clapham *et al.*, 1999; Clapham & Baker, 2008; Thomas *et al.*, 2016). In the Southern Hemisphere, more than two million whales have been caught on the Antarctic whaling grounds during the 20th century (Clapham & Baker, 2008). Antarctic blue whales were one of the preferred targets of commercial whaling between 1904 and 1964, when the International Whaling Commission officially banned whaling of this subspecies. Illegal Soviet whaling nevertheless continued until 1973 (Zemsky *et al.*, 1995; Yablokov *et al.*, 1998; Branch *et al.*, 2004). Within a few decades, an estimated amount of more than 360,000 individual Antarctic blue whales were taken, causing near-extinction of the population (Tønnessen & Johnsen, 1982; Branch *et al.*, 2004; Clapham & Baker, 2008). In 1973, only about 360 individuals were left, representing less than 1% of the estimated original population size of 239,000 individuals (Branch *et al.*, 2004). Since then, the Antarctic blue whale population is thought to increase steadily at an annual growth rate of 7.4% (Branch *et al.*, 2004). Most recent abundance estimates assessed the population size to range between 1000 and 2300 individuals (Branch & Butterworth, 2001a; Branch *et al.*, 2004; Branch, 2007) and Antarctic blue whales are still listed as critically endangered by the IUCN (Reilly *et al.*, 2008c).

6.2. Pre-whaling migratory behavior of baleen whale populations

As elucidated in chapter 4, historic catch data already suggested a diverse repertoire of the migratory strategies of (Antarctic) blue whales and other baleen whale species, although these data may not reflect the behavioral traits of (undisturbed) pre-whaling baleen whale populations. (Partial) residency has been suggested to have occurred at both high and low latitudes, based on the observation of a year-round presence of Antarctic blue whale individuals on the whaling grounds off South Georgia in the Southern Ocean and off Namibia in the Atlantic Ocean (Mackintosh & Wheeler, 1929; Harmer, 1931; Hjort *et al.*, 1932). Furthermore, seasonally changing compositions of populations on the feeding grounds implied a differential migratory behavior, with a temporally staggered migration based on the individuals' sex, age or reproductive state (Mackintosh & Wheeler, 1929). However, these observations were conducted during the whaling era when baleen whale populations already experienced significant changes in abundance and demography (Clapham & Baker, 2008; Rocha *et al.*, 2014). Thus, the migratory patterns and strategies inferred based on historic catch data may not necessarily represent the state and migratory behavior of pre-whaling baleen whale populations undisturbed by human intervention (i.e. the *status quo ante*).

This raises the question of how insights into the actual behavior of pre-whaling baleen whale populations can be obtained. In this context, genetic data have the potential to (to a certain degree) improve our understanding of the movement behavior of past (i.e. pre-whaling) populations (e.g. Baker *et al.*, 1990; Sremba *et al.*, 2012). This is based on the fact that the alteration in a species' genetic diversity that accompanies a demographic change is subject to a time delay and accumulates over a large number of generations after a population bottleneck (Palsbøll *et al.*, 2013). The longevity of baleen whales, presumably ranging up to 100 years (Taylor *et al.*, 2007; Bannister, 2009; Sears & Perrin, 2009), suggests that some of the individuals that lived through the bottleneck could still be alive today, thus incorporating the genetic diversity of pre-whaling populations. Furthermore, baleen whales exhibit comparatively long generation times, i.e. average times between two generations in a population (Taylor *et al.*, 2007). In turn, the longevity and long generation times of baleen whales along with the relatively recent occurrence and short duration of the bottleneck may have dampened the loss in genetic diversity (e.g. Baker *et al.*, 1993; Branch & Jackson, 2008; Sremba *et al.*, 2012). Hence, in the case of baleen whales, genetic data collected shortly after populations have undergone a bottleneck are likely to be representative of a historic (*status quo ante*), rather than the current population state, i.e. the *status quo* (Palsbøll *et al.*, 2013). This in turn provides the possibility of improving our understanding of pre-whaling baleen whale populations by using genetic data. Given that genetic data are representative of past patterns in a species' (migratory) behavior, inferences from genetic data may differ from current behavioral observations. Such differences could therefore shed light on potential effects of population bottlenecks on baleen whale migratory behavior.

In several baleen whale species, there is genetic evidence for a maternally determined population structure and hence strong maternal site fidelity to feeding or breeding grounds, including Antarctic blue whales, humpback whales and fin whales (e.g. Baker *et al.*, 1990; Clapham & Seipt, 1991; Baker *et al.*, 1993; Stevick *et al.*, 2006; Rizzo & Schulte, 2009; Sremba *et al.*, 2012). Furthermore, in humpback whales, comparisons between maternally inherited mtDNA and biparentally inherited nuclear DNA indicated that male gene-flow is greater than female gene-flow (Baker *et al.*, 1998). These findings suggest a gender-biased migration between different breeding grounds with male individuals dispersing more than females (Baker *et al.*, 1990; Baker *et al.*, 1993; Baker *et al.*, 1998; Rizzo & Schulte, 2009). Alternatively, a male mediated gene-flow could also be a result of occasional mating between otherwise discrete populations during migration (Baker *et al.*, 1998). Furthermore, there is genetic evidence for a differential use of migratory routes in male and female humpback whales (Valsecchi *et al.*, 2010). Off eastern Australia, differences in the haplotypic composition between northbound migrating male and female individuals indicated that the two sexes of a matrilineal stock use different migratory corridors (Valsecchi *et al.*, 2010).

Although only few genetic studies have been conducted on Antarctic blue whales to date, there is genetic evidence of a certain degree of connectivity of Antarctic blue whales in the Southern Ocean, indicating that dispersal behavior may have existed (or still exist) in Antarctic blue whales. Recently, it has been suggested that at least three genetically distinct Antarctic blue whale populations exist on the Southern Ocean feeding grounds, which on the one hand may indicate little connectivity between populations (Attard *et al.*, 2016). On the other hand however, some individuals appeared to have a mixed ancestry, suggesting at least some gene-flow between populations (Attard *et al.*, 2016). Given the maternally determined population structure and assumed site fidelity to the Southern Ocean feeding grounds in Antarctic blue whales (Sremba *et al.*, 2012), population interchange might be mainly mediated by male individuals, in analogy to what has been reported for humpback whales (Baker *et al.*, 1990; Baker *et al.*, 1998). However, in-depth understanding of the interchange between Antarctic blue whale populations is lacking to date and the existence of different populations and the degree of connectivity between these potential populations on the feeding grounds are still subject to debate (see e.g. International Whaling Commission, 2016). The findings of Attard *et al.* (2016) implying the existence of genetically largely distinct Antarctic blue whale populations in the Southern Ocean are in contrast to observations (based on Discovery marks and photo identification) made during or after the commercial whaling era. These observations indicate large-scale longitudinal movements of individual whales within and between seasons (Brown, 1962; Branch *et al.*, 2007; Andrews-Goff *et al.*, 2013; Olson *et al.*, 2016). The observed circum-polar movements in the Southern Ocean have been considered to suggest that Antarctic blue whales are likely to be a single population (Branch *et al.*, 2007; International Whaling Commission, 2016). The differences between genetic data and visual and marking-based observations could potentially reflect a change in the migratory behavior of Antarctic blue whales associated with the population bottleneck, e.g. regarding the relative importance of longitudinal dispersal of the species on the feeding grounds.

6.3. Potential effects of commercial whaling on baleen whale migratory behavior

In migratory species, a decrease in the number of individuals with cultural knowledge on migration, e.g. on migratory routes or destinations, has the potential to directly affect the migratory ability of a population or species (Shaw & Couzin, 2013). The severity and temporal scale of the bottleneck effects on the migratory behavior of a species is likely to depend on whether this behavior is transferred genetically or culturally over time (see Petitgas *et al.*, 2010). In baleen whales, the population structure and migratory behavior is governed by strong maternal site fidelity to specific habitats. Such cultural, migratory knowledge is considered to be transferred via social learning within the populations (e.g. Baker *et al.*, 1990; Clapham & Seipt, 1991; Stevick *et al.*, 2006; Clapham *et al.*, 2008; Valenzuela *et al.*, 2009; Sremba *et al.*, 2012; Barendse *et al.*, 2013) (see also chapter 5.1.4). In turn, the availability and transmission of cultural, migratory knowledge in a population is likely to have decreased when individuals exhibiting such knowledge were caught during whaling (Brown & Laland, 2003; Clapham *et al.*, 2008; Shaw & Couzin, 2013). Such a loss of cultural knowledge on e.g. suitable migratory destinations and routes is presumed to have mediated the abandonment of previous migratory routes or former, frequently used, habitats (Clapham *et al.*, 2008; Valenzuela *et al.*, 2009). A lack of recolonization was reported for blue whales formerly inhabiting waters off South Georgia and Japan, for humpback whales off South Georgia, off New Zealand and in the southeastern Caribbean, as well as for bowhead whales off Spitsbergen (e.g. Moore *et al.*, 1999; Swartz *et al.*, 2003; Wiig *et al.*, 2007; see also Clapham *et al.*, 2008 and references therein). Similarly, southern right whale populations, which were also drastically exploited during the whaling era (Reilly *et al.*, 2013), presently occupy only one of six former feeding grounds in the South Atlantic Ocean (Valenzuela *et al.*, 2009).

Potential negative effects of population bottlenecks on baleen whale migration may to some extent have been buffered by the behavioral plasticity of a species. Behavioral plasticity may favor the establishment of new migratory patterns, the maintenance of connectivity between populations, the re-colonization of areas or the formation of new breeding aggregations in baleen whales (see also Carroll *et al.*, 2014; Clapham & Zerbini, 2015). In an undisturbed population, cultural inheritance of a strong site fidelity to specific habitats, as presumed to occur in baleen whales, may limit the exploration of new feeding opportunities, despite the availability of more suitable, high-quality habitats elsewhere (Matthiopoulos *et al.*, 2005; Clapham *et al.*, 2008; Valenzuela *et al.*, 2009; Carroll *et al.*, 2014). Hence, traditional, culturally transferred, behavioral traits may restrict populations in their potential range and hamper potential (re)colonization processes of former or new habitats (Matthiopoulos *et al.*, 2005). This phenomenon has also been suggested to maintain migratory behavior under fluctuating environmental conditions (Corten, 2002) and to some degree hamper the recovery of collapsed fish stocks (Petitgas *et al.*, 2010).

Under a loss of cultural knowledge due to drastic changes in a populations' size, demography and population structure, the relative importance of alternative, exploratory migratory behaviors in a population may increase. In particular, immigration from other populations has been suggested to be an important factor in securing the survival of drastically exploited populations in marine and terrestrial mammals (e.g. Hoelzel *et al.*, 1993; Flagstad *et al.*, 2003; Carroll *et al.*, 2014; Clapham & Zerbini, 2015). Clapham & Zerbini (2015) suggested the 'social aggregation hypothesis' to provide a partial explanation for the observed recovery in some humpback whale populations. This hypothesis suggests that the strong tendency of humpback whales to aggregate in their breeding season favors the immigration of whales from adjacent populations. The authors further argued that the failure of recolonization of some former humpback whale habitats may not necessarily reflect a lack of recovery but rather a post-whaling shift in migratory routes and destinations towards higher-density areas (Clapham & Zerbini, 2015). Similarly, differences in the inferences of connectivity of Antarctic blue whales in the Southern Ocean based on either genetic data or visual and marking data (Branch *et al.*, 2007; Attard *et al.*, 2016; see chapter 6.2) could potentially reflect that the relative importance of dispersal behavior has increased in the post-whaling Antarctic blue whale population(s). In other baleen whale populations however, excessive broad-scale exploitation may have precluded the possibility to maintain connectivity between populations. In turn, this may have affected the effectiveness of re-population of deserted habitats by immigration of individuals from adjacent populations (Clapham *et al.*, 2008).

6.4. Parallel evidence on population bottleneck effects in other migratory species

Studies from other migrating animal populations provide parallel evidence that population bottlenecks, accompanied by a damage of the population structure, can cause a breakdown of socially transmitted traditions, such as migratory behavior (Petitgas *et al.*, 2010). Similarly to baleen whales, the migratory behavior of many fish species is thought to be socially transferred, in particular in long-living species (McQuinn, 1997; Corten, 2002; Petitgas *et al.*, 2010). Bottleneck situations, such as stock collapses under intense fishing or an imbalanced recruitment process due to a depletion of the adult stock, were accompanied by changes in fish migration (Petitgas *et al.*, 2010; MacCall, 2012). These changes include the disappearance of migratory routes or the development of new migration patterns (McQuinn, 1997; Corten, 2002). In addition, in depleted fish stocks, an entrainment of individuals in the traditional migratory behaviors of their respective stock due to social learning processes was suggested to inhibit the recovery of depleted populations and recolonization of abandoned habitats (Petitgas *et al.*, 2010). Similarly, experiments with storks and whooping cranes showed that naïve, captive-reared birds are unlikely to complete the autumn migration towards the wintering grounds successfully when adult animals are absent (e.g Fagan *et al.*, 2012; Mueller *et al.*, 2013). These observations confirm that the absence of experienced individuals can considerably affect the migratory behavior and migratory success in some species (Fagan *et al.*, 2012; Mueller *et al.*, 2013).

Besides the importance of culturally transferred migratory knowledge, there may also be other components affecting or determining the behavior of migratory species. Such factors, e.g. environmental conditions and genetically inherited traits, might buffer the effects of a population bottleneck. In short-living fish species that do not rely on social learning, migratory patterns have been hypothesized to be mediated by environmental conditions. In these species, stock collapses were observed to not entail long-lasting effects on migratory behavior (Petitgas *et al.*, 2010). In some migrating bird species, innate programs might also be important to direct migratory movements. These programs may encode the direction or distance to migrate in some species, enabling a successful migration of naïve birds also when experienced adult individuals are absent (Alerstam *et al.*, 2003; Åkesson & Hedenström, 2007; Bauer *et al.*, 2011). However, the influence and importance of environmental triggers and genetic imprinting on migratory behavior is not well understood to date and may differ between species. It hence cannot be excluded that such additional factors might influence a species' migratory behavior as well and potentially buffer the effects of a population bottleneck to at least some degree.

6.5. Ecosystem-effects of baleen whale migration

Migration is considered an important factor in contributing to long-term stability of ecosystems and shaping ecosystem dynamics. Changes in a species' migratory behavior can hence entail large-scale ecosystem-effects, as suggested both in the terrestrial and the aquatic realm (e.g. Fryxell & Sinclair, 1988; Brönmark *et al.*, 2010; Holdo *et al.*, 2011; Chapman *et al.*, 2012). In migratory ungulates, a cessation of migration not only entailed changes in the trophic cascade, but presumably also affected local vegetation, soil stability and climatic conditions (Fryxell & Sinclair, 1988; Holdo *et al.*, 2011). Similarly, (partial) migration of fish influences the dynamics of lower trophic levels (Brodersen *et al.*, 2008) and is considered to be a crucial factor in regulating regime shifts between different ecological states of entire lake ecosystems (Brönmark *et al.*, 2010; Chapman *et al.*, 2012).

The depletion in baleen whale populations due to commercial whaling is likely to have affected a number of ecosystem processes, including the availability and flux of nutrients, energy flow and food web structure (Croll *et al.*, 2006; Ainley *et al.*, 2010a). The ecological role of baleen whales is considered to involve both bottom-up effects (such as nutrient cycling and transport or habitat modification) and top-down effects (e.g. consumption or predator-prey interactions) (e.g. Bowen, 1997; Van Opzeeland, 2010). Changes in the migratory behavior, such as altered migratory routes or abandonment of former habitats, lead to a (local) decrease in the abundance of baleen whales in an area (see e.g. Clapham *et al.*, 2008). In the Southern Ocean, a declining baleen whale abundance in an area is likely to be associated with a decrease in the availability of iron as a result of the crucial role of baleen whales in nutrient cycling processes and subsequent stimulation of primary productivity (Lavery *et al.*, 2014; Ratnarajah *et al.*, 2014; Surma *et al.*, 2014). The post-whaling decrease in the baleen whale abundance in an area (either directly due to heavy exploitation or indirectly due to alterations in migratory behavior) therefore is likely to have caused a decrease in the (local) productivity of the respective ecosystems, leading to cascading effects in the food web (Surma *et al.*, 2014).

Furthermore, changes in the migratory behavior and abundance of a baleen whale species may also cause changes in the competition for prey resources both intra- and interspecifically (e.g. Laws, 1977; Lockyer, 1984; Ballance *et al.*, 2006; Branch & Williams, 2006). Decreases in a species' abundance have been suggested to cause an intra-specific competitive release, e.g. resulting in higher growth rates and subsequently, a decreased age at sexual maturity in baleen whales (Lockyer, 1979; Lockyer, 1984). Between (krill consuming) species, a decreasing competition for prey resources, associated with the decline of blue, fin and humpback whale populations, has been suggested to cause increases in the abundance of species that were less or not at all targeted by commercial whaling, such as minke whales, sei whales, pinnipeds and penguins (e.g. Laws, 1977; Kawamura, 1978; 1994; Ballance *et al.*, 2006). However, the degree and effects of intra- and inter-specific competition among marine mammals are not fully understood[d], not least because comparative data on populations during or shortly after whaling are scarce (Kawamura, 1994; Clapham & Brownell, 1996).

Changes in the abundance and migratory behavior of baleen whales may also have the potential to affect higher trophic levels. Mammal-eating killer whales have been suggested to switch their prey in response to a decreased baleen whale abundance (Springer *et al.*, 2003). In turn, this prey switch may have increased predation pressure on other species, such as sea lions and elephant seals (Springer *et al.*, 2003; Branch & Williams, 2006). However, the actual dependence of killer whales on baleen whale prey as well as the hypothesis of a killer whale prey switch are still under debate (Clapham, 2001; Connor & Corkeron, 2001; Mizroch & Rice, 2006; Mehta *et al.*, 2007; Pitman *et al.*, 2015).

In summary, changes in the abundance of baleen whales in an area have been suggested to entail large-scale effects on several ecosystem processes, potentially affecting different trophic levels. These effects are likely to interact or be coupled with various other, abiotic and biotic, factors, including various global change-related ecosystem alterations but also multi-species interactions within the marine food webs (Mori & Butterworth, 2004; Smetacek & Nicol, 2005; Croll *et al.*, 2006; Trathan *et al.*, 2012; Thomas *et al.*, 2016). Hence, careful consideration of potential interrelations between different impact factors and associated uncertainties is essential when aiming at assessing potential ecosystem-effects of an altered migratory behavior and abundance of baleen whales.

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[d] But see Friedlaender *et al.* (2008) and Friedlaender *et al.* (2015) who reported differences in foraging strategies between sympatric baleen whales species and suggested that such differences may help to avoid interspecific competition in baleen whales.

7. OUTLOOK: HOW IMPORTANT IS THE SOUTHERN OCEAN AS ANTARCTIC BLUE WHALE HABITAT?

An understanding of the importance of a specific habitat for the focal species is one of the most critical prerequisites for the development of effective long-term conservation strategies such as the designation of marine protected areas or the mitigation of anthropogenic impacts on baleen whale populations. In this context, future research on Antarctic blue whale distribution and migration patterns should explicitly focus on further exploring the importance of the Southern Ocean and subpolar waters as Antarctic blue whale habitat. This requires an understanding of multiple related aspects, such as: Which and how many individuals overwinter at high(er) latitudes (and which do not), i.e. does facultative residency represent a common migratory trait of Antarctic blue whales on both individual and population-level? Does mating regularly take place in (sub)polar waters during austral winter? Which areas are crucial summer and winter (and potential mating) habitats for Antarctic blue whales, and hence are critical for population recovery?

In the following sections, I will outline future research needs that will help gauging deeper insights into these open questions.

Northward extension of the spatial coverage of the PAM network in the Southern Ocean

Spatial extension of the PAM data coverage in the Southern Ocean, e.g. in its Atlantic sector, is highly desirable to better understand the winter distribution of Antarctic blue whales and hence, the location of critical habitats for the population’s recovery. In the Weddell Sea, a substantial number of passive acoustic recorders remains yet to be recovered and data to be analyzed, allowing a spatial extension of the existing passive acoustic Weddell Sea data set in the near future (Fig. 11). Analyses of PAM data recorded in the inner southern Weddell Sea can provide further insights into the southerly extent of the Antarctic blue whale distribution range throughout the year (Fig. 11). Furthermore, publication IV implied that the waters close to the sea ice edge might form an important winter habitat for Antarctic blue whales, potentially providing foraging opportunities. In the future, it would therefore be worthwhile to consider expanding the Weddell Sea PAM network northwards in order to specifically target the area of the winter sea-ice edge and the Southern Boundary of the Antarctic Circumpolar Current, which is located between 55°S and 60°S in the subpolar South Atlantic Ocean (Orsi *et al.*, 1995) and known to be an ecologically important region, inhabiting high densities of krill (Tynan, 1998; Atkinson *et al.*, 2008). In this context, a northward extension of the PAM network could also include the deployment of passive acoustic recording devices in the highly productive South Georgia region (Atkinson *et al.*, 2008). This area has been an important year-round blue whale habitat as indicated by early whaling data (e.g. Mackintosh & Wheeler, 1929), but few blue whales are observed in this area today (Clapham *et al.*, 2008). Future long-term PAM projects could help to explore the occurrence of Antarctic blue whales in the waters off South Georgia and, possibly, monitor the recolonization of this former habitat.

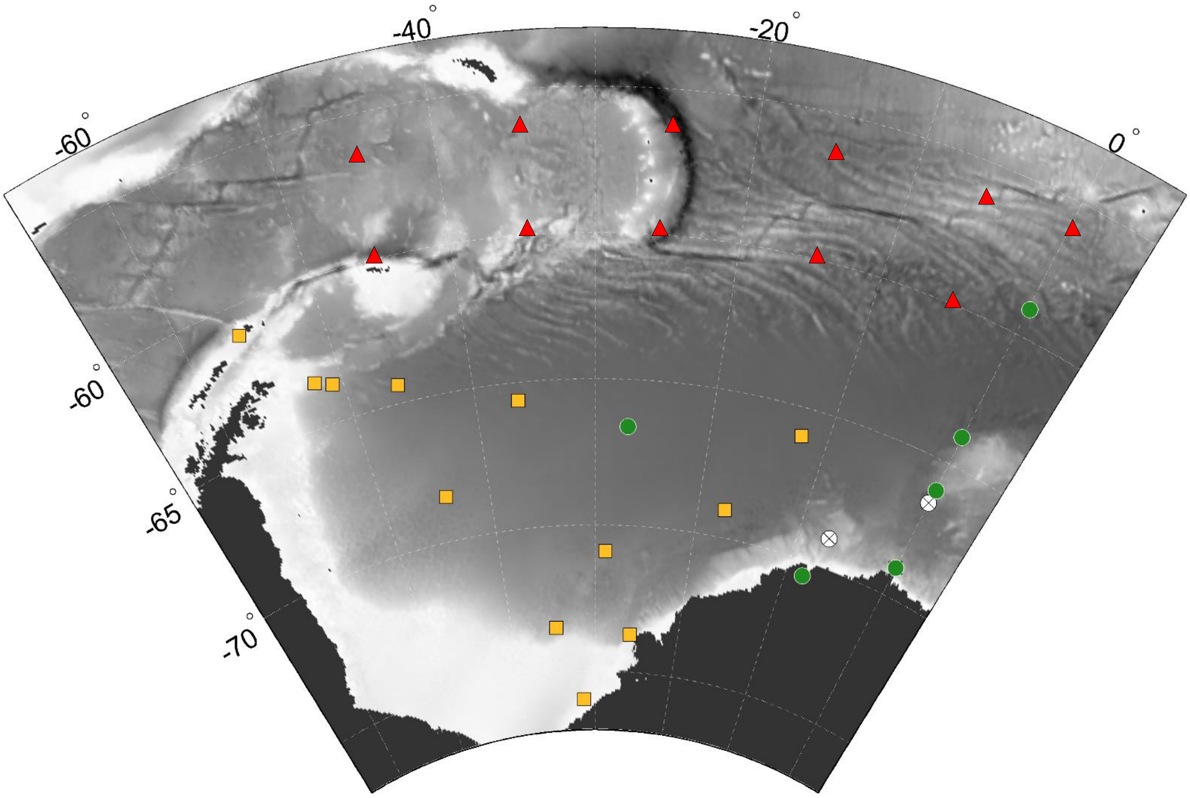

Fig. 11: *Overview of passive acoustic recording positions in the Weddell Sea and Atlantic sector of the Southern Ocean. Green dots represent positions from which PAM data were available and analyzed in the framework of the present thesis. White crossed dots indicate positions from which PAM data were recovered but excluded from further analyses (see Publication III for further details). Orange squares indicate recording sites from which PAM data were not yet recovered or analyzed. Red triangles indicate potential future recording positions.*

On a circumpolar scale, some areas of the Southern Ocean are rarely monitored to date, e.g. the IWC management areas I and VI in the Southern Ocean (see Fig. 4 in Samaran *et al.*, 2012 for an overview on PAM efforts in the Southern Hemisphere). This issue could be overcome by the establishment of a large-scale, circum-Antarctic network of passive acoustic recorders (referred to as ‘SOHN’) as is currently being aspired by the ‘Blue and Fin Whale Acoustics Trends Project’[e] of the Southern Ocean Research Partnership (SORP) (see Van Opzeeland *et al.*, 2013a for further details). In the future, the spatial scale and resolution of the SOHN project could also be extended in order to overcome the scarcity of knowledge on potential migratory corridors and critical overwintering habitats of Antarctic blue whales. A higher spatial resolution of the circum-Antarctic PAM network, obtained by increasing the number of deployed passive acoustic recorders, would help to investigate fine-scale distribution patterns and to identify important habitats of Antarctic blue whales in the Southern Ocean. Furthermore, a northward extension of the circum-Antarctic PAM network could involve the establishment of latitudinal transects of passive acoustic devices, causing the PAM network to range from high-latitude feeding grounds of Antarctic blue whales in the Southern Ocean to mid- and potentially low-latitude areas in the Atlantic, Pacific and Indian

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[e] The Blue and Fin Whale Acoustics Trends Project is one of five original research projects of SORP and currently involves international collaboration among research institutes from Australia, France, Germany, South Africa, the UK and the USA (Van Opzeeland *et al.*, 2013a).

Oceans[f]. Subsequently, such a dense, large-scale PAM network would have the potential to provide unprecedented information not only on the location of important feeding habitats of Antarctic blue whales in the Southern Ocean, but also on locations of potential migratory routes and overwintering habitats (and, possibly, breeding areas) within and outside the Southern Ocean.

Obtaining positional information on Antarctic blue whales

Long-term information on the location of vocalizing Antarctic blue whales can reveal fine-scale distribution patterns of the animals over the course of the year and can facilitate identifying the location of important winter habitats. Furthermore, such information can show how much time Antarctic blue whales spend in a particular area, hence help assessing the relative importance of this habitat. Detailed positional information could for instance be obtained by (satellite) tracking approaches. Besides providing fine-scale information on the location of the tagged individuals, tracking approaches also provide the opportunity to obtain additional data on the identity of the individuals (Double *et al.*, 2013). Such information benefits inferences on whether the tendency to skip migration differs between classes of whales and, given that the tag is attached long enough, how often skipping migration may occur in an individuals' life. The advances of tracking approaches are to some extent derogated by a low probability to encounter Antarctic blue whales, resulting in a comparatively low number of individuals tagged (Andrews-Goff *et al.*, 2013). In turn, the obtained data may not be representative on a population-level yet. This difficulty could be significantly decreased by passive acoustic tracking, which has been successfully used to localize and trace Antarctic blue whales in the Southern Ocean (Miller *et al.*, 2015). PAM further provides another possibility to acquire positional information on Antarctic blue whales. Long-term positional data could be obtained by setting-up small-scale arrays of passive acoustic recording devices, which are capable of localizing the direction of a sound source by analyzing time differences of arrivals of signals at different devices (e.g. Širović *et al.*, 2007; Simard & Roy, 2008), or by deploying recording devices equipped with directional sensors (e.g. Greene Jr *et al.*, 2004; Blackwell *et al.*, 2007; see also Sousa-Lima *et al.*, 2013). Such PAM applications would provide a better understanding of the area monitored and the animal density in this area (see also Marques *et al.*, 2013) and can subsequently enable estimations on how many (vocalizing) individuals overwinter in a particular area.

Obtaining behavioral information during austral winter

An enhanced understanding of the vocal behavior of Antarctic blue whales, e.g. on intra-population differences in call production or on functionality of their calls, could considerably improve inferences on which Antarctic blue whale individuals skip migration and overwinter in the Southern Ocean. In particular, PAM-based inferences on the distribution, migratory behavior and habitat use of certain Antarctic blue whale classes, e.g. in terms of sex, age or reproductive state, would require information on whether and how these classes are acoustically distinguishable as well as on the functionality and behavioral context of different call types. The scarcity of such information could be overcome by combining multiple research approaches. A future multi-level research project could include data collection on: 1) the vocal behavior of individual Antarctic blue whales, particularly during winter months, e.g. by using acoustic tags, 2) the sex or age of the tagged individual, e.g. from biopsy samples collected during tag deployment, and 3) the individual behavior (ideally during call production), e.g. based on visual observations, acoustic tags allowing inferences on an

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[f] While a broad-scale PAM array has already been established in the Indian Ocean (see e.g. Stafford *et al.*, 2011; Samaran *et al.*, 2013), there has been comparatively little PAM research effort in the South Atlantic and Pacific Oceans, particularly with respect to the oceanic areas (but see Stafford *et al.*, 2004; Samaran *et al.*, 2012; Buchan *et al.*, 2015).

individuals' behavior (Bailey *et al.*, 2010) or data collected by unmanned systems (Christiansen *et al.*, 2016; Nowacek *et al.*, 2016).

Obtaining information on Antarctic blue whale behavior during winter is highly desirable not only to better understand their acoustic ecology, but also to explore the types of behaviors Antarctic blue whales are engaged in during austral winter in their (sub)polar habitats. Collecting behavioral data is however complicated by the high costs of accessing ice-covered areas during winter months. Furthermore, the location of overwintering habitats of Antarctic blue whale individuals is still largely unknown and is furthermore likely to be spatially variable depending on environmental factors (Tynan, 1998; Van Opzeeland *et al.*, 2013b). Hence, future research would benefit from large-scale and long-term positional information as outlined above, helping to identify important 'hot spots' for Antarctic blue whales during austral winter and thus research key areas. Another opportunity to obtain behavioral information on Antarctic blue whales could be the use of unmanned underwater systems equipped with camera gear (Nowacek *et al.*, 2016). On shorter time scales, a specifically modified AUV equipped with a camera system could be used to track and follow tagged individuals, as has been used to study white sharks ('REMUS SharkCam', see e.g. Kukulya *et al.*, 2015). Recent technological developments and advances allowed collecting (near)real-time data on the acoustic presence of vocalizing marine animals from ocean gliders (e.g. Baumgartner *et al.*, 2013; Baumgartner *et al.*, 2014; Klinck *et al.*, 2016). In future projects, such unmanned autonomous underwater systems could be developed further to exhibit integrated directional acoustic sensors. These could enable the device to localize and track vocalizing marine animals and be used by the unmanned underwater system to actively adapt its course towards the detected acoustic source. By further equipping it with a camera system, the instrument would be able to collect visual behavioral information on the focal individual. Such information could potentially help to shed light on whether mating regularly takes place in high-latitude waters. Furthermore, such insights would considerably improve our understanding on which areas might be particularly critical for population recovery and, consequently, are of primary concern regarding conservation applications.

8. CONCLUDING REMARK

During the past decades, advances in marine mammal monitoring techniques have enabled refining our understanding of distribution and migration patterns of Antarctic blue whales. We now better understand the large-scale distribution range of Antarctic blue whales in the Southern Hemisphere over the course of the year. Additionally, recent findings, including the ones presented in this thesis, challenged the migration paradigm of an obligate, complete and uniform migration by illustrating that Antarctic blue whales exhibit a diverse migratory repertoire, including facultative, partial and differential migration.

The findings of this dissertation will hopefully stimulate and guide future research to further unveil the distribution and complex migratory repertoire of Antarctic blue whales. Such knowledge is invaluable to directly inform future conservation and mitigation applications, such as the establishment of a marine protected area in the Weddell Sea, currently being aspired by the Commission for the Conservation of Antarctic Marine Living Resources (‘CCAMLR’) (e.g. Teschke *et al.*, 2015). Future research projects could for instance help identifying important migration corridors and critical habitats for feeding, overwintering and mating of baleen whales in the Southern Ocean as well as at mid and low latitudes. Such insights will contribute to the identification of key habitats of marine species and to the development of effective conservation measures. Furthermore, an enhanced understanding of the *status quo* of baleen whales will benefit our ability to assess potential impacts of current threats, such as the ongoing global change or the increasing human intervention in the world’s oceans, on their populations.

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PUBLICATIONS

Outline of publications

The present dissertation was written on a cumulative basis and comprises 6 publications: 2 papers published in peer-reviewed journals, 1 publication being a paper presented to the Scientific Committee of the International Whaling Commission (‘IWC’) in 2015, and 3 manuscripts in preparation.

All publications are presented as independent pieces of work in the current thesis and are listed in order of their appearance below, including the status, content and author contributions for each of the publications.

Publication I: *Status: Published 2015 (peer-reviewed)*

Effects of subsampling of passive acoustic recordings on acoustic metrics.

Karolin Thomisch, Olaf Boebel, Daniel P. Zitterbart, Flore Samaran, Sofie Van Parijs, Ilse Van Opzeeland (2015), Journal of the Acoustical Society of America 138:267-278

This study investigates how different subsampling schemes affect the accuracy of acoustic presence and call rate assessments in passive acoustic data representing different vocalization patterns of baleen whales. The accuracy of both acoustic presence and call rate estimates is negatively impacted by a reduction of the duty cycle. Furthermore, at a given duty cycle, the accuracy of daily acoustic presence estimates is enhanced by using frequent short listening periods rather than few, long listening periods. Subsampling effects are most pronounced when the vocal activity of the focal species is low or temporally clustered. This study highlights the importance of informed decisions on suitable subsampling schemes for passive acoustic data collection or analysis.

I conducted all manual analyses of the passive acoustic data collected by PALAOA. Pre-processed data sets containing information on call detections of Antarctic blue whales from the Indian Ocean and North Atlantic right whales from the North Atlantic Ocean were contributed by the fourth and fifth author, respectively. Together with the second, third and sixth author, I developed the metrics and routines for subsampling of the continuous passive acoustic data sets and analyses of the subsampled data sets. I wrote the initial draft of the manuscript and all further versions of the manuscript, which resulted from discussions with all other authors.

Publication II: *Status: Published 2015 (IWC paper)*

Blue whale sightings in Antarctica west of the Greenwich meridian, January 2015.

Steve C. V. Geelhoed, Bram Feij, Jan-Andries van Franeker, Helena Herr, Nicole Janinhoff, Shannon McKay, Sebastian Müller, Karolin Thomisch, Hans Verdaat, Sacha Viquerat (2015), Paper SC/66a/SH/11 presented to the Scientific Committee of the International Whaling Commission, May 2015, San Diego, CA.

This study reports blue whale (*Balaenoptera musculus*) sightings in the Atlantic sector of the Southern Ocean during cruise PS89 of RV Polarstern from December 2014 to February 2015, based on 5 different sources of both dedicated and opportunistic marine mammal sightings. Within 5 days during mid-January, 20 sightings of 26 individual blue whales were made. These findings add to previous observations of a blue whale hot spot off Queen Maud Land between 0°E and 20°E and imply a spatial extension of this hot spot into the eastern Weddell Sea.

I contributed to species identification on photographs taken from the bridge of RV Polarstern during opportunistic cetacean sightings and logged using the custom-written software WALOG[g]. The first author wrote the initial draft of the manuscript. Together with all other authors, I contributed to preparation and development of the manuscript.

Publication III: *Status: Published 2016 (peer-reviewed)*

Spatio-temporal patterns in acoustic presence and distribution of Antarctic blue whales (*Balaenoptera musculus intermedia*) in the Weddell Sea.

Karolin Thomisch, Olaf Boebel, Christopher W. Clark, Wilhelm Hagen, Stefanie Spiesecke, Daniel P. Zitterbart, Ilse Van Opzeeland (2016), Endangered Species Research 30: 239-253

This study explored spatial and temporal patterns in the distribution of Antarctic blue whales based on passive acoustic monitoring data collected in the Atlantic sector of the Southern Ocean between 2008 and 2013. Antarctic blue whales were acoustically present year-round in the study area, with most calls detected between January and April. During austral winter, vocalizations were recorded at latitudes as high as 69°S with sea ice cover exceeding 90%, indicating that part of the Antarctic blue whale population overwinters in Antarctic waters. The study adds to increasing evidence of a diverse migratory repertoire of Antarctic blue whales, potentially comprising partial and differential migration.

I conducted all passive acoustic data analyses. The second and the seventh author designed the study. Data from the recording site at 59°S, 0°E (MARU recorder) were made available for analyses by the third author. The fifth author held responsibility for recorder deployment and recovery of passive acoustic recording devices deployed within the HAFOS array as well as data storage on board RV Polarstern. Together with the sixth author, I developed and tested the automated Z-call detector and BWI metric applied in this study. Data on daily sea ice concentrations were provided by the second author. I wrote the all versions of the manuscript and all co-authors provided scientific and editorial advice.

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[g] Further details on WALOG software and data protocols are given in Burkhardt (2009) and Bombosch (2013).

Publication IV: *Status: Manuscript in preparation*

Spatio-temporal patterns in the presence of frequency-modulated calls of Antarctic blue whales in the Weddell Sea.

Karolin Thomisch, Olaf Boebel, Christopher W. Clark, Stefanie Spiesecke, Ilse Van Opzeeland, Manuscript in preparation

This study is based on frequency-modulated (FM) downsweep calls of Antarctic blue whales recorded between 2008 and 2013 in the Weddell Sea to further explore Antarctic blue whale distribution patterns. FM-calls were frequently present during austral summer at all recording sites, implying a wide distribution range of Antarctic blue whales. During winter months, part of the population is likely to remain close to the sea ice edge, as indicated by the persistent FM-call presence at 59°S, 0°E. FM-calls were largely absent during austral winter south of 60°S, which is in contrast to the year-round presence of Antarctic blue whale Z-calls throughout the study area. Differences between FM-call and Z-call presence may reflect different propagation ranges of these calls. Alternatively, the absence of FM-calls south of 60°S during winter might indicate a change in the (vocal) behavior of Antarctic blue whales during winter months.

I conducted all passive acoustic data analyses. The second and the fifth author designed the study. Data from the recording site at 59°S, 0°E (MARU recorder) were made available for analyses by the third author. The fourth author held responsibility for recorder deployment and recovery as well as data storage on board RV Polarstern. I wrote the all versions of the manuscript, with all co-authors providing ideas and scientific advice.

Publication V: *Status: Manuscript in preparation*

Intra- and interannual patterns in the acoustic presence of large cetacean species in a presumed breeding area off Namibia.

Karolin Thomisch, Olaf Boebel, Jennifer Bachmann, Svenja Neumann, Stefanie Spiesecke, Ilse Van Opzeeland

In this study, temporal patterns in the acoustic presence of large cetacean species were examined in the South Atlantic Ocean off Namibia based on passive acoustic data collected between 2011 and 2013. Antarctic minke whales, fin whales and humpback whales were seasonally present during austral winter, likely indicating that the animals migrate to high(er) latitudes during austral summer months. Antarctic blue whales were present throughout the recording period, potentially implying that part of the population remains at low latitudes year-round. This study hence confirms the ecological importance of the oceanic waters off Namibia as a suitable wintering and, possibly, breeding habitat for several cetacean species.

The study was designed by the second and the sixth author and myself. I conducted all analyses with regard to Antarctic blue whale acoustic presence using automated detection approaches for Antarctic blue whale Z-calls and BWI. The third and fourth authors conducted the manual (visual and aural) analyses of the passive acoustic data sets determining the daily acoustic presence for all other cetacean species. I wrote the initial draft of the manuscript and all further versions of the manuscript, which resulted from discussions with all other authors.

Publication VI: *Status: Manuscript in preparation*

Temporal shifts in the vocalization frequency of Antarctic blue whales in the Atlantic sector of the Southern Ocean and the South Atlantic Ocean.

Karolin Thomisch, Olaf Boebel, Stefanie Spiesecke, Ilse Van Opzeeland

The study reports inter- and intra-annual temporal patterns in the vocalization frequency of Antarctic blue whales based on passive acoustic data collected between 2008 and 2013. Inter-annually, the Antarctic blue whale peak vocalization frequency declined steadily at all recording sites. The annual rates of decline reported here are lower than those reported in previous studies, potentially indicating spatial differences or a temporal deceleration in the decrease rates of the Antarctic blue whale peak vocalization frequency. Intra-annually, a sinusoidal pattern was evident in the peak frequency in the recordings from the Southern Ocean, but not in those from the Atlantic Ocean off Namibia. The reasons for the observed temporal patterns in Antarctic blue whale vocalization frequency are not understood to date and several hypotheses have been provided, which are briefly summarized and discussed in this manuscript.

I conducted all analyses of the passive acoustic data in order to investigate temporal patterns in the peak frequency of Antarctic blue whale Z-calls. The fourth author held responsibility for recorder deployment and recovery as well as data storage on board RV Polarstern. The manuscript was written by myself with advice by all co-authors.

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Publication I:

Effects of subsampling of passive acoustic recordings on acoustic metrics.

Karolin Thomisch, Olaf Boebel, Daniel P. Zitterbart, Flore Samaran, Sofie Van Parijs, Ilse Van Opzeeland

Journal of the Acoustical Society of America (2015) 138:267-278

Effects of subsampling of passive acoustic recordings on acoustic metrics

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Passive acoustic monitoring is an important tool in marine mammal studies. However, logistics and finances frequently constrain the number and servicing schedules of acoustic recorders, requiring a trade-off between deployment periods and sampling continuity, i.e., the implementation of a subsampling scheme. Optimizing such schemes to each project's specific research questions is desirable. This study investigates the impact of subsampling on the accuracy of two common metrics, acoustic presence and call rate, for different vocalization patterns (regimes) of baleen whales: (1) variable vocal activity, (2) vocalizations organized in song bouts, and (3) vocal activity with diel patterns. To this end, above metrics are compared for continuous and subsampled data subject to different sampling strategies, covering duty cycles between 50% and 2%. The results show that a reduction of the duty cycle impacts negatively on the accuracy of both acoustic presence and call rate estimates. For a given duty cycle, frequent short listening periods improve accuracy of daily acoustic presence estimates over few long listening periods. Overall, subsampling effects are most pronounced for low and/or temporally clustered vocal activity. These findings illustrate the importance of informed decisions when applying subsampling strategies to passive acoustic recordings or analyses for a given target species. *© 2015 Author(s). All article content, except where otherwise noted, is licensed under a Creative Commons Attribution 3.0 Unported License*. [http://dx.doi.org/10.1121/1.4922703]

[JFL] Pages: 267–278

I. INTRODUCTION

Passive acoustic monitoring (PAM) is a widely used tool in marine mammal research concerning primarily spatio-temporal distribution patterns and behavior of vocalizing species (e.g., Mellinger *et al.*, 2007; Van Parijs *et al.*, 2009; Van Opzeeland *et al.*, 2010). Recent methodological advances have broadened the field of PAM applications to also include abundance estimations for some marine mammals (Küsel *et al.*, 2011; Marques *et al.*, 2011; Ward *et al.*, 2012; Harris *et al.*, 2013). While dependent on vocalizations from the target species, PAM exhibits several advantages over traditional visual surveys, such as the possibility to collect data under poor weather conditions, during darkness and in areas with dense ice cover, allowing marine mammal monitoring in regions and at times otherwise inaccessible (both logistically and financially) (e.g., Mellinger *et al.*, 2007). In particular, autonomous passive acoustic recorders are the tool of choice for collecting long-term data series in remote areas that are inaccessible to ships during much of the year, such as the Arctic and Southern Oceans (e.g., Širović *et al.*, 2009; Samaran *et al.*, 2010; Stafford *et al.*, 2012; Sousa-Lima *et al.*, 2013; Van Opzeeland *et al.*, 2013). In many cases, logistic and financial constraints determine the frequency at which recorders are serviced, resulting in time spans of up to two to three years between recorder deployment and retrieval (e.g., Širović *et al.*, 2004; Miksis-Olds *et al.*, 2010; Rettig *et al.*, 2013). However, to date, the majority of autonomous recording instruments do not quite feature sufficient capacity in terms of battery life and/or data storage to record continuously for such prolonged deployment periods at high sampling rates (e.g., Rettig *et al.*, 2013).

Nevertheless, as multi-year data are indispensable to capture long-term trends in temporal and seasonal occurrences of species, full coverage of the period between recorder deployment and retrieval is highly desirable. This often requires recordings to be subsampled (e.g., Burtenshaw *et al.*, 2004; Gedamke *et al.*, 2007; Stafford *et al.*, 2012; Rettig *et al.*, 2013), i.e., to be collected at a repetitive pattern of sampling periods and non-sampling periods at a given repetition cycle. Likewise, for human

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screening of comprehensive, continuous data sets, researchers may resort to analyzing subsets of the data to accelerate the analysis process (e.g., Oleson *et al.*, 2007; Van Opzeeland *et al.*, 2010).

Subsampling of a given percentage of time might, however, be implemented in different ways, with the extremes being either many short listening periods (sampling bouts) or few long listening periods. This option immediately gives rise to the question of potential impacts of the subsampling scheme on ecological inferences drawn from the ensuing data which, in turn, leads to the question for the most suitable sampling scheme for a given species. Simply put, if the recording period is limited, for example, to 1 h during a day, one wonders whether sampling once daily for an hour, twice daily for half an hour, or four times a day for 15 min represents the vocal behavior of a given species best.

The choice of a specific subsampling scheme will be driven by the research question, power and storage capacity of the recording equipment and most importantly the desire not to introduce any biases to the data which can be achieved by seeking an optimal sampling scheme based on pre-existing knowledge on vocalization patterns (e.g., Sousa-Lima *et al.*, 2013). Impacts of subsampling are likely to depend strongly on the characteristics of the focal species' vocal behavior: In case of frequent, regular calls, results from subsampled data may remain representative of the respective period. However, if vocal activity occurs rarely or exhibits a distinct diurnal pattern, sampling exclusively at off-periods would result in substantial misrepresentations of the focal species' acoustic presence. Consequently, suitable subsampling requires tuning to the acoustic behavior of the focal species, such as rate and temporal structure of call production.

Acoustic presence (a binary parameter) and call rate (a continuous numeric parameter) are two frequently used metrics to investigate various aspects of marine mammal ecology (e.g., Mellinger *et al.*, 2007; Širović *et al.*, 2007; Van Opzeeland *et al.*, 2013), such as spatio-temporal patterns in occurrence and distribution, locations of feeding or overwintering habitats as well as density estimations (see also Table I and references therein). In turn, an unbiased assessment of a focal species' acoustic presence is essential for descriptions of its occurrence and distribution on spatial and/or temporal scales (Table I).

Continuous passive acoustic recordings of North Atlantic right whales (NARW, *Eubalaena glacialis*) and Antarctic blue whales (ABW, *Balaenoptera musculus intermedia*) were used in this study to investigate the potential impacts of different subsampling schemes on acoustic presence and call rates by comparing the ensuing results with regard to their representativeness.

II. MATERIALS AND METHODS

A. Passive acoustic data acquisition

Continuous passive acoustic data were collected at three different locations. On the Ekström ice shelf at 70° 31′ S, 8° 13′ W, the PerenniAL Acoustic Observatory in the Antarctic Ocean (PALAOA) collects continuous underwater recordings from a coastal Antarctic environment since 2005 with a Reson TC4032 hydrophone, deployed at approximately 160 m depth (Boebel *et al.*, 2006; Kindermann *et al.*, 2008). In the Indian Ocean, southwest of Amsterdam Island ('SWAMS', 42° 59′ S, 74° 35′ E), continuous acoustic recordings were collected from October 2006 to April 2008 with an ITC-1032 hydrophone moored at 1000 m depth (see Samaran *et al.*, 2013 for further details). In Massachusetts Bay, MA, continuous acoustic data were recorded from January 2006 to February 2007 by means of marine autonomous recording units (MARUs) deployed at depths ranging from 41 to 76 m

TABLE I. Acoustic parameters used in the present case study and possible inferences on the focal species' ecology based on these parameters as reported by previous studies.

Parameter	Direct and further inferences	References (exemplary)[a]
Acoustic presence	Occurrence of a focal species at recording location(s) with potential indications on suitability of habitat for overwintering/breeding/feeding/etc.	(Mussoline *et al.*, 2012; Rankin *et al.*, 2005; Samaran *et al.*, 2013; Širović *et al.*, 2009; Stafford *et al.*, 2004)
	Spatial and temporal patterns in distribution of focal species in certain area	(Gedamke *et al.*, 2007;[b] Matthews *et al.*, 2014; Mussoline *et al.*, 2012; Samaran *et al.*, 2013; Širović *et al.*, 2004)
	Diel vocalization patterns	(Mussoline *et al.*, 2012)
	Associations with abiotic or biotic factors	(Burtenshaw *et al.*, 2004)[b]
Vocalization rate	Abundance and density estimations of animals at recording location/in study area	(Marques *et al.*, 2013; Širović *et al.*, 2004)
	Estimation of historical catch numbers of different blue whale populations from calling patterns	(Monnahan *et al.*, 2014)
	Movement/migration patterns of animals	(Samaran *et al.*, 2013; Širović *et al.*, 2004; Širović *et al.*, 2009)
	Diel vocalization patterns	(Matthews *et al.*, 2014; Stafford *et al.*, 2005; Wiggins *et al.*, 2005)
	Associations with abiotic or biotic factors	(Širović *et al.*, 2004; Širović and Hildebrand, 2011)
	Effects of anthropogenic noise on focal species	(Di Iorio and Clark, 2010; McDonald *et al.*, 1995; Melcón *et al.*, 2012)

[a] References were selected exemplarily, mainly representing passive acoustic research on the focal species of this study, i.e., blue whale (*Balaenoptera musculus)* and North Atlantic right whale (*Eubalaena glacialis*).

[b] Studies based on subsampled acoustic data.

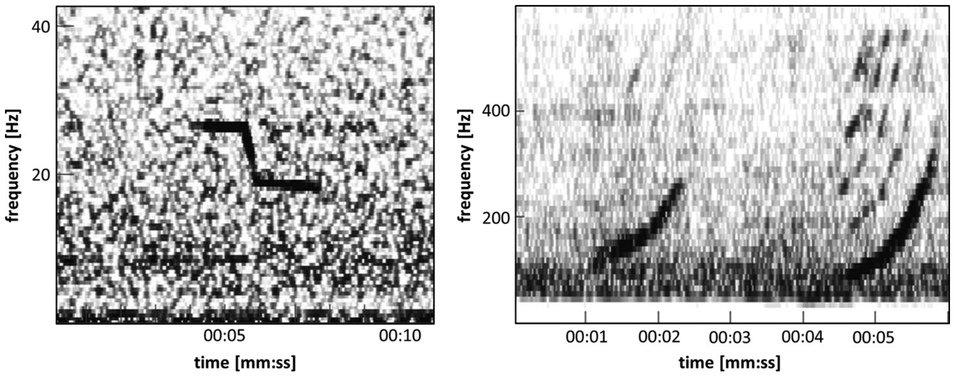

FIG. 1. Spectrogram of Antarctic blue whale Z-call (left panel) and North Atlantic right whale up-call vocalization (right panel). Sound file of NARW up-call was downloaded from http://www.nefsc.noaa.gov/psb/acoustics/sounds.html.

at 10 separate locations throughout the Stellwagen Bank National Marine Sanctuary (see Mussoline *et al.*, 2012 for further details).

B. Focal species and vocalizations

The continuous passive acoustic recordings used in this study contained a variety of marine mammal sounds, yet only ABW Z-calls and NARW up-calls are examined herein. ABW Z-calls (Fig. 1) consist of three components, starting with a constant frequency tone at 27 Hz which lasts for about 8–12 s, followed by a short downsweep to 19 Hz of about 1–2 s duration and a longer (8–12 s) slightly frequency modulated tone at about 18–19 Hz (e.g., Ljungblad *et al.*, 1998; Rankin *et al.*, 2005). The NARW's up-call is a frequency modulated call lasting approximately 1 s with an increasing frequency from 50 to 200 Hz (Fig. 1), which is considered to serve as contact call (Clark, 1982; Parks and Clark, 2007).

C. Passive acoustic data sets

Five data subsets, each comprising seven days, were extracted from the three continuous data sets described in Sec. II A. Each subset is representative of a different pattern of calling behavior including: (1) variable acoustic activity, (2) clear song sequences, and (3) vocal activity featuring a clear diel pattern.

1. *Variable, temporally unstructured acoustic activity with both high and low calling rates*

To explore how subsampling may affect data featuring variable acoustic activity, i.e., without any clear song pattern or diurnal trend, two sets from the PALAOA data were chosen on the basis of results from previous analyses of seasonal vocal activity of Antarctic blue whales (Van Opzeeland, 2010) (Fig. 2). Generally, Z-calls are considered to be repeated every 60 to 65 s in patterned sequences ("song") (e.g., Ljungblad *et al.*, 1998; Širović *et al.*, 2004), however, clear song sequences were not present in this selection of PALAOA data. Instead, the acoustic activity was variable with periods of higher and lower calling activity. The selected data were resampled at 6 kHz and ABW Z-call detection was performed visually by manually screening 1-min spectrograms (FFT 8,192 points, Hanning window, time, and frequency resolution 1.3 s, 0.75 Hz) with Adobe Audition 2.0, resulting in call count data at 1-min resolution. "Regime A–high call rate" represented high vocal activity of an average of 55 ± 18 (standard deviation) Z-calls per hour, whereas "regime B–low call rate" represented data with medium vocal activity of 20 ± 8 Z-calls per hour on average.

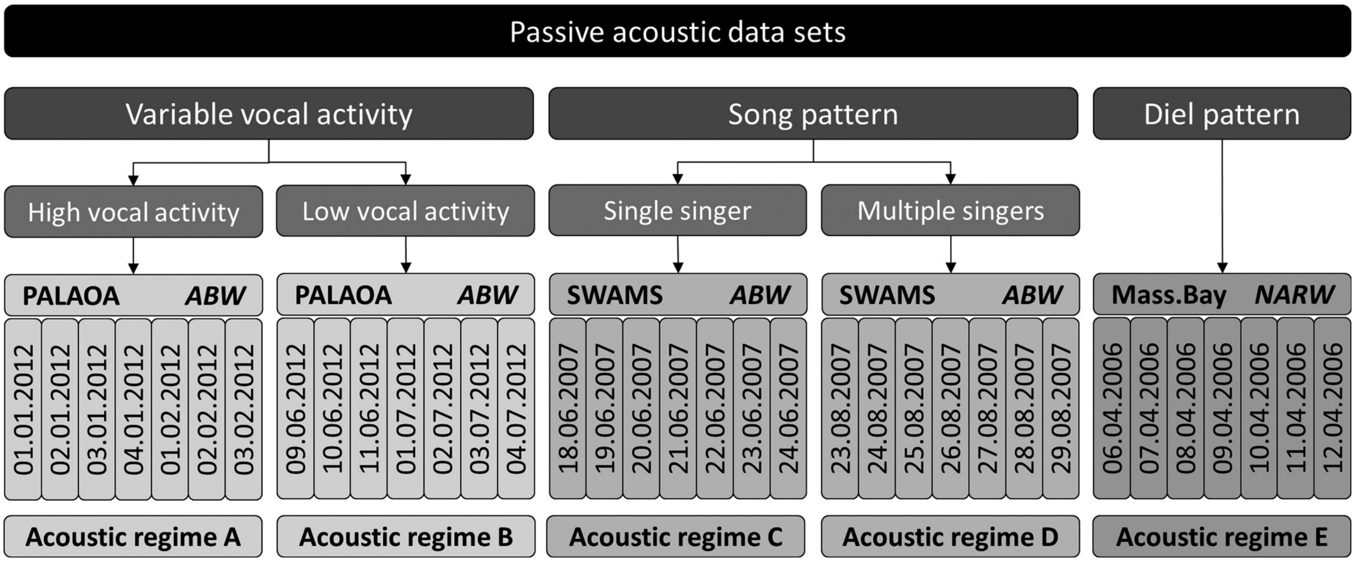

FIG. 2. Passive acoustic data sets used for exploring the effects of different subsampling schemes on call rate and acoustic presence estimation.

No diurnal patterns were evident in these data. Data sets comprised four consecutive days from January and three consecutive days from February (1–4 January 2012 and 1–3 February 2012) for regime A and three consecutive days from June and four consecutive days from July (9–11 June 2012 and 1–4 July 2012) for regime B (Fig. 2). The number of consecutive days was constrained by the presence of noisy periods on some days, caused, for example, by glacier calving. Noisy days were excluded as these potentially affected the reliability of call counts.

2. Structured acoustic activity with clear song sequences by single and multiple individuals

The Indian Ocean data contained sequences of ABW Z-call vocalizations organized in regular song structures. Calls were automatically detected using a template detector in XBAT (Figueroa and Robbins, 2008; see Samaran *et al.*, 2013 for further details). ABW Z-call song featuring inter-call intervals of 60–65 s typically stem from a single calling individual (e.g., Širović *et al.*, 2004) and such events were hence considered as representing single singers. Periods with shorter inter-call intervals are representative of the presence of multiple singers. Seven consecutive recording days from June 2007 (18–24 June 2007) containing individual song were selected to form "regime C–single song," with 17 ± 8 Z-calls per hour on average (Fig. 2). "Regime D–multiple song" comprised a second set of seven consecutive days (23–29 August 2007, Fig. 2) of continuous recordings with 35 ± 22 Z-calls per hour on average, containing ABW song sequences with shorter inter-call intervals (with ~30% of inter-call intervals ranging between 15 and 45 s). No diurnal patterns were evident in these data.

3. Call activities exhibiting strong diel patterns

The Stellwagen Bank acoustic data, containing NARW vocalizations, were analyzed in XBAT, using a custom-written automated call detection algorithm to detect NARW up-calls (see Mussoline *et al.*, 2012 for further details). Seven consecutive recording days (6–12 April 2006, representing pooled call detections from nine different locations) with distinct diel fluctuations [i.e., increased NARW vocal activity during twilight and at night (Mussoline *et al.*, 2012)] were selected to comprise "regime E–diel patterns" (Fig. 2). Hourly call rates ranged from 0 to 137 up-calls per hour (mean 12 ± 6 up-calls per hour).

D. Subsampling schemes

Subsampling schemes are defined by their ***cycle periods*** (τ_c, "sampling intervals") and ***duty cycles D,*** commonly given in percent but as a fractional number hereinafter (Table II and Fig. 3) The corresponding ***listening period*** $\boldsymbol{\tau_l}$ (i.e., length of a sampling bout) is then given by $\boldsymbol{\tau_l = D \cdot \tau_c}$. In the course of a day, the cycle is repeated $24\,\mathrm{h}/\tau_c = N$ times (***number of cycles per day***), with τ_c usually chosen such that $N \in \mathbb{N}$ (Fig. 3).

The potential repercussions of different sampling schemes are explored in this publication by varying (a) the *cycle period* (τ_c) (or correspondingly the *number of cycles per day N*) and (b) the *duty cycle D*. Table III lists the analyzed combinations of cycling periods and duty cycles that result in full minute listening periods. A given duty cycle D may be realized differently in terms of cycle period and corresponding listening period (rows of Table III), resulting in different sampling strategies (e.g., a single long listening period versus multiple shorter windows distributed evenly over the course of a day).

In PAM studies, commonly little consideration is given to when exactly a cycle period commences within a day, while the start of a listening period mostly matches that of the corresponding cycle period. However, (phase) shifts of either are feasible. Within a cycle period (τ_c) the number of independent (non-overlapping) listening periods equals ***1/D***, called the ***number or realizations r*** hereinafter (Fig. 3). For our statistical analysis of the effects of data subsampling, all possible $1/D$ realizations were processed to estimate the variability of call rates and acoustic presence estimations (Table II). This procedure provided $7/D$ ($1/D$ realizations times seven days) independent estimates of acoustic presence and call rates per regime, respectively.

1. Daily acoustic presence estimations from subsampled data

For continuous data, a species was considered present if at least one call was evident during a day. For subsampled data, a focal species was considered acoustically present if at

TABLE II. Index of abbreviations and symbols.

Symbol	Definition
$\boldsymbol{\tau_c}$	Cycle period [h], i.e., the interval at which data collection is repeated
$\boldsymbol{N}$	Number of cycles per day
$\boldsymbol{\tau_l}$	Duration of listening period [min], i.e., the period over which data are acquired continuously
$\boldsymbol{D}$	$= \tau_l / \tau_c$; duty cycle
1/D	$= \tau_c / \tau_l$; number of independent realizations of a given sampling scheme, i.e., number of listening periods per cycle
$\boldsymbol{d}$	Metric depicting correctness of acoustic presence determination in subsampled data compared to true acoustic presence in continuous data; $\boldsymbol{d} = 1$ representing correct acoustic presence estimation and $\boldsymbol{d} = 0$ representing incorrect acoustic presence estimation
$\boldsymbol{p_p}$	Probability to correctly assess acoustic presence of a focal species during the day
$\boldsymbol{p_c}$	Probability to assess call rate of a focal species within a certain range (i.e., 10%, 50%, and 100%, respectively) of the true call rate

TABLE III. Listening periods for tested subsampling schemes (i.e., listening period [min] per cycle [h]), representing different duty cycles. Duty cycles highlighted in bold indicate subsampling schemes that were used for comparative analyses and interpretation of subsampling effects on passive acoustic data in the present study.

Duty cycle		Cycle period τ_c							
D	D [%]	1 h	2 h	3 h	4 h	6 h	8 h	1/D	No. of independent realizations per regime
1/2	**50.0**	30 min	60 min	90 min	120 min	180 min	240 min	2	14
1/3	33.0	20 min	40 min	60 min	80 min	120 min	160 min	3	21
1/4	**25.0**	15 min	30 min	45 min	60 min	90 min	120 min	4	28
1/5	20.0	12 min	24 min	36 min	48 min	72 min	96 min	5	35
1/6	16.7	10 min	20 min	30 min	40 min	60 min	80 min	6	42
1/8	12.5		15 min		30 min	45 min	60 min	8	56
1/9	11.1			20 min		40 min		9	63
1/10	**10.0**	6 min	12 min	18 min	24 min	36 min	48 min	10	70
1/12	8.3	5 min	10 min	15 min	20 min	30 min	40 min	12	84
1/15	6.7	4 min	8 min	12 min	16 min	24 min	32 min	15	105
1/16	6.3				15 min		30 min	16	112
1/18	5.6			10 min		20 min		18	126
1/20	**5.0**	3 min	6 min	9 min	12 min	18 min	24 min	20	140
1/24	4.2		5 min		10 min	15 min	20 min	24	168
1/30	3.3	2 min	4 min	6 min	8 min	12 min	16 min	30	210
1/32	3.1						15 min	32	224
1/36	2.8			5 min		10 min		36	252
1/40	2.5		3 min		6 min	9 min	12 min	40	280
1/45	2.2			4 min		8 min		45	315
1/48	2.1				5 min		10 min	48	336
1/60	**1.7**	1 min	2 min	3 min	4 min	6 min	8 min	60	420
cycles per day N		**24**	**12**	**8**	**6**	**4**	**3**		

least one call was detected in any of the N listening periods of that day (Table III). Daily acoustic presence was estimated from the call counts in the rth realization in all N cycles of the jth day. If the assessments of acoustic presence from subsampled data and from continuous data matched, the decision was considered correct ($\boldsymbol{d} = 1$), and incorrect otherwise ($\boldsymbol{d} = 0$).

To evaluate the probability $\boldsymbol{p_p}$ of having properly determined the acoustic presence during that day, d was determined for each of the *1/D* independent realizations r of the listening period per day (Table II). This procedure resulted in *1/D* independent estimates $\boldsymbol{d_{r,j}}$ of correctness of presence assessment per day. The probability $\boldsymbol{p_p}$ was calculated from all $7/D$ independent $d_{r,j}$ estimates in each acoustic regime, permitting to establish an average probability of correct acoustic presence determination and its standard deviation ($n = 7/D$) for each sampling scheme:

$$\overline{p_p} = \frac{D}{7} \cdot \sum_{j=1}^{7} \sum_{r=1}^{1/D} d_{r,j}. \tag{1}$$

Between-regime comparisons of the results were conducted for selected duty cycles ($\frac{1}{2}$, $\frac{1}{4}$, $\frac{1}{10}$, $\frac{1}{20}$, and $\frac{1}{60}$).

2. Daily call rate estimations from subsampled data

Continuous call count data were subsampled according to the schemes listed in Table III, and hourly call rates $\bar{\gamma}$ were estimated from the call rates γ_i of the rth realization in all N cycles of the jth day:

$$\overline{\gamma_{r,j}} = \frac{1}{N} \sum_{i=1}^{N} \gamma_{i,r,j}. \tag{2}$$

This estimation was accomplished for all possible realizations r of listening periods within a cycle providing 1/D independent daily call rates $\overline{\gamma_{r,j}}$ per day (Fig. 4).

To assess the variability of call rate estimates within a given sampling scheme, the ratios of call rates from subsampled data and true call rates from continuous data were calculated for all $\overline{\gamma_{r,j}}$:

$$\text{ratio}_{r,j} = \frac{\overline{\gamma_{r,j}} - y_{\text{true}}}{y_{\text{true}}}. \tag{3}$$

This procedure was repeated for all 1/D $\text{ratios}_{\text{r,j}}$ at each day and resulted in $7/D$ independent estimates per regime providing average and standard deviation of call rate estimations at a given subsampling scheme. As animal abundance estimates from acoustic data strongly depend on the accuracy of call rate assessments, the probability $\boldsymbol{p_c}$ of estimating the actual call rate within a range of 10%, 50%, and 100%, respectively, was calculated (Table II). Results from selected duty cycles ($\frac{1}{2}$, $\frac{1}{4}$, $\frac{1}{10}$, $\frac{1}{20}$, and $\frac{1}{60}$) were used for between-regime comparisons.

III. RESULTS

Impacts of different subsampling schemes on daily acoustic presence were evaluated by determining the probability of a correct decision regarding acoustic presence.

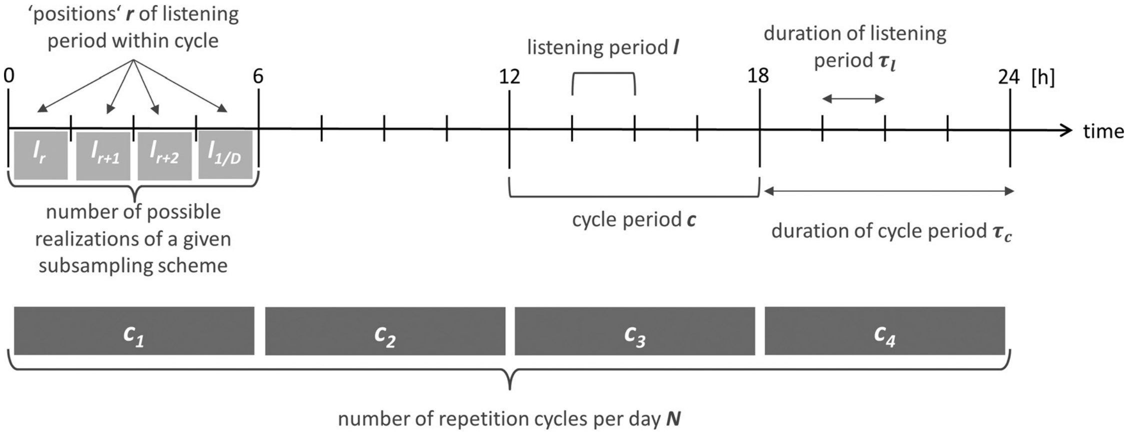

FIG. 3. Exemplary scheme of terms used in the context of subsampling of passive acoustic data.

Subsampling effects on call rate estimates were assessed by considering the probability of call rate estimates better than 10%, 50%, and 100% of the true call rate.

A. Acoustic presence

Analyses of the continuous data sets reveal that ABWs were acoustically present on all days in regimes A, B, C, and D, while NARW up-calls were detected during all days of regime E. The average time-span of hourly acoustic presence varied between regimes, with 24 ± 0 h of acoustic presence per day for regime A and B, 19.43 ± 5.77 h of acoustic presence per day for regime C, 23 ± 2.24 h of acoustic presence per day for regime D and 19.14 ± 2.41 h of acoustic presence per day for regime E.

The probability p_p to correctly assess daily acoustic presence of ABWs and NARWs on the basis of subsampled data was dependent on duty cycle, cycle period and acoustic regime (Fig. 5). While acoustic presence was always assessed correctly for high duty cycles ($D > \frac{1}{4}$), small duty cycles ($D \leq \frac{1}{10}$) underestimated the acoustic presence for some regimes (Fig. 5). Similarly, for a given duty cycle, the probability of estimating presence correctly was smaller for long cycles τ_c (>6 h), i.e., few cycles per day. The repercussions of subsampling also depended strongly on the acoustic regime, i.e., on the vocalization pattern of the focal species. For regimes A, B, and D, subsampling had no or only minor effects on the likelihood of correct presence estimation, even at small duty cycles (Fig. 5). In regime A, acoustic presence was always assessed correctly, regardless of the duty cycle, while in regime B and D presence assessment was correct in at least 97% of cases for all duty cycles (Fig. 5). Contrastingly, effects of subsampling were more pronounced for regimes C and E. While duty cycles of $D > \frac{1}{4}$ did not affect the probability to correctly estimate acoustic presence, this probability decreased at smaller duty cycles for both regimes (Fig. 5). For example, acoustic presence was correctly assessed with a probability of 73% to 90% at $D = \frac{1}{60}$ for regime E, with probabilities decreasing with increasing cycle periods (Fig. 5).

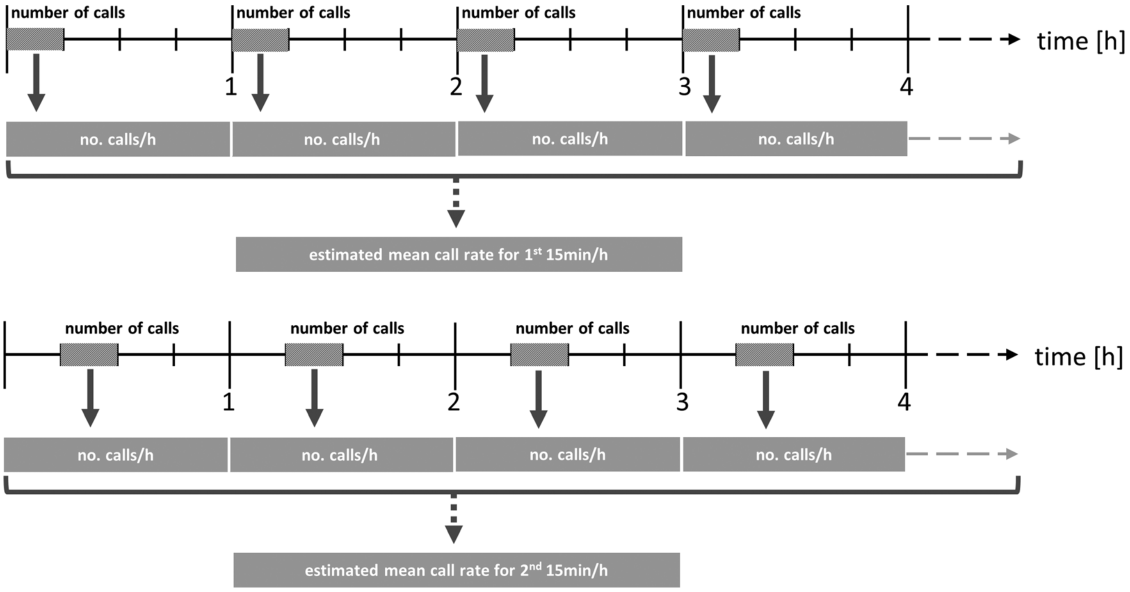

FIG. 4. Exemplary scheme of analysis algorithm to estimate hourly call rates from subsampled passive acoustic data assuming a subsampling scheme of 15 min per hour ($\text{DC} = [1/4]$). Upper panel: first run of algorithm estimating hourly call rates in the first 15 min per hour, lower panel: second run of algorithm estimating hourly call rates in the second 15 min per hour.

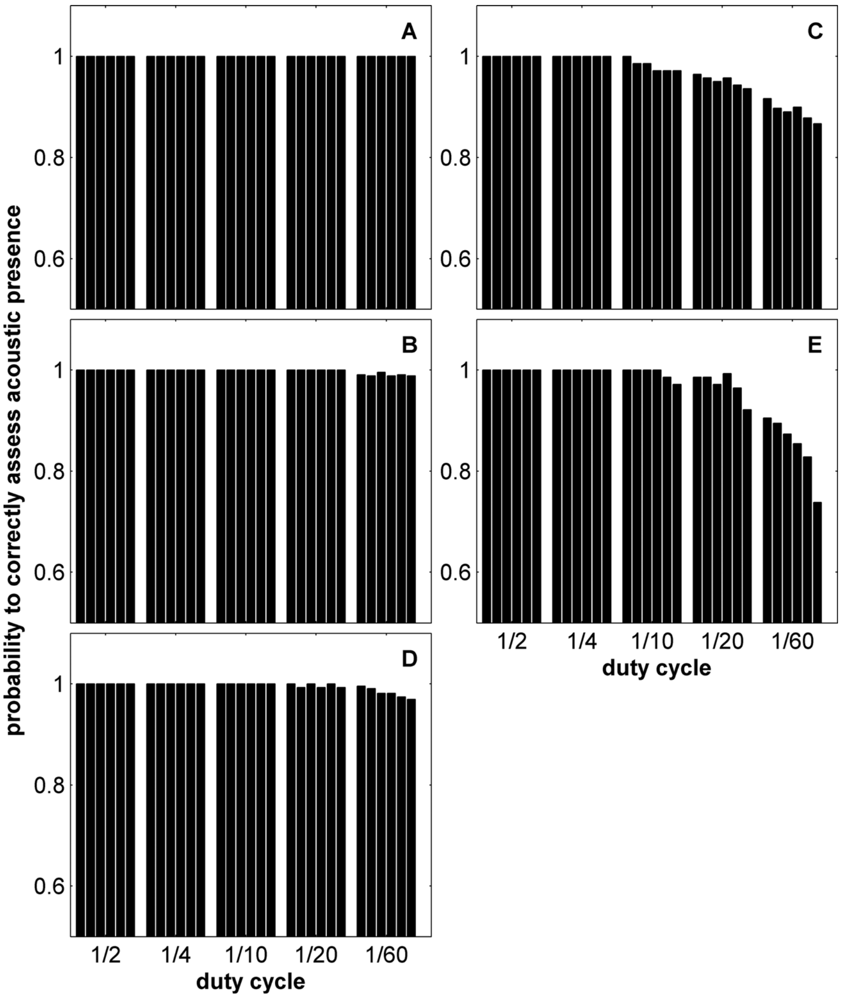

FIG. 5. Between-regime comparisons of probabilities to correctly assess acoustic presence of ABWs and NARWs from subsampled data at different sampling schemes. Letters indicate acoustic regimes with (A) regime A (high ABW call rates), (B) regime B (lower ABW call rates), (C) regime C (single ABW singer), (D) regime D (multiple ABW singers), and (E) regime E (NARW vocalizations with distinct diel pattern). Within a given duty cycle, bars represent different cycle periods τ_c (from left to right: 1, 2, 3, 4, 6, and 8 h, respectively).

B. Call rate estimations

The total number of ABW calls detected in the original data sets varied between regimes with 9183 calls in regime A (54.64 ± 17.73 calls per hour), 3353 calls in regime B (19.95 ± 7.96 calls per hour), and 2830 (16.85 ± 8.81 calls per hour) and 5823 calls (34.67 ± 21.65 calls per hour) in regimes C and D, respectively. For regime E, 1945 NARW calls (11.58 ± 6.14 calls per hour) were detected.

Call rates based on subsampled data varied significantly depending on the sampling scheme applied (Fig. 6). Generally, the variability of call rate estimates increased with decreasing duty cycle, i.e., call rates based on subsampling with large duty cycles ($D > \frac{1}{4}$) differed less from the true call rate than call rates based on small duty cycles ($D < \frac{1}{20}$) (Fig. 6). For a given duty cycle, increasing cycle periods τ_c resulted in a higher variability within the call rate estimates, i.e., a more widely spread data distribution and potentially higher deviations from the true call rate (Fig. 6). While this effect was clearly detectable in regime C, D, and E, it was less evident in regimes A and B. In turn, effects of subsampling on call rate estimations also depended strongly on the vocal behavior of the focal species, i.e., the data regime analyzed.

In order to quantify the validity of the call rate estimates from subsampled data, the probability p_c that the call rate estimated from a given subsampling scheme is within a specified range X (with X being 10%, 50%, and 100%, respectively) of the true call rate was assessed (Fig. 7). As expected, the probability to obtain call rate estimates within a certain range of the true call rate depended on the subsampling scheme chosen (i.e., p_c decreased as duty cycle decreased and/or cycle period increased) as well as on the acoustic regime analyzed (Fig. 7). However, effects of subsampling scheme and acoustic regime were much more pronounced at 10% accepted deviation between estimated and true call rates compared to a deviation range of 100%.

The probability p_c to estimate the call rate within 10% of the true call rate was highest for regime A and considerably decreased with duty cycle and cycle period in all regimes (Fig. 7). In regime E, the lowest probability was observed with $p_c < 0.5$ at $D = \frac{1}{2}$ and $p_c < 0.2$ at $D \leq \frac{1}{10}$ (Fig. 7). For estimating the call rates within a 50% range from the true call rate, the probability was highest for regime A with a probability of 1 for all $D \geq \frac{1}{10}$ and of minimally 0.95 at $D \leq \frac{1}{20}$ (Fig. 7). Except for at $D = \frac{1}{2}$ where all call rate estimates were within a 50% range of the true call rate, smaller probabilities were observed for regimes B, C, and D with minimal p_c values of 0.8, 0.55, and 0.76, respectively, at $D = \frac{1}{60}$ (Fig. 7). Regime E exhibited the smallest probabilities at all subsampling schemes analyzed with p_c falling below 0.5 at large cycle periods of duty cycles $D \leq \frac{1}{10}$ (Fig. 7). Finally, the probability to estimate the true call rate

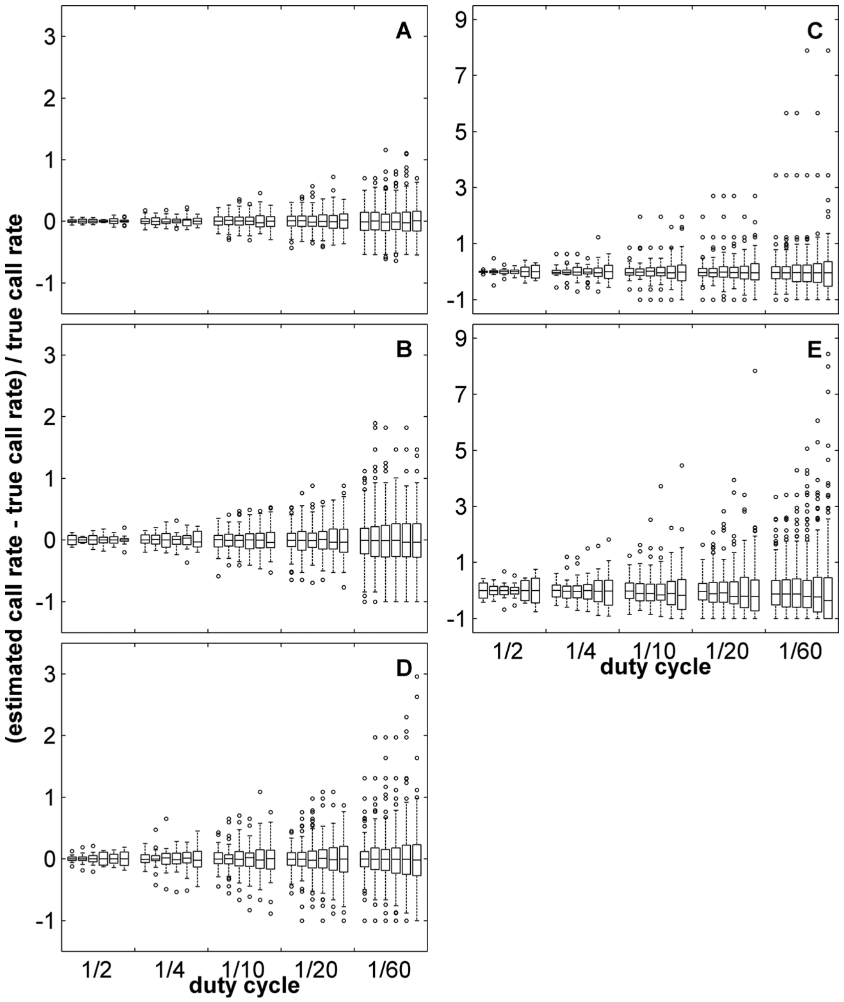

FIG. 6. Between-regime comparisons of ratios of estimated call rates from subsampled data to true call rates at different subsampling schemes. Letters indicate acoustic regimes with (A) regime A (high ABW call rates), (B) regime B (lower ABW call rates), (C) regime C (single ABW singer), (D) regime D (multiple ABW singers), and (E) regime E (NARW vocalizations with distinct diel pattern). Within a given duty cycle, boxplots represent different cycle periods τ_c (from left to right: 1, 2, 3, 4, 6, and 8 h, respectively). Note that regimes C and E are differently scaled.

within 100% deviation from the true call rate ranged from 0.97 to 1 for all sampling schemes tested for regimes A, B, and D with little effects of duty cycle and cycle period (Fig. 7). For regime C and E, this probability was smaller for all $D < \frac{1}{2}$ with minimal values of 0.92 and 0.85, respectively (Fig. 7).

IV. DISCUSSION

The present case study shows that subsampling of passive acoustic data can substantially bias acoustic presence estimates or affect the accuracy with which call rates of a focal species are determined, respectively. However, the extent of this effect depends on the subsampling strategy that is applied and the acoustic behavior of the focal species.

A. Overall effect of subsampling acoustic data

Unsurprisingly, large duty cycles generally represented acoustic presence and call rates more accurately than small duty cycles. The acoustic presence of the focal species was increasingly underestimated with decreasing duty cycles. These findings match the trends observed by Riera *et al.* (2013), showing that a duty cycle of $\frac{1}{3}$ resulted in a 24% decline in encounter detections of killer whale calls and a consequent underestimation of the time whales were acoustically present in the data set compared to a larger duty cycle of $\frac{2}{3}$. In the present study, medium to small duty cycles ($D \leq \frac{1}{10}$) resulted in acoustic presence underestimations of up to 26% for regime E, especially for large cycle periods. These results indicate that temporal clustering of vocal activity is a decisive factor determining the reliability of acoustic presence estimation from subsampled data. In turn, selecting many short samples at short cycle periods may increase the chance of correctly assessing daily acoustic presence, particularly for acoustic data exhibiting strong temporal fluctuation in calling activity.

The accuracy of call rate estimates varied widely across different subsampling schemes without any consistent under- or overestimation of call rates. Deviations from the true call rate were highly variable between regimes and ranged from 100% underestimation to up to 900% overestimation. Generally, the deviation of call rate estimates from the true call rate increased with decreasing duty cycle and increasing cycle periods. This effect was most pronounced in regimes C and E, indicating that the high variability may be a consequence of the (irregular) temporal clustering of calls and/or low calling rates in these regimes.

B. Data regimes

The present study indicates that the organization of vocal activity, i.e., regular (song, regime C and D) or irregular (regime A and B) organization, does not considerably

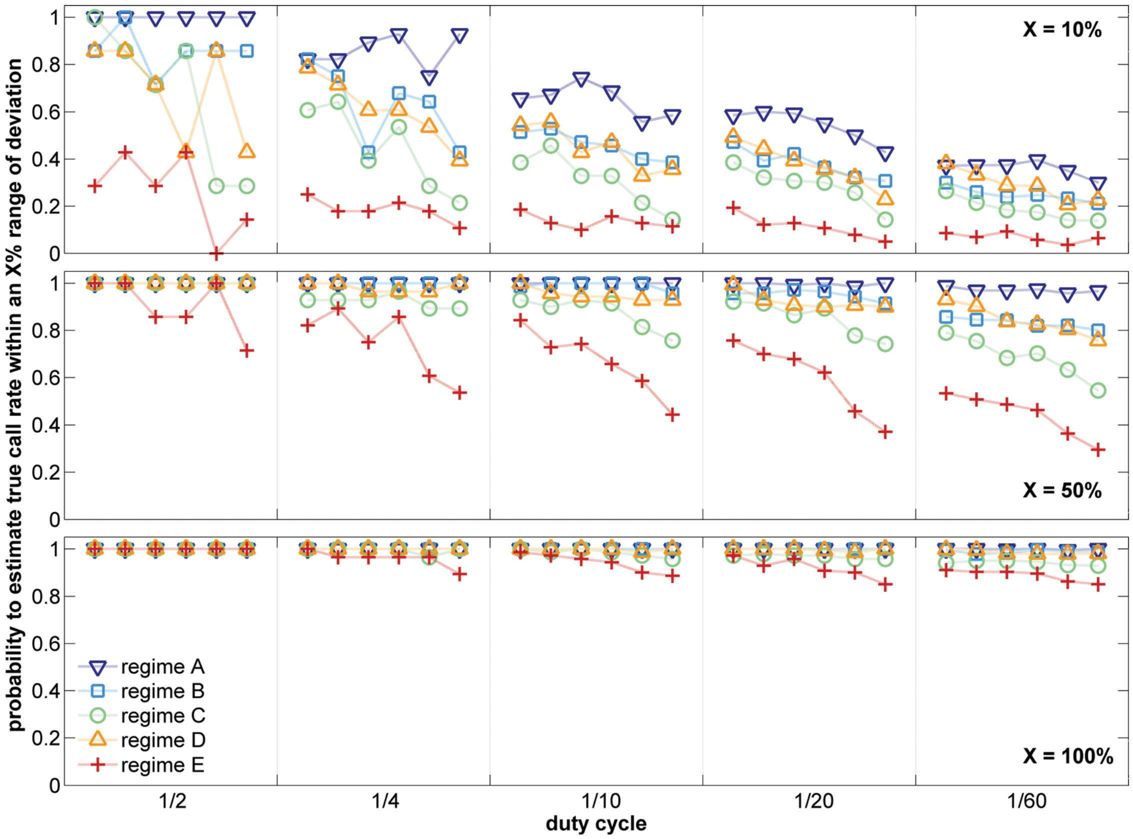

FIG. 7. Between-regime comparisons of probabilities to estimate call rates from subsampled data within a specified range X [with X being 10% (upper panel), 50% (middle panel), and 100% (lower panel), respectively] of the true call rate at different subsampling schemes. Regimes A–E (indicated by different colors) represent different vocal characteristics of the focal species as given in Fig. 6. Within a given duty cycle, markers indicate different cycle periods τ_c (from left to right: 1, 2, 3, 4, 6, and 8 h, respectively).

impact the effects of subsampling. Instead, the calling activity level and potential temporal clustering of the focal species' vocal behavior determine the accuracy with which subsampled data can represent the actual patterns in acoustic behavior. Generally, species with high vocalization rates that call throughout the day are more likely to be detected even with small duty cycles compared to irregularly and/or rarely calling species (Miksis-Olds *et al.*, 2010). This is also reflected in differences in the accuracies of call rate estimates when regime pairs A and B as well as C and D are compared; both basically exhibit the same temporal structure but differ in the frequency of occurrence of calls, showing the more calls, the higher the accuracy of call rate estimates. Highest deviations between estimated and true call rates were observed in regime E, representing vocal behavior with a comparatively low vocalization rate and a distinct diel pattern.

In the context of using passive acoustic data for density estimation of calling animals, highly accurate call rate estimates and/or knowledge on the potential uncertainty of these estimates is crucial, as call rate linearly enters the density estimates (Marques *et al.*, 2013). Under subsampling, most reliable results may be obtained by employing a subsampling strategy that collects short samples at short cycle periods. This will positively affect the accuracy with which cue rates can be assessed as more of the natural variability can be covered by the sampling scheme.

However, subsampling acoustic recordings is not suitable for species vocalizing rarely or to reliably capture unpredictable temporal clusters of acoustic activity, for example, when the species of interest passes the recorder's acoustic range only sporadically. Existing knowledge on the frequency and timing of occurrences of temporal clusters in vocal activity may aid the choice of a subsampling scheme, provided that the patterns in vocal behavior of the focal species are sufficiently well understood.

C. Subsampling strategies

Before deciding on a subsampling strategy, several aspects concerning the research goal need consideration, such as: What is the main purpose of the recording? What is the temporal scale relevant to the investigation (e.g., is collecting multi-year data worth the cost of subsampling to cover the entire deployment period)? What knowledge on acoustic behavior of the focal species is already available, and is this representative for the study area and/or recording season?

Single species studies, for example, investigating acoustic animal density in a given area, might benefit from adjusting the recording parameters as much as possible to the target species. When data storage is the limiting factor, studies investigating low-frequency baleen whale species may decide to lower the sample rate to the minimum required to capture only the calls of interest to maximize the time span over which acoustic data can be collected. Alternatively, adaptive subsampling may be considered to selectively capture only the events or species of interest throughout the entire period, although this method is not appropriate to record rarely calling species or short events (e.g., Miksis-Olds *et al.*, 2010; Sousa-Lima *et al.*, 2013). Furthermore, pilot studies during which continuous records are collected in or near the area of interest or information from previous investigations may provide a basis to decide on if and/or which duty cycles are suitable to reliably capture the vocalizations of interest. Recording in a *Matryoshka mode* may provide a solution to collect detailed "snapshots" that can be used to, for example, gauge acoustic animal densities during specific parts of the year. *Matryoshka* mode, referring to the Russian nested dolls, employs continuous or large duty cycles that are again set to cycle over a larger time scale.

For studies aiming to explore acoustic biodiversity or soundscape ecology in an area for which no acoustic records exist yet, it may be inevitable to collect continuous records given that principally all events are of interest. By, for example, continuously collecting a week of data each month, a relatively reliable overview of the event types and species that are (substantially) acoustically present in the vicinity of the recorder may be gained throughout the entire recording time span, depending on the storage and battery capacity of the recording instrument. To reliably capture transiting species or species that frequent the region only sporadically, truly continuous records are the only possibility to collect reliable information. When logistically and financially possible, multiple recorders programmed to record subsequently after the previous one has stopped may allow covering the entire period that the devices are in the water with (near-)continuous acoustic data.

Alongside maximizing the probability of capturing the species of interest, requirements on the acoustic data to answer specific research questions should also be taken into account. For example, humpback whale (*Megaptera novaeangliae*) acoustic presence may be reliably estimated from short samples at short cycle periods data with relatively small duty cycles, however assessing the number of singers and in-detail analyses of song structure require substantially longer samples.

The decision on a certain subsampling strategy is often not primarily (or not at all) driven by biological parameters or considerations. The only recording parameter that in most cases is adapted to meet the specific research objectives is the sample rate, which (when too low) may result in missed call events or species misidentification due to, for example, aliasing (Oswald *et al.*, 2004). The fact that other vocal characteristics of the focal species are not evaluated when deciding on sampling strategies is in most cases not an active decision but rather the result of lacking knowledge on the acoustic behavior for many species (e.g., Mellinger *et al.*, 2007). However, informed decisions on subsampling strategies can only be based on a solid understanding of vocal behavior for which, ironically, a representative acoustic sampling strategy is fundamental. If such information is not available, it may be preferable to collect continuous samples of limited duration across the year.

Technological developments may sooner or later allow autonomous collection of continuous acoustic records over long time scales with high sample rates, relaxing the need to record in subsampling mode due to instrument limitations. Nevertheless, these extensive data sets also need to be analyzed and stored which are other aspects where subsampling again may come into play. However, in contrast to subsampled recordings, subsampled analyses allow evaluation of the representativeness of the selected sampling strategy by comparisons to the continuous data records, according to the principle applied in the present case study.

V. CONCLUSION

The present case study demonstrates that subsampling acoustic data might have substantial effects on the assessment of acoustic presence and call rate, depending on the vocal characteristics of the focal species. If subsampling at a given duty cycle is mandatory due to logistic constraints, data collection in many short listening periods is preferable. Such sampling scheme results in many sampling cycles per day and hence, enables optimal representation of potential variability in the vocal behavior throughout the day and is best suited for assessments of both acoustic presence and call rate of the focal species.

Vocal characteristics as represented by different acoustic regimes in this study partly affected the accuracy of acoustic presence and call rate estimates from subsampled data. The organization of vocal activity (i.e., in terms of regular or irregular structure of vocalizations) did not markedly affect the results from subsampled data. Contrastingly, differences in vocalization rates had considerable impact on acoustic presence and call rate estimates from subsampled data, with accuracy improving with increasing call rates (in the continuous data). Furthermore, temporal clustering of vocal activity (i.e., diel vocalization pattern) considerably decreased the accuracy with which acoustic presence and call rates were assessed in the present study.

Subsampling during data collection may not be necessary in studies on species vocalizing at low frequencies as the sampling rate may be adjusted to a comparatively low level and in turn, recording continuously during the entire deployment period may be possible. However, subsampling may increasingly become necessary when shifting the focus towards species with high-frequency vocalizations as well as in multi-species studies covering a broad frequency range to investigate an area's acoustic biodiversity or soundscape. While technological advancements concerning power supply and data storage capacities will likely allow acquisition of large (near-)continuous data sets in the near future, human screening of the data will in many cases still be necessary to a certain degree, for example, for verification of automatic detection outcomes, and in turn, may still require subsampling of the total data to be manageable.

Polar oceans are areas where subsampling of acoustic recordings occurs relatively frequently as a consequence of the logistic difficulties of accessing the area. For many species inhabiting the polar oceans, relatively little is known on acoustic diversity, interactions, and acoustics-based animal densities, whereas gaining insights as to how climate-induced ecosystem changes affect the species in these areas is particularly crucial in the context of monitoring and managing potential changes. Optimizing passive acoustic data collection procedures in terms of sampling strategies lies at the heart of improving the current status of knowledge and providing fundamental information for future management and conservation strategies.

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Publication II:

Blue whale sightings in Antarctica west of the Greenwich meridian, January 2015.

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Blue whale sightings in Antarctica west of the Greenwich meridian, January 2015

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ABSTRACT

During the RV Polarstern PS 89 (ANT-XXX/2) expedition from Cape Town to Atka Bay and back, 20 sightings of 26 individual blue whales *(Balaenoptera musculus)* were recorded in Antarctic waters west of the Greenwich Meridian between 16-20 January 2015. These observations suggest a more westerly extension of a reported hot spot between the Greenwich Meridian and 20°E.

KEYWORDS: ANTARCTIC, BLUE WHALE, SHIP-BASED SURVEY, OPPORTUNISTIC DATA

INTRODUCTION

Three subspecies of blue whale (*Balaenoptera musculus*) are recognized; the Northern blue whale (*B.m.musculus*) inhabits the Northern hemisphere, while the Antarctic blue whale (*B.m. interm*edia) and the pygmy blue whale (*B.m.brevicauda*) occur in the Southern Hemisphere (Rice, 1998). Both subspecies differ acoustically (Ljungblad et al., 1998) and show slight differences in morphology (Attard et al., 2012; Branch et al., 2007a, Omura et al., 1970). The Pygmy blue whale is distributed in lower latitudes and occurs mainly in the southern Indian Ocean and the south-western Pacific Ocean (Rice, 1998). Antarctic blue whales are known to have a circumpolar distribution in Antarctic waters during austral summer and early autumn (e.g., Branch et al., 2007b). Contrasting with traditional migration hypotheses, the year-round presence of Antarctic blue whales in Antarctic waters south of 55°S was revealed by acoustic detections off the western Antarctic Peninsula (Sirovic et al., 2009), in the southern Indian Ocean (Samaran et al., 2010, 2013) and in eastern Antarctica (Gedamke et al., 2007; Sirovic et al., 2009). To estimate population sizes of Antarctic blue whales annual sighting surveys compiling three circumpolar cruises were conducted under the auspices of the IWC's International Decade of Cetacean Research (IDCR) and Southern Ocean Whale Ecosystem Research (SOWER) programmes in 1978/79-1983/84, 1985/86-1991/92 and 1991/92-2003/04 (Branch et al., 2007b; Branch & Butterworth, 2001). Despite the enormous effort of these surveys, information on the abundance and distribution of blue whales in Antarctic waters remains scarce due to the species reduced density caused by commercial whaling as well as the area's remoteness. In this paper we document a series of sightings of blue whales in the Antarctic waters west of the Greenwich meridian made on board the multidisciplinary expedition by the German research vessel Polarstern (PS 89 ANT-XXX/2) following Cape Town-Atka Bay-Cape Town in December 2014-February 2015.

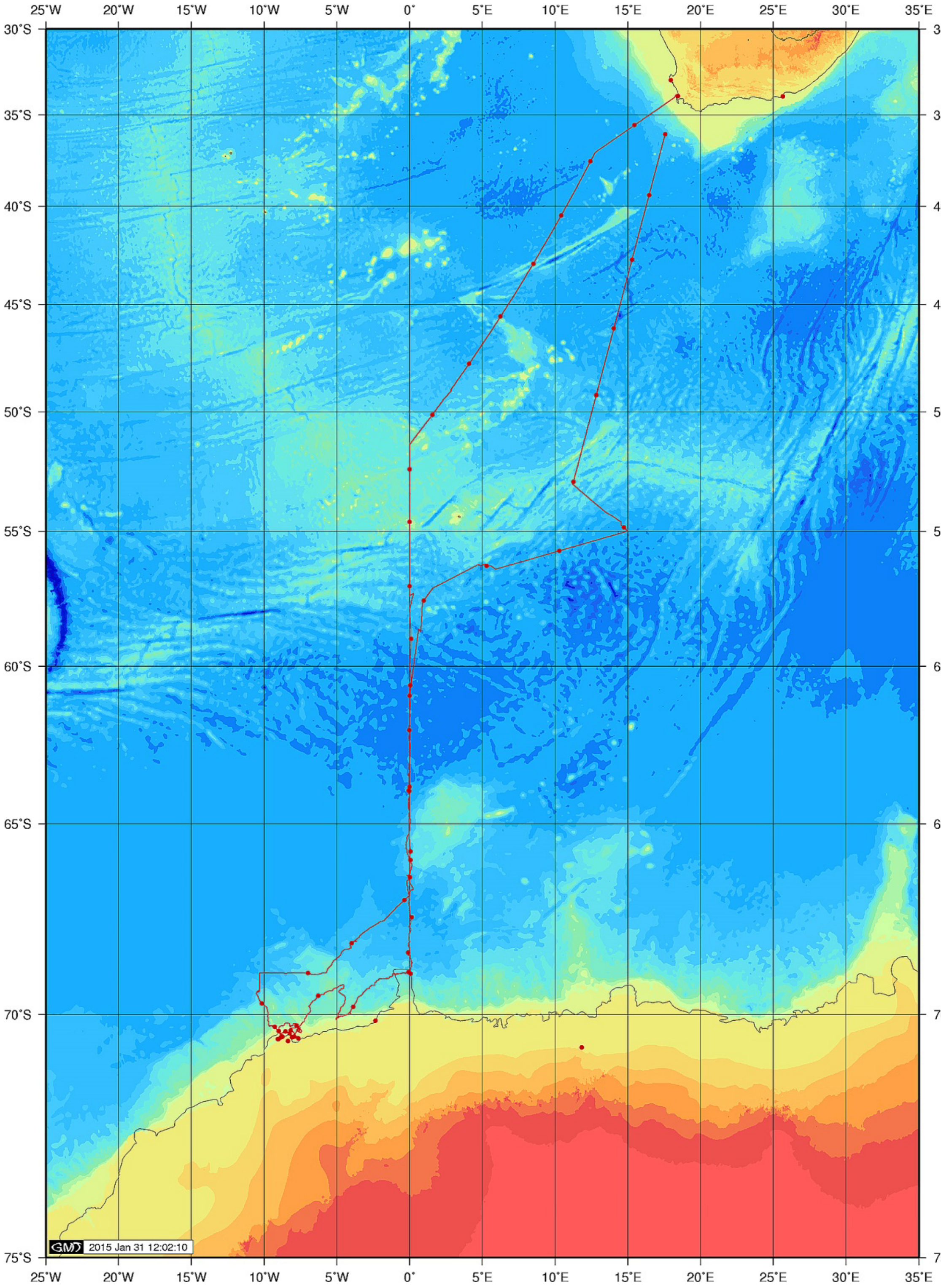

Figure 1. Cruise track from RV Polarstern during PS 89 (ANT-XXX/2) expedition Cape Town-Atka Bay-Cape Town, 2 December 2014 – 1 February 2015. Dots represent sampling stations, moorings and deployment sites for oceanographic research.

METHODS

During PS 89 (ANT-XXX/2) expedition on board RV Polarstern from Cape Town to Atka Bay, located off the Ekström ice shelf in the Weddell Sea, and back (2 Dec 2014-1 Feb 2015, Fig 1), marine mammals were recorded by three different teams from different platforms, as well as opportunistically, adding up to 5 different sources for collected marine mammal sightings: 1) dedicated marine mammal survey using line transect distance sampling from the crow's nest, 2) dedicated marine mammal survey using line transect distance sampling from a helicopter, 3) dedicated top predator (birds and marine mammals) strip transect survey from the monkey deck, 4) non-dedicated observations from the bridge, and 5) non-dedicated opportunistic observations.

Platforms 1-3 use standardized methods during survey effort. Platform 1-2 use line-transect distance sampling. The track from the crow's nest 29.5 meters above sea level was linked to the ship course, whereas the helicopter survey design was created ad hoc depending on weather and ice conditions. On both platforms two independent observers searched for and collected data on marine mammals along the track line using the naked eye. In the crow's nest binoculars were used to aid identification. Sighting details such as date, time, species, number and behaviour were recorded. If possible pictures were taken to document observations of scarce species and help with species ID. Coordinates were directly recorded by means of a handheld GPS connected to a computer running the sightings recording software VOR (Hiby & Lovell, 1998). Additional information (cue, distance perpendicular to the transect line, sighting conditions, environmental data) was recorded by a third person acting as data recorder.

Line-transect surveys of top predators were made from open observation posts installed on the monkey deck. Standard strip band transect methods are used, with snapshot methodology for birds in flight, and additional distance sampling line-transect methods for marine mammals. One observer searched for and collected data on seabirds and marine mammals along the track line using the naked eye. Binoculars were used to aid identification. Sighting details such as date, time, species, number and behaviour, and environmental data were recorded. If possible pictures were taken to document observations of scarce species and help with species ID. Coordinates were directly recorded by means of a handheld GPS The surveyed bandwidth was 300 m, that is 150 m to both sides. Marine mammals outside the surveyed bandwidth were recorded as well. The angle and distance from the ship were measured additionally to calculate the perpendicular distance to the transect line.

From the non-dedicated platforms 4 and 5 opportunistic observations were made. Observers searched for animals with the naked eye or with binoculars. Date, time, species, number and behaviour were recorded. If possible pictures were taken to document observations of scarce species. Coordinates were either directly recorded or derived from the observation time. Additional information on sighting and other environmental conditions was collected on an ad-hoc basis. The number of observers for the non-dedicated platforms 4 and 5 varied between one and five; observations from the bridge were primarily collected by the bridge officers. Other cruise participants and observers that were off effort from their dedicated surveys made all non-dedicated observations on platform 5.

Observation effort varied per day and is impossible to quantify for the non-dedicated observations. Especially the effort from the bridge is non-homogenous, since officers are primarily tasked with other duties and collect sighting data in addition to other tasks. During the time period 16-20 January dedicated survey effort amounted to a total of 7.9 hrs from the crow's nest and 51.5 hrs from the monkey deck (table 1). Helicopter-based surveys were not conducted. All surveys from the crow's nest were conducted simultaneously with the observations from the monkey deck.

Table 1. Observation effort per platform, 16-20 January 2015. No helicopter surveys (2) were conducted. Effort from the bridge (4) and from non-dedicated opportunistic observations (5) cannot be quantified.

Date	*Effort (hrs)*				
	1	*2*	*3*	*4*	*5*
16-1-2015	*3.2*	-	*11.8*	*NA*	*NA*
17-1-2015	*1.7*	-	*12.3*	*NA*	*NA*
18-1-2015	-	-	*6.2*	*NA*	*NA*
19-1-2015	-	-	*11.3*	*NA*	*NA*
20-1-2015	*2.7*	-	*9.8*	*NA*	*NA*
Total	*7.9*	-	*51.5*	*NA*	*NA*

Sightings were validated and checked for double counts by the authors. Only sightings that were documented with pictures or that were based on a combination of several distinctive characteristics (e.g. surfacing pattern, colouration, shape and size of dorsal fin) were qualified as certain blue whale. Other sightings were qualified as uncertain blue whale or no blue whale. Double counts were excluded by comparing times, and other collected sighting data (e.g. group size, distance to the ship, swim direction). Communication between the observers shortly after sightings were made filtered out most double counts. In case of doubt only one sighting was entered in the database.

Weather and sighting conditions ranged from very poor to excellent, with strong winds and heavy snowfall on 17-18 January 2015. Those days observations were carried out under very poor sighting conditions. The weather and ice conditions made some alterations to the proposed ship track necessary and did not permit helicopter surveys.

RESULTS AND DISCUSSION

From 16-20 January 2015, 20 unique sightings of 26 blue whales were made (table 2, fig 2). Despite survey effort no blue whales were seen outside this period. The majority of the sightings was made during non-dedicated opportunistic observations (n = 14). No calves were observed. Most sightings were of single animals, but some groups of two individuals were recorded. The average group size was 1.3 animals. Sightings were unevenly distributed with two 'concentrations'; north of the ice edge around 69°S (16 Jan 2015, 12 individuals and along the north-western slope of the Lichtner Seamount (18 Jan 2015, 7 individuals). It should be noted, however, that the sighting conditions on 17-18 January were poor.

Though information on the subspecies-level of the sighted individuals could not be ascertained in the field we assume all animals were Antarctic blue whales. This is supported by an observed geographic variation of the subspecies with Antarctic blue whales mainly occurring in high-latitude waters south of 55°S during summer (Kato et al., 1995). In contrast, pygmy blue whales were rarely sighted south of 55°S (Kato et al., 1995), therefore, it seems reasonable to assume that most of the blue whale sightings in high-latitude water represent Antarctic blue whales. Further evidence is provided by studies reporting acoustic presence of Antarctic blue whales all around Antarctica during austral summer (Gedamke et al., 2007, 2010; Ljungblad et al., 1998; Rankin et al., 2005; Sirovic et al., 2004, 2009).

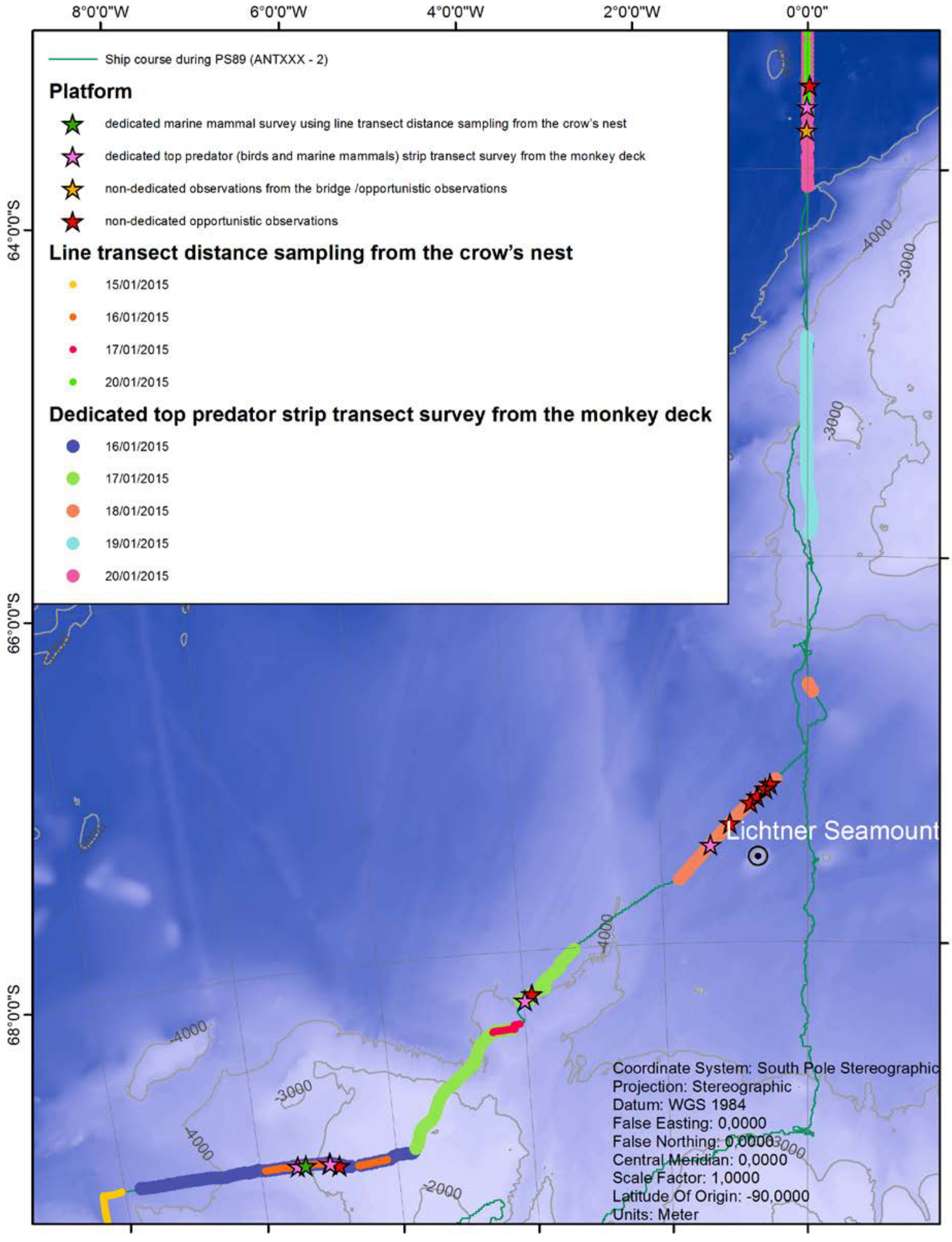

Figure 2. Blue whale sightings in Antarctica west of the Greenwich meridian, during the PS89 (ANT XXX-2) expedition, 16-20 January 2015.

Table 2. Blue whale sightings in Antarctica west of the Greenwich meridian, 16-20 January 2015. Platform numbers refer to 1) dedicated marine mammal survey using line transect distance sampling from the crow's nest, 2) dedicated marine mammal survey using line transect distance sampling from a helicopter, 3) dedicated top predator (birds and marine mammals) strip transect survey from the Monkey Island, 4) non-dedicated observations from the bridge, and 5) non-dedicated opportunistic observations.

Date	*Time*	*Number*	*Lon (W)*	*Lat (S)*	*Platform*
16-1-2015	*5:40*	*1*	*7.449*	*69.0016*	*3*
16-1-2015	*5:57*	*1*	*7.33249*	*69.0031*	*1*
16-1-2015	*6:53*	*2*	*6.98731*	*69.0062*	*5*
16-1-2015	*6:57*	*1*	*6.98731*	*69.0062*	*5*
16-1-2015	*7:32*	*1*	*6.98731*	*69.0062*	*5*
16-1-2015	*9:00*	*2*	*6.98731*	*69.0062*	*5*
16-1-2015	*14:40*	*2*	*6.9767*	*69.0074*	*3*
16-1-2015	*16:26*	*2*	*6.8453*	*69.023*	*5*
16-1-2015	*17:17*	*1*	*6.8453*	*69.023*	*5*
17-1-2015	*14:30*	*1*	*3.9793*	*68.2567*	*3*
17-1-2015	*15:32*	*1*	*3.8758*	*68.2251*	*5*
18-1-2015	*8:00*	*1*	*1.3147*	*67.4888*	*3*
18-1-2015	*9:05*	*1*	*1.0473*	*67.3798*	*5*
18-1-2015	*10:19*	*1*	*0.7638*	*67.273*	*5*
18-1-2015	*10:40*	*1*	*0.6760*	*67.2417*	*5*
18-1-2015	*11:08*	*2*	*0.5602*	*67.2004*	*5*
18-1-2015	*11:24*	*1*	*0.4965*	*67.1778*	*5*
20-1-2015	*15:03*	*2*	*0.0050*	*63.8*	*4 & 5*
20-1-2015	*16:30*	*1*	*0.0001*	*63.6795*	*3*
20-1-2015	*17:16*	*1*	*0.0288*	*63.5708*	*5*

Worldwide exploitation depleted the population(s) of blue whales, with Antarctic blue whales being the preferred target of commercial whaling (Branch et al., 2004). The pre-whaling population of estimated 239,000 individuals has been decimated to a minimum in 1973 (Branch et al., 2004). After implementation of protection measures, commercial whaling on blue whales was banned in the 1960's. Reported population estimates of Antarctic blue whales are based on three circumpolar surveys carried out under the auspices of the IWC's International Decade of Cetacean Research (IDCR) and Southern Ocean Whale Ecosystem Research (SOWER) programmes in 1978/79-1983/84, 1985/86-1991/92 and 1991/92-2003/04 (Branch et al, 2007b; Branch & Butterworth, 2001). These surveys were conducted south of 60°S till the ice edge and yielded population estimates of 453 (CV = 0.40), 559 (CV = 0.47) and 2,280 (CV = 0.36), respectively (Branch, 2007). Based on data from these surveys, the rate of Antarctic blue whale population increase was estimated to be 8.2% per year (95% CI 1.6-14.8%) (Branch 2007) and the minimum abundance of Antarctic blue whales to be as low as 395 (CI 235-804) in the early 1970's, less than 2% of the pre-exploitation level (Branch, 2008). At present, Antarctic blue whales are listed as 'critically endangered' by the International Union for Conservation of Nature (Reilly et al., 2013). Circumpolar SOWER surveys were not continued after the 2003/04 season and no new abundance estimates are available. The stated numbers nowadays are at least ten years out of date. For generating a new circumpolar abundance estimate of Antarctic Blue whales, today the Antarctic Blue whale project, an international collaboration led by the Australian Antarctic Division, employs mark-recapture techniques rather than conventional sighting surveys. Over a number of seasons genetic as well as photo-ID sampling will collect data on individual blue whales around Antarctica, to ultimately contribute to a new abundance estimate. For this purpose, high encounter rates of blue whales are of utmost importance to increase the sampling size. Information on areas of high blue whale densities are thus of great interest to the project.

Highest encounter rates of blue whales (0.17-0.52 sighting/1000 km) were found close to the sea ice edge in the area between 20°W-50°E during the IWC IDCR/SOWER surveys (Branch et al., 2007b). Recently, a survey was conducted in the area 0- 20°E along zigzag transect lines from the ice edge to 67˚S, within the period 13-23 January 2014 (Findlay et al., 2014). During 82 hours of dedicated survey effort covering almost 1000 nm (ca 1800 km), 14 observations of 20 blue whales were recorded, corresponding to an encounter rate of almost 0.78 sighting/1000 km. Findlay et al. (2014) concluded that the relatively high number of Antarctic blue whale individuals sighted supports previous findings by the IDCR/SOWER cruises reporting the waters from 0-to 20°E off the Queen Maud Land coast as a hotspot area for Antarctic blue whales.

Our results are well in line with the hotspot areas identified from historical whaling records, SOWER and IDCR surveys, more recent surveys and acoustic detections, but they suggest a more westerly extension of the reported hot spot between the Greenwich Meridian and 20°E (Findlay et al., 2014).

In addition to the six sightings during dedicated survey effort fourteen sightings were made during opportunistic observations. Since information on the abundance and distribution of blue whales in Antarctic waters remains scarce, opportunistically collected data can be an important additional source of information, preferably made available to the Southern Ocean Research Partnership (SORP) and the Antarctic Blue Whale Project. Photos that qualify for photo-ID purposes and have geographical information can be added to the Antarctic Blue Whale catalogue and the collection of identified individuals. Thus contributing to the ultimate goal of a new circumpolar abundance estimate. In this regard, opportunistically collected data are of the same value as data from dedicated surveys – every blue whale sighting and especially every identified individual counts.

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Spatio-temporal patterns in acoustic presence and distribution of Antarctic blue whales (*Balaenoptera musculus intermedia)* in the Weddell Sea.

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Spatio-temporal patterns in acoustic presence and distribution of Antarctic blue whales *Balaenoptera musculus intermedia* in the Weddell Sea

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ABSTRACT: Distribution and movement patterns of Antarctic blue whales *Balaenoptera musculus intermedia* at large temporal and spatial scales are still poorly understood. The objective of this study was to explore spatio-temporal distribution patterns of Antarctic blue whales in the Atlantic sector of the Southern Ocean, using passive acoustic monitoring data. Multi-year data were collected between 2008 and 2013 by 11 recorders deployed in the Weddell Sea and along the Greenwich meridian. Antarctic blue whale Z-calls were detected via spectrogram cross-correlation. A Blue Whale Index was developed to quantify the proportion of time during which acoustic energy from Antarctic blue whales dominated over background noise. Our results show that Antarctic blue whales were acoustically present year-round, with most call detections between January and April. During austral summer, the number of detected calls peaked synchronously throughout the study area in most years, and hence, no directed meridional movement pattern was detectable. During austral winter, vocalizations were recorded at latitudes as high as 69° S, with sea ice cover exceeding 90%, suggesting that some Antarctic blue whales overwinter in Antarctic waters. Polynyas likely serve as an important habitat for baleen whales during austral winter, providing food and reliable access to open water for breathing. Overall, our results support increasing evidence of a complex and non-obligatory migratory behavior of Antarctic blue whales, potentially involving temporally and spatially dynamic migration routes and destinations, as well as variable timing of migration to and from the feeding grounds.

KEY WORDS: Passive acoustic monitoring · Antarctic blue whale · *Balaenoptera musculus intermedia* · Baleen whale migration · Southern Ocean

INTRODUCTION

For most baleen whales, seasonal long-distance migrations between cold, productive, high-latitude feeding areas and warmer, low-latitude breeding grounds are considered a fundamental life cycle feature (Kellogg 1929, Mackintosh 1942, 1966). The factors driving baleen whale migration are still under debate and have been suggested to involve a higher survival rate for calves due to calmer waters and a decreased risk of predation by killer whales at low latitudes (Corkeron & Connor 1999, Ford & Reeves

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2008), as well as energetic advantages which increase the future reproductive success of calves born in warm waters (Clapham 2001). Nevertheless, evidence is accumulating that the concept of a complete annual migration in baleen whales is unlikely to hold true for many baleen whale species (e.g. Ingebrigsten 1929, Kellogg 1929, Brown et al. 1995, Dawbin 1997, Širović et al. 2004, Branch et al. 2007). Instead of migrating to lower latitudes after the feeding season, part of the population remains in polar and subpolar waters during winter, indicating partial migration (see also Dingle & Drake 2007) in many species (e.g. Bockstoce et al. 2005, Moore et al. 2006, Stafford et al. 2007, Acevedo et al. 2011, Van Opzeeland et al. 2013b).

For blue whales *Balaenoptera musculus* in the Southern Ocean, historical catch data suggest that migration is not obligatory and that timing of migration may vary between individuals (e.g. Mackintosh & Wheeler 1929, Harmer 1931, Hjort et al. 1932). Blue whales were caught off South Georgia year-round (Harmer 1931, Hjort et al. 1932, Branch et al. 2007), suggesting this species exhibits partial or differential migration (i.e. part of the population either does not migrate or delays migration based on age, sex or reproductive stage). Furthermore, the composition of the blue whale population on the Southern Ocean whaling grounds changed considerably over austral summer, further supporting the hypothesis of a differential migratory behavior (Mackintosh & Wheeler 1929). While adult whales were predominant in the population during austral spring, immature whales and lactating females did not arrive on the feeding grounds until February (Mackintosh & Wheeler 1929, Harmer 1931, Hjort et al. 1932). Blue whale migratory behavior is therefore likely to be complex and staggered, resulting in a continuous, procession-like movement to and from feeding grounds (Mackintosh & Wheeler 1929, Harmer 1931). Although both Antarctic blue whales (ABWs) *Balaenoptera musculus intermedia* and pygmy blue whales *B. m. brevicauda* inhabit the Southern Hemisphere, the latter were rarely sighted south of 55° S (Kato et al. 1995); therefore, most inferences on blue whale sightings from high-latitude waters are likely to represent ABWs.

After commercial whaling was banned, extensive visual sighting surveys were conducted in the Southern Ocean to monitor population abundance and behavior of ABWs, amongst other species (e.g. Kasamatsu et al. 1988, Branch & Butterworth 2001, Branch et al. 2007). However, the species' low encounter rate, elusive character and low abundance, as well as the area's seasonal inaccessibility largely impede year-round data collection on ABW occurrence. But to explore patterns in the spatial distribution and — potentially staggered — migration of ABWs, year-round data are nevertheless a prerequisite.

Passive acoustic monitoring allows investigation of the large-scale spatio-temporal distribution of vocalizing individuals and, when applied in an array or network, provides information on movement patterns of vocalizing whales (e.g. Širović et al. 2004, Samaran et al. 2013, Risch et al. 2014). Furthermore, passive acoustic monitoring has the potential to yield seasonally unbiased information on marine mammal acoustic presence, hence being particularly valuable in remote areas which are not accessible year-round for visual surveys (e.g. Širović et al. 2004, Mellinger et al. 2007, Rettig et al. 2013, Van Opzeeland et al. 2013b). ABWs are particularly eligible for passive acoustic studies due to the repetitive production of different types of distinctive low-frequency vocalization (e.g. Ljungblad et al. 1998, Rankin et al. 2005) and the large propagation distances of these vocalizations (e.g. Širović et al. 2007, Miller et al. 2015). Consequently, passive acoustic monitoring has been increasingly used to study ABWs in the Southern Ocean, e.g. off the western Antarctic Peninsula, off eastern Antarctica and in the Ross Sea (Širović et al. 2004, 2009, Gedamke & Robinson 2010, Miller et al. 2015). Similar to findings from blue whale populations inhabiting the North Atlantic and North Pacific Oceans (e.g. Clark & Gagnon 2002, Charif & Clark 2009, Stafford et al. 2009), the acoustic presence of ABWs exhibits a clear seasonal pattern in the Southern Ocean (Širović et al. 2004, 2009, Gedamke et al. 2007), often with a peak in call numbers during the respective summer season. Nevertheless, off the western Antarctic Peninsula, ABWs are acoustically present year-round, implying either a time-lagged migration or that some individuals omit migration to lower latitudes (Širović et al. 2004). However, to our knowledge, previous passive acoustic studies in the Southern Ocean have not been based on large-scale multi-year recorder networks in the open ocean, and hence little is known about distribution and movement patterns of ABWs in pelagic zones.

Here, we use multi-year data, recorded between 2008 and 2013 in the Weddell Sea and along the Greenwich meridian in the Atlantic sector of the Southern Ocean, to study the year-round distribution of vocalizing ABWs. One objective of our study was to investigate spatio-temporal patterns in the acoustic presence and distribution of ABWs within the study area, both intra- and inter-annually. Furthermore, we examined whether large-scale movement patterns can be detected from passive acoustic data in order to gain insight into the migratory behavior of ABWs. In this context, we explored the relation between the number of detected calls and the sea ice concentration within the study area to identify potential determinants and drivers of ABW distribution and migration patterns.

MATERIALS AND METHODS

Acoustic data

Between March 2008 and November 2013, passive acoustic recordings were collected by 14 moored devices, which were deployed in the Weddell Sea and along the Greenwich meridian for differing periods (Fig. 1, Table 1). The study area ranged from 59 to 69° S and from 0 to 27° W (Fig. 1). The study period comprised 3 consecutive periods of recorder deployment: March 2008–December 2010; December 2010–December 2012; and December 2012–December 2014 (hereafter referred to as deployment periods I, II and III, respectively; see also Table 1). Most of the recording sites were monitored for at least 2 deployment periods (for nomenclature of recording sites and deployment periods see Table 1).

The acoustic recorders were either a self-contained lander or attached to oceanographic deep-sea moorings of the Hybrid Antarctic Float Observation System (HAFOS) (Rettig et al. 2013). A total of 3 types of acoustic recording device were utilized: SonoVaults (Develogic GmbH) (Rettig et al. 2013); Autonomous Underwater Recorder for Acoustic Listening (AURAL; Model 2, Multi-Électronique) (e.g. Simard et al. 2008); and a Marine Acoustic Recording Unit (MARU; contributed by the Bioacoustic Research Program, Cornell University, NY) (e.g. Parks et al. 2009). The acoustic recorders were moored at different depths and set to different duty cycles due to recorder-specific depth ratings and constraints of battery life and data storage capacities (see Table 1 for details of recorder specifications) (Rettig et al. 2013). Passive acoustic data were stored in 5 and 4.5 min files for the AURAL recorders, in 6 min files for the MARU device and in 10 min files for the SonoVault systems.

After retrieval, data quality of the recordings was inspected using long-term spectrograms of the recordings (calculating power spectral densities using Welch, fast Fourier transform [FFT] 16 384, Hamming window, 50% overlap). The AURAL recorders operated flawlessly for the entire period of their deployment. The SonoVault recorders stopped recording prior to their recovery due to battery exhaustion. Electronic noise was observed in both MARU and SonoVaults. In 2 SonoVaults (SV1002 and SV1005), persistent broadband noise masked parts of the acoustic signal. For this reason, these 2 recorders were excluded from further analyses. In the MARU, tonal noise occurred, which did not affect our analyses. Nonetheless, data recorded by MARU were excluded from all amplitude-related analyses due to the occasional occurrence of broadband noise. Further, 1 SonoVault (SV0001) failed to record underwater sound altogether, presumably due to a defective hydrophone or hydrophone connection.

In summary, the operational period of acoustic devices with utilizable recordings ranged from 6 to 34 mo (Table 1). Prior to further

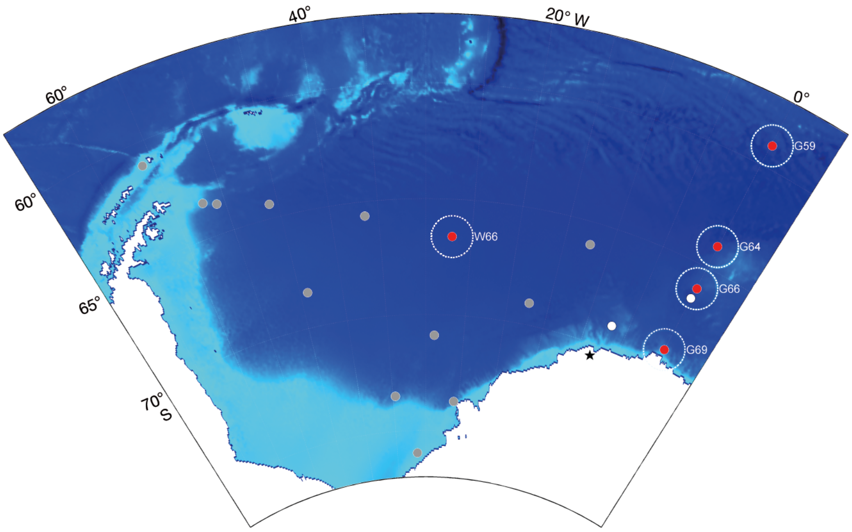

Fig. 1. Locations of autonomous recording devices, deployed between March 2008 and January 2013, in the Weddell Sea and Atlantic sector of the Southern Ocean. Positions of the acoustic recorders analyzed in this study (red dots), positions of recorders excluded from the analyses due to electronic noise (white dots) and locations of recorders not yet recovered (grey dots) are shown. Recorder IDs are shown in white (see also 'Materials and methods'; Table 1); (★) indicates the location of the Perennial Acoustic Observatory in the Antarctic Ocean (PALAO). Dashed circles indicate the area (radius of 100 km from the respective recording sites) used to calculate sea ice concentration

Table 1. Locations and recording parameters of passive acoustic recorders deployed within the Hybrid Antarctic Float Observation System (HAFOS) array in the Weddell Sea. Recording sites are assigned IDs representing the geographic location by a combination of letters (with 'G' and 'W' indicating a recording site on the Greenwich meridian and in the inner Weddell Sea, respectively) and numbers roughly reflecting the recording sites' latitudinal position; Roman numerals (I, II or III) indicate the respective deployment period (2008–2010, 2010–2012 and 2012–2014, respectively). Deployment period given as mm/yyyy. Sampling scheme is given in sampling duration (min) per sampling interval (min). Correction factor *f* indicates the recorder-specific factor used to extrapolate call numbers from subsampled recordings to an assumed continuous recording scheme

Recording site ID	Latitude	Longitude	Recorder ID	Deployment period	Deployment depth (m)	Sampling frequency (kHz)	Sampling scheme (min/min)	*f*	Operational period (mo)
G59-I	59° 10.03′ S	000° 00.17′ E	MARU01	12/2008–12/2009	4838	2.00	6/60	10	12
G59-II	59° 03.02′ S	000° 06.63′ E	AWI227-11 SV0002	12/2010–12/2012	1007	5.33	Continuous	–	8
G59-III	59° 02.63′ S	000° 04.92′ E	AWI227-12 SV1025	12/2012–12/2014	1020	5.33	Continuous	–	7
G64-II	63° 59.56′ S	000° 02.65′ W	AWI229-09 SV1000	12/2010–12/2012	969	5.33	Continuous	–	6
G64-III	63° 59.66′ S	000° 02.65′ W	AWI229-10 SV1010	12/2012–12/2014	969	5.33	Continuous	–	8
G66-I	66° 01.13′ S	000° 04.77′ E	AWI230-06 AU0085	03/2008–12/2010	189	32.77	5/240	48	34
G66-II	66° 01.90′ S	000° 03.25′ E	AWI230-07 SV1001	12/2010–12/2012	934	5.33	Continuous	–	21
G66-III	66° 02.12′ S	000° 02.98′ E	AWI230-08 SV1009	12/2012–12/2014	949	5.33	Continuous	–	9
G67-II[a]	66° 30.71′ S	000° 01.51′ W	AWI231-09 SV1002	12/2010 12/2012	1083	5.33	Continuous	–	21
G69-I	68° 59.74′ S	000° 00.18′ E	AWI232-09 AU0086	03/2008–12/2010	206	32.77	5/240	48	34
G69-III	68° 59.86′ S	000° 06.51′ W	AWI232-11 SV1011	12/2012–12/2014	958	5.33	Continuous	–	11
W66-II	66° 36.70′ S	027° 07.31′ W	AWI209-06 AU0086	12/2010–01/2013	207	32.77	4.5/180	40	24
W69-II[a]	69° 00.30′ S	006° 58.89′ W	AWI244-02 SV1005	12/2010 12/2012	1003	5.33	Continuous	–	28
W69-III[a]	69° 00.35′ S	006° 58.97′ W	AWI244-03 SV0001	12/2012 01/2015	998	5.33	Continuous	–	11

[a] Passive acoustic data sets that were excluded from further analyses due to flawed recordings containing broadband electronic noise

analyses, for all recorder types, passive acoustic data were downsampled (including an anti-aliasing FIR [finite impulse response] lowpass filter) to a uniform sampling rate of 250 Hz to obtain standardized data covering the frequency range of interest, i.e. below 125 Hz.

Sea ice data

Sea ice cover in the study area was calculated using satellite data collected from 2008 to 2013 with a resolution of 6.25 × 6.25 km (Spreen et al. 2008). Daily ice concentrations were calculated for an area of 3.1×10^4 km^2 (representing a radius of 100 km) around each recording site, including all data points located at a distance ≤100 km from the recording location. Given the large propagation ranges of ABW vocalizations and, hence, the potentially widespread spatial distribution of the recorded individuals around a respective recording location, we consider a radius of 100 km to be representative of sea ice conditions that ABWs are exposed to during their transit through or stay in the study area.

Acoustic data analysis

ABW vocalizations

One well-known ABW vocalization is the stereotyped, high-energy Z-call (named after its Z-shaped spectrographic signature) (Fig. 2) that is often produced in repetitive song patterns at regular intervals of about 62 ± 5 s (Ljungblad et al. 1998, Širović et al. 2004, McDonald et al. 2006). A Z-call is composed of 3 units, starting with a constant frequency tone within the range of 26 to 28 Hz lasting about 9 s (Unit A), which is followed by a short downsweep (ca. 1 s) to about 19 Hz (Unit B) and a slightly frequency-modulated tone of 18 to 19 Hz lasting 8 to 12 s (Unit C) (Ljungblad et al. 1998, Širović et al. 2004, Rankin et al. 2005). Long-term declines in vocalization frequency are evident in blue whale populations worldwide (McDonald et al. 2009, Gavrilov et al. 2012), and were also evident in the current data set. However, in-depth analyses of the decline pattern were beyond the scope of the present study.

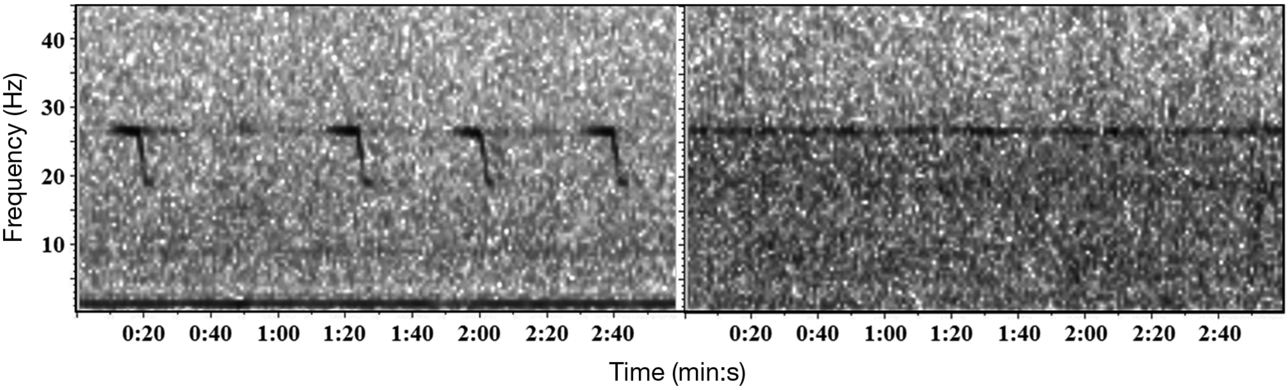

Fig. 2. Spectrogram of Antarctic blue whale song sequence of Z-calls (left panel) and chorus (right panel) recorded on 12 December 2010 at 59° 03′ S, 0° 07′ E and 10 March 2011 at 66° 37′ S, 27° 08′ W, respectively (sample rate 250 Hz [after downsampling]; spectrogram settings: FFT 512 points, Hanning window, 50% overlap)

Automated detection of single ABW Z-calls

ABW Z-calls were detected by cross-correlating spectrograms with a pre-defined spectrogram template (e.g. Mellinger & Clark 2000). Spectrograms were calculated for each audio file (FFT 1024, 500 point Hamming window, 75% overlap; resulting in frequency resolution of ca. 0.25 Hz and time resolution of ca. 0.5 s). The template was created by averaging 100 temporally aligned spectrogram snippets of high-quality Z-calls (i.e. with all 3 call units being present) from 6 recorders and distributed over an overall period of 39 mo from December 2008 to February 2012 to ensure representativeness. This set of snippets also includes 12 Z-calls from recorder SV1002 (which was excluded from further analyses), which were recorded during a brief period without broadband noise. The final template had a frequency range of 18.5 to 28 Hz and was of 12 s duration (i.e. shorter than a 3-unit Z-call), containing 8 s of Unit A, Unit B (=1 s) and 3 s of Unit C. These settings avoided biasing the detection results towards complete 3-unit Z-calls, because recorded ABW calls did not always comprise all 3 units, but most comprised (part of) Unit A or Units A + B (see also Rankin et al. 2005, Miller et al. 2015). Spectrogram cross-correlation was performed in time/frequency space for each audio file and in a frequency band from 17.5 to 29 Hz. Inter- and intra-annual variations in the ABW Z-call frequency, e.g. the long-term decline in vocalization frequency, can affect the performance of a detector operating in a fixed frequency range. Therefore, the bandwidth of the frequency range to be analyzed (= 11.5 Hz) was intentionally set broader than the Z-call template's bandwidth (= 9.5 Hz) to allow cross-correlation in both time and frequency space, accounting for a potential frequency shift of ABW Z-calls over time. A minimum separation of 15 s between detected events was preset to prevent biasing the results by detecting multipath arrivals of the same call, as exploratory manual analyses showed occurring in the MARU recordings.

Selection of a suitable detection threshold, which defines whether calls are considered present or not, is likely subject to biological, physical and methodological factors. The whales' calling behavior, location- and recorder-specific ambient noise levels, and the detector's performance all affect the number of effectively detected calls. To nevertheless allow comparisons of detection rates between the acoustic data sets recorded by different devices, at least to a certain extent, recorder-specific detection thresholds were adjusted to achieve a constant false alert rate for all recorders. Thresholds were calculated by correlating the Z-call template with a 'noise band' (29.5 to 39 Hz), which does not contain any ABW Z-call units. Any detection within the noise band would therefore represent a false alert. Previous exploratory manual analyses showed that a correlation coefficient of 0.3 was the threshold at which all manually perceivable (true positive) Z-calls were detected. To determine the recorder-specific thresholds, a set of false positive detections was generated for each recorder by running the detector over the noise band with a threshold of 0.3. From these false alerts, 1000 events were selected randomly and ranked according to their associated correlation coefficients. The minimum correlation coefficient associated with the best correlated 1% of false detections was selected. This procedure was repeated 1000 times per recorder and the respective minimum correlation coefficients were averaged (n = 1000) to obtain a recorder-specific threshold (Table 2). While this approach is not sufficient to provide resilient data for abundance estimates or determining ABW call rates, relative and recorder-specific threshold setting provided a means to reliably compare detections between recorders for exploring spatio-temporal patterns in acoustic presence throughout our study area.

ABW Z-call detection was performed based on these thresholds representing a 1% false alert level, and numbers of calls detected per week (7 d bins) were calculated and used to correlate numbers of detected calls with sea ice concentration over time at the different recording sites. Assuming a uniform ABW call distribution without a diel pattern in our study area (see also Thomisch et al. 2015), weekly detection numbers from subsampled recordings were extrapolated to an assumed continuous recording period for direct comparability among data sets, using a recorder-specific factor that corrects for the respective duty cycle (Table 1). In addition, daily mean numbers of Z-call detections per minute were calculated. Time series of these daily mean detection rates were filtered to reduce variability in detected call numbers between days in order to focus on large-scale patterns in Z-call detections (Savitzky-Golay filtering, window length = 31, step size = 1, regression based on polynomial order 2). In contrast to smoothing approaches using linear regressions, the Savitzky-Golay filter (based on polynomial regression) keeps the actual data distribution intact in terms of small-scale patterns, such as local minima and maxima.

Table 2. Thresholds for Z-call detection using spectrogram cross-correlation and total number of detected Antarctic blue whale (ABW) Z-calls in passive acoustic data sets from the Weddell Sea and Atlantic sector of the Southern Ocean. Detection was based on a false-alert rate (FAR) of 1% as determined from detector performance within a frequency band (29.5–39 Hz) not containing any Z-calls. Determined detection thresholds (representing minimally required correlation coefficients) are given as mean (used for detection process) ± SD. For a detailed description of detection threshold determination, see 'Materials and methods'

Recording site	Recorder ID	Detection threshold for FAR 1%	Total no. detected ABW Z-calls at FAR 1%
W66	AWI209-06 AU0086	0.4573 ± 0.0084	18 180
G59	MARU01	0.4939 ± 0.0075	7553
	AWI227-11 SV0002	0.4725 ± 0.0078	147 964
	AWI227-12 SV1025	0.4729 ± 0.0077	112 004
G64	AWI229-09 SV1000	0.4704 ± 0.0088	159 336
	AWI229-10 SV1010	0.4748 ± 0.0088	132 847
G66	AWI230-06 AU0085	0.4709 ± 0.0101	9398
	AWI230-07 SV1001	0.4680 ± 0.0085	611 580
	AWI230-08 SV1009	0.4679 ± 0.0082	206 335
G69	AWI232-09 AU0086	0.4693 ± 0.0071	9287
	AWI232-11 SV1011	0.4647 ± 0.0083	211 724

Quantification of ABW chorus: Blue Whale Index (BWI)

Z-calls (or, more explicitly, Unit A of the Z-calls) produced by distant ABWs create a tonal 'chorus' within the 26 to 28 Hz frequency band (Gedamke et al. 2007). Hence, detections of only single Z-calls may underestimate the acoustic presence of ABWs (Fig. 2). A Blue Whale Index (BWI) was designed to quantify the proportion of time during which the ABW chorus was more energetic than background noise, taking into account acoustic energy from both nearby and distant ABWs. The BWI is based on comparing energy levels in 3 different frequency bands, representing acoustic power in the signal band (S) and in 2 adjacent noise bands. The signal band, with 26 ≤ frequency ≤ 28 Hz, comprises the ABW Z-call Unit A. The 2 noise bands, N_l with 23 ≤ frequency ≤ 24 Hz and N_u with 29 ≤ frequency ≤ 30 Hz, contain no spectral energy from ABW Z-call Unit A's, yet possibly negligible amounts of energy from Z-call Unit B's.

Band energy of the signal band was calculated by averaging power spectral densities (PSD; temporal resolution 0.5 s, frequency resolution 0.25 Hz) between 26 and 28 Hz. Combined noise band (N_c) energy was obtained by averaging PSD values between 23 and 24 Hz, and 29 and 30 Hz. This process results in time series of the signal band $\varepsilon(S)$ and the combined noise band $\varepsilon(N_c)$ between 4.5 and 10 min length, corresponding to the respective file length. From these, moving averages of band energy of $\varepsilon(S)$ and $\varepsilon(N_c)$ were calculated using a 5.5 s long averaging window in 0.5 s steps t_i (i.e. over k = 11 samples) to obtain mean energy levels of signal band $\overline{S}$ and combined noise band $\overline{N}_c$, respectively:

$$\overline{S} = \frac{1}{k}\sum_{t_i=1}^{k}\varepsilon_S(t_i) \qquad (1)$$

and

$$\overline{N}_c = \frac{1}{k}\sum_{t_i=1}^{k}\varepsilon_{N_c}(t_i) \qquad (2)$$

Standard deviation of the combined noise band $\varepsilon(N_c)$ was calculated accordingly.

For each data point (i.e. every 0.5 s), we tested whether the mean signal band energy level was larger than the sum of the mean plus twice the standard deviation of the energy level in the combined noise band, i.e. if

$$10 \times \log_{10}(\overline{S}) > 10 \times \log_{10}(\overline{N}_c) + 2 \times \{10 \times \log_{10}[\mathrm{SD}(N_c)]\} \tag{3}$$

The BWI was defined as the ratio of occurrences when this criterion was met versus the total number of data points per file. For each file, this provides the percentage of time dominated by ABW acoustic energy in the signal band. Given that the BWI test criterion continuously adjusts to local ambient noise levels, it prevents interpreting (broadband) noise as ABW chorus. Accordingly, acoustic signatures such as fin whale pulses that contribute energy to both the signal and noise band will not meet the BWI criterion and, hence, do not bias the BWI.

Similar to the single Z-call data, time series of daily mean BWIs were calculated and smoothed using Savitzky-Golay filtering (window length = 31, step size = 1, regression based on polynomial order 2).

Recorder independence and distance estimations

For reliable interpretation of single Z-call detections at different recording sites, it is essential to know whether recording sites are independent in terms of the recorded signals. For 2 recorder pairs, we tested whether the same ABW Z-call sequences were detectable at 2 recording sites quasi-simultaneously (see the Supplement at www.int-res.com/articles/suppl/n030p239_supp.pdf). Furthermore, rough estimates of distances of ABWs from recording sites were calculated for each Z-call detection, assuming a source level of 189 dB (Širović et al. 2007) and using different reported transmission loss models (Širović et al. 2007, Breitzke & Bohlen 2010, Van Opzeeland et al. 2013b) (see the Supplement for detailed information on amplitude measurements and distance estimation).

RESULTS

Recorder independence

The estimated distances of vocalizing ABWs from the recorders ranged from less than 2 km to more than 700 km. However, for all recording sites, the majority of calls were estimated to have come from whales within a 200 km range of the recorder (see Fig. S1 in the Supplement at www.int-res.com/articles/suppl/n030p239_supp.pdf). Consistent with this finding, Z-call sequences were rarely detected on more than one recorder at a time (Table S4 in the Supplement). Although a little overlap in the recorded signals may occur between adjacent recorders, this is unlikely to bias the results substantially. For further data interpretation, we therefore considered data sets from different recorders to be acoustically independent of each other.

Acoustic presence

ABWs were acoustically present at all recording sites in all years covered by this study. The total number of detected ABW Z-calls varied highly among recorders, depending on the sampling scheme as well as on the respective overall operational period of recorders, and ranged from 7553 detections at Site G59 (MARU) to 611 580 at G66 (SV1001) at a detection threshold level accepting 1 % false alerts (Table 2). Of all recording days at a respective site, 99 % showed acoustic presence of ABWs at W66, 81 % at G59, 100 % at G64, 94 % at G66 and 83 % at G69, based on detections of single Z-calls.

Manual perusal of the data revealed that song bouts with Z-calls repeated at regular intervals were present occasionally in our passive acoustic recordings. For the larger part, vocal activity was variable and temporally unstructured (i.e. occurring in irregular bouts).

Spatio-temporal patterns in ABW Z-call detections and acoustic energy

Single Z-calls

The number of detected calls was lower in the AURAL and MARU recordings than in SonoVault data during austral winter, presumably for a combination of reasons, including sampling scheme (see also Thomisch et al. 2015), occurrence of broadband noise and deployment depth.

A clear seasonal pattern in the number of detected ABW Z-calls was evident at all locations and in all years (Fig. 3). At most sites, detected call numbers showed a steep increase starting between December and January (except for G66-II and W66, where detection numbers started to increase in October), a peak between January and March (austral summer), and a decrease from April to September. ABWs remained acoustically present year-round with small

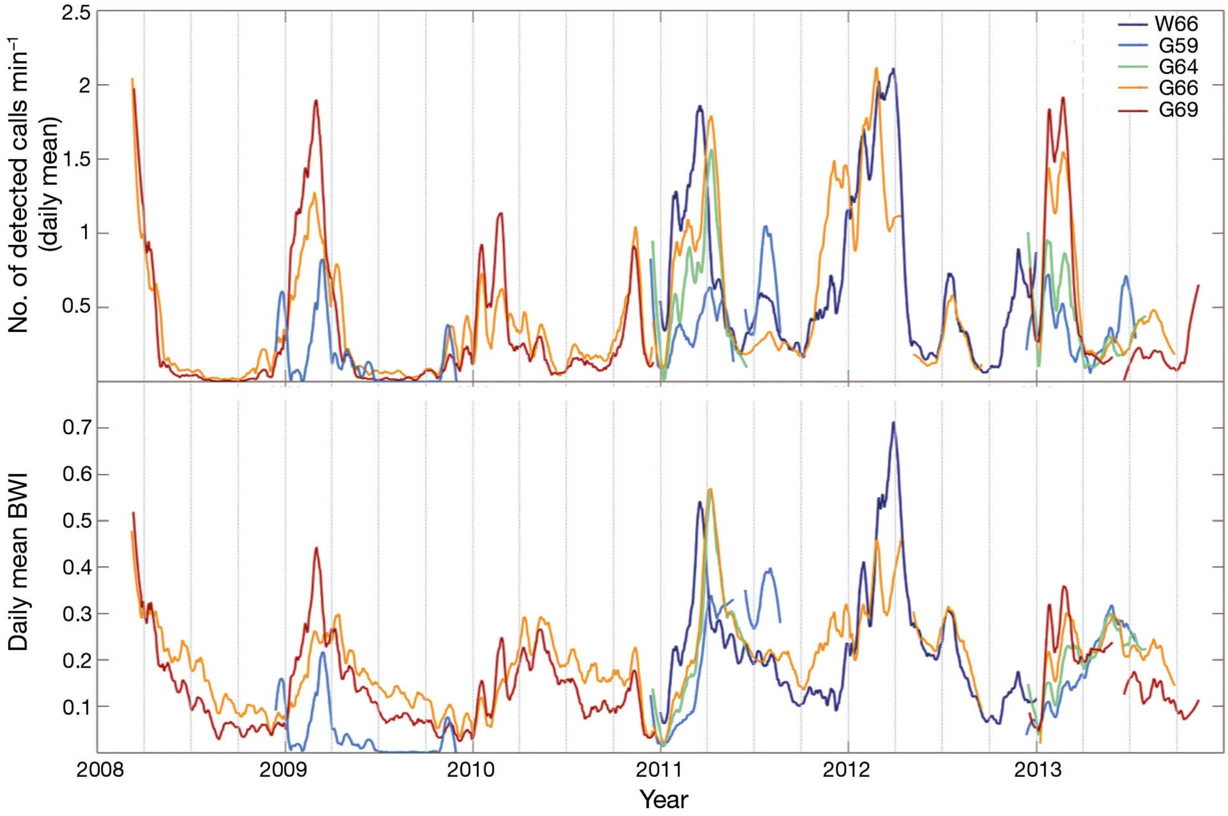

Fig. 3. Time series of Antarctic blue whale call detections and blue whale index (BWI) at different recording locations in the Weddell Sea and along the Greenwich meridian. Upper panel: daily mean number of detected Z-calls per minute, based on detections at a threshold level of 1 % false alerts. Lower panel: BWI based on spectral energy in 26 to 28 Hz frequency band. Time series were smoothed using Savitzky-Golay filter (window length = 31, polynomial order = 2); colors represent different recording locations; vertical grey lines indicate beginnings of quarters of the year

numbers of Z-calls also detected during austral winter at all locations. At G59-II and -III, G66 and W66, the number of detected calls showed a secondary peak during winter (see also Table 1 for information on IDs). Only at G59-I were very few ABW vocalizations detected from July to October. Visual screening of winter recordings (July to October) from G59-I, however, revealed the presence of some faint Unit A's of Z-calls in July and August, which were discarded during automatic detection as these failed to meet the threshold requirements. ABW vocalizations were not detected visually in September and October at G59-I either.

At W66, G66 and G69, the timing of the peak in call detections during austral summer was relatively stable over time, while it varied between years at G59 (with most calls detected between November and April) and at G64 (most calls detected between December and April) (Fig. 4). Interestingly, in austral summer 2010/2011, most calls were detected in early April at G59, G64 and G66, which was markedly delayed compared to all other recording years.

No, or only small, temporal shifts in the timing of the peak in call detections were discernable between recording locations in a meridional direction, i.e. north–south along the Greenwich meridian (Fig. 4). Only during austral summer 2008/2009 was a succession in the timing of the peaks in call detections evident, with numbers of detections peaking first at G59 at the end of December, followed by peaks at G66 at the end of February and at G69 at the beginning of March (Figs. 3 & 4). In mid-March 2009, a secondary peak in detections was evident at G59. During all other years, the number of Z-call detections peaked synchronously at all recording sites along the Greenwich meridian. In a zonal direction, peaks in ABW call numbers showed temporal differences between W66 and G66. In the 2010/2011 season, the number of detected ABW calls was highest in mid-March at W66, which was about 3 wk earlier compared to the peak at G66. By contrast, in the following year, the

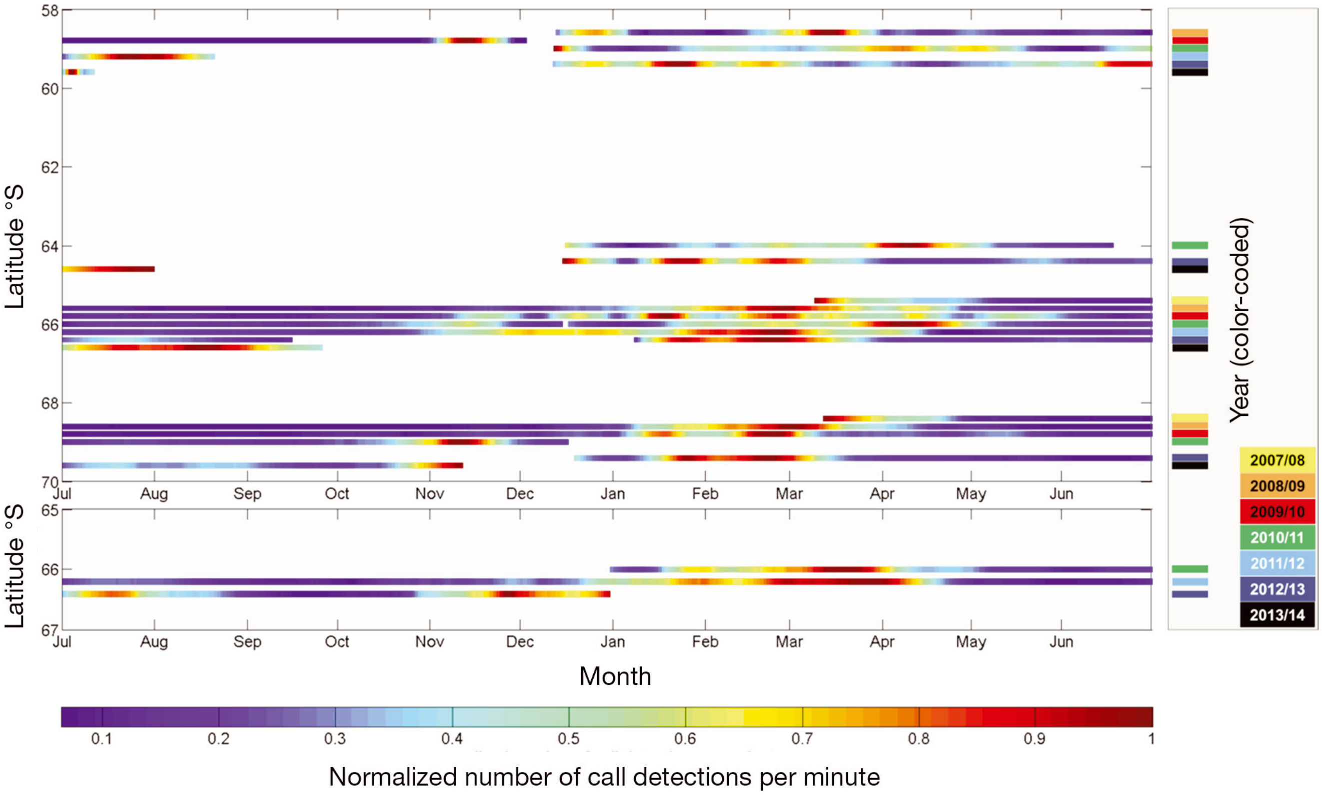

Fig. 4. Timing of peaks in numbers of Antarctic blue whale (ABW) call detections at different recording sites located along the Greenwich meridian (upper panel) and in the inner Weddell Sea (lower panel) over time. Recording sites were located at 59°, 64°, 66°, 66° 30′, 68° and 69° S, respectively (see Fig. 1, Table 1), but are depicted slightly shifted depending on recording season for clearer presentation. Different bands represent different years/seasons (with a season defined as starting in July and ending in June of the next year) and are color-coded on the right. Colors of the bands themselves indicate the (normalized) level of ABW Z-call detections (numbers of detected calls per minute)

number of detections peaked first at G66 in late February 2012 (occurring about 5 wk earlier in 2012 than in 2011) and about 1 mo later (i.e. late March) at W66. Secondary peaks during austral winter were discernable at both recording sites during July.

BWI

For all sites and in all years, the mean BWI exhibited values above zero throughout the year, indicating that acoustic energy attributed to ABWs was always present in the recordings from the study area (Fig. 3). Similar to data from Z-calls, BWI data from G59-I formed an exception, with the mean BWI ranging close to zero from July through October. No clear differences in BWI between northern and southern recording sites were observed.

The BWI time series mirrored the seasonal variations in the number of Z-call detections at all recording sites, except for a slower decrease in autumn following the BWI summer peak (Fig. 3). At most of the recording locations (W66, G59, G64-II, G66-II and G69-III), the BWI peak closely matched in time with the peak in Z-call detections. At G64-III, G66-I and G69-I, a delay of several weeks was observed between the timing of the BWI peak and the peak in single Z-call detections.

Z-call detections in relation to sea ice concentration

There was a distinct negative relation between the number of detected ABW Z-calls and ice coverage in the study area (Fig. 5). Over the study period, sea ice retreated between October and January, and started to form between March and July, depending on the recording site. Periods with open waters (defined as sea ice concentration <15%) were considerably longer at the northern recording sites (lasting up to 7 mo at G59) than at the southern recording sites (0 to

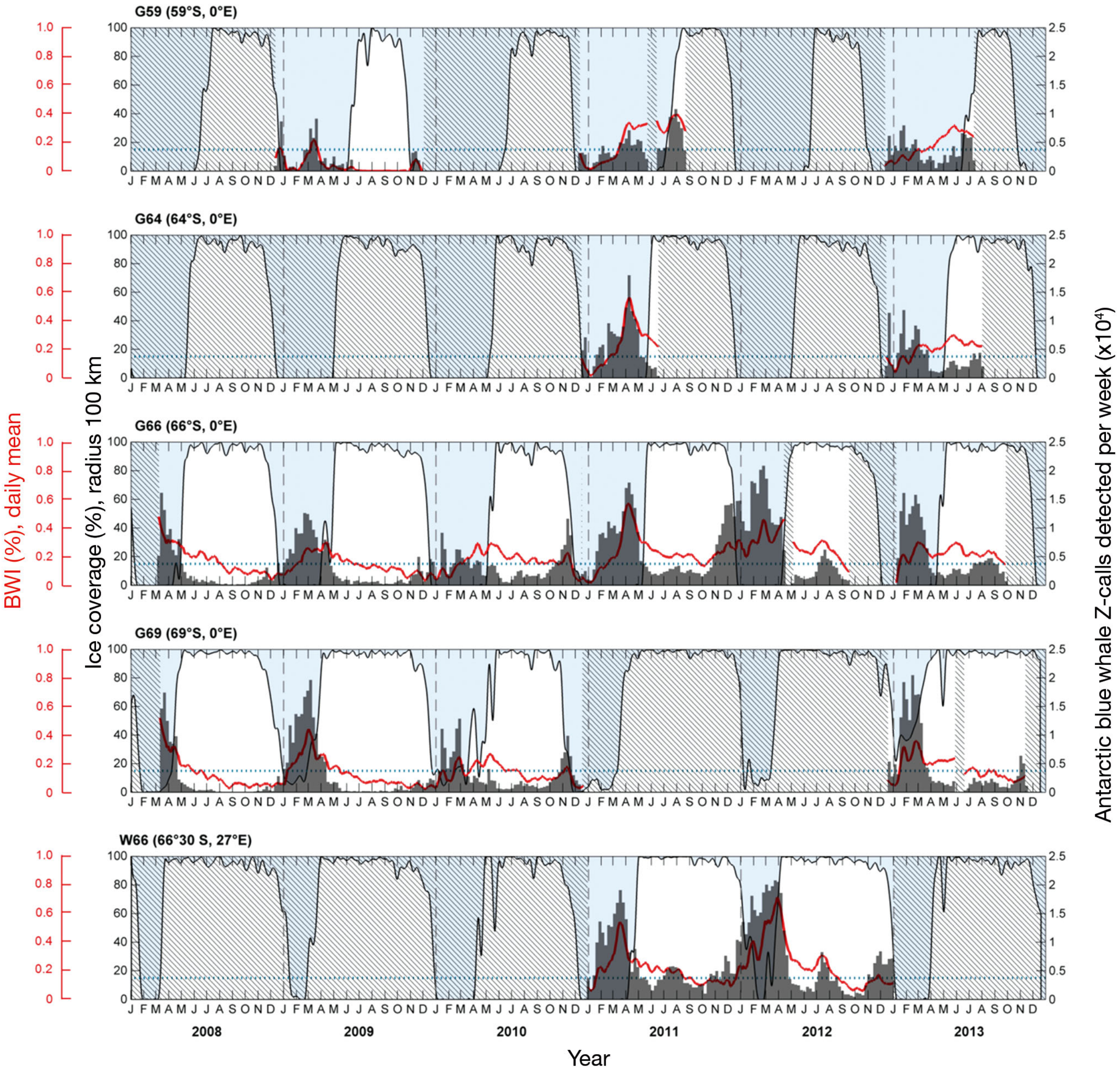

Fig. 5. Antarctic blue whale Z-call detections per week (dark grey bars, 7 d bins), BWI (red line, daily means) and sea ice concentration (black solid line, daily means within a 100 km radius) at different recording sites from 2008 to 2013. White areas indicate sea ice coverage and blue areas indicate open water. Blue dotted line represents sea ice edge (15 % ice cover). Hatched areas indicate periods when no recordings are available. Vertical dashed grey lines indicate beginnings of years of the study period. Z-call detections from subsampled recordings were normalized to weekly values for direct comparability between data sets

2 mo at G69). In general, most vocalizations were detected during periods with no (W66, G59, G64, G66 and G69-I) or moderate (G69-III) sea ice concentrations, while considerably less calls were detected during periods with high (>90 %) sea ice coverage. At most locations (G59, G64, G66-I and G69), changes in the number of detections appeared to be closely related to changing ice conditions, i.e. sea ice retreat or formation. However, at W66, G66-II and G66-III, Z-calls were also detected during periods of high (>90 %) sea ice concentration in winter. Furthermore, the number of detections already began to increase weeks to months before the sea ice retreated. At G69, the sea ice did not fully retreat during austral summer 2013; also at this location, many ABW Z-call detections were associated with moderate ice conditions (about 40 % ice cover in January and February).

DISCUSSION

ABW distribution in the Weddell Sea

The acoustic presence of ABWs along the Greenwich meridian in the Southern Ocean and in the inner Weddell Sea mirrors patterns in historic catch data, indicating a wide meridional distribution of ABWs in the Atlantic sector of the Southern Ocean (see review of Branch et al. 2007). At each of the recording sites, ABWs were acoustically present for more than 80% of all recording days each year, indicating that they are reliably present in Southern Ocean waters during much of the year, irrespective of ice conditions. Interestingly, in contrast to the present study and the historic catch data, post-whaling visual surveys showed that ABWs predominantly occurred close to the pack ice edge and continental shelf in austral summer (Branch et al. 2007). Although it cannot be excluded that the sighting effort was biased to some extent towards the summer months and the ice edge south of 60° S, the overall reduced density of exploited ABW populations may also have caused whales to concentrate at the ice edge where krill is most abundant (Branch et al. 2007). Our data show ABW acoustic presence from 59 to 69°S, implying a distribution of ABWs similar to that observed during the whaling era.

A recovery of the ABW population might have caused individuals to disperse and return to their former, much wider, distribution range (Branch et al. 2004, 2007). Nevertheless, possibilities to infer (local) abundances from our passive acoustic data are limited due to a detector artifact. Therefore, further inferences on whether potential changes in distribution could be reflective of increases in ABW abundance are impeded. The detector enables a total maximum of 4 vocalizations per minute to be detected, given a template duration of 12 s and a predefined minimum separation of 15 s between detected events (i.e. between the same part of 2 adjacent vocalizations). Assuming calls occur at regular intervals of about 1 min, the maximum number of calling whales that it is technically possible to detect with our algorithm is 4 individuals. The BWI measurements do not suffer from these detector-specific limitations, as these determine ABW energy on a continuous time basis. However, inferences on the number of individuals from the BWI are not possible without essential knowledge of, for example, detection likelihood, the individual cue rate and how this relates to the BWI, information which is currently lacking for ABWs. Furthermore, it is likely that song sequences of ABW Z-calls represent a male reproductive display, analogous to behavioral patterns in other baleen whale species (e.g. Tyack 1981, Croll et al. 2002, Oleson et al. 2007). Abundance estimates based on Z-call activity would therefore only account for the reproductively active male part of the population.

Acoustic presence in ice-covered areas

The present study found ABWs to be acoustically present in ice-free waters as well as under moderate ice concentrations during austral summer, and in areas with >90% ice cover during winter. Off the western Antarctic Peninsula, a negative correlation between ABW Z-calls and sea ice concentration suggested that ABWs are absent or scarce in ice-covered areas (Širović et al. 2004, Širović & Hildebrand 2011, Dziak et al. 2015). Nevertheless, Double et al. (2015) also reported vocal aggregations of ABWs located in areas with non-navigable ice conditions in the Ross Sea during austral summer. Despite the fact that different metrics have been used by different studies to determine ice concentration and ice edge location, the results of Double et al. (2015), along with our findings, indicate that ABW distribution in open ocean environments, such as the Ross and Weddell Sea, is not principally restricted to ice-free waters, but that ABWs are capable of navigating (heavily) ice-covered areas as well.

Differences in krill distribution and hence food availability between the western Antarctic Peninsula and the Weddell and Ross Sea may explain the differential usage of ice-covered waters by ABWs. The waters west of the Antarctic Peninsula are highly productive in terms of phytoplankton and krill abundance during austral summer, governed by the proximity and seasonal convergence of the ice edge and the southern boundary of the Antarctic Circumpolar Current in this region (e.g. Tynan 1998, Atkinson et al. 2008). During winter, krill overwinter at greater depth on the shelf (Siegel 2005, Nicol 2006). ABWs in the western Antarctic Peninsula area may therefore primarily exploit high-density food patches coinciding with the ice edge during austral summer, while feeding in this area is possibly too inefficient during winter. Conversely, in the Weddell Sea, postlarval krill are less abundant and distributed over a wider geographic range than off the western Antarctic Peninsula (Tynan 1998). Nevertheless, an almost year-round, close association of krill with the under-ice-habitat persists in the Weddell/Lazarev Sea (Flores et al. 2012) and may therefore provide a reliable food source for ABWs and other baleen whales that is virtually continuously available in the ice-covered waters of our study area.

Acoustic presence during austral winter

Our data provide the southernmost record of ABW winter presence in the Southern Ocean. High ice concentrations during winter most likely inhibit large-scale movements of ABWs, particularly at the southernmost recording sites. Hence, ABW winter presence indicates that part of the population skips the energy-costly migration to lower latitudes and overwinters in cold, ice-covered waters of the Weddell Sea. By thus reducing energy expenditure, along with the opportunity for prolonged exploitation of food sources, this may primarily benefit female whales, especially young barren individuals without dependent calves (e.g. Brown et al. 1995). Furthermore, baleen whale mating is known not to be restricted spatially and temporally to low-latitude breeding grounds, but also occurs at high latitudes and outside the breeding season (Clark & Clapham 2004). The presence of (presumably exclusively male) Z-calls therefore possibly indicates that a certain portion of ABW males also benefits from skipping migration by opportunistically mating with females that may have failed to conceive during summer and then overwinter in the Weddell Sea.

Besides the Weddell Sea, ABWs were also present year-round off South Georgia (Harmer 1931, Hjort et al. 1932), off the western Antarctic Peninsula (Širović et al. 2004, Dziak et al. 2015), in the southern Indian Ocean (Samaran et al. 2013) and in eastern Antarctica (Gedamke et al. 2007, Širović et al. 2009). Our study therefore adds to accumulating evidence that annual migration is not obligatory for ABWs and overwintering in the Southern Ocean may occur regularly and over large spatial scales. Local, potentially recurring, polynyas may enable ABWs and other marine mammals to overwinter in otherwise ice-covered areas (Ainley et al. 2010), but are likely to spatially constrain animal movements to open water areas during winter (see also Van Opzeeland et al. 2013b). Decreasing trends in the sea ice extent and the length of the sea ice season (e.g. de la Mare 1997, Parkinson 2002, Cotté & Guinet 2007) may potentially enable more extensive animal movements in the Weddell Sea during winter, but are likely to have severe effects on the Weddell Sea ecosystem due to an accompanying decline in krill densities (Atkinson et al. 2004).

Inferring ABW migratory movements in the Weddell Sea from passive acoustic data

ABWs are thought to emit Z-calls while travelling or migrating (Širović et al. 2009, Širović & Hildebrand 2011), hence spatio-temporal differences in the timing of peak call numbers might reveal migratory movements of ABWs in our study area (see also Širović et al. 2004). However, we observed a virtually simultaneous gradual increase in vocal activity from November onwards. Moreover, the number of detected calls peaked synchronously along the Greenwich meridian, and hence, no evidence for a directed, meridional migration of vocalizing (presumably male) ABWs could be detected. Our data thus contrast with the observations of Double et al. (2015) that suggested a simultaneous onset of ABW acoustic activity after vocal inactivity at the beginning of the feeding season.

Our results possibly indicate that ABWs exhibit a complex migratory behavior, featuring partial and differential migration, as reported for many baleen whale species (e.g. Kellogg 1929, Mackintosh & Wheeler 1929, Brown et al. 1995, Dawbin 1997, Craig et al. 2003, Širović et al. 2004). A (temporally or spatially) segregated and dynamic migration may result in a complex, staggered pattern of ABW movements to and from the feeding grounds, involving continuous arrivals and departures of individuals (see also Mackintosh & Wheeler 1929, Harmer 1931, Širović et al. 2004, Samaran et al. 2013). Future studies employing satellite and passive acoustic tags or visual observations of acoustically tracked individuals (Miller et al. 2015) will be most valuable to further our understanding of the (vocal) behavior in different ABW sex or age classes and, in turn, enable more comprehensive inferences on the (acoustic) ecology of ABWs.

CONCLUSIONS

This study is the first to report year-round acoustic presence of ABWs in the Weddell Sea and along the Greenwich meridian based on multi-year passive acoustic data. Our results suggest that the Weddell Sea, and in particular coastal polynyas, serve as an important habitat for ABWs and other baleen whales throughout the year, most likely by supplying food resources and reliable access to open water for breathing (see also Van Opzeeland et al. 2013b).

The synchronous peak of call numbers and the virtually continuous presence of calls are potentially indicative of temporally and spatially dynamic migration routes or destinations, as well as a temporally segregated migration depending on sex, age and reproductive status of the animals. Hence, our results add to the increasing evidence that a complex and dynamic migratory behavior, potentially including both partial and differential migration, is the rule rather than the exception for baleen whales. Further, evidence is accumulating that baleen whale feeding grounds are not static and confined locations, but rather dynamic areas providing a suitable habitat in terms of sea ice conditions, primary productivity and, in turn, krill abundance (Tynan 1998, Van Opzeeland et al. 2013b). Accordingly, blue whale feeding does not appear to be restricted in time and space, but has been observed to occur throughout the migration cycle year-round (Mate et al. 1999, Hucke-Gaete et al. 2004, Bailey et al. 2009, Silva et al. 2013). In turn, intra- and inter-annually variable environmental conditions that determine prey abundance and distribution, such as sea ice or ocean dynamics, may significantly influence the migratory behavior of baleen whales in terms of timing, routes and destinations (Mackintosh & Wheeler 1929, Reilly & Thayer 1990, Bailey et al. 2009).

A detailed understanding of distribution and migration patterns of baleen whales is of particular importance for assessing the effects of global change on high trophic levels. Recently, humpback and fin whales in the Gulf of Saint Lawrence were reported to migrate to their feeding grounds 2 wk earlier than 3 decades ago, possibly representing an earlier onset of primary production due to increased sea surface temperature and earlier sea ice breakup caused by global warming (Ramp et al. 2015). However, such notions need to be viewed critically in light of the overall variability of migratory patterns, or the direct and indirect long-term effects of commercial whaling on entire ecosystems. In this context, standardized data collection is essential to guarantee an accurate and integrative analysis of data, stemming from different areas, years and, in the case of passive acoustic data, different recording devices. Currently, the Southern Ocean Research Partnership (SORP) aims to set up the Southern Ocean Hydrophone Network (SOHN), a circumpolar hydrophone array intended to collect standardized, synchronously recorded passive acoustic data over multiple years with ABWs as a focal species (Van Opzeeland et al. 2013a). Once implemented, SOHN will provide detailed information on ABW occurrence and distribution on a circum-Antarctic scale, indispensable for the design of effective conservation measures such as the designation of ecologically relevant marine protected areas.

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Spatio-temporal patterns in acoustic presence and distribution of Antarctic blue whales *Balaenoptera musculus intermedia* in the Weddell Sea

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INDEPENDENCE OF ACOUSTIC RECORDINGS

Interpretation of acoustic data in terms of distribution and migratory behavior requires an understanding whether signatures detected at neighboring recording sites are independent of each other or if the same signatures are recorded on both sensors. Here we tested for acoustic independence of recorders by employing two different approaches:

A. compare the distance between recorder pairs with estimates of detection range of Antarctic blue whale calls and

B. look for unique sequences of ABW Z-calls that are coherently detectable in recordings from neighboring sensors by cross-correlation and supporting manual analyses.

In summary, the results of approach A indicated that detected individuals were in most cases closer than 200 km to at least one of the recorders, while results from approach B indicated that sequences were rarely detected simultaneously by even the closest neighboring recorders. Both findings consistently imply independence of our acoustic recorders, permitting interpretation of possible temporal differences in acoustic presence as migratory movements.

APPROACH A: DISTANCE ESTIMATIONS

Methods

Estimates of the distance of the vocalizing individuals from the respective recording site were obtained from received levels of detected ABW Z-calls. Prior to analysis, SonoVault recorders deployed from 2012 to 2014 were calibrated using a Brüel & Kjaer pistonphone calibrator (type 4229) with a custom-made adapter (by Develogic GmbH, Hamburg Germany), applying the same SonoVault configuration settings as during the recording period (Table S1). Sound pressure level calculations for the remaining recorder deployments are based on manufacturer information according to chosen amplifier settings.

Upper components (12 s duration) of auto-detected Z-calls were extracted from band-pass filtered audio files (Butterworth filter, pass band 25–29 Hz) and the sound pressure level SPL_{RMS} [dB re: 1µPa] within the 25–29 Hz band of each Z-call event was determined. The 25-29 Hz frequency band represents the peak (i.e., loudest) frequency range of an ABW Z-call, and matches the approach taken in the analysis by Širović et al. (2004). Approximate distances between vocalizing ABWs and the respective recorder location were calculated assuming a source level of 189 dB re: 1 µPa at 1m over 25–29 Hz and a transmission loss

TL[dB] = 17.8 $\log_{10}(r)$ as reported by Širović et al. (2007). However, as this transmission loss law was calculated based on data from bottom-moored recorders in waters off the Western Antarctic Peninsula (Širović et al. 2004), it might not necessarily be applicable for our study area and our study setup, with recorders moored at typically 1000 m depth in most cases. Hence, additional distance estimates were calculated applying TL[dB] = 20.0 $\log_{10}(r)$ and TL[dB] = 20.9 $\log_{10}(r)$ to assess the potential uncertainty in the range of the estimated distances. The former represents a spherical spreading loss modeled for the propagation of seismic signals, which comprise most energy at frequencies below 100 Hz, in the Weddell Sea (Breitzke & Bohlen 2010). The transmission loss law of TL[dB] = 20.9 $\log_{10}(r)$ represents almost spherical spreading plus some attenuation and was empirically determined for RAFOS sound source sweeps of approx. 260 Hz in a coastal Antarctic environment neighboring our study area (Van Opzeeland et al. 2013).

The MARU recorder was excluded from all amplitude related analyses due to unresolved strong fluctuations in the received levels in all frequency bands of interest, potentially caused by broad-band electronic noise. Additionally, the record of device AWI230-07 SV1001 exhibited an unexpected decrease in the received levels, probably caused by a flawed internal resistor (Develogic GmbH, pers. comm.). Over a period of seven days (22 to 28 March 2011) the received levels decreased slowly but steadily. While this period was excluded from further analyses, the period after 28 March 2011 was corrected for this offset by adding a frequency band-specific correction value (equaling 9.25 dB for the 25–29 Hz frequency range) to account for the amplitude drop.

The transmission loss laws used for our study were obtained for acoustic environments other than our study area (Širović et al. 2007) and for signals other than ABW calls (Breitzke & Bohlen 2010, Van Opzeeland et al. 2013). To take this to some extent into account, we employed all three different transmission loss laws to calculate the detection range of ABW Z-calls.

Results

Mean distance estimates (as based on a transmission loss of TL = 17.8 $\log_{10}(r)$) ranged between 87 and 144 km and were generally larger for AURAL recorders than for SonoVault devices (Fig. S1, Table S2). Although the maximum detection ranges of Z-calls may extend up to 700 km or more for some recorders, the bulk of estimated distances nevertheless ranged below 200 km for all recorders (Fig. S1, Table S2). As data were recorded concurrently at locations of at least 222 km apart, this indicates that a rather small percentage of Z-calls may have been audible at more than one recording site, whereas most recorded vocalizations will have been audible at only one recorder.

The range of distance estimates varied considerably depending on the transmission loss coefficient applied. Using a transmission loss of TL= 20.0 $\log_{10}(r)$ yielded mean distance estimates ranging between 25 and 36 km, with the majority of vocalizations (95th percentile) emitted within 100 km of the respective recorders (Table S2). Applying a transmission loss of TL= 20.9 $\log_{10}(r)$ yielded mean distance estimates ranging between 16 and 25 km, with the majority of vocalizations (95th percentile) produced in a range of up to 60 km (Table S2).

Previous studies reported detection ranges of ABW vocalizations of up to 600 nm (>1100 km) at maximum (Širović et al. 2007, Miller et al. 2015), similar to the maximum range estimates obtained in our study and hence supporting the plausibility of the distances estimated in our study. Calculations employing each of the three transmission laws, however, indicated that by far the most Z-calls were produced by animals that were closer than 200 km from the recorder. Our recorders are can therefore be considered independent from each other with respect to ABW Z-calls.

APPROACH B: CROSS-CORRELATION OF Z-CALL SEQUENCES

Methods

Three data sets (recorded at 64°S (G64, SV1010), 66°S (G66, SV1009) and at 69°S (G69, SV1011)) were selected for this test based on their close proximity (227 km between G64 and G66 and 330 km between G66 and G69, respectively) and hence, their potential acoustic dependence in terms of ABW Z-calls.

Assuming a constant sound propagation speed of 1500 m s^{-1}, the maximal travel time difference of sound between adjacent sites was expected to be about ±151 s (G64-G66) and ±220 s (G66-G69), respectively (source in-line with recorder pair). The internal clock drifts of the selected recorders were calculated to account for -26.5 seconds (G64, SV1010), -14 seconds (G66, SV1009) and -46 seconds (G69, SV1011) per year (Table S3). In turn, the maximal expected time lag of the same sound recorded at neighboring sites was 164 s and 252 s, respectively.

Z-call detection times were mapped onto binary (time) vectors of 5 s resolution, i.e., each 5-second-bin was assigned a logical "1" if a Z-call occurred within the interval, and a logical "0" otherwise. Binary vectors from G66 were cross-correlated with those from G64 and G69, respectively (Fig. S2). To allow for potential time lags between recordings of sequences, clock drifts and different travel times, a 10 minute long segment (template from -5 min to +5 min) from the binary vector of recorder A was cross-correlated with a 30 minute period (-15 min to +15 min) from the binary vector of recorder B, for each pair of data sets (Fig. S2: Step 1). The template's duration of 10 min is assumed to capture a significant portion of ABW song (Ljungblad et al. 1998, Širović et al. 2004). The cross-correlation procedure resulted in time series of correlation coefficients of 30-minutes length at 5 s resolution (Fig. S2: Step 2). Times at which the correlation coefficient exceeded 0.9 were stored (Fig. S2: Step 3).

For those events (i.e., times at which the cross-correlation coefficient exceeded 0.9), time lags between the detection time in recorder A and in recorder B were calculated. Taking into account a potential time delay between signal detections in recordings from different sites, only those events were considered that exhibited less than 10 minutes time delay between the detection times in different devices. Consecutive 10 minute templates (progressively shifted by 5 min) and 30 minute periods (shifted accordingly, Fig. S2: Step 4) were correlated for the entire duration of each record. Cross-correlation was performed in both directions for each pair of data sets, i.e., first, 10 minute templates of recorder A were correlated with 30 minute periods of recorder B and second, 10 minute templates of recorder B were correlated with 30 minute periods of recorder A. To assess the acoustic independence of data sets, only those events based on sequences of 3 or more Z-calls per 10 minute template were used, as they are unlikely to be caused by coincidence given that at least 2 intervals between consecutive vocalizations are required to match in both data sets.

To substantiate the results of the cross-correlation approach, manual checks were performed to determine whether a set of selected sequences of Z-calls from the recordings of one recorder was also detectable in the recordings of the adjacent recorder(s). A total of 12 sequences was selected from the recorders SV1009, SV1010 and SV1011, with the sequences comprising Z-calls consisting of one (unit A), two (units A + B) or all three units (A + B + C), respectively. This approach aimed to take into account song sequences of individuals vocalizing close to the respective recorder (i.e., with all three units being discriminable), and those of more distant individuals potentially sojourning between two recording sites (i.e., not all three units being detectable at the recording sites, see also Miller et al. (2015)). The corresponding period during which Z-call sequences were observed at one recording site was visually scanned in the recordings of the respective adjacent recorder(s), while allowing for potential time delays due to time lag between recordings of sequences, potential clock drifts and different travel times of the signals.

Results

For the cross-correlation of data sets recorded at G64 and G66 (distance 227 km), no events were detectable in both data sets, hence implying that data sets recorded at G64 and G66 can be assumed independent (Table S4). For cross-correlation of data sets recorded at G66 and G69 (distance 330 km), 6 events were based on 3 or more Z-calls and exhibited a time lag of <10 minutes between the two data sets, i.e., were detected in both data sets (Table S4). Hence, the data sets recorded at G66 and G69 are not completely independent from each other. However, although some overlap is likely to occur in the recorded signals from these two adjacent recording sites, the very limited number of interdependent sequences found is unlikely to bias the results substantially.

Similarly, manual analyses indicated that none of the Z-call sequences selected was discriminable in two recorders at the same time. Although this approach does not represent a quantitative analysis, it further supports the results of the distance estimation and cross-correlation approach, indicating that recorders can be considered acoustically independent from each other.

Figures & Tables

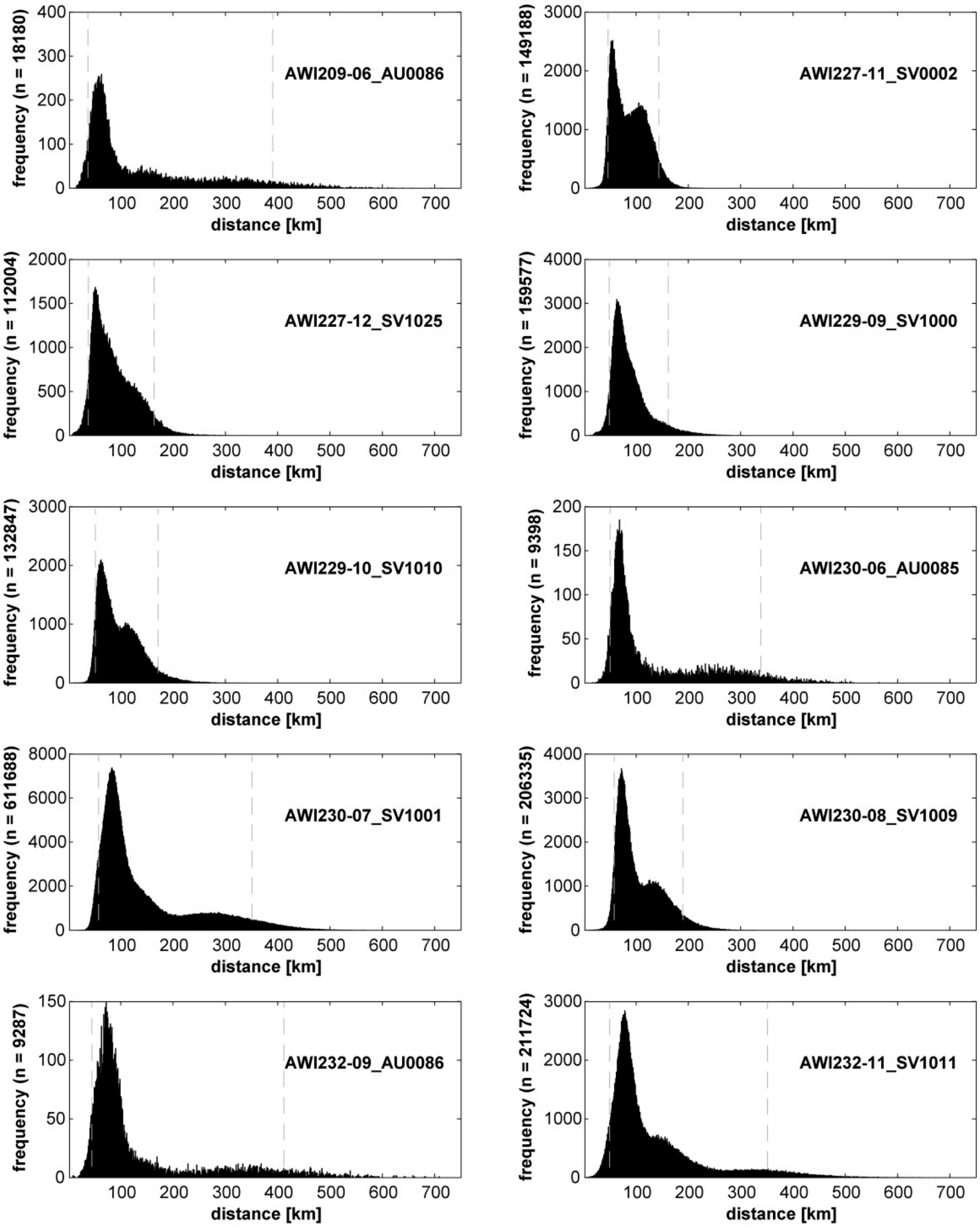

Fig. S1: Distribution (absolute frequency) of estimated distances [km] of the vocalizing ABW individuals from the respective recording site; distance calculations based on received levels in the 25-29 Hz frequency band of all Z-calls detected at a false alert rate of 1%, assuming a source level of 189 dB and a transmission loss TL[dB] = 17.8 $\log_{10}(r)$ (Širović et al. 2007); vertical dashed lines indicate the 5th and 95th percentile of estimated distances, respectively; subplots ordered by location as given by recorder ID in Table 1 (main article); note that y-axes are differently scaled due to the varying number of Z-call detections per recorder.

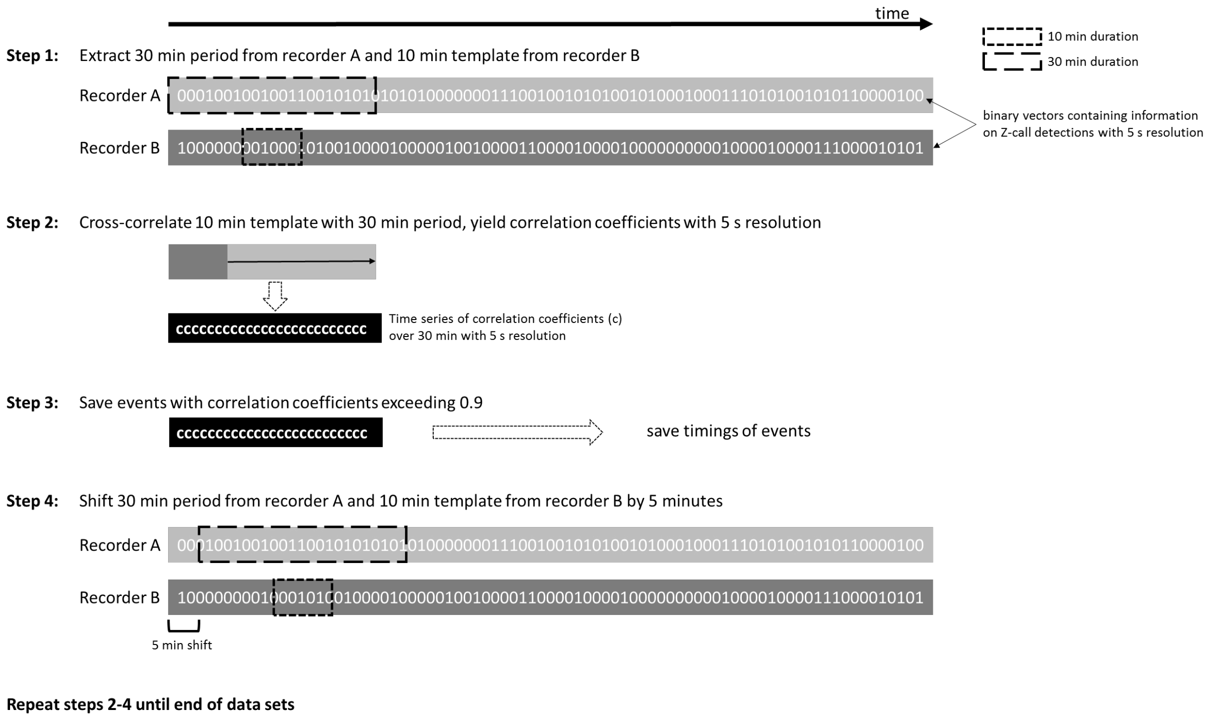

Fig. S2: Scheme of cross-correlation procedure to test independence of acoustic recordings.

Table S1: Post-calibration of SonoVault recorders deployed from 2012 to 2014 (after battery replacement) was conducted with a Brüel & Kjaer pistonphone calibrator (type 4229) with a custom-made adapter (by Develogic GmbH, Hamburg Germany). Actual gain G_{cal} (i.e., set gain + digitization gain) was calculated by $\boldsymbol{G_{cal}[dB] = 20 \cdot log_{10}(signal_{out}) - S - SPL_{in}}$ with $signal_{out}$ being the recorded sound pressure level [dB_{rms}] of the calibration signal SPL_{in}. Normalized signal values from .wav files were corrected for ADC input voltage of 2.5 V. Hydrophone sensitivity S and sound pressure level of the calibration signal are given for a frequency of 250 Hz and 251.2 Hz ± 0.1%, respectively.

recorder ID	**hydrophone sensitivity S [dB]**	**set gain G_{set} [dB]**	**ADC input U_{in} [V]**	**Sound pressure level of calibration signal SPL_{in} [dB]**	**calculated gain G_{cal} [dB]**
AWI227-12 SV1025	-192.50	24.00	2.5	153.85	24.89
AWI229-10 SV1010	-192.30	24.00	2.5	153.85	24.52
AWI230-08 SV1009	-193.00	24.00	2.5	153.85	25.32
AWI232-11 SV1011	-192.60	30.00	2.5	153.85	27.94

Table S2: Potential range of distance estimations [km] of vocalizing individuals from the recording site using TL[dB] = 17.8 $log_{10}(r)$ as estimated for Antarctic blue whale Z-calls in the Western Antarctic Peninsula area (Širović et al. 2007), TL[dB] = 20 $log_{10}(r)$ as calculated for seismic signals in the Weddell Sea (Breitzke & Bohlen 2010) and TL[dB] = 20.9 $log_{10}(r)$ as determined for sounds at approx. 260 Hz in coastal Antarctic waters near our study area (Van Opzeeland et al. 2013).

	range of distance estimates [km] at TL = 17.8 $log_{10}(r)$			**range of distance estimates [km] at TL = 20.0 $log_{10}(r)$**			**range of distance estimates [km] at TL = 20.9 $log_{10}(r)$**		
recorder ID	**5th %ile**	**mean**	**95th %ile**	**5th %ile**	**mean**	**95th %ile**	**5th %ile**	**mean**	**95th %ile**
AWI209-06 AU0086	37.07	136.53	390.04	11.65	36.08	94.64	7.79	23.63	57.78
AWI227-11 SV0002	46.15	87.91	143.30	14.16	24.97	38.82	9.38	16.25	24.63
AWI227-12 SV1025	37.92	86.89	163.29	11.89	24.62	43.60	7.94	16.08	27.53
AWI229-09 SV1000	48.38	87.13	161.03	14.77	24.75	43.07	9.77	16.12	27.20
AWI229-10 SV1010	50.95	97.07	171.08	15.46	27.24	45.45	10.21	17.68	28.64
AWI230-06 AU0085	49.97	130.71	338.12	15.20	34.96	83.34	10.04	22.77	51.16
AWI230-07 SV1001	57.23	144.15	350.51	17.15	38.22	86.06	11.27	24.75	52.76
AWI230-08 SV1009	57.71	105.15	188.98	17.28	29.25	49.66	11.35	18.92	31.17
AWI232-09 AU0086	44.60	132.50	411.43	13.74	35.18	99.25	9.11	23.04	60.47
AWI232-11 SV1011	49.36	131.82	350.84	15.04	35.34	86.13	9.94	22.94	52.80

Table S3: Calculation of time drift in SonoVault (SV) recorders from recorded RAFOS (Ranging And Fixing Of Sound) sound source signals. While a RAFOS source was hosted by the same mooring as the respective SonoVault (SV1010) for mooring AWI229, for mooring AWI230 (with recorder SV1009) time drift calculations were based on recorded signals from RAFOS sources at 227 km and 53 km distance, for mooring AWI232 (with recorder SV1011) time drift calculations were based on recorded signals from a RAFOS source at 276 km distance. Columns 3-4 and 5-6 indicate the time of reception of a RAFOS signal at the beginning and end of the recording period, respectively.

recorder ID	**RAFOS ID**	**date d_1**	**time t_1**	**date d_2**	**time t_2**	**period covered $D = d_2 - d_1$ [d]**	**$\Delta t = t_2 - t_1$ over D [s]**	**time drift RAFOS per day [s d^{-1}]**	**time drift RAFOS over D [s]**	**time drift SV over D [s]**	**time drift SV [s a^{-1}]**
AWI229-10 SV1010	AWI229-10_D0026	15.12.2012	12:29:59.1	01.08.2013	12:29:43.2	229	-15.9	-0.0027	-0.6183	-16.5183	-26.3283
AWI230-08 SV1009	AWI229-10_D0026	07.01.2013	12:32:23.7	26.09.2013	13:32:15.0	262	-8.7	-0.0027	-0.7074	-9.4074	-13.1057
	AWI231-10_D0024	07.01.2013	13:00:09.2	26.09.2013	12:59:59.0	262	-10.2	0	0.0000	-10.2000	-14.2099
AWI232-11 SV1011	AWI231-10_D0024	20.12.2012	13:02:53.9	12.11.2013	13:02:13.0	327	-40.9	0	0.0000	-40.9000	-45.6529

Table S4: Cross-correlation of Z-call detection results from data sets collected by SonoVault (SV) recorders at neighboring recording sites (G64: SV1010, G66: SV1009, G69: SV1011) to assess independence of recordings. Only events (i.e., times at which the cross-correlation coefficient exceeded 0.9) based on sequences of ≥ 3 Z-calls per 10 minute template, that exhibited less than 10 minutes delay between the detection time in different devices, were considered for assessing the independence of data sets.

Z-call number (per 10 min template)	**Number of events with correlation coefficients ≥ 0.9**	
	SV1009 & SV1010	SV1009 & SV1011
3	0	5
4	0	0
5	0	0
6	0	1
Σ of events detectable at both recorders	**0**	**6**

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Publication IV:

Spatio-temporal patterns in the presence of frequency-modulated calls of Antarctic blue whales in the Weddell Sea.

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Manuscript in preparation

Title: Spatio-temporal patterns in the presence of frequency-modulated calls of Antarctic blue whales in the Weddell Sea

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Abstract

Despite recent advances in marine mammal monitoring technologies, distribution and migration patterns of Antarctic blue whales in the Southern Ocean are far from being fully understood. This study aims at investigating fine-scale patterns in Antarctic blue whale (*Balaenoptera musculus intermedia*) distribution based on frequency-modulated (FM) downsweep calls recorded between 2008 and 2013 by 11 passive acoustic recorders deployed in the Weddell Sea and along the Greenwich meridian and one coastal-based long-term acoustic observatory. Hourly FM-call presence was assessed based on automated call detection using a custom-written Generalized Power Law detector, and subsequent manual validation. Our results show that FM-calls were frequently present throughout the study area during austral summer, indicating a wide distribution of Antarctic blue whales. During austral winter, persistent FM-call presence at 59°S implied that part of the population remains close to the sea ice edge during winter months. In contrast, south of 60°S, FM-calls were largely absent during austral winter, which contrasts with previous findings showing a year-round presence of Antarctic blue whale Z-calls throughout the Weddell Sea. The observed intra-annual differences between FM-call and Z-call presence may result from differences in the spatial scale over which each of these call types propagates, with FM-calls likely reflecting distribution patterns on a smaller spatial scale compared to Z-calls. Alternatively, the (near-)absence of FM-calls south of 60°S during winter could indicate a change in the species' (vocal) behavior. Although their functionality is not fully understood, FM-calls may function as social calls and potentially be of lesser relevance during winter due to a sparser distribution of Antarctic blue whales.

Keywords

passive acoustic monitoring, *Balaenoptera musculus intermedia*, frequency-modulated downsweeps, Antarctic blue whale distribution, migratory behavior, Southern Ocean

Introduction

Passive acoustic monitoring has been proven to be an important tool to investigate distribution and movement patterns of Antarctic blue whales (*Balaenoptera musculus* *intermedia*) in the Southern Hemisphere, particularly in remote and seasonally inaccessible areas such as the Southern Ocean (e.g. Širović *et al.*, 2004; Stafford *et al.*, 2004; Samaran *et al.*, 2013; Thomisch *et al.*, 2016). Most passive acoustic studies investigating Antarctic blue whale distribution are based on Z-calls: low-frequency vocalizations which are very amenable for passive acoustic monitoring as they are highly stereotypic, species-specific for Antarctic blue whales and produced year-round (Ljungblad *et al.*, 1998; Rankin *et al.*, 2005; Samaran *et al.*, 2013; Thomisch *et al.*, 2016). Z-calls are often produced in repetitive song patterns, which, in analogy to behavioral patterns in other baleen whales, presumably reflect a male reproductive display (e.g. Tyack, 1981; Croll *et al.*, 2002; Oleson *et al.*, 2007c). Due to the large detection ranges of Z-calls of up to several hundred kilometers (Širović *et al.*, 2007; Samaran *et al.*, 2010a; Miller *et al.*, 2015; Thomisch *et al.*, 2016), inferences on small-scale distribution patterns of Antarctic blue whales are impeded by the lack of positional data of the calling individuals.

However, apart from Z-calls, Antarctic blue whales (as well as other blue whale populations (e.g. Oleson *et al.*, 2007b; Oleson *et al.*, 2007c; Gavrilov *et al.*, 2011)) are known to produce highly variable frequency-modulated calls (FM-calls) in the frequency range between 100 and 30 Hz, which have also been referred to as ‘D-calls’ (e.g. Rankin *et al.*, 2005; Gedamke & Robinson, 2010; Double *et al.*, 2015). Unlike Z-calls, FM-calls have been found to be produced by both males and females within groups of foraging blue whales and hence are presumed to fulfill a social function (McDonald *et al.*, 2001; Oleson *et al.*, 2007b; Oleson *et al.*, 2007c). Furthermore, source levels and hence overall detection ranges of blue whale FM-calls are presumed to be lower compared to Z-calls (Thode *et al.*, 2000; Gavrilov *et al.*, 2011; Miller *et al.*, 2015), although no quantitative estimates of source levels and detection ranges of Antarctic blue whale FM-calls are available to date. However, given the presumed differences in functionality and detection ranges between Antarctic blue whale Z-calls and FM-calls, comparisons of the timing of FM-call and Z-call usage in an area may have the potential to provide further information on the behavioral context of call production and to improve our understanding of distribution and habitat usage of Antarctic blue whales on different spatial scales (e.g. Samaran *et al.*, 2010b; Širović & Hildebrand, 2011).

The present study investigates spatial and temporal patterns in the presence of Antarctic blue whale FM-calls in the Atlantic sector of the Southern Ocean from passive acoustic data collected between 2008 and 2013. Relationships between FM-call presence, sea ice concentration, and two metrics representing Antarctic blue whale Z-call presence were explored in order to gain further insight into Antarctic blue whale distribution and migration patterns.

Material & Methods

Acoustic data collection

In the pelagic Antarctic environment, passive acoustic data were collected by 11 autonomous recording devices deployed at various depths in the Weddell Sea and along the Greenwich meridian, either as a self-contained lander or attached to oceanographic deep-sea moorings of the Hybrid Antarctic Float Observation System (HAFOS) (Fig. 1, Table 1) (Rettig *et al.*, 2013; Thomisch *et al.*, 2016).

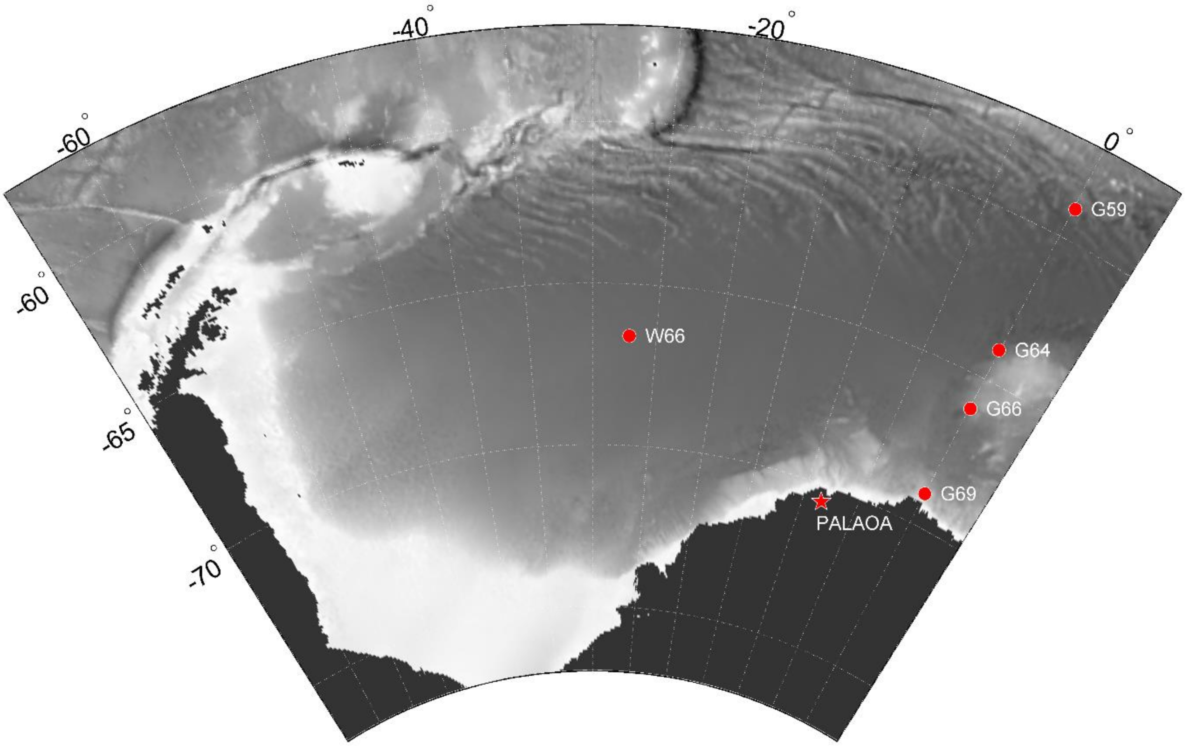

Fig. 1: Locations of autonomous recording devices (red circles), deployed between March 2008 and January 2013, in Weddell Sea and Atlantic sector of the Southern Ocean. Recorder IDs are shown in white (see also Material & Methods section, Table 1).

The deployment periods comprised three consecutive periods of recorder deployment between March 2008 and November 2013 (Table 1). Passive acoustic data were collected by three types of acoustic recording devices: SonoVaults (manufactured by Develogic GmbH, Hamburg, Germany) (Rettig *et al.*, 2013), AURALs (Autonomous Underwater Recorder for Acoustic Listening - Model 2, manufactured by Multi-Electronique (MTE) Inc., Rimouski, Quebec, Canada) (e.g., Simard *et al.*, 2008) and a MARU (Marine Acoustic Recording Unit, contributed by the Bioacoustic Research Program, Cornell University, Ithaca, NY, USA) (e.g., Parks *et al.*, 2009).

Furthermore, passive acoustic data from the Perennial Acoustic Observatory in the Antarctic Ocean (‘PALAOA’) located on the Ekström ice shelf at 70°31’S, 8°13’W were included. PALAOA collects continuous underwater recordings from a coastal Antarctic environment since 2005 with a Reson TC4032 hydrophone, deployed at approximately 160 m depth (see Klinck *et al.*, 2016 for further technical details on data acquisition). In the present study, PALAOA data recorded from 2008 to 2013 were analyzed.

Further details on passive acoustic devices, data acquisition and preprocessing are provided in Table 1 and Thomisch *et al.* (2016).

Table 1: Locations and recording parameters of passive acoustic recorders deployed within the HAFOS (Hybrid Antarctic Float Observation System) array in the Weddell Sea as well as of PALAOA. Recording sites are assigned with IDs representing the geographic location by a combination of letters (with ‘G’ and ‘W’ indicating a recording site on the Greenwich meridian and in the inner Weddell Sea, respectively) and numbers roughly reflecting the recording sites’ latitudinal position, Roman numerals (‘I’, ‘II’ or ‘III’) indicate the respective deployment period (2008-2010, 2010-2012 and 2012-2014, respectively); the sampling schemes are listed in terms of sampling duration [min] per sampling interval [min]; the correction factor f indicates the recorder-specific factor used to normalize the number of hours with FM-call presence in subsampled recordings for the duty cycle.

Recording site ID		Latitude	Longitude	Recorder ID	Deployment period	Depl. depth [m]	Sampl. freq. [kHz]	Sampl. scheme [min]/[min]	Corr. factor *f*	Operat. period [months]
G59	I	59 10.03 S	000 00.17 E	MARU01	12/2008-12/2009	4838	2.00	6/60	1	12
	II	59 03.02 S	000 06.63 E	AWI227-11 SV0002	12/2010-12/2012	1007	5.33	continuous	-	8
	III	59 02.63 S	000 04.92 E	AWI227-12 SV1025	12/2012-12/2014	1020	5.33	continuous	-	7
G64	II	63 59.56 S	000 02.65 W	AWI229-09 SV1000	12/2010-12/2012	969	5.33	continuous	-	6
	III	63 59.66 S	000 02.65 W	AWI229-10 SV1010	12/2012-12/2014	969	5.33	continuous	-	8
G66	I	66 01.13 S	000 04.77 E	AWI230-06 AU0085	03/2008-12/2010	189	32.77	5/240	4	34
	II	66 01.90 S	000 03.25 E	AWI230-07 SV1001	12/2010-12/2012	934	5.33	continuous	-	21
	III	66 02.12 S	000 02.98 E	AWI230-08 SV1009	12/2012-12/2014	949	5.33	continuous	-	9
G69	I	68 59.74 S	000 00.18 E	AWI232-09 AU0086	03/2008-12/2010	206	32.77	5/240	4	34
	III	68 59.86 S	000 06.51 W	AWI232-11 SV1011	12/2012-12/2014	958	5.33	continuous	-	11
W66	II	66 36.70 S	027 07.31 W	AWI209-06 AU0086	12/2010-01/2013	207	32.77	4.5/180	3	24
PALAOA		70 31‘ S	008 13‘ W	PALAOA	12/2005-ongoing	160	192	continuous	-	67

Automated detection of Antarctic blue whale FM-calls

Automatic detection of Antarctic blue whale FM-calls was performed using the generalized power law (GPL) detector developed by Helble *et al.* (2012). The GPL detector is based on Nuttall’s power-law processor, which is the optimal method to detect transient signals of unknown location, structure, extent and strength (Nuttall, 1994; 1996), but it was modified to take into account highly variable ocean noise conditions (see Helble *et al.*, 2012 for further details). The GPL detector was originally developed to detect humpback whale song units (Helble *et al.*, 2013; Helble *et al.*, 2015) and was adapted to time and frequency characteristics of Antarctic blue whale FM-calls for this study. Although Antarctic blue whale FM-calls are more stereotyped than humpback whale calls, they still exhibit considerable variability in frequency, duration, bandwidth, and slope. Therefore, cross-correlation and kernel-based detectors were not useful for this dataset as they tended to miss a considerable number of calls. The GPL detector is general enough to accommodate Antarctic blue whale FM-call variability, with some additional filters added from its original form to capitalize on the more stereotyped aspects of the calls. Calls were “templated” using the procedure outlined in Sect. IIA of Helble *et al.* (2015), and filters were applied to the spectral features, namely: the duration of the signal was required to be between 1 and 10 s, the bandwidth of the templated calls was required to span at least 3.1 Hz, and the slope of the template signal was required to be between -35.12 and -1.4 $Hz \cdot s^{-1}$.

Detector performance was estimated by visual inspection of spectrograms using two test data sets, i.e., a summer data set and a winter data set comprising five (28 January - 01 February 2013) and three (08 - 10 August 2011) continuous days of data collected at G69-III and G59-II (see Table 1), respectively. Spectrograms (FFT 256 points, Hanning window, 50% overlap) of the data, which were downsampled to a sample rate of 250 Hz, were visually inspected using Raven Pro (Bioacoustics Research Program, 2011). Start and end times of all detected Antarctic blue whale FM-calls were logged. Based on comparison of these manually obtained detection times to those of automatically detected FM-call events, the GPL detector yielded a precision (defined as the fraction of calls from the ground truth that were automatically detected, see also Roch *et al.* (2011)) equaling 59% and 47% for the summer and winter data set, respectively (Table 2). The recall (defined as the fraction of automatic detections that were also part of the ground truth, i.e. the true positive rate) of the GPL detector accounted for 67% and 75% in the summer and winter data set, respectively, when compared to the human annotated dataset (Table 2).

Table 2: Estimation of the GPL detector performance in detecting Antarctic blue whale FM-calls using two manually analyzed sets of continuous passive acoustic data; in this study, precision (in italics) is not a determinant of detector performance since all automatically detected events were subsequently verified by trained human analysts and all false positive detections were discarded.

	test data set 'summer'	**test data set 'winter'**
data	28 January – 01 February 2013	08 – 10 August 2011
ID recording position	G69-III (device SV1011)	G59-II (device SV0002)
manually detected FM-calls	5,106	1,408
automatically detected FM-calls	3,439	1,056
false alarms	2,382	1,178
precision [%]	*59*	*47*
recall [%]	67	75

Prior to FM-call detection, all passive acoustic data were downsampled to a sample rate of 2000 Hz (including an antialiasing FIR lowpass filter) due to detector-specific requirements. Furthermore, PALAOA data, which were originally stored in 1 minute files, were merged to 10 minute files prior to automated call detection in order to compile a uniform data set. Following GPL processing, all detected events were post-processed by trained human analysts using a graphical user interface (GUI), which is part of the GPL software. Reporting actual numbers of detections is only informative when the respective detection range is known to allow comparisons of vocal activity recorded in different seasons and at different recording sites. In the absence of such detailed information, Antarctic blue whale FM call presence was determined on an hourly basis in the present study, i.e. FM-calls were considered present within a given hour if at least one detected FM-call event was verified by the human analysts. Information on biological context (e.g. acoustic presence of other species during the respective hour and day) was gathered during austral autumn and winter (May to October) to facilitate differentiating between Antarctic blue whale FM-calls and similar downsweep vocalizations of Antarctic minke whales (Dominello & Širović, 2016). To avoid potential misidentification and subsequent overestimation of Antarctic blue whale FM-call presence, potential FM-call detections were discarded when Antarctic minke whale ‘bioduck’ vocalizations (Risch *et al.*, 2014) were visually and aurally identified during the same day.

Daily number of hours containing Antarctic blue whale FM-calls were calculated. For acoustic data sets subsampled at intervals of less than one hour, the number of hours with FM-call presence was normalized to 24 hours, using a recorder-specific correction factor (Table 1). Time series of FM-call presence were compared to time series of the number of Antarctic blue whale Z-call detections and the blue whale index ‘BWI’, as previously reported by Thomisch *et al.* (2016). Z-call time series data represent the number of Z-call detections per day. The BWI quantifies the portion of time when acoustic energy from Antarctic blue whales surpassed ambient noise (see methods section in Thomisch *et al.*, 2016 for further details). Time series of numbers of Z-call detections per day and daily mean BWI were smoothed using Savitzky-Golay filtering (window length = 31, step size = 1, regression based on polynomial order 2). In contrast to smoothing approaches using linear regressions, the polynomial regression of the Savitzky-Golay filter has the advantage of retaining the actual data distribution in terms of small-scale patterns, such as local minima and maxima (see also Thomisch *et al.*, 2016).

Sea ice concentrations

Sea ice coverage at each recording position was calculated using satellite data collected from 2008 to 2013, with changes in the spatial resolution of the data (6.25 · 6.25 km from January 2008 to October 2011 and from January 2013 onwards; and 13.2 · 15.5 km otherwise) due to instrument failures (Spreen *et al.*, 2008). Antarctic blue whale FM-calls are considered to be received over shorter distances than Antarctic blue whale Z-calls (Miller *et al.*, 2015), however quantitative estimates of detection ranges in the Weddell Sea are not available yet. In the present study, daily ice concentrations were calculated within a radius of 50 km of each recording site, including all data points located in a distance of smaller or equal 50 km from the recording location.

Results

Antarctic blue whale FM-calls were recorded at all recording sites and during all years (Fig. 2, Table 3). FM-calls were present during up to 7 months per year at G59, up to 6 months per year at G64, up to 5 months per year at G66, and up to 7 months per year at G69 (see Table 1 for nomenclature of recording sites). At W66, FM-calls were detected during up to 4 months per year. At PALAOA, FM-calls were present during up to 9 months per year (Table 3).

At most recording sites, FM-call presence showed a clear seasonal pattern. Most FM-calls were recorded between January and April at G64, G66, G69, W66 and PALAOA, although the exact timing of peak FM-call presence varied between recording sites and years (Fig. 2, Table 3). At PALAOA, daily FM-call presence was particularly high from January to March, equaling up to 24 hour day^{-1} over several weeks, in particular in 2009, 2012 and 2013 (Fig. 2). FM-calls were also detected during austral autumn and winter, i.e. in May and June at G64, in May at G66, in May and July at G69, as well as in May, June, August and September at PALAOA (Table 3). However, the number of hours with FM-call presence was low during these months and often based on few FM-call detections per day. At G59, the seasonal pattern in FM-call presence showed a more pronounced inter-annual variation compared to the other recording sites (Fig. 2, Table 3). At G59-I, FM-calls were frequent in January as well as in March and April, while few FM-calls were present from May to October. At G59-II, high FM-call presence occurred from May to August, while few FM-calls were recorded from

January to April. At G59-III, no clear seasonal pattern was evident, and FM-calls were present throughout the recording period from December to July.

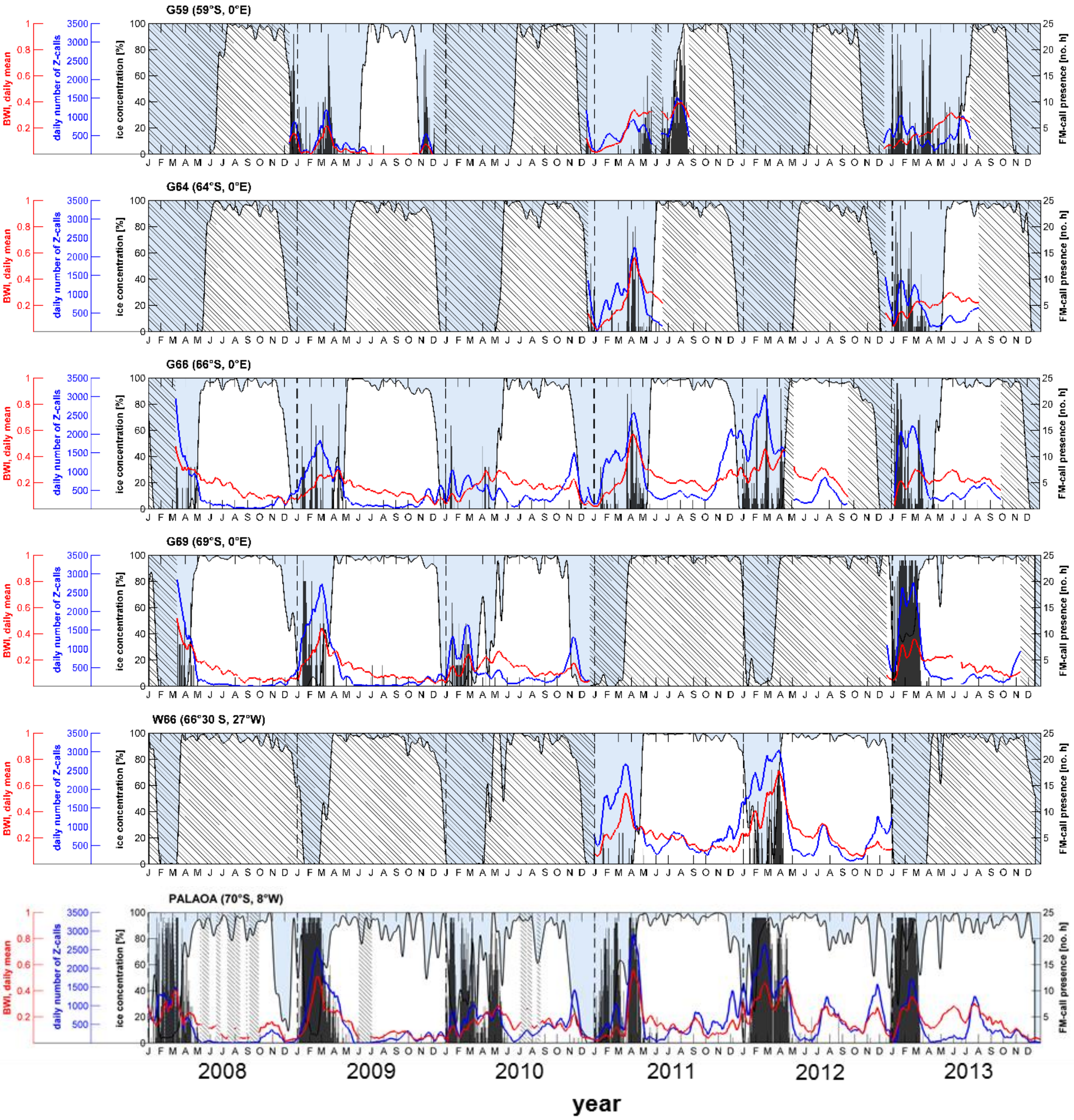

Fig. 2: Daily number of hours with presence of Antarctic blue whale FM-calls (black bars) in the Weddell Sea and along the Greenwich meridian from 2008 to 2013. Blue solid line indicates daily mean number of Z-call detections, while red solid line represents daily mean BWI (Thomisch et al., 2016). Sea ice concentration (black solid line) was calculated within a 50 km radius of the recording sites, with white areas indicating sea ice coverage and blue areas indicating open water. Hatched areas indicate periods when no passive acoustic data were available. Vertical dashed grey lines represent beginnings of years of the study period. For subsampled recordings, numbers of hours with FM-call presence and Z-call detections were normalized to daily values for direct comparability between data sets.

Table 3: Monthly presence of Antarctic blue whale FM-calls at different recording sites along the Greenwich meridian and in the Weddell Sea. Black bars with white crosses indicate periods when FM-calls were present, light grey bars represent periods when no FM-calls were detected, white areas indicate periods without passive acoustic recordings. Nomenclature of recording sites according to Table 1.

		month											
recording site	**year**	**J**	**F**	**M**	**A**	**M**	**J**	**J**	**A**	**S**	**O**	**N**	**D**
G59	2008												x
	2009	x	x	x	x	▒	x	▒	▒	▒	▒	x	x
	2010												x
	2011	▒	x	x	x	x	x	x	x				
	2012												x
	2013	x	x	x	x	x	x	x	▒				
G64	2008												
	2009												
	2010												x
	2011	x	x	x	x	x	x						
	2012												x
	2013	x	x	x	x	▒	▒	▒	▒				
G66	2008			x	x	x	▒	▒	▒	▒	▒	▒	▒
	2009	x	x	x	x	▒	▒	▒	▒	▒	▒	▒	x
	2010	x	▒	▒	x	▒	▒	▒	▒	▒	▒	▒	▒
	2011	x	x	x	x	x	▒	▒	▒	▒	▒	▒	▒
	2012	x	x	x	x	▒	▒	▒	▒	▒			
	2013	x	x	x	x	▒	▒	▒	▒	▒			
G69	2008			x	x	x	▒	▒	▒	▒	▒	▒	▒
	2009	x	x	x	x	x	▒	x	▒	▒	▒	▒	x
	2010	x	x	x	x	▒	▒	▒	▒	▒	▒	▒	▒
	2011												
	2012												x
	2013	x	x	x	▒	▒	▒	▒	▒	▒	▒	▒	
W66	2008												
	2009												
	2010												x
	2011	x	x	x	x	▒	▒	▒	▒	▒	▒	▒	▒
	2012	x	x	x	x	▒	▒	▒	▒	▒	▒	▒	▒
	2013	▒											
PALAOA	2008	x	x	x	x	x	x	▒	▒	x	▒	▒	x
	2009	x	x	x	x	x	░	▒	x	▒	▒	x	x
	2010	x	x	x	x	x	▒	░	x	▒	▒	x	x
	2011	x	x	x	x	x	x	▒	▒	▒	▒	▒	x
	2012	x	x	x	x	x	x	▒	x	▒	▒	x	x
	2013	x	x	x	▒	▒	x	▒	▒	▒	▒	▒	▒

From December to April, the temporal pattern in FM-call presence resembled the seasonal pattern in both number of Z-call detections and BWI at most recording sites. During this period, local or global maxima or minima in FM-call presence occurred synchronously to maxima or minima in the number of detected Z-calls and BWI at G59-I, G64-II, G66-II, G69-I, G69-III, W66-II and PALAOA (Fig. 2). In contrast, from May to November, Antarctic blue whales were still acoustically present at G64-III, G66, G69, W66 and PALAOA as indicated by the number of Z-call detections and the BWI, while FM-calls were rarely present or absent at all recording sites during this period, except at G59-II and III (Fig. 2, Table 3).

Generally, periods with high FM-call presence concurred with periods of little or no ice cover at the respective recording sites, while no or few calls were recorded during austral winter when sea ice concentrations were high (Fig. 2). However, FM-calls were also present during periods when the ice concentration exceeded 50% within a 50 km radius of G59-II (July - August), G69-III (February - March), W66-II (March - April) and PALAOA (March-April).

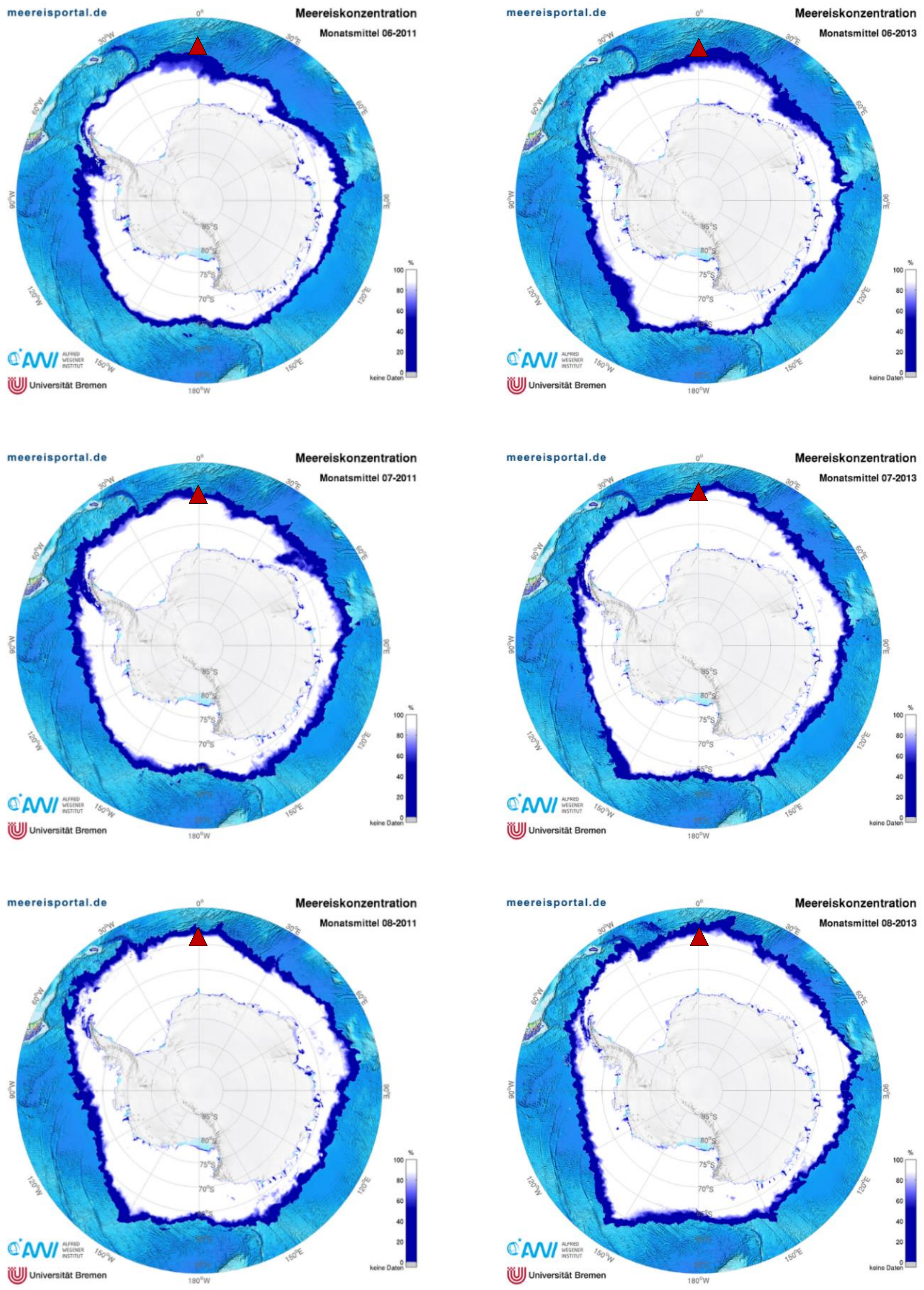

Fig. 3: Monthly mean sea ice concentrations in the Southern Ocean from June to August in 2011 (left panels) and 2013 (right panels). Red triangle indicates the position of recording site at 59°S (G59).

Discussion

Avoiding misidentification of Antarctic blue whale FM-calls with other baleen whale downsweep calls

Periods with low numbers of (potential) call detections are particularly vulnerable to misrepresentation of patterns in Antarctic blue whale acoustic presence that may arise by confusing FM-calls with similar vocalizations of other species. Apart from Antarctic blue whales, frequency-modulated vocalizations within the range from 30 to 100 Hz are known to be produced by pygmy blue whales *Balaenoptera musculus brevicauda* (e.g. Gavrilov *et al.*, 2011), Antarctic minke whales *Balaenoptera bonaerensis* (e.g. Dominello & Širović, 2016), fin whales *Balaenoptera physalus* (e.g. Thompson *et al.*, 1992), sei whales *Balaenoptera borealis* (e.g. Baumgartner & Fratantoni, 2008; Calderan *et al.*, 2014) and humpback whales *Megaptera novaeangliae* (e.g. Darling, 2015), which complicates the attribution of such low-frequency vocalizations to a species with certainty based on characteristics of frequency and duration (see also Ou *et al.*, 2015). Pygmy blue whales are known to mainly inhabit waters north of 55°S (Kato *et al.*, 1995). This, along with the fact that further pygmy blue whale signatures were absent from our recordings, leaves it unlikely that pygmy blue whale downsweep calls cause a likely source of confusion with Antarctic blue whale FM-calls in the present study. Misidentification of FM-calls is presumably most likely to arise from Antarctic minke whale downsweep calls, which closely resemble Antarctic blue whale FM-calls in terms of frequency range, duration and spectrographic shape (Rankin *et al.*, 2005; Double *et al.*, 2015; Dominello & Širović, 2016). Antarctic minke whales are known to occur frequently in the Southern Ocean during austral winter (Thiele *et al.*, 2004; Van Dam & Kooyman, 2004; Van Opzeeland, 2010; Dominello & Širović, 2016). Therefore, all FM-call detections at days with acoustic presence of Antarctic minke whales were discarded to overcome potential overestimation of Antarctic blue whale presence. Although a certain level of underestimation of Antarctic blue whale FM-call presence cannot be excluded, the number of (potential) FM-call detections between May and November was already low at G64, G66, G69 and W66. Hence, our post-processing approach has not drastically altered the overall pattern in occurrence of Antarctic blue whale FM calls (Table 4).

Functionality and behavioral context of Antarctic blue whale vocalizations

The observed temporal differences in the presence of FM-calls (i.e. seasonally present) and Z-calls (present year-round) possibly affirm that the production of these call types is associated with differential behavioral states in Antarctic blue whales. Blue whale FM-calls are thought to have a social function and were previously observed to be associated with feeding activities (Oleson et al., 2007b), while blue whale song (i.e. composed of Z-calls in Antarctic blue whales) is assumed to have a reproductive function, presumably representing a male reproductive display (Oleson et al., 2007c). In eastern North Pacific blue whales, Oleson et al. (2007c) observed temporal separation in the presence of FM-calls and song on both daily and seasonal scales and suggested that singing and foraging activities are generally incompatible. In the Weddell Sea however, both FM-calls and Z-calls were most frequent during austral summer months. Hence, the lack of a temporal delay between these call types during summer potentially indicates a mixture of behavioral states within the Antarctic blue whale population in the Southern Ocean, with some animals foraging while others may be involved in behaviors related to reproduction. Foraging activity and hence FM-call production may in contrast cease during austral winter, whereas the presumably dispersed mating season of Antarctic blue whales may lead to the continued production of Z-calls (see also Mackintosh & Wheeler, 1929).

Table 4: Number of days and hours with potential FM-call detections that were excluded from further analyses due to simultaneous acoustic presence of Antarctic minke whales. Nomenclature of recording sites according to Table 1. Note that the data sets associated with different recording sites are of variable duration (see Table 1 for further information on operational periods).

recording site	G59-I	G66-II	G66-III	G69-I	G69-III	PALAOA
no. of days with excl. hours	4	7	12	2	24	37
total no. of excl. hours	10	11	23	2	27	52
mean no. of excl. hour day^{-1}	2.50	1.57	1.92	1.00	1.13	1.41
minimum no. of excl. hours day^{-1}	1	1	1	1	1	1
maximum no. of excl. hours day^{-1}	5	3	5	1	2	8

However, FM-calls may not be indicative of foraging behavior of Antarctic blue whales per se but could also reflect social interactions between individuals on comparatively small spatial scales, since they were observed to be produced by individuals within groups of blue whales Oleson et al. (2007b). In baleen whales, social sounds are likely to be related to the mediation of social group composition and interactions between socials groups (e.g. Tyack, 1983; Dunlop et al., 2008). Downsweep calls of other baleen whale species have been hypothesized to fulfill a function in maintaining contact and spacing between individuals on the feeding areas, potentially in order to reduce direct intra-specific competition for food (Edds-Walton, 1997; 2000) Hence, downsweep calls may be produced more frequently when animal density in an area is high (Dominello & Širović, 2016), which is supported by the observed positive correlation between blue whale FM-call presence and the number of individuals present in an area (Oleson et al., 2007a). In turn, intra-annual variations in FM-call presence might also indicate fluctuations in the need for short-distance communication in terms of contact calling to maintain space between individuals. Particularly during austral winter, a sparse distribution and low density of Antarctic blue whales near the recording sites may result in the observed pattern of near-absence of FM-calls, while persistent Z-call presence might be reflective of off-season reproductive behavior on the feeding grounds or of long-distance communication among distant individuals.

Furthermore, the presumed functionality of downsweep calls in reducing competition for food may provide a possible explanation of the similarity in frequency characteristics, duration and shape of frequency modulated downsweeps among different baleen whale species, including pygmy blue whales, fin whales, sei whales, humpback whales and minke whales (e.g. Thompson et al., 1992; Edds-Walton, 2000; Dunlop et al., 2007; Baumgartner & Fratantoni, 2008; Samaran et al., 2010b; Calderan et al., 2014; Darling, 2015; Double et al., 2015; Ou et al., 2015; Dominello & Širović, 2016). Hence, downsweep calls may potentially mediate social interactions between individuals not only intra-specifically but on an inter-specific scale. In this context, the static and dynamic characteristics of social calls may transmit different types of information, e.g. sex, size, dominance rank or motivational state of the caller (e.g. Taylor & Reby, 2010; Dunlop, 2016), and the responses to social calls may differ among individual receivers (e.g. Tyack, 1983; Clapham, 2000).

Spatio-temporal patterns in Antarctic blue whale distribution

Antarctic blue whale FM-calls were present most frequently between January and April at all recording sites during most years, while FM-calls were largely absent south of 60°S during austral winter months.

During austral summer months, the simultaneous FM-call presence at the various recording sites indicates a wide latitudinal distribution of Antarctic blue whales on their Weddell Sea feeding ground. Blue whales have been observed foraging throughout their migratory cycle (Mate et al., 1999; Bailey et al., 2010; Silva et al., 2013) and prey availability is considered a major determinant of Antarctic blue whale distribution, potentially year-round (Branch et al., 2007). In the Weddell Sea, krill is known to be widely distributed (e.g. Tynan, 1998; Flores et al., 2012), which hence may favor a broad Antarctic blue whale distribution, particularly during summer (see also Thomisch et al., 2016). If FM-calls are exclusively produced in a behavioral context related to foraging, our results could indicate that Antarctic blue whales forage throughout the Weddell Sea during austral summer. In turn, simultaneous presence of FM-calls at all recording sites could reflect a differential migratory behavior of Antarctic blue whales. Some individuals may follow the retreating sea ice edge southwards, while others may remain in the productive waters of the Southern Boundary of the Antarctic Circumpolar Current to forage during summer months (Tynan, 1998; Branch et al., 2007; Thomisch et al., 2016).

During austral winter, FM-calls were largely absent south of 60°S, but were present at site G59 during winter months in 2011 and 2013, implying that this area serves as an important habitat for Antarctic blue whales well into austral winter. During July and August 2011 and from June to July 2013, the sea ice edge was located close to site G59 (Fig. 3). South of 60°S, high ice concentrations likely constrain large scale movements of Antarctic blue whales and confine individuals to (local) open water areas and hence, are likely to proximately determine distribution patterns of baleen whales during winter months (Van Opzeeland *et al.*, 2013; Thomisch *et al.*, 2016). Our results hence indicate that the waters close to the ice edge likely provide suitable habitat conditions for Antarctic blue whales during winter months, enabling part of the Antarctic blue whale population to remain, and potentially overwinter, close to the ice edge. Furthermore, the occasional presence of FM-calls at PALAOA during autumn and winter months might indicate that some individuals overwinter in coastal Antarctic waters. Overwintering of baleen whales in these waters may be favored by the presence of coastal polynyas and possibly foraging opportunities given the close association of krill with the under-ice habitat during austral winter (Marschall, 1988; Flores *et al.*, 2012; Van Opzeeland *et al.*, 2013).

At the offshore recording sites, the absence of FM-calls south of 60°S during austral winter stands in stark contrast to the persistent presence of Z-calls at all of this study's offshore recording sites year-round (see also Thomisch et al., 2016). Alternatively or in addition to the possibility of a change in the species' (vocal) behavior during the winter months, differential seasonal patterns in FM-call and Z-call presence may in part be caused by differences in the propagation ranges of the calls and hence, the spatial scales which are represented by each of these metrics. Antarctic blue whale FM-calls are presumed to propagate over shorter distances than Z-calls, which are likely to be propagated over hundreds of kilometers (Širović et al., 2007; Samaran et al., 2010a; Miller et al., 2015; Thomisch et al., 2016). Hence, FM-calls are likely to represent Antarctic blue whale distribution over a smaller spatial scale compared to Z-calls, which - given a sparser Antarctic blue whale distribution during the austral winter - potentially contributes to the (near-)absence of FM-calls at most recording sites during winter months. Quantitative estimates of detection ranges of Z-calls and FM-calls in the Weddell Sea are lacking yet, but are subject of ongoing work. Such estimates will substantially improve our understanding of Antarctic blue whale distribution and habitat usage on (presumably) different spatial scales in the near future.

Outlook

This manuscript is still in preparation. Further analyses are in progress and involve sound propagation modelling for Antarctic blue whales vocalizations in the study area in order to estimate transmission loss and hence, detection ranges of FM-calls and Z-calls in the Weddell Sea. The results on Antarctic blue whale FM-call presence obtained from the passive acoustic recorders moored within the Weddell Sea and those recorded by PALAOA (including also data on Z-call detections and BWI in the PALAOA data) will likely form separate manuscripts at a later stage.

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Publication V:

Intra- and interannual patterns in the acoustic presence of large cetacean species in a presumed breeding area off Namibia.

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Manuscript in preparation

Title: Intra- and interannual patterns in the acoustic presence of large cetacean 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, but the spatio-temporal distribution and migratory behavior of cetaceans off southern Africa is still poorly understood. Our study aimed to investigate temporal patterns in the acoustic presence of large cetacean species in a presumed baleen whale breeding area off Namibia by using passive acoustic recordings collected between November 2011 and May 2013. Our results showed seasonal acoustic presence of humpback whales, fin whales and Antarctic minke whales from November to December and from June to August, and acoustic absence from February to May. Their acoustic absence possibly reflects that most animals migrate to other (high-latitude) areas to feed in austral summer. By contrast, Antarctic blue whale were acoustically present during all recording months, suggesting that part of the population remains at lower latitudes year-round. Odontocete click trains were recorded from November to March and May in 2012 and 2013, respectively. Their temporal patterns in acoustic presence varied between years, possibly reflecting small-scale fluctuations in odontocete distribution patterns as a consequence of variations in environmental conditions. Our study confirms the presumed ecological importance of the oceanic area off Namibia, likely providing (part of) a suitable wintering and, potentially, breeding range or migratory corridor for several cetacean species. 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 for a partial, rather than complete, baleen whale migration.

Keywords

baleen whale breeding grounds, Antarctic blue whales, partial migration, passive acoustic monitoring, Namibia, South Atlantic Ocean

Introduction

Technological advances have contributed significantly to an increased understanding of animal migratory behavior (see Dingle, 2014, and references therein). Across many animal taxa this has led to new insights, revealing that migratory patterns are far from uniform for species, populations and even individuals (see Chapman *et al.*, 2011; Avgar *et al.*, 2014;

Geijer *et al.*, 2016 for reviews). For marine mammals, passive acoustic monitoring has proved to provide an important tool with which large-scale spatio-temporal patterns in occurrence and distribution can be non-invasively mediated (e.g., Mellinger *et al.*, 2007; Van Parijs *et al.*, 2009, Au & Lammers 2016). Evidence is accumulating that migration in many species, also in marine mammals, is not obligate and much more dynamic than previously assumed. Passive acoustic data from the Southern Ocean showed that fin whales (*Balaenoptera physalus*), Antarctic blue whales (*B. intermedia musculus*; Širović *et al.* 2004, Thomisch et al. 2016) and humpback whales (*Megaptera novaeangliae*; Van Opzeeland *et al.* 2013) were 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 part of the population is likely to overwinter in the cold, largely ice-covered Southern Ocean (Van Opzeeland *et al.*, 2013; Thomisch *et al.*, 2016), defying the paradigm of a complete baleen whale migration. Such partial migration, i.e., a population composed of migratory and resident individuals, has been suggested to be advantageous in the context of increasing fecundity (Brown *et al.*, 1995; Shaw & Levin, 2011). In baleen whales, predominantly females may benefit from omitting migration and remaining on the feeding grounds to maximize growth and body mass, which forms an important factor determining sexual maturity (Lockyer, 1984; Brown *et al.*, 1995). However, complementary knowledge from breeding areas on whether partial migration also entails individuals remaining in low-latitude breeding areas year-round, is to date sparse and mainly based on historic catch data and the Discovery tagging program (Best, 2007; Reilly *et al.*, 2008). In fact, the locations of breeding and wintering areas in the South Atlantic Ocean are still largely unknown for many baleen whales. Within the eastern South Atlantic Ocean, different parts of the Angola Basin are thought to represent important winter habitats and potential breeding grounds for several species, particularly Antarctic blue whales, fin whales, Antarctic minke whales and sei whales (Best, 2007; Weir, 2010). Furthermore, the area may also provide foraging opportunities for cetaceans during summer, driven by the highly productive Benguela upwelling system (Best, 2007; Barendse *et al.*, 2011).

To better understand the ecological importance of the Angola Basin as a potential breeding ground for baleen whales, we investigate inter- and intra-annual patterns in cetacean acoustic presence using long-term passive acoustic data collected in the waters off Namibia.

Methods

Passive acoustic data

Between November 2011 and May 2013, passive acoustic data were collected using two SonoVault recorders (further referred to as ‘SV’; manufactured by Develogic GmbH, Hamburg, Germany). The recorders were deployed in the Atlantic Ocean off Namibia, north-west of Walvis ridge (20° 58’ S, 5° 59’ E, Table 1, Fig. 1) at a depth of about 740 m. Devices were configured to record continuously at a sample rate of 5,333 Hz.

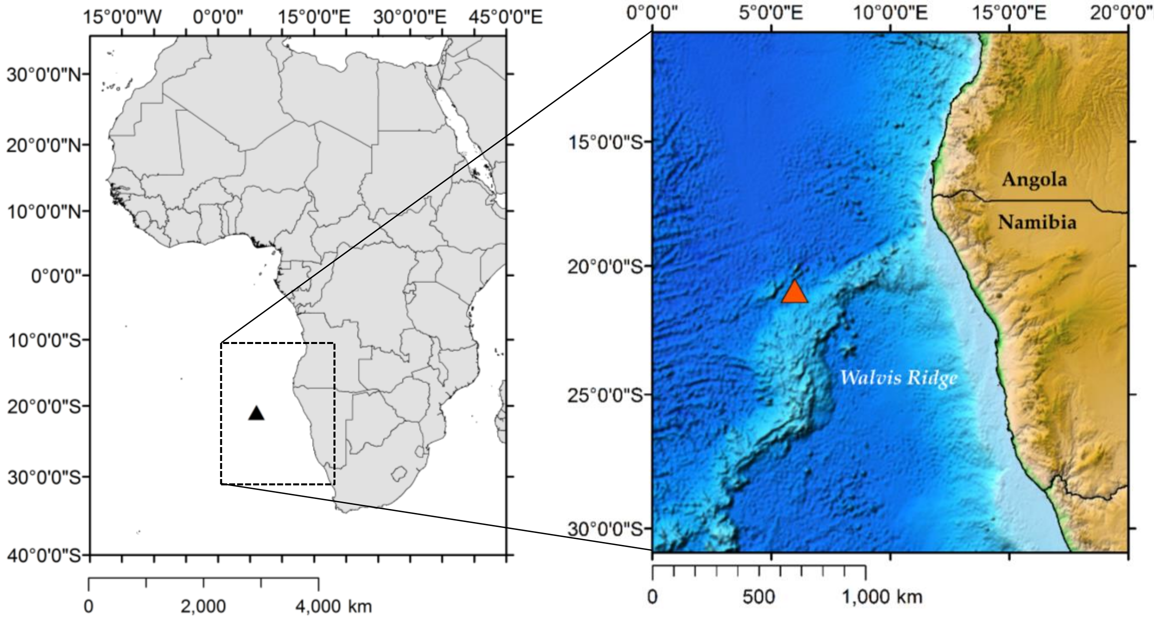

Fig. 1: *Map of Africa for overview with recorder position (black triangle) in the Atlantic Ocean (left panel), and bathymetry map showing recorder position (red triangle) off Namibia, northwest of Walvis Ridge (right panel). Maps were created using the ETOPO1 global relief model map provided by the NOAA National Centers for Environmental Information, NCEI (based on dataset of Amante & Eakins, 2009), and the World Countries Basemap by Esri, DeLorme Publishing Company, CIA World Factbook.*

The recorders were deployed between 25 November 2011 and 22 November 2012 (device SV1008) and between 22 November 2012 and 24 November 2014 (device SV1019). Both recorders stopped operating prior to their recovery due to battery exhaustion, with SV1008 recording until 25 August 2012 and SV1019 recording until 30 May 2013. The duration of the utilizable recordings was 274 days and 189 days for SV1008 and SV1019, respectively (Table 1, Fig. 2).

Table 1: Locations and recording parameters of passive acoustic SonoVault recorders deployed off Namibia.

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	5,333	continuous	274
20°58,54' S	5°59,07' E	SV1019	11/2012-11/2014	11/2012-05/2013	736	5,333	continuous	189

Manual data analysis

All passive acoustic recordings were visually and aurally analysed using XBAT (Extensible Bioacoustic Tool; Figueroa & Robbins, 2008) (spectrogram settings of FFT between 512 and 2058 points, Hanning window, resulting in frequency resolution of ca. 3-9 Hz and time resolution of ca. 0.1-0.4 s). Detected vocalizations were classified to species level wherever possible based on spectrograms and signature descriptions from literature (e.g., Watkins et al., 1987; Ljungblad et al., 1998; Dunlop et al., 2007; Risch et al., 2014b; Dominello & Širović, 2016). Data analysis was performed qualitatively on a daily scale, i.e., a species was considered acoustically present at a particular day if at least one call was observed during that day. To inspect low frequency (i.e., <125 Hz) acoustic 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 and time resolution of ca. 1 s). 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.

Automated analysis of Antarctic blue whale Z-calls

For a more detailed analysis of the acoustic activity of Antarctic blue whales, Z-calls were automatically detected in the downsampled recordings (250 Hz sample rate). Z-calls are highly stereotypic, low-frequency vocalizations, typically consisting of three units within the frequency range of 18-28 Hz (Ljungblad et al., 1998; Rankin et al., 2005). Z-calls 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). Z-call detection was performed via spectrogram correlation (e.g., Mellinger & Clark, 2000), with an estimated false alert rate of 1% (see Thomisch et al. (2016) for method description). Weekly sums of Z-call detections were calculated (7-day bins).

Vocalizations produced by distant ABW individuals deteriorate with distance, resulting in a tonal ‘chorus’ within the 26–28 Hz frequency band (Gedamke et al., 2007), which complicates the detection of single Z-calls. To capture the intensity of the chorus, a blue whale index (BWI) was developed (see Thomisch et al., 2016) to quantify the time during which the ABW chorus (26–28 Hz band) dominated over ambient noise (23–24 Hz and 29–30 Hz bands). BWI’s 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 days, step size = 1 day, regression based on polynomial order 2).

Results

Acoustic biodiversity

Four baleen whale species were identified based on their species-specific vocalizations: Antarctic blue whales, fin whales, Antarctic minke whales (*Balaenoptera bonaerensis*) and humpback whales. 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 toothed whales. 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 signals.

During the overall recording period of 17 months, humpback whale sounds were recorded during 9 months, while both fin and Antarctic minke whales were acoustically present during 5 months (Fig. 2). Odontocete clicks were detected during 11 months (Fig. 2). The automated analyses showed that Antarctic blue whales were acoustically present throughout the recording period (Fig. 3).

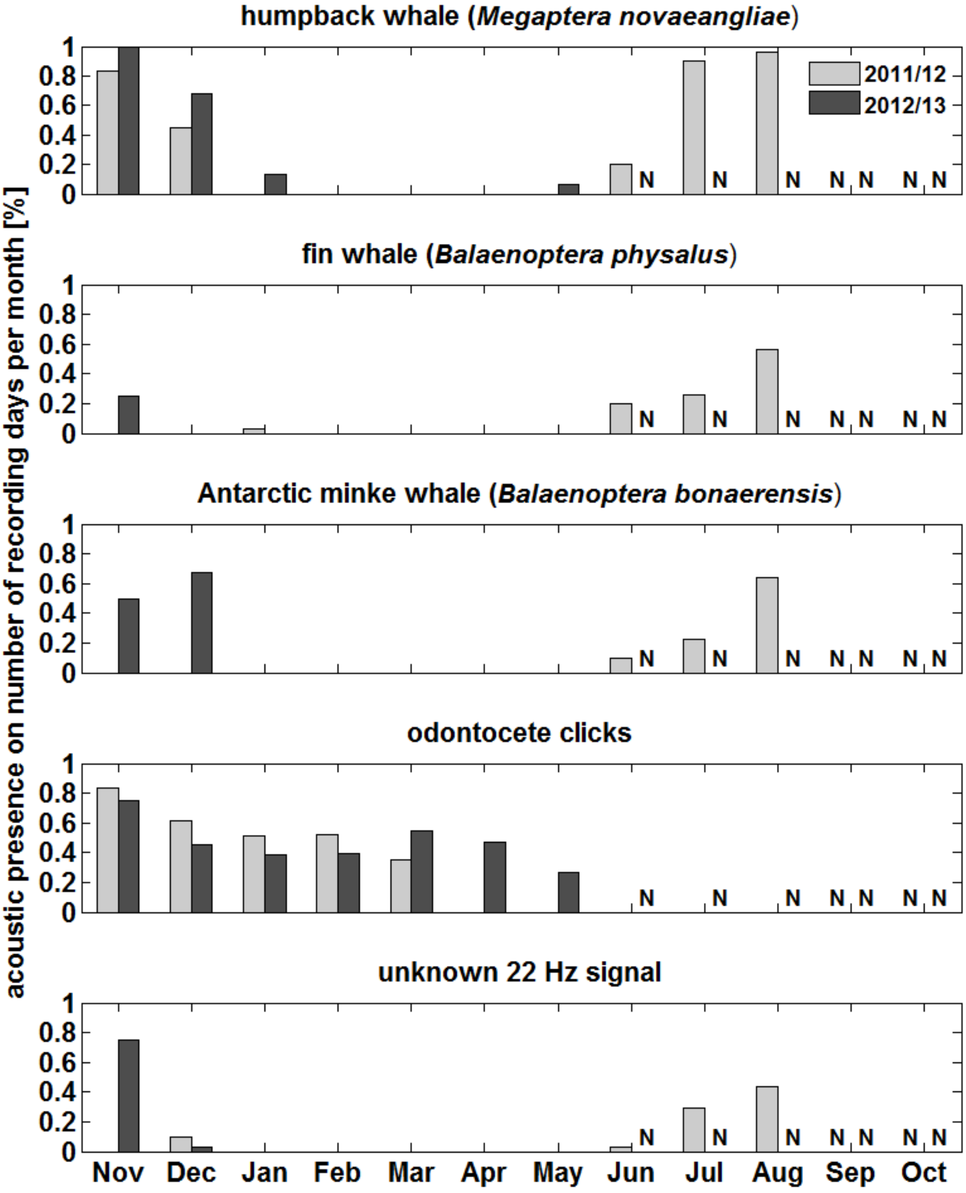

Fig. 2: *Acoustic presence of cetacean species off Namibia from November 2011 to August 2012 (light grey bars, recorded by SV1008) and from November 2012 to May 2013 (dark grey bars, recorded by SV1019). Presence of letter 'N' indicates months when no passive acoustic data were available.*

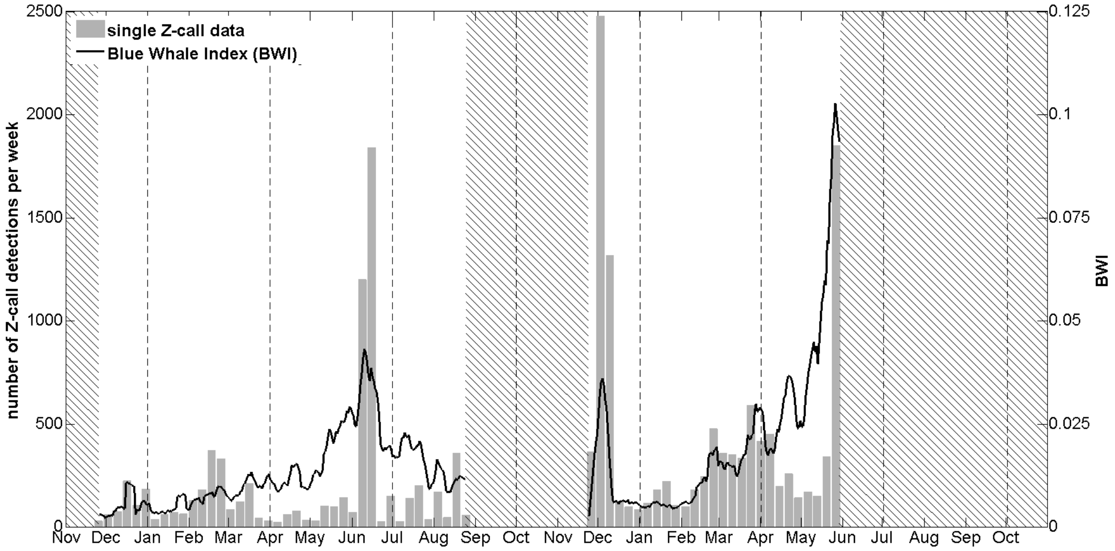

***Fig. 3:** Acoustic presence of Antarctic blue whales off Namibia from November 2011 until October 2013, showing the numbers of Z-call detections per week (grey bars; in 7-day bins) and the daily mean BWI (black line, smoothed using Savitzky-Golay filter; window length = 31 days, polynomial order = 2). Hatched areas represent periods without recordings; dashed lines represent beginnings of quarters of the years.*

Furthermore, sounds of unknown, but presumably biological, origin were recorded. One sound frequently recorded throughout the recording period, and hereinafter referred to as ‘22 Hz signal’, featured a frequency of about 22.5 Hz, lasted about 8-10 s and occurred in long sequences with inter-signal intervals of ca. 2.5 minutes (Fig. 4). Occasionally, frequency-modulated sounds of about 1 s duration were recorded, sweeping downwards from 130 to 40 Hz (with harmonics between 260 and 120 Hz) and occurring in groups of two or three sounds (Fig. 5). These sounds 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' in Dominello & Širović, 2016) and to frequency-modulated calls of Antarctic blue whales recorded in the Southern Ocean (Rankin *et al.*, 2005). Antarctic blue, minke and sei whales may winter in the waters off Namibia (Best, 2007), however, attributing the sound to one of these species with certainty is not possible without concurrent visual information.

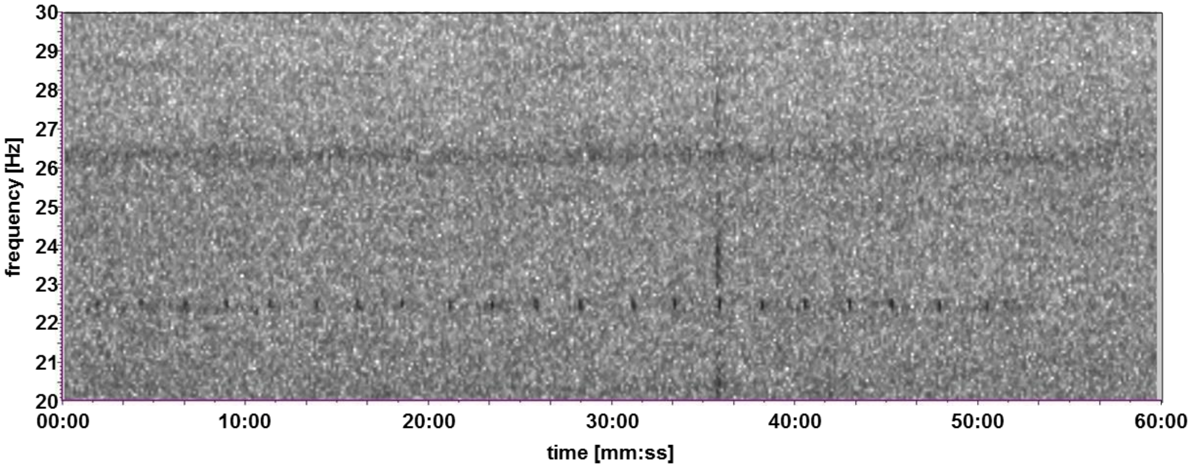

Fig. 4: *Spectrogram of unknown '22 Hz signal' (frequency of ca. 22.5 Hz, duration of 8-10 s, inter-signal intervals of ca. 2.5 minutes), recorded by SV1008 at 01 July 2012.*

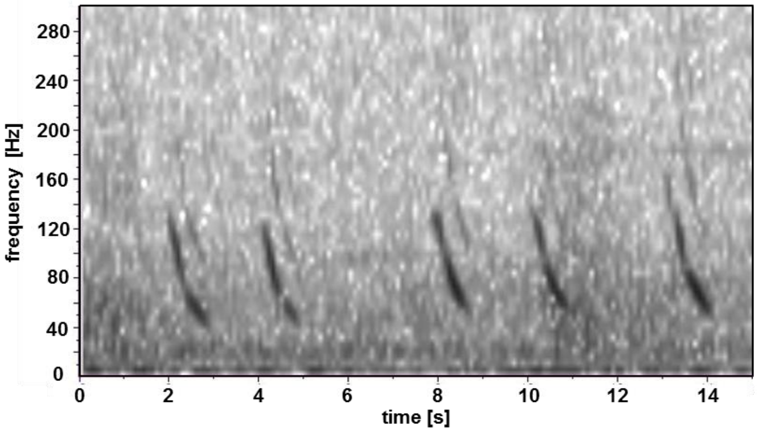

Fig. 5: *Spectrogram of unknown sound (frequency range ca. 40 – 130 Hz, duration about 1 s), recorded by SV1008 at 07 June 2012.*

Apart from cetacean vocalizations, anthropogenic sound, originating from vessels and seismic surveys, significantly shaped the acoustic environment throughout the recording period, with both vessel and seismic noise being present for more than ≥ 90% of recording days during all months (Table 2).

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

	seismic signals		**vessel noise**	
month	2011/12	2012/13	2011/12	2012/13
November	100 %	100 %	100 %	100 %
December	100 %	100 %	100 %	100 %
January	100 %	100 %	100 %	97 %
February	100 %	100 %	100 %	93 %
March	100 %	100 %	94 %	100 %
April	97 %	100 %	100 %	90 %
May	100 %	100 %	100 %	97 %
June	100 %	no data	97 %	no data
July	100 %	no data	100 %	no data
August	97 %	no data	100 %	no data

Intra- and inter-annual patterns in acoustic presence

During the study period, the acoustic presence of most baleen whale species identified exhibited both intra- and inter-annual patterns. Humpback whales were acoustically present from November 2011 to February 2012 and in May 2012 as well as from November to December 2012 and from June to August 2012 (Fig. 2). In both recording periods, humpback whales were acoustically absent from February to April. During recording period 2011/2012, fin whales were acoustically present only in November and absent from December to May (Fig. 2). In 2012/2013, they were recorded in January and from June to August in 2013 and acoustically absent from November to December and from February to March. 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. 2). Antarctic blue whales were acoustically present during the entire recording period (Fig. 3). During the recording period in 2011/2012, the number of detected Antarctic blue whale calls and the BWI were low from November until May and peaked in mid-June (Fig. 3). In 2012/13, the acoustic activity peaked first in early December, thereafter decreased from mid-December to early February when it started to increase again. The acoustic activity then increased considerably towards late May 2013.

Odontocete clicks were present from November and to March as well as from November to May during recording period 2011/2012 and 2012/2013, respectively, with peak acoustic presence in November in both years (Fig. 2).

The 22-Hz signal was recorded in November and December 2011, in December 2012 as well as from June to August 2012, with peak acoustic presence in November 2011 (Fig. 2).

For humpback whales and Antarctic blue whales, the intra-annual patterns in acoustic presence were similar in both recording periods, potentially depicting greater seasonality in the species' (acoustic) presence (Fig. 2, Fig. 3). For fin whales and Antarctic minke whale (as well as the 22 Hz signal), the pattern of acoustic presence varied inter-annually with little to no acoustic presence of the species in austral spring and summer during 2011/12, but (at least some) acoustic presence during this period in 2012/2013 (Fig. 2). Similarly, no odontocete clicks were present from April to August 2012, whereas clicks were recorded during April and May 2013, respectively.

Discussion

Ecological importance of the eastern South Atlantic Ocean

The waters off south-west Africa are greatly influenced by the Benguela Current 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 foraging for many cetacean species (Best, 2007). 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 (Harmer, 1931; Best, 2007). Also, the waters off Namibia and Angola are known to have formed an important whaling ground for sperm whales (Townsend, 1935).

Conclusions on the actual location of calling whales in this study are largely impeded by the fact that the acoustic recorders were single sensors and moored in the SOFAR channel, hence complicating estimations of the distance between calling whales and the recorder. The recorded Antarctic blue whale calls mainly comprised only the upper, loudest and hence furthest propagated Z-call unit, indicating that vocalizing individuals were likely to reside at some distance from the recording site (see Miller *et al.*, 2015). Propagation ranges of thousands of kilometers for low-frequency signals (i.e., blue or fin whale vocalizations) are most likely to be achieved when both sender and receiver of a signal are located close to the axis of the SOFAR channel (Urick, 1983; Richardson *et al.*, 1995), which is at about 800 m depth in the study area (Northrop & Colborn, 1974). Given an average baleen whale diving depth of less than 200 m (Panigada *et al.*, 1999; Acevedo-Gutiérrez *et al.*, 2002; Stewart, 2009; Friedlaender *et al.*, 2014) and an estimated maximum depth for producing low-frequency vocalizations of less than 100 m (Aroyan *et al.*, 2000; Thode *et al.*, 2000), the SOFAR channel is unlikely to enable latitudinal long-range communication of baleen whales across ocean basins (see also Jones *et al.*, 2011). However, the depth of the SOFAR channel axis decreases with increasing latitudes and reaches the sea surface at around 50°S in the Atlantic Ocean (Northrop & Colborn, 1974), potentially enabling long-range propagation of low-frequency vocalizations produced near-surface in a longitudinal direction. Antarctic blue whales vocalizing at around 50°S might therefore possibly still be detectable off Namibia, potentially providing an alternative explanation for the observed year-round acoustic presence of Antarctic blue whales.

By contrast, the odontocete clicks recorded in this study are likely detectable only over comparatively short distances due to their high directionality and frequency range (e.g., Møhl *et al.*, 2003). Hence, acoustic presence (or absence) of odontocetes likely represents their occurrence close to our recording site. Recorded odontocete click trains may potentially have originated from sperm whales, which are known to produce different types of clicks depending on behavioral context (Madsen *et al.*, 2002; Møhl *et al.*, 2003; Oliveira *et al.*, 2013) and were reported present year-round off the west coast of Africa (Townsend, 1935; Best, 2007). However, our passive acoustic data, sampled at 5,333 Hz, did not capture enough of the frequency range of sperm whale clicks (centroid frequency of 15 kHz) to allow reliable analyses (Madsen *et al.*, 2002).

The absence of a bimodal pattern in the acoustic winter presence of the four baleen whale species possibly suggests that the waters off Namibia represent the northern limit of migration in the South Atlantic Ocean, at least for separate populations of these species (see also Best, 2007). This possibly adds a new aspect to the presumed locations of humpback whale breeding grounds. For breeding stock B1, breeding grounds were reported to be located off Angola, Congo and Gabon (International Whaling Commission, 2011). Humpback whales feeding off South Africa are considered part of a separate breeding stock (B2) for which the breeding ground locations are not known (Barendse *et al.*, 2011; International Whaling Commission, 2011) and could therefore potentially be located in the vicinity of our recording site. However, baleen whale migratory routes and timing are known to differ both within and between age- and sex-classes of a population, as well as, in terms of migratory routes, between northward and southward migrations (Kellogg, 1929; Mackintosh & Wheeler, 1929; Bannister & Gambell, 1965; Brown *et al.*, 1995; Dawbin, 1997). It therefore has to be kept in mind that local, single sensor acoustic data may only represent that part of the population that occurs or passes in relative proximity of the recorder. Furthermore, inferences on the number of calling individuals in recordings from single, fixed sensors require 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 however was beyond the scope of this study. Hence, inferences on whether our data represent significant parts of baleen whale (breeding) populations or single, roaming individuals are not possible.

The seasonal pattern in acoustic presence of the 22 Hz signal resembled that of other baleen whales, indicating that this sound is potentially produced by a mysticete species. An alike signature, recorded off New Zealand, was previously attributed to Bryde's whales (*Balaenoptera brydei*) (McDonald, 2006). Bryde's whales are known to occur in the Southeast Atlantic year-round (Best, 2001) and could potentially have produced the unknown signature. Alternatively, the 22 Hz signal is similar to presumed blue whale calls recorded in the central North Pacific (Fisher-Pool *et al.*, 2015). However, without concurrent visual information it is not possible to attribute this signal to any specific source with certainty.

Temporal patterns in acoustic presence off Namibia - Evidence for (partial) migration?

Off Namibia, intra-annual variability in the acoustic presence most likely reflects decreased presence of the four baleen whale species during spring and summer, as (at least parts of) the populations leave the area to feed in higher latitude waters, and increased presence during winter for overwintering and, potentially, breeding in the South Atlantic Ocean. Furthermore, temporal patterns in the presence of odontocete clicks could possibly reflect seasonal distribution patterns of odontocetes in the waters off Namibia. However, as mentioned previously, odontocete clicks can only be detected over short distances and small scale changes in prey distribution may already drastically affect local acoustic presence (see also Whitehead, 2003; Mizroch & Rice, 2013).

Our study adds to existing evidence for partial migration in Antarctic blue and minke whales. Along with findings from the Indian Ocean (see Samaran *et al.*, 2013), the continuous acoustic presence of Antarctic blue whales off Namibia possibly indicates that some individuals skip migration to high latitudes to remain in warmer waters during summer, potentially to some extent fueled by prey available in high-productivity waters of the Benguela region and the associated high-turbulence eddy regime. These 'resident' whales have been suggested to be juvenile individuals based on catch data (Mackintosh & Wheeler, 1929). Juvenile whales with a poor body condition predominated in winter catches from 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 on the feeding grounds during austral winter, as indicated by year-round catches and acoustic presence of Antarctic blue whales in the Southern Ocean (Harmer, 1931; Hjort *et al.*, 1932; Širović *et al.*, 2004; Branch *et al.*, 2007; Širović *et al.*, 2007; Thomisch *et al.*, 2016). However, it has to be taken into consideration that a continuous acoustic presence of baleen whales off Namibia may also be caused by behavioral features other than partial migration. A wide spectrum of migratory strategies within many baleen whale species, including intra-specific differences in migratory timing, 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 (see e.g., Mackintosh & Wheeler, 1929; Brown *et al.*, 1995; Geijer *et al.*, 2016). Similarly, Antarctic minke whales were reported 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, when they were also reported to exhibit highest acoustic presence in the Southern Ocean (Van Opzeeland, 2010; Dominello & Širović, 2016).

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 individuals' life time fecundity and may occur most frequently under stochastic environmental conditions associated with a high risk of mortality during migration (Shaw & Levin, 2011). Mainly female individuals are thought to benefit from skipping migration (Lockyer, 1984; Brown *et al.*, 1995). However, our recordings contained (partial) song sequences of Antarctic blue whales, fin whales and humpback whales, which are 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 understood yet, 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 breeding grounds and seasons (e.g., Norris *et al.*, 1999; Clark & Ellison, 2004; Širović *et al.*, 2013; Risch *et al.*, 2014a; Thomisch *et al.*, 2016). In-depth analyses of baleen whale vocalizations, e.g. unraveling acoustic characteristics and patterns in sound production, were however beyond the scope of the present study, but are planned for the near future to provide further insights into the (acoustic) ecology of the species in temperate waters off Namibia.

Conclusion

Our study highlights the importance of the eastern South Atlantic Ocean as a potential breeding, overwintering and feeding habitat for different large cetacean species and adds to increasing evidence that partial, rather than complete, migration is a common feature of many migratory species, including baleen whales. In particular for Antarctic blue whales, our results, along with previous findings, expand the concept of 'low-frequency breeding [partial] migrations', where non-migrating individuals are thought to forego reproduction in favor of increased life-time fecundity (e.g., Shaw & Levin, 2011). The simultaneous acoustic presence of Antarctic blue whales in both high- and low-latitude waters year-round (Širović *et al.*, 2004; Branch *et al.*, 2007; Samaran *et al.*, 2013; Thomisch *et al.*, 2016, present study) likely represents the presence of reproductively active males and may hence indicate the occurrence of mating or other behaviors related to reproduction outside the presumed breeding areas and season (see also Clark & Clapham, 2004).

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, gas and oil exploration (Weir & Pierce, 2013). In this context, 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. Furthermore, further in-depth analyses on noise level patterns are required to assess potential effects of the quasi-continuous presence of anthropogenic noise on cetaceans off Namibia.

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Publication VI:

Temporal shifts in the vocalization frequency of Antarctic blue whales in the Atlantic sector of the Southern Ocean and the South Atlantic Ocean

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Manuscript in preparation

Title: Temporal shifts in the vocalization frequency of Antarctic blue whales in the Atlantic sector of the Southern Ocean and the South Atlantic Ocean

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Abstract

In this study, we present preliminary results on temporal patterns in the peak vocalization frequency of Antarctic blue whales (*Balaenoptera musculus intermedia*) based on passive acoustic recordings from the Atlantic sector of the Southern Ocean and recordings collected off Namibia in the South Atlantic Ocean. Our results show an inter-annual decline in the peak frequency of single Z-calls and the Antarctic blue whale chorus at all recording sites. The decline in peak vocalization frequency of the Antarctic blue whale chorus ranged between 0.114 and 0.131 Hz year^{-1}. These rates are lower than those reported in previous studies, possibly reflecting spatial differences or a temporal deceleration in the inter-annual decline of the Antarctic blue whale vocalization frequency. Intra-annually, the peak vocalization frequency showed a sinusoidal pattern in the Atlantic sector of the Southern Ocean, in line with findings from waters off eastern Antarctica and western Australia. An intra-annual trend was not evident in the recordings from waters off Namibia. However, the omnipresent anthropogenic broad-band noise in these recordings impeded further conclusions on whether the lack of an intra-annual pattern is an actual characteristic of the vocal behavior of Antarctic blue whales at this low-latitude recording site. Further work will involve the analysis of potential temporal patterns in the peak frequency of other marine mammal species' vocalizations and of an anthropogenic sound source and is expected to provide an important basis for refining our understanding of the potential drivers of temporal shifts in the vocalization frequency of Antarctic blue whales.

Introduction

Antarctic blue whale (*Balaenoptera musculus intermedia*) Z-calls were recorded in high-, mid- and low-latitude waters year-round (e.g. Širović *et al.*, 2004; Samaran *et al.*, 2013; Thomisch *et al.*, 2016; Thomisch *et al.*, in preparation) and have been found to exhibit both inter- and intra-seasonal variations in their peak frequency at different recording sites (Gavrilov *et al.*, 2012; Miller *et al.*, 2014). Inter-annually, the peak vocalization frequency of Antarctic blue whales showed a steady decline of > 0.1 Hz per year both in temperate and polar waters. The factor(s) driving this steady decrease are not understood to date and several hypotheses for the decline have been proposed. McDonald *et al.* (2009) suggested post-whaling population recovery associated with changes in sexual selection and vocal behavior to be the most likely explanation for the observed decline. Increasing blue whale population densities may have led to a change in sexual selection pressure on males by altering the tradeoff between the ability to be heard over great distances, represented by the calls' amplitude, and the ability to produce sounds at a low pitch, i.e. the vocalization frequency (McDonald *et al.*, 2009). Other hypotheses concern a potential post-whaling increase in whale body size, global warming, increasing ocean noise levels as well as interference from other animal sounds (McDonald *et al.*, 2009).

Intra-annually, the vocalization frequency time series has been shown to exhibit a sinusoidal seasonal pattern (Gavrilov *et al.*, 2012; Miller *et al.*, 2014). The peak vocalization frequency declined over the course of the season, but showed an increase at the beginning of the following season to approximately meet the mean peak vocalization frequency of the previous year (Gavrilov *et al.*, 2012; Miller *et al.*, 2014). Intra-annual shifts in the Antarctic blue whale vocalization frequency are also not fully understood to date. Factors proposed to (partially) account for the intra-annual patterns include the Doppler effect as well as gradual changes in body condition or vocalization depths over the course of a season (Gavrilov *et al.*, 2012; Miller *et al.*, 2014).

Comparing concurrently collected data from low, mid and high latitudes represents a promising approach to explore the ubiquitousness and synchronicity of temporal variations in the peak vocalization frequency of Antarctic blue whales among their habitats at both high and low latitudes. Here, we investigate the temporal patterns in the Antarctic blue whale peak vocalization frequency based on individual Z-calls and the chorus from passive acoustic data collected between 2008 and 2013. These data were recorded in both coastal and oceanic waters of the Atlantic sector of the Southern Ocean as well as at one oceanic location off Namibia, South Atlantic Ocean.

Methods

Data collection

Passive acoustic data were collected by 14 autonomous recording devices that were deployed at six locations within the Weddell Sea and at one location in the South Atlantic Ocean off Namibia (Fig. 1). Most of the recording devices were attached to oceanographic deep-sea moorings of the Hybrid Antarctic Float Observation System (HAFOS) and one (MARU recorder) was a self-contained lander. Furthermore, the Perennial Acoustic Observatory in the Antarctic Ocean (‘PALAOA’), representing the southernmost recording site, collects passive acoustic data from a coastal Antarctic underwater environment (Fig. 1, Table 1) (Boebel *et al.*, 2006; Rettig *et al.*, 2013; Thomisch *et al.*, 2016). The study period ranged from January 2008 to December 2013 (see Table 1) for details on recording sites, deployment and recording periods).

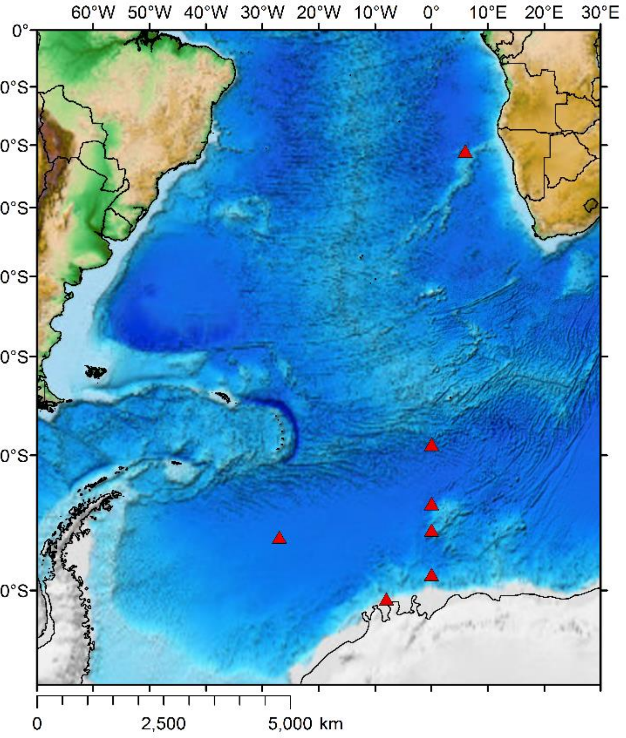

Fig. 1: *Overview of recording positions in the Atlantic sector of the Southern Ocean and in the South Atlantic Ocean off Namibia. Map was created using the ETOPO1 global relief model map provided by the NOAA National Centers for Environmental Information, NCEI (based on dataset of Amante & Eakins, 2009), and the World Countries Basemap by Esri, DeLorme Publishing Company, CIA World Factbook.*

In the oceanic areas, passive acoustic data were collected by two types of acoustic recording devices: SonoVaults (manufactured by Develogic GmbH, Hamburg, Germany) (Rettig *et al.*, 2013) and AURALs (Autonomous Underwater Recorder for Acoustic Listening - Model 2, manufactured by Multi-Electronique (MTE) Inc., Rimouski, Quebec, Canada) (e.g., Simard *et al.*, 2008) and a MARU (Marine Acoustic Recording Unit, contributed by the Bioacoustic Research Program, Cornell University, Ithaca, NY, USA) (e.g., Parks *et al.*, 2009). Due to recorder-specific constraints of deployment depth, battery life and data storage capacities, the acoustic recorders were moored at different depths and set to different duty cycles (Table 1) (Rettig *et al.*, 2013). Passive acoustic data were stored in 5 and 4.5 minute files (AURAL recorders), in 10 minute files (SonoVault systems) and in 6 minute files (MARU device). MARU recordings were however excluded from further analyses due to the occurrence of broad-band noise, which may have biased frequency measurements.

In the coastal Antarctic environment, PALAOA collects continuous underwater recordings from a coastal Antarctic environment since 2005 with a Reson TC4032 hydrophone, deployed at approximately 160 m depth (Boebel *et al.*, 2006; Kindermann *et al.*, 2008; Klinck *et al.*, 2016). Data were stored in 1 minute files. Early phase PALAOA data, i.e. prior to 2008, were excluded from further analyses here due to the frequent changes in the recording parameters, which affected the frequency measurements.

Table 1: Locations and recording parameters of passive acoustic recorders deployed in the Atlantic sector of the Southern Ocean and in the South Atlantic Ocean off Namibia. Recording sites are assigned with IDs representing the geographic location by a combination of letters (for offshore recording positions in the Atlantic sector of the Southern Ocean, 'G' and 'W' indicate a recording site on the Greenwich meridian and in the inner Weddell Sea, respectively and numbers roughly reflecting the recording sites' latitudinal position; 'PALAOA' and 'NAM' indicate the positions of the PALAOA observatory and off Namibia, respectively); sampling scheme is given in sampling duration [min] per sampling interval [min]; correction factor f indicates the recorder-specific factor used to extrapolate the number of hours with FM-call presence in subsampled recordings to an assumed continuous recording scheme.

Recording site ID	Latitude	Longitude	Recorder ID	Deployment period	Depl. depth [m]	Sampl. freq. [kHz]	Sampling scheme [min]/[min]	Corr. factor *f*	Analysed period [months]
G59	59 10.03 S	000 00.17 E	MARU01	12/2008-12/2009	4838	2.00	6/60	1	12
	59 03.02 S	000 06.63 E	AWI227-11 SV0002	12/2010-12/2012	1007	5.33	continuous	-	8
	59 02.63 S	000 04.92 E	AWI227-12 SV1025	12/2012-12/2014	1020	5.33	continuous	-	7
G64	63 59.56 S	000 02.65 W	AWI229-09 SV1000	12/2010-12/2012	969	5.33	continuous	-	6
	63 59.66 S	000 02.65 W	AWI229-10 SV1010	12/2012-12/2014	969	5.33	continuous	-	8
G66	66 01.13 S	000 04.77 E	AWI230-06 AU0085	03/2008-12/2010	189	32.77	5/240	4	34
	66 01.90 S	000 03.25 E	AWI230-07 SV1001	12/2010-12/2012	934	5.33	continuous	-	21
	66 02.12 S	000 02.98 E	AWI230-08 SV1009	12/2012-12/2014	949	5.33	continuous	-	9
G69	68 59.74 S	000 00.18 E	AWI232-09 AU0086	03/2008-12/2010	206	32.77	5/240	4	34
	68 59.86 S	000 06.51 W	AWI232-11 SV1011	12/2012-12/2014	958	5.33	continuous	-	11
W66	66 36.70 S	027 07.31 W	AWI209-06 AU0086	12/2010-01/2013	207	32.77	4.5/180	3	24
PALAOA	70 31' S	008 13' W	PALAOA	12/2005-ongoing	160	192	continuous	-	67
NAM	20 57.90' S	005 58.82' E	AWI247-02 SV1008	11/2011-11/2012	741	5.33	continuous	-	9
	20 58.54' S	005 59.07' E	AWI247-03 SV1019	11/2012-11/2014	736	5.33	continuous	-	6

Data analysis

Antarctic blue whale Z-calls typically consist of three units, comprising a tonal unit at 26-28 Hz of 8-12 s duration (unit A), a downsweep of 1-2 s to about 19 Hz (unit B) and a slightly frequency-modulated unit at 20-18 Hz of 8-12 s duration (unit C), although also 1-unit or 2-unit calls have been recorded (Ljungblad et al., 1998; Rankin et al., 2005). With increasing distance from the recording site, vocalizations produced by distant Antarctic blue whales deteriorate into a tonal 'chorus' within the 26-28 Hz frequency band (Gedamke et al., 2007), which can serve as an alternative measure of Antarctic blue whale (acoustic) presence in an area (Thomisch et al., 2016).

Prior to analyses, passive acoustic data were downsampled (including an antialiasing finite impulse response lowpass filter) to a uniform sampling rate of 250 Hz for all recorder types. The procedure applied by Gavrilov et al. (2012) and Miller *et al.* (2014), which focused on the Antarctic blue whale chorus (i.e. representing Z-call unit A), was expanded in the present study by incorporating both unit A and unit C of Antarctic blue whale chorus and individual Z-call detections. Regarding the Antarctic blue whale chorus, Power Spectral Densities (PSDs) were calculated for each (downsampled) file over the entire, recorder-specific, file duration (FFT of 16,384, resulting in a frequency resolution of 0.02 Hz). For each file, the peak frequency was determined within the frequency ranges of 25 <= f <= 29 Hz (representing unit

A) and 17 <= f <= 21 Hz (representing unit C). Additionally, peak frequencies were determined for individual Antarctic blue whale Z-calls. Z-calls were automatically detected in the downsampled recordings via spectrogram correlation (e.g., Mellinger & Clark, 2000), using the detection procedure described in Thomisch et al. (2016). PALAOA files, originally stored as files of 1 min duration, were merged to 10 minute files prior to Z-call detection to compile a uniform data set. Peak frequencies were determined from PSDs over the duration of each individual Z-call detection within the frequency ranges of 25 <= f <= 29 Hz and 17 <= f <= 21 Hz.

Time series of daily mean peak frequencies for Z-call unit A and C were calculated for both individual Z-calls and chorus. From these, annual mean vocalization frequencies were calculated for each recording year of each recording device. Inter-annual trends in the vocalization frequencies were calculated by linear regression analysis. For recorders deployed in November or December, mean vocalization frequencies of the deployment year were however excluded from regression analysis, as they base on only one or two months of recordings. Furthermore, linear regression analyses were only performed for the data set from a particular recording site when annual mean values from at least three years were available. This applies to the data sets collected at G66, at G69 and by PALAOA.

Results

Inter-annual patterns in peak vocalization frequency of Antarctic blue whales

In the Atlantic sector of the Southern Ocean, passive acoustic data from all recording sites (i.e. from G59, G64, G66, G69, W66 and PALAOA) showed an inter-annual trend with decreasing vocalization frequencies in unit A (25-29 Hz frequency range) in both individual Z-calls and chorus over time (Fig. 2, Fig. 3, Fig. 4, Fig. 5, Table 2). At G66, the peak frequency of unit A decreased at an almost equal rate in Z-calls (0.132 Hz year^{-1}) and chorus (0.131 Hz year^{-1}) (Fig. 3, Fig. 4, Table 3). At G69, the peak frequency of unit A decreased by 0.140 Hz year^{-1} and 0.129 Hz year^{-1} in Z-calls and chorus, respectively (Fig. 3, Fig. 4, Table 3). In passive acoustic recordings of PALAOA, the vocalization frequency of unit A declined at a rate of 0.134 Hz year^{-1} in individual Z-calls and by approx. 0.114 Hz year^{-1} in the Antarctic blue whale chorus (Fig. 5, Table 3).

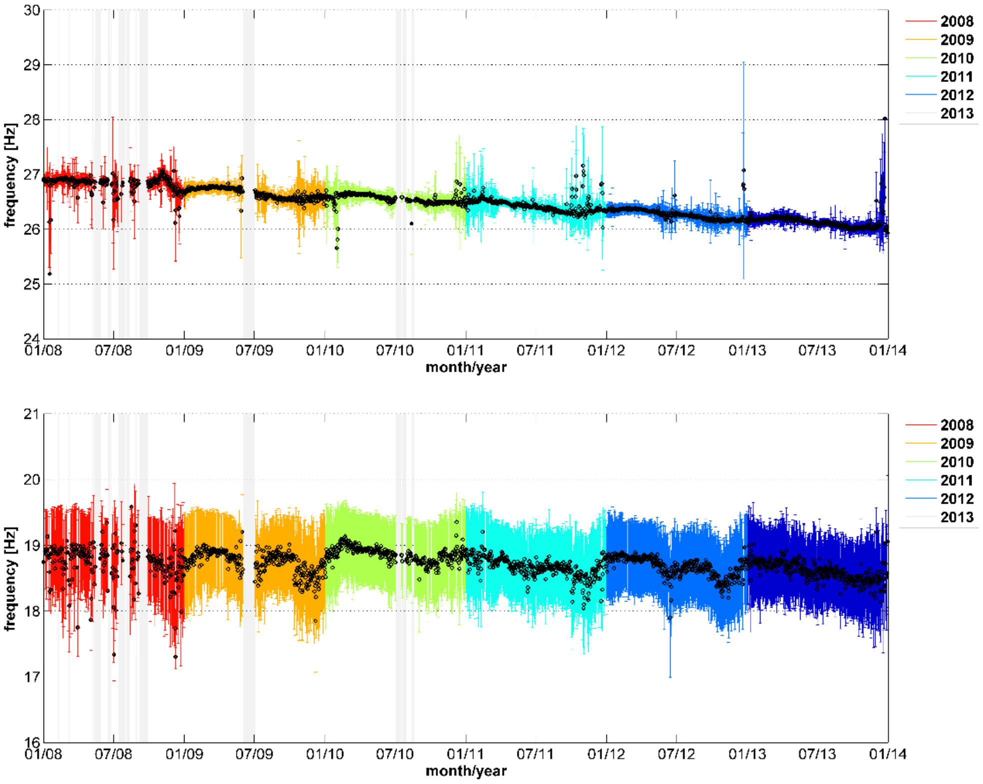

Fig. 2: *Temporal patterns in peak frequency of unit A (25-29 Hz; upper panel) and unit C (17-21 Hz; lower panel) of single Z-call detections from passive acoustic data recorded by PALAOA from 2008 to 2013. Daily mean values are indicated by black dots and standard deviations are color-coded representing different years. See Supplement Fig. S 1 for temporal patterns in peak frequency of Antarctic blue whale chorus recorded at PALAOA.*

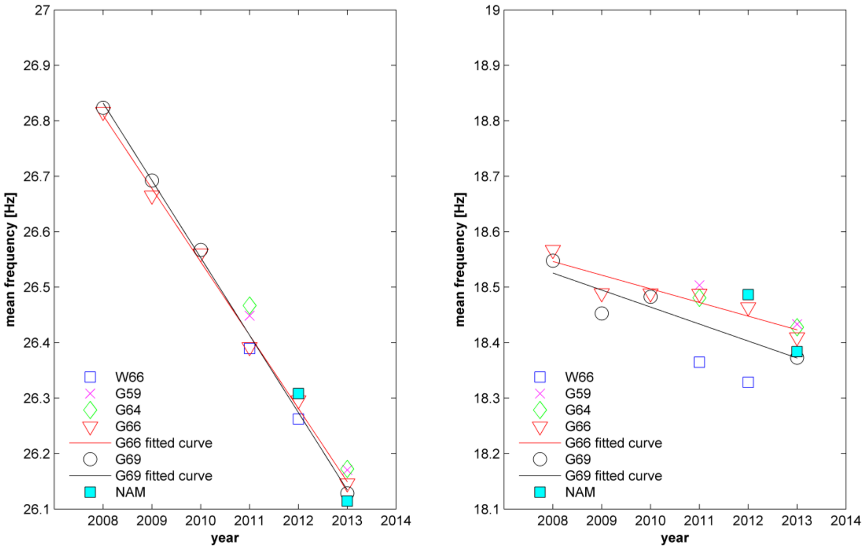

Fig. 3: *Inter-annual shift of mean frequencies of unit A (left panel) and unit C (right panel) of Antarctic blue whale Z-calls in passive acoustic data recorded in the Weddell Sea (W66), along the Greenwich meridian (G59, G64, G66 and G69) and South Atlantic Ocean (NAM) between 2008 and 2013. Recorder IDs indicate deployment positions according to Table 1. Markers indicate annual mean vocalization frequencies, lines indicate linear regressions for data sets from G66 and G69.*

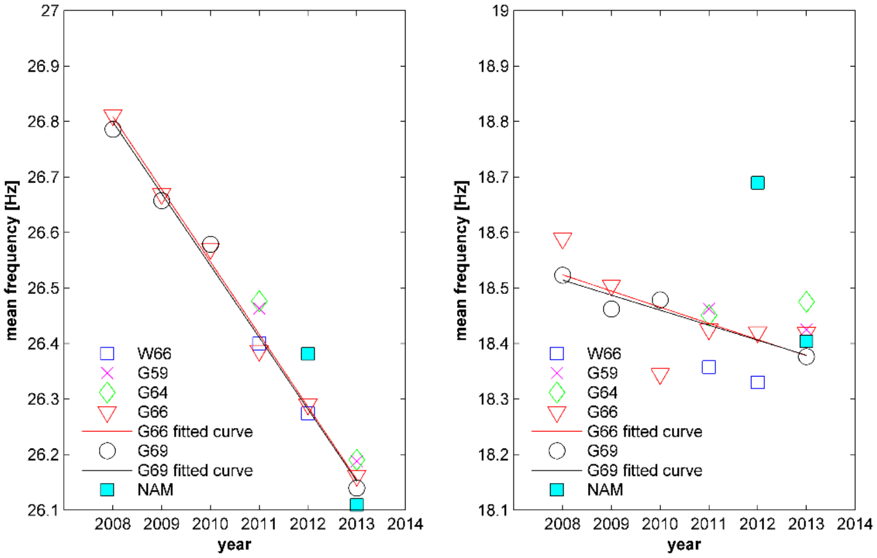

Fig. 4: *Inter-annual shift of mean frequencies of unit A (left panel) and unit C (right panel) of Antarctic blue whale chorus in passive acoustic data recorded in the Weddell Sea (W66), along the Greenwich meridian (G59, G64, G66 and G69) and South Atlantic Ocean (NAM) between 2008 and 2013. Recorder IDs indicate deployment positions according to Table 1. Markers indicate annual mean vocalization frequencies, lines indicate linear regressions for data sets from G66 and G69.*

For unit C (17-21 Hz frequency range), the peak vocalization frequency seemed to show a slight inter-annual decline at G59, G64 (at this site only for individual Z-calls), G66, G69 and W66 for both individual Z-calls and chorus (Fig. 3, Fig. 4, Table 2, Table 3). At G66 and G69, the peak frequency for both individual Z-calls and chorus decreased at a rate ca. 0.03 year^{-1}. At PALAOA, the peak frequency of unit C decreased by about 0.032 Hz year^{-1} for individual Z-call detections. In contrast, linear regression analysis suggested an overall increase of Antarctic blue whale chorus unit C by ca. 0.008 Hz year^{-1} at PALAOA, but a clear inter-annual pattern was not evident (Fig. 5, Table 3).

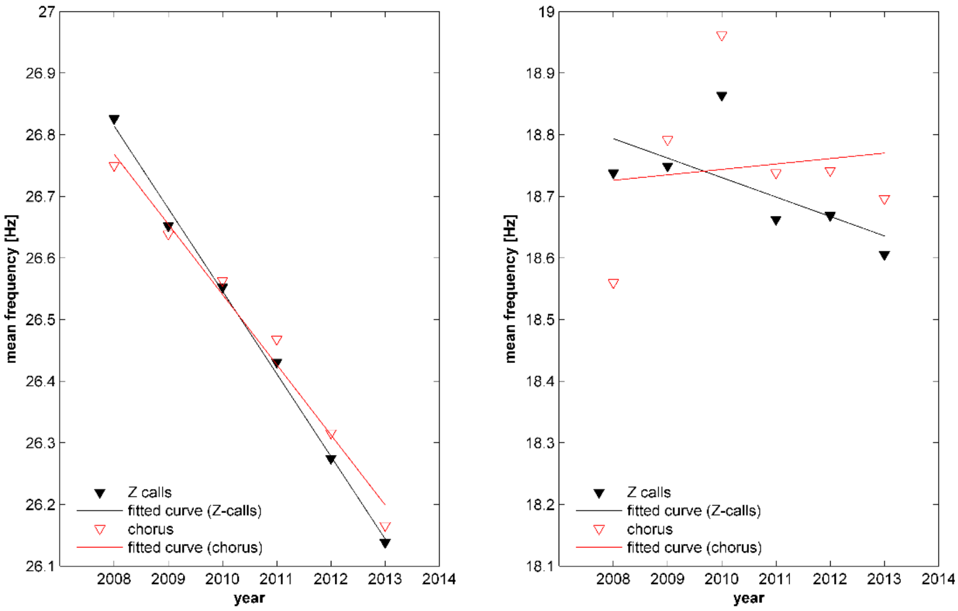

Fig. 5: *Inter-annual shift of mean frequencies of unit A (left panel) and unit C (right panel) of ABW Z-calls (black lines and markers) and chorus (red lines and markers) in passive acoustic data recorded by PALAOA between 2008 and 2013.*

In passive acoustic data collected off Namibia, unit A and C of both individual Z-calls and chorus seemed to decrease between years, however only two years of passive acoustic data were available from this location (Fig. 3, Fig. 4, Table 2).

Table 2: Annual mean peak vocalization frequencies [Hz] of unit A (25-29 Hz range, upper part of table) and unit C (17-21 Hz range, lower part of table) of individual Z-call detections and chorus of Antarctic blue whales in passive acoustic data sets recorded in the Atlantic sector of the Southern Ocean and in the South Atlantic Ocean. Recording site IDs are given according to Table 1.

		Z-CALLS							CHORUS						
	year	**W66**	**G59**	**G64**	**G66**	**G69**	**PALAOA**	**NAM**	**W66**	**G59**	**G64**	**G66**	**G69**	**PALAOA**	**NAM**
unit A (25-29 Hz)	2008				26.82	26.82	26.83					26.81	26.79	26.75	
	2009				26.67	26.69	26.65					26.67	26.66	26.64	
	2010				26.56	26.57	26.55					26.57	26.58	26.56	
	2011	26.39	26.45	26.47	26.39		26.43		26.40	26.46	26.48	26.39		26.47	
	2012	26.26			26.30		26.28	26.31	26.27			26.29		26.32	26.38
	2013		26.17	26.17	26.15	26.13	26.14	26.11		26.19	26.19	26.16	26.14	26.17	26.11
	year	**W66**	**G59**	**G64**	**G66**	**G69**	**PALAOA**	**NAM**	**W66**	**G59**	**G64**	**G66**	**G69**	**PALAOA**	**NAM**
unit C (17-21 Hz)	2008				18.57	18.55	18.88					18.59	18.52	18.68	
	2009				18.49	18.45	18.91					18.50	18.46	18.92	
	2010				18.49	18.48	19.03					18.35	18.48	19.16	
	2011	18.36	18.50	18.48	18.49		18.84		18.36	18.46	18.45	18.43		18.97	
	2012	18.33			18.46		18.82	18.49	18.33			18.42		18.88	18.69
	2013		18.43	18.43	18.41	18.37	18.75	18.38		18.43	18.48	18.42	18.38	18.90	18.40

Table 3: Inter-annual trends in peak vocalization frequencies (‘PVF’) within unit A (25-29 Hz) and unit C (17-21 Hz) of individual Z-call detections and chorus of Antarctic blue whales in passive acoustic data sets from PALAOA, G66 and G69.

		Z-call unit A (25-29 Hz)		Z-call unit C (17-21 Hz)	
metric	**recording site**	**annual mean change in PVF (Hz)**	**95% confidence intervals (Hz)**	**annual mean change in PVF (Hz)**	**95% confidence intervals (Hz)**
Z-CALLS	PALAOA	-0.134	[-0.146, -0.122]	-0.032	[-0.082, 0.019]
	G66	-0.132	[-0.143, -0.121]	-0.025	[-0.040, -0.009]
	G69	-0.140	[-0.154, -0.125]	-0.031	[-0.072, 0.011]
CHORUS	PALAOA	-0.114	[-0.137, -0.093]	0.008	[-0.088, 0.1052]
	G66	-0.131	[-0.144, -0.117]	-0.029	[-0.077, 0.019]
	G69	-0.129	[-0.166, -0.093]	-0.027	[-0.053, -0.001]

Intra-annual patterns in peak vocalization frequency of Antarctic blue whales

At all recording sites in the Atlantic sector of the Southern Ocean, intra-seasonal patterns in peak vocalization frequency were evident in unit A of both individual Z-calls and chorus. Generally, the peak vocalization frequency of unit A of both Z-calls and chorus was at its maximum within the first quarter of the year, then decreased gradually and reached its minimum between July and November, after which it started to increase again in most years (Fig. 2, Fig. 6, see also Supplement Fig. S 1). The peak frequency of unit C showed a similar intra-annual pattern at G59, G64 and W66, increasing during the first quarter of the year, peaking between March and May and decreasing afterwards (see Supplement Fig. S 2). At G66, G69 and PALAOA, the peak frequency of unit C generally decreased over the course of the year, although the intra-annual pattern was less distinct at these recording sites.

Off Namibia, no clear intra-seasonal pattern was evident in the peak vocalization frequency of unit A and C of individual Z-calls and chorus (see Supplement Fig. S 3 and Fig. S 4).

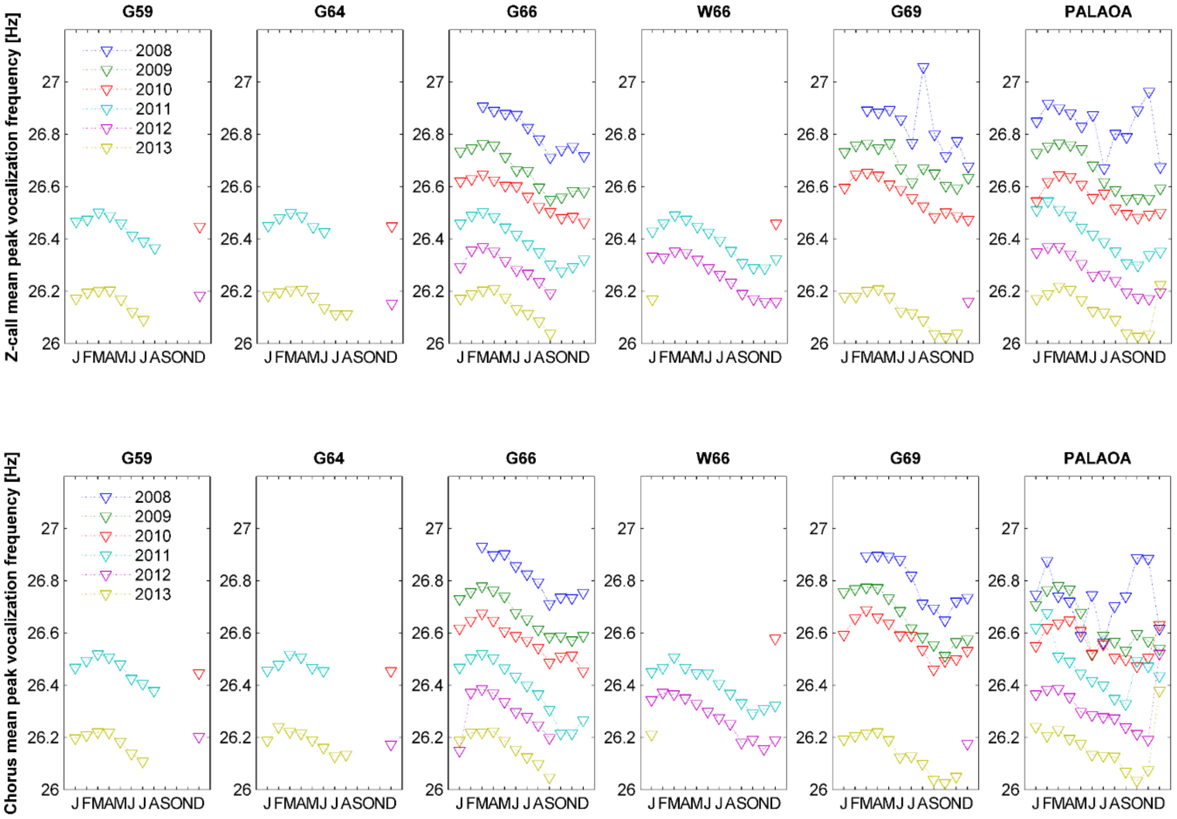

Fig. 6: *Intra-annual patterns in monthly mean frequencies of unit A of individual Z-calls (upper panel) and chorus (lower panel) of Antarctic blue whales in passive acoustic data recorded at different recording sites between 2008 and 2013. Recording years are color-coded and recorder IDs indicate deployment positions according to Table 1.*

Discussion

In the present study, the peak vocalization frequency of Antarctic blue whales was found to exhibit inter- and intra-annual patterns in both call unit A (25-29 Hz frequency range) and call unit C (17-21 Hz frequency range) at most recording locations in the Weddell Sea and the South Atlantic Ocean in both single Z-calls and Antarctic blue whale chorus. Previously, the high variability in the vocalization frequency among single Z-calls of individual whales has been considered to impede analyses on temporal shifts in the vocalization frequency of Antarctic blue whales based on single Z-calls (see Gavrilov *et al.*, 2012; Miller *et al.*, 2014). Our study has nevertheless shown that both single Z-calls and chorus are suitable to investigate temporal patterns in the Antarctic blue whale vocalization frequency, at least at large temporal scales, such as months or years.

An inter-annual decline in the vocalization frequency applying to both unit A and unit C of single Z-calls and chorus was evident at almost all recording locations. However, the decreasing trend in the peak frequency of unit C was weaker and less pronounced than for unit A, which may partly be due to the larger band width of unit C in contrast to the more tonal unit A (see e.g. Ljungblad *et al.*, 1998). The observed annual rates of decline in frequency of unit A of the Antarctic blue whale chorus during the period from 2008 to 2013 (i.e. -0.114 Hz year^{-1}, -0.131 Hz year^{-1} and -0.129 Hz year^{-1} at PALAOA, G66 and G69, respectively) are lower than the decrease rates reported by McDonald *et al.* (2009) and Gavrilov *et al.* (2012). These authors reported annual rates of ca. -0.145 Hz year^{-1} from 1995 to 2005 (McDonald *et al.*, 2009) and of -0.135 Hz year^{-1} from 2002 to 2010 (Gavrilov *et al.*, 2012). These findings may indicate large-scale geographical differences in the annual rates of decline in the peak vocalization frequency, as have been reported to occur between (acoustic) blue whale populations (McDonald *et al.*, 2009). Annual rates of decrease ranged from 0.07 Hz year^{-1} in blue whale calls recorded in the Southeast Indian Ocean to 0.56 Hz year^{-1} to those recorded in the Northern Indian Ocean (McDonald *et al.*, 2009). On a smaller scale, the hypothesis of spatial variations in the peak vocalization frequency decline might be supported by the observation that the annual rate of decrease also varied between different recording positions of the present study. Alternatively, or in addition, the results of the present study may indicate that the rate of decrease is currently decelerating, although prolonged time series of frequency measurements are required to substantiate this hypothesis. Further insights on long-term inter-annual patterns in the Antarctic blue whale vocalization frequency may be obtained from passive acoustic data collected by recorders that are currently deployed in the Atlantic sector of the Southern Ocean and scheduled for recovery in 2016/17.

In the Atlantic sector of the Southern Ocean, the intra-annual pattern in the vocalization frequency of Antarctic blue whales was in accordance with the patterns observed in temperate waters off Australia (Gavrilov *et al.*, 2012) and in polar waters off eastern Antarctica (Miller *et al.*, 2014). The lack of a discernible intra-annual pattern in the peak calling frequency of Antarctic blue whales off Namibia may indicate that the factor (or factors) causing the intra-annual shifts at high and mid latitudes is not present in warm, low-latitude waters. However, the predominance of anthropogenic noise (such as shipping noise and seismic explorations), which was omnipresent in the passive acoustic recordings (Thomisch *et al.*, in preparation), may have at least partly blurred potential intra-annual frequency shifts of the Antarctic blue whale vocalizations.

Several factors have been proposed to cause or contribute to the observed inter- and intra-annual changes in the peak vocalization frequency of Antarctic blue whales. Below, the most important hypotheses on these temporal shifts are summarized and evaluated based on the present study's results where possible.

Population recovery

McDonald *et al.* (2009) hypothesized that the overall inter-annual decrease in the vocalization frequency might be mediated by a post-whaling recovery of the blue whale populations. The recovery may result in a decreased need to communicate over long distances, affecting the tradeoff in sexual selection between amplitude and pitch of a call or song. As a consequence, males may switch to lower vocalization frequencies over time at the cost of a lower source level and lower propagation ranges of the calls (McDonald *et al.*, 2009). The Antarctic blue whale population has been estimated to recover from whaling at an annual rate of approximately 7.4% (Branch *et al.*, 2004). Recent passive acoustic studies indicate a wide distribution of Antarctic blue whales throughout the Weddell Sea (Thomisch *et al.*, 2016; Thomisch *et al.*, in prep.). This is in accordance to the former, wide Antarctic blue whale distribution range indicated by whaling data, but contrasts with the narrow distribution range observed in post-whaling visual surveys (Branch *et al.*, 2007). The post-whaling contraction of the Antarctic blue whale distribution range has been hypothesized to be an effect of the reduced animal density (Branch *et al.*, 2007). In this context, the recent observation of a wide distribution range based on passive acoustic data from the Weddell Sea may provide indirect evidence of a recovery of the Antarctic blue whale population (see Thomisch *et al.*, 2016). However, if and how a population recovery may affect male Antarctic blue whale vocal behavior remains yet to be verified.

Ambient noise levels

In vocalizing animal species, shifts in the calling frequencies have also been suggested to reflect responses to environmental conditions, such as increasing ambient noise levels (e.g. Brumm & Slabbekoorn, 2005; Slabbekoorn & Ripmeester, 2008). Bird species in urban environments have been shown to raise the frequency of their song, presumably to prevent acoustic masking by increasing urban noise levels (Slabbekoorn & Ripmeester, 2008). In the marine realm, increased ambient noise levels, e.g. due to shipping or airgun signals, are considered to potentially entail changes in the vocal characteristics of baleen whales, including increasing call amplitudes (e.g. Holt *et al.*, 2009; Parks *et al.*, 2011) and decreasing vocalization frequencies (Castellote *et al.*, 2012) under elevated noise conditions. The center frequency of fin whales song notes was negatively correlated to background noise levels (Castellote *et al.*, 2012), possibly supporting McDonald *et al.* (2009) who suggested increasing ocean noise levels to contribute to the decline in blue whale vocalization frequency. However, a decrease in the vocalization frequency is likely to be related to higher energetic costs of signal production or decreased source levels. This contrasts with the assumption that call source levels should be raised in order to compensate for increasing noise levels (see also McDonald *et al.*, 2009). The hypothesis of a negative correlation between baleen whale peak vocalization frequency and ambient noise levels is potentially further challenged by observations on intra-annual patterns of both metrics. Intra-annual patterns in the Antarctic blue whale peak vocalization frequency seem to correspond to seasonal fluctuations in ambient noise levels (Thomisch *et al.*, 2015; Menze *et al.*, 2017), hence possibly indicating a positive correlation between these two metrics. Future work will further explore this potential interrelation by analyzing seasonal fluctuations in ambient noise levels at all recording sites of the present study.

Ocean acidification and global warming

Global change has been hypothesized to contribute to the observed inter-annual long-term decline in blue whale peak vocalization frequency (McDonald *et al.*, 2009; Sehgal *et al.*, 2010). Both global warming and ocean acidification have the potential to alter the propagation characteristics of a sound. Increasing global temperatures cause higher average sound velocities and increasing ocean acidification is associated with a decreasing attenuation of a signal by absorption, both possibly causing a decline in the signal's peak frequency (McDonald *et al.*, 2009). However, McDonald *et al.* (2009) assumed the potential changes in a signal's frequency related to global warming and ocean acidification to be too small to account for the observed temporal patterns in the blue whale vocalization frequency. In contrast, modelling results of Sehgal *et al.* (2010) indicated that ocean acidification could be a major contributor to the long-term decline in blue whale peak vocalization frequency. Future modeling of sound propagation characteristics in the Weddell Sea may provide a basis to further explore potential correlations between Antarctic blue whale peak frequencies, sound propagation characteristics and oceanographic conditions in the Atlantic sector of the Southern Ocean. Furthermore, future work will involve analyses of signals produced by a known artificial sound source as well as by other species. Temporal patterns in the peak frequency of moored, oceanographic (RAFOS) sound sources will be examined. These sound sources are deployed at several location within the Weddell Sea HAFOS array and produce tonal signals at ca. 260 Hz. Analyzing the signals of an artificial sound source will help to reveal whether external abiotic factors might possibly cause or contribute to the observed temporal patterns in Antarctic blue whale vocalization frequency. In terms of other species, further planned analyses will involve fin whales and leopard seals, which are acoustically present in the Atlantic sector of the Weddell Sea and, in case of fin whales, also in the South Atlantic Ocean. These future analyses will aid exploring whether inter- and intra-annual changes are unique to Antarctic blue whales or whether such shifts occur in other species as well.

Variations in calling depths

The calling depths of Antarctic blue whales have been hypothesized to gradually change over the course of a season. Such changes might result in intra-annual shifts in the peak vocalization frequency of the whales, given that the resonance frequency of a whale body is considered to decline at decreasing diving depths (Gavrilov *et al.*, 2011; Gavrilov *et al.*, 2012). Gavrilov *et al.* (2011) outlined that a resonance frequency of 24 Hz of a body at 25 m depth would drop to 23 Hz at 23.3-23.5 m depth. Hence, the observed intra-annual pattern in the peak vocalization frequency could be explained by slight changes in the diving depth of vocalizing Antarctic blue whales over the course of season, possibly due to changes in the water temperature or blubber mass (Gavrilov *et al.*, 2012). However, it remains yet to be verified whether such seasonal changes in diving depth occur in Antarctic blue whales.

Body condition

Miller *et al.* (2014) suggested that the intra-annual trend may partly be mediated by changes in the body composition of the Antarctic blue whale individuals present on the high-latitude feeding grounds. Miller *et al.* (2014) pointed out that the intra-annual variations in the peak frequencies of Antarctic blue whales vocalizations are loosely correlated to the assumed migration of Antarctic blue whales to and from the Southern Ocean. Furthermore, for small males (<19 m length), they found a positive correlation between the monthly measurements of blubber thickness of whales caught in the Southern Ocean (as reported by Mackintosh & Wheeler, 1929) and monthly variations in the peak vocalization frequency (as reported by Miller *et al.*, 2014). These findings might indicate that the intra-annual increase in peak frequency during austral summer reflects improving body conditions of smaller males migrating to and foraging on the feeding grounds (Miller *et al.*, 2014). However, a correlation between blubber thickness and vocalization frequency was absent in larger (>23 m) males (Miller *et al.*, 2014). In this context, it also remains to be verified if these smaller males are the individuals that produce the Z-calls and the Antarctic blue whale chorus exhibiting the intra-annual variation. Antarctic blue whale Z-calls are often produced in repetitive song patterns (Širović *et al.*, 2004), which are presumed to reflect a reproductive display of, presumably reproductively active, male blue whale individuals (Oleson *et al.*, 2007). Male Antarctic blue whales are thought to reach sexual maturity at a length of 22 m (Sears & Perrin, 2009). In turn, smaller, possibly immature, subadult males may not necessarily produce Z-calls or contribute significantly to the Antarctic blue whale chorus. Hence, a deeper understanding of the vocal behavior Antarctic blue whales is crucial to further explore whether intra-annual variations in their peak vocalization frequency are related to the presence and body condition of particular classes of Antarctic blue whales in the Southern Ocean.

Outlook

This manuscript is still in an early phase of preparation. Further work involves the exploration of possibilities to include one further recorder into the frequency analyses (the MARU position). Moreover, further analyses encompass the investigation of temporal patterns in the peak frequency of calls of biological (e.g. fin whales and leopard seals) and anthropogenic sound sources in the study area. These analyses are expected to provide a deeper understanding on whether similar temporal shifts in a signals' peak frequency occur in other species or sound sources as well. Obtaining such knowledge represents an essential step towards the identification of factors driving the observed changes in the vocalization frequency of Antarctic blue whales and, possibly, other species.

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Supplemental figures

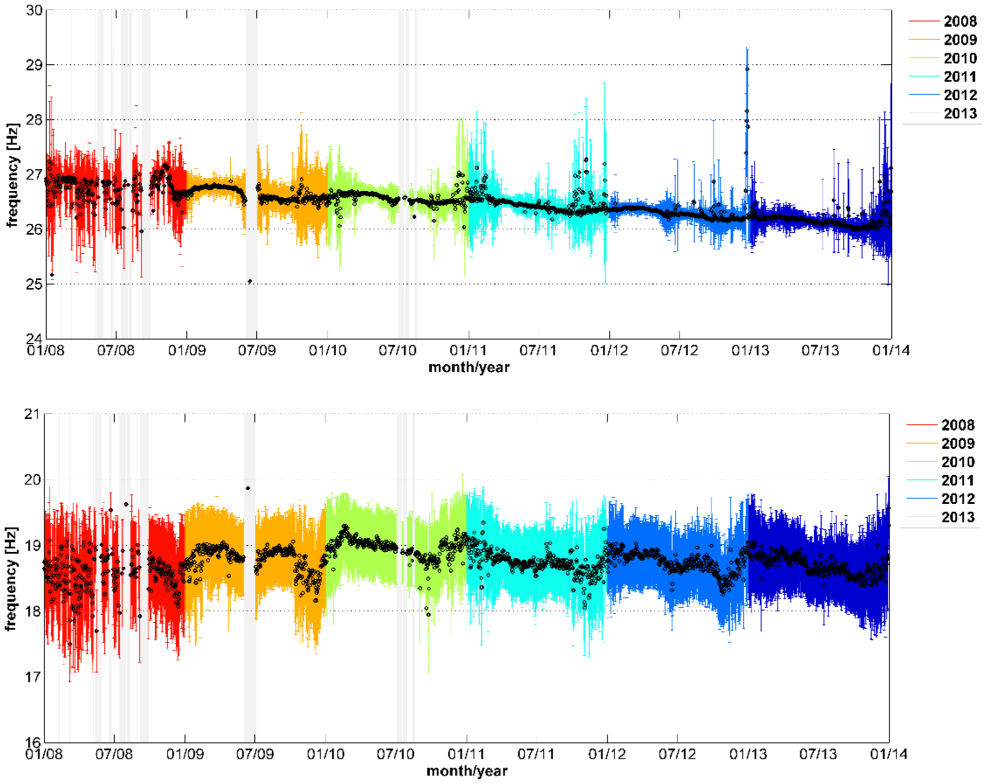

Fig. S 1: *Temporal patterns in peak frequency of unit A (25-29 Hz; upper panel) and unit C (17-21 Hz; lower panel) of Antarctic blue whale chorus from passive acoustic data recorded by PALAOA from 2008 to 2013. Daily mean values are indicated by black dots and standard deviations are color-coded representing different years.*

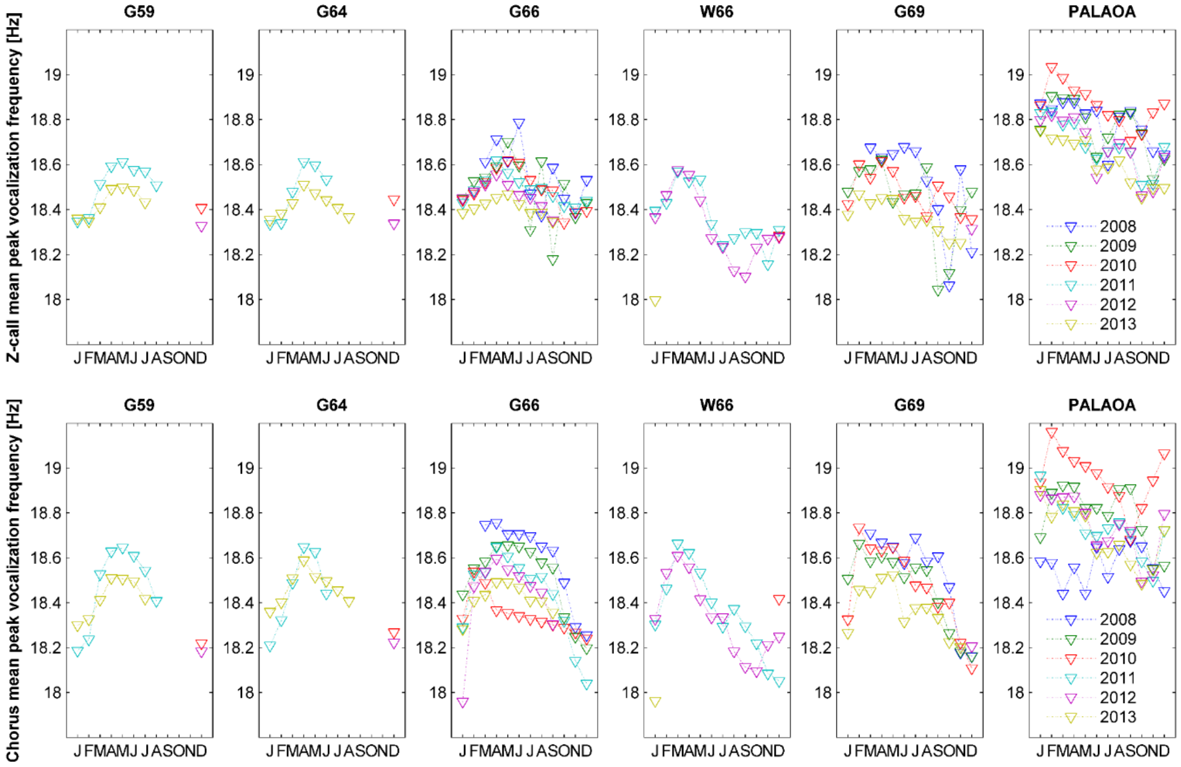

Fig. S 2: *Intra-annual patterns in monthly mean frequencies of unit C of individual Z-calls (upper panel) and chorus (lower panel) of Antarctic blue whales in passive acoustic data recorded at different recording sites between 2008 and 2013. Recording years are color-coded and recorder IDs indicate deployment positions according to Table 1.*

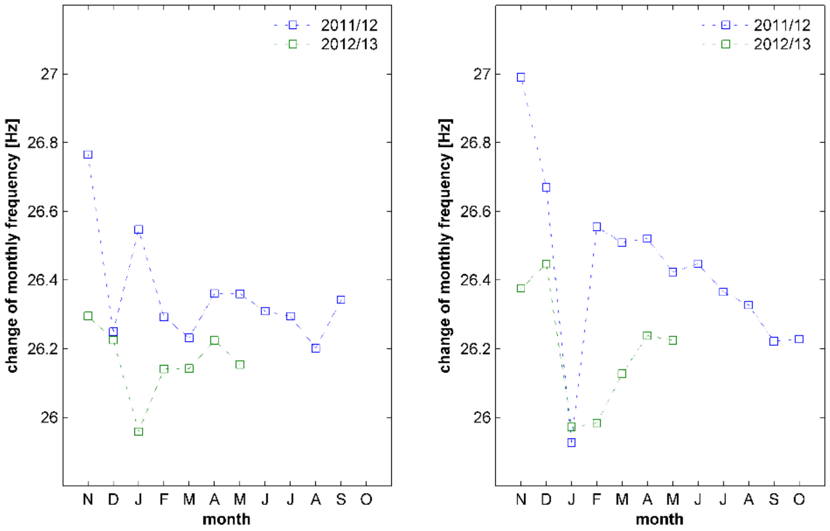

Fig. S 3: *Intra-annual pattern in the peak frequency of unit A of individual Z-calls (left panel) and chorus (right panel) of Antarctic blue whales in passive acoustic data recorded in the South Atlantic Ocean off Namibia between November 2011 and May 2013.*

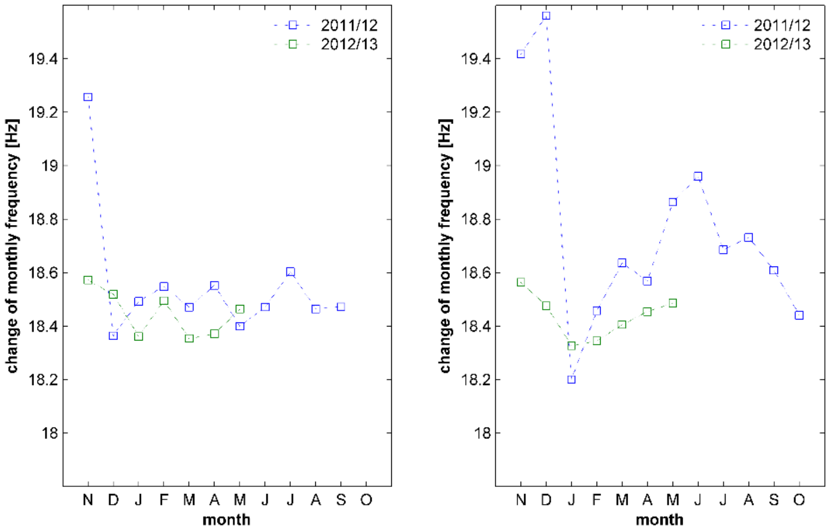

Fig. S 4: *Intra-annual pattern in the peak frequency of unit C of individual Z-calls (left panel) and chorus (right panel) of Antarctic blue whales in passive acoustic data recorded in the South Atlantic Ocean off Namibia between November 2011 and May 2013.*

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