Spatio-temporal patterns in humpback whale (*Megaptera novaeangliae*) acoustic presence and acoustic behavior in the Atlantic sector of the Southern Ocean

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Spatio-temporal patterns in humpback whale (*Megaptera novaeangliae*) acoustic presence and acoustic behavior in the Atlantic sector of the Southern Ocean

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Table of Contents

Abstract

Humpback whale males produce songs which are comparable in complexity and behavioral function to bird songs. Humpback whale songs are hierarchically structured, undergo constant change, and are breeding population-specific. These songs and other social vocalizations are produced in various behavioral contexts and along most of the geographic range of humpback whales including winter breeding habitats, summer feeding habitats and on migration routes. In remote areas, such as the Southern Ocean, which humpback whales visit primarily in summer, passive acoustic recordings can provide valuable insights to address open questions including: 'Where and when are humpback whales present in the Southern Ocean?', 'How do they use high latitude habitats?' or 'How do they respond to changes in the environment?'.

In the scope of this PhD thesis, I analyzed passive acoustic recordings from the Atlantic sector of the Southern Ocean (ASSO) to investigate spatio-temporal patterns in the acoustic presence and behavior of humpback whales and relate these patterns to potential ecological drivers.

In the first chapter, spatial and intra-annual patterns of humpback whale acoustic presence were investigated at 12 recording position in the ASSO. The passive acoustic data revealed two humpback whale hotspots at the western and eastern edges of the ASSO with higher acoustic activities towards lower latitudes. At these hotspots, humpback whale acoustic presence was also registered during austral winter, indicating that at least part of the humpback whale population remains in polar waters year-round.

In *Chapter II*, the analysis of a multi-year passive acoustic dataset from the ASSO yielded unique insights into the response of humpback whales to climate oscillations. Considerable humpback whale acoustic presence (i.e., multiple days in different months) was recorded in five out of seven years at different locations. In two years, almost no humpback whale acoustic presence was registered, which coincided with a strong El Niño event and a simultaneously long positive phase of the Southern Annular Mode. These climate oscillations most likely alter baleen whale prey availability in the Southern Hemisphere and thus affect migration routes and destinations of humpback whales.

Chapter III describes a new method for the automized and standardized classification of humpback whale vocalizations to circumvent the drawbacks of the common manual parameterization and categorization in the analyses of, for example, humpback whale songs.

The combination of standardized and automatically computed acoustic metrics to train a supervised classification model proved useful for the simple, rapid and highly reproducible identification and comparison of vocalization types and shows high potential for broad application purposes in bioacoustics.

In *Chapter IV*, humpback whale singing activity was evaluated for 13 recording positions in the ASSO over seven years. The data show that humpback whale males regularly sing during late summer and autumn on the feeding grounds in the ASSO implying that reproductive activities may be shifted at least partly to areas outside the breeding grounds. Song analyses and preliminary comparisons with song material from breeding populations, additionally, reveal that at least three humpback whale populations share the ASSO feeding area. This discovery illustrates the importance of the ASSO area for the preservation of humpback whale populations from the Atlantic but also the Pacific Ocean.

Overall, the findings presented in this thesis highlight the significance of the investigation of long-term and large-scale dataset in order to understand migration patterns, habitat preferences, and the effects of environmental variation on highly mobile marine species. For humpback whales and the ASSO, the results of this thesis present fundamental knowledge that can guide the conservation and management of populations and ecosystems.

Zusammenfassung

Die Gesänge der männlichen Buckelwale sind in Komplexität und Funktion vergleichbar mit den Gesängen der Singvögel. Buckelwalgesänge sind hierarchisch strukturiert, werden kontinuierlich verändert und sind populationsspezifisch. Diese Gesänge und andere soziale Vokalisationen werden in unterschiedlichen Verhaltenskontexten und im gesamten Ausbreitungsgebiet der Buckelwale einschließlich der im Winter besuchten Fortpflanzungsgebiete, der im Sommer besuchten Fressgebiete und entlang der Migrationsrouten produziert. In entlegenen Gebieten wie z.B. dem Südpolarmeer, welches die Buckelwale hauptsächlich im Sommer besuchen, können passiv-akustische Aufnahmen wertvolle Einblicke ermöglichen, um offene Fragen zu beantworten, wie z.B.: ‚Wo und wann sind Buckelwale im Südpolarmeer präsent?', 'Welches Verhalten zeigen sie in antarktischen Habitaten?' oder ‚Wie reagieren sie auf Veränderungen ihrer Umwelt?'.

Im Rahmen dieser Doktorarbeit habe ich passiv-akustische Aufnahmen aus dem atlantischen Sektor des Südpolarmeeres (ASSP) ausgewertet, um die räumlich-zeitlichen Muster der akustischen Präsenz und des akustischen Verhaltens von Buckelwalen zu studieren und diese Muster mit potentiellen ökologischen Faktoren in Zusammenhang zu bringen.

Im ersten Kapitel wurden räumliche und saisonale Muster der akustischen Präsenz von Buckelwalen an 12 Aufnahmepositionen im ASSP untersucht. Die passiv-akustischen Daten offenbarten zwei "Buckelwal-Hotspots" an den nordöstlichen und nordwestlichen Randgebieten des ASSP. An diesen Hotspots wurde die akustische Präsenz von Buckelwalen auch im südlichen Winter registriert, was darauf hinweist, dass zumindest ein Teil der Buckelwalpopulationen ganzjährig in Südpolargebieten verbleibt.

In *Kapitel II* hat die Analyse von mehrjährigen passiv-akustischen Daten aus dem ASSP einzigartige Einblicke in die Reaktion von Buckelwalen auf Klimaveränderungen ermöglicht. Erwähnenswerte akustische Präsenzen von Buckelwalen (i.e. mehrere Tage in unterschiedlichen Monaten) wurden in fünf von sieben Jahren an verschiedenen Orten aufgenommen. In den verbleibenden zwei Jahren wurden nahezu keine Buckelwalpräsenzen registriert, dies in zeitlicher Übereinstimmung mit einem starken El Niño Ereignis und einer gleichzeitig langen positiven Phase der Antarktischen Oszillation. Diese Klimaveränderungen haben vermutlich Auswirkungen auf die Verfügbarkeit der Beute der Bartenwale in der Südhemisphäre und beeinflussen somit Migrationsrouten und -ziele der Buckelwale.

Kapitel III beschreibt eine neue Methode für die automatisierte und standardisierte Klassifizierung von Buckelwalvokalisation, mit welcher man die Nachteile der häufig verwendeten manuellen Parametrisierung und Kategorisierung zur Analyse von z.B.

Buckelwalgesängen umgehen kann. Eine Kombination von standardisierten und automatisch berechneten akustischen Metriken wurde verwendet, um ein überwachtes Klassifizierungsmodell zu trainieren. Diese Methode hat sich bewährt zur einfachen, schnellen und reproduzierbaren Tonkategorisierung und hat Potential zu vielfältigen Anwendungen in der Bioakustik.

In *Kapitel IV* wurde die Gesangsaktivität von Buckelwalen für 13 Aufnahmepositionen im ASSP über sieben Jahre evaluiert. Die erhobenen Daten zeigen, dass Buckelwalmännchen regelmäßig von Spätsommer bis Herbst in den Fressgebieten des ASSP singen. Dies impliziert, dass Fortpflanzungsaktivitäten zumindest zum Teil auch im Südpolarmeer stattfinden. Gesangsanalysen und vorläufige Vergleiche mit Gesängen aus den Fortpflanzungsgebieten haben zusätzlich gezeigt, dass sich mindestens drei Buckelwalpopulationen die Fressgebiete des ASSP teilen. Diese Entdeckung stellt einen wichtigen Hinweis auf die Bedeutung des ASSP zur Erhaltung von Buckelwalpopulationen des atlantischen und sogar des pazifischen Ozeans dar.

Die in dieser These präsentierten Ergebnisse weisen auf die Bedeutsamkeit der Auswertung von Langzeitdatensätzen hin, um Migrationsmuster, Habitatpräferenzen und die Effekte von Umweltveränderungen auf Bartenwale zu erforschen. Speziell für die Erhaltung und das Management von Buckelwalen und der Ökosysteme des ASSP liefern die Ergebnisse dieser Doktorarbeit fundamentale Erkenntnisse.

Introduction

Sounds in the ocean – acoustic communication in cetaceans

The evolution of complex acoustic communication systems

Communication by sound is wide-spread within different taxa, such as birds, mammals, insects and fishes (Bradbury and Vehrencamp, 1998). Hearing and communication by sound is considered as one of the more recently developed senses (Norris and Evans, 1988; Bradbury and Vehrencamp, 1998). The evolution of this additional sense has been related to the increasing complexity of information in surrounding ecosystems which increased the need for a larger variety of communication forms (Norris and Evans, 1988). Bradbury and Vehrencamp (1998), additionally, suggest that initial acoustic displays evolved as by-products of movements used for visual or tactile displays. Also, the mainly nocturnal activity of ancestral species has been correlated with the evolution of acoustic signals for communication (Chen and Wiens, 2020). The evolutionary processes and drivers are specific to each species or group of species and cannot be generalized to one common evolutionary pathway. A variety of selective forces, e.g., the physical properties of the environment, morphological restrictions and biological interactions, often act as trade-offs, finally creating a complex network of evolutionary drivers (Ryan, 1986). This competition of selective forces led to the independent evolution of multiple different forms of acoustic communication both in air and in water, such as the defensive tail rattle of rattlesnakes or the acoustic display of piranhas produced through muscle contractions of the swimbladder (Bradbury and Vehrencamp, 1998; Ladich, 2000; Fine and Parmentier, 2015).

Underwater, the communication by sound seems to take a particularly crucial role. Common senses to communicate or orientate over considerable distances in terrestrial environments are sight, smell and hearing (Bradbury and Vehrencamp, 1998). The marine environment presents significant restrictions to sight and smell. Throughout much of the ocean (i.e., at depth greater than tens of meters), light is absorbed completely and consequently visibility is poor, whereas in surface waters, turbidity can cause additional restrictions in visibility (Wozniak and Dera, 2007). Thus, the range of sight underwater is greatly reduced compared to in air and the communication by color, facial expression or gesture is limited (Pryor, 1990; Price *et al.*, 2008; Miller, 2009). In many terrestrial species, smell is important to

locate food sources and predators or to transfer information for social interaction (Wyatt, 2003). Due to the slow diffusion of chemicals in water, underwater communication by odorous substances is only suitable for short distances, extended time scales or in combination with strong directional currents (i.e., the olfactory identification of suitable habitats in reef fish larvae; Rogers and Kaplan, 2002; Munday *et al.*, 2009). Baleen whales seem to circumvent this disadvantage by detecting chemical signals in the air above the sea surface while they are breathing (i.e., sensing the odor dimethyl sulfide released by certain species of phytoplankton; Torres, 2017b). Long-range communication is necessary for various ecological and social processes, such as the attraction of mates or the localization of potential prey (Bradbury and Vehrencamp, 1998). Due to the unique physical properties of the ocean, for example the density and salinity of sea water, sound is the only option by which to communicate across greater distances than tens of meters (Tyack, 2008). In contrast to visual or olfactory cues, sound can travel several kilometers within water without substantial information loss (Tyack, 1998). Especially, low frequency sounds are favorable for long distance communication, because these sounds can travel great distances in the deep ocean where almost no disturbances (i.e., absorption or reflections of sound waves) cause transmission loss (Bass and Clark, 2003). Additionally, sound travels ~4.5 times faster in water compared to air due to the higher density of sea water, ensuring propagation efficiency when occupying acoustic signals for communication in the ocean (Nummela and Thewissen, 2008).

Cetaceans evolved specialized sound production mechanisms to further improve acoustic communication efficiency in the marine environment. Cetaceans have a larynx originating from their terrestrial ancestor (Fordyce, 2018). The need for long-range communication in baleen whales (related to large-scale distributions) most likely drove the evolution of a specialized homolog of human vocal folds (Reidenberg and Laitman, 2007). Baleen whales evolved vocal folds which are U-shaped, termed the U-fold (Reidenberg and Laitman, 2007). Unlike the vocal folds of terrestrial mammals, which are perpendicular to the airflow, the U-fold is oriented parallel to the airflow (Figure 1) (Reidenberg and Laitman, 2007). This modification is potentially beneficial for the production of very low frequency sounds, which allow baleen whales to communicate over tens to hundreds of kilometers (Reidenberg and Laitman, 2007). The development of the specific sound production mechanism in toothed whales was probably related to the advantages of using echolocation during past environmental changes (e.g.,

changing continental positions, ocean circulations, and/or food resources; Tyack and Miller, 2002; Berta *et al.*, 2014). Although, toothed whales feature a larynx including functional vocal folds, these cetaceans seem not to make use of the larynx for sound generation (Cranford *et al.*, 1996). The sound source of toothed whale vocalizations is the nasal passage connecting the lungs with the blowhole (Dormer, 1979; Cranford, 2000). In their nasal passage, toothed whales developed a so-called monkey-lips-dorsal-bursae (MLDB) complex (Cranford *et al.*, 1996). The MLDB complex is composed of one or two pairs of phonic lips (a keratinous structure with a slit-like passage, sometimes also termed monkey lips) and two bursae (Figure 1) (Cranford *et al.*, 1996). With a complex system of air sacs, toothed whales force air through the phonic lips, thereby generating vibrations, i.e., a sound (Tyack and Miller, 2002). Dolphins, for example, have two pairs of phonic lips which allow for simultaneous echolocation and communication (Cranford *et al.*, 2011).
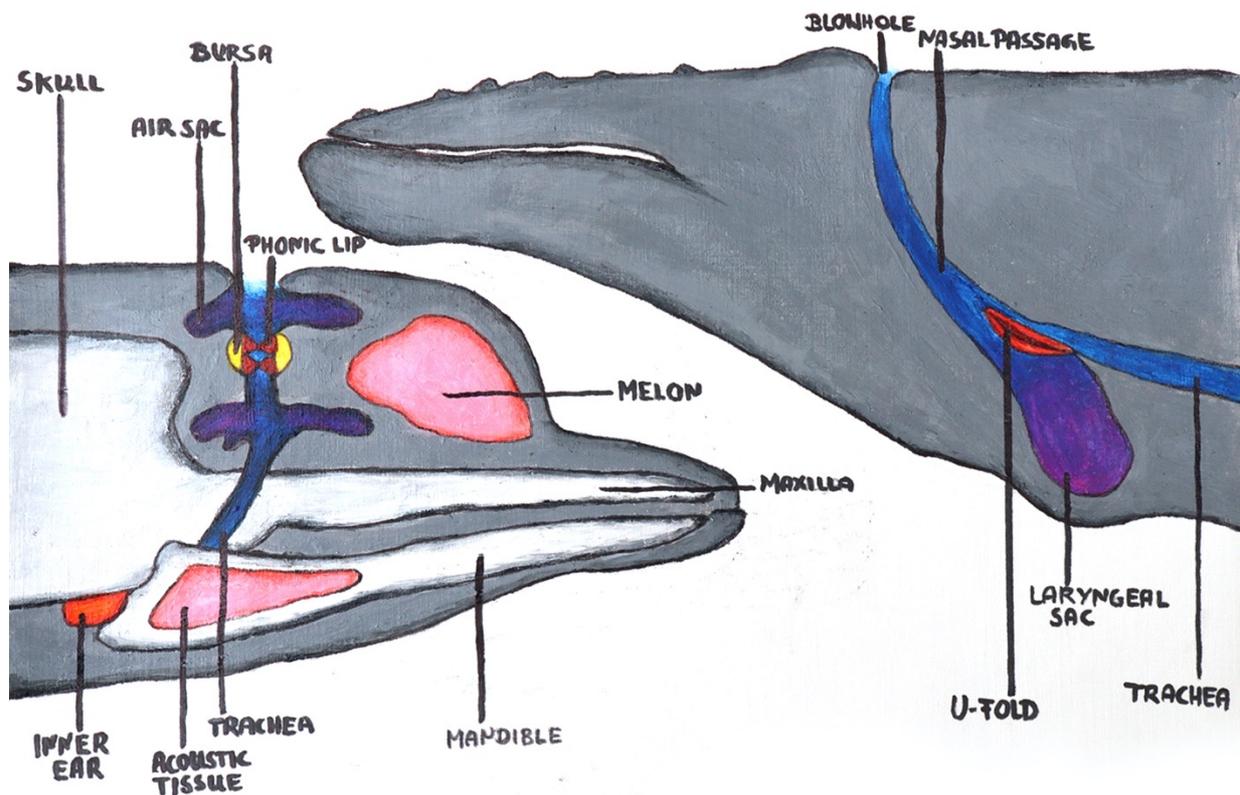

Figure 1. Sound production and reception organs in cetaceans. Left: Toothed whale sound production pathway via phonic lips and melon and sound perception pathway via acoustic tissue as part of the mandible and the inner ear (adapted from Cranford et al., 1996). Right: Baleen whale sound generation organs (adapted from Reidenberg and Laitman, 2007). © Marie Schall

Besides environmental properties and physiological restrictions, biological interactions are an important factor shaping the evolution of acoustic communication systems (Ryan, 1986). This is true for inter-specific interactions such as predator-prey interactions or ecological facilitation (Ryan, 1986; Kyhn *et al.*, 2009), but especially a high level of intra-specific interaction favors the development of complex acoustic communication systems. The 'social complexity hypothesis' implies that complex social systems, defined by the number of interacting individuals, the different types of social roles, and the variability of interactions, drive communicative complexity in terms of signaling repertoire and number of components of a given signal (Freeberg *et al.*, 2012). Social systems, in cetaceans, such as fission-fusion (i.e., flexible size and composition of social group) and matrilineal societies, are highly complex and created the need for sophisticated vocal communication systems (Marino, 2002; Marino *et al.*, 2007). Across all species of cetaceans, a variety of specializations has been discovered in their vocal communication systems and the question of 'What is the purpose of communication?' in this context is of particular interest to the scientific community.

What is the purpose of communication?

The variety of vocalization types in cetaceans is thought to be indicative of the information types which are encoded to be directed to other individuals, groups, or populations (Payne and Mcvay, 1971; Ford, 1991; Janik *et al.*, 2006). Cetacean vocalizations cover frequencies from only tens of Hertz (Hz) to more than 100 kilohertz (kHz) determining the spatial scale of communication (Au and Hastings, 2008). The resulting sizes of vocalization repertoires in cetacean species in combination with their aquatic lifestyle makes it challenging to study the information content of signals in the respective species and different contexts. Cetacean vocalization repertoires and the complexity of information content continuously extend due to their cognitive abilities, allowing two main types of learning: Cetaceans are capable of both contextual vocal learning and vocal production learning, which is rare in mammals (Janik and Slater, 1997). Contextual vocal learning allows cetaceans to associate existing vocalizations with novel contexts which changes the information content transferred by a given signal (Janik, 2014). Vocal production learning opens the possibility to learn new signals from conspecifics or even other species which facilitates the continuous development of vocalization repertoires (Janik, 2014). Although most

information types transferred by cetacean vocalizations, are still poorly understood, at least three main types of information could be identified, namely individual identity, group affiliation and differentiation, and reproductive display.

Individual identity, in most species, is conveyed by subtle voice features that affect all vocalizations produced (Janik *et al.*, 2006). However, voice features can easily be masked by background noises and therefore lost during transmission (e.g., Aubin and Jouventin, 1998). In bottlenose dolphins (*Tursiops truncatus*; and maybe some other dolphin species), the communication of individual identity seems to take a specifically important role. These dolphins developed a vocalization type termed *signature whistle* which conveys individual identity in a much more efficient way than voice features (i.e., comparable to human names; Janik *et al.*, 2006). Through vocal production learning, bottlenose dolphin calves develop their own signature whistle, frequently modifying sounds from their acoustic environment (including conspecific vocalizations) and individuals of a group are able to copy another individual's signature whistle in social interactions (Tyack, 1997; Janik *et al.*, 2006). Signature whistles allow for individual recognition and social cohesion in the complex fission-fusion society of bottlenose dolphins and prioritize individual over group recognition (Janik and Sayigh, 2013).

Group-specific vocalization types, in contrast, enhance affiliation among group members and differentiation among distinct groups. These group-specific vocalization types are also termed dialects and are mainly known from killer whales (*Orcinus orca*) and sperm whales (*Physeter macrocephalus*) (Ford, 2018). Killer and sperm whales both live in (stable) matrilineal groups which include multiple generations. These groups often locally interact with other groups of the same species and use group-specific vocalization types (i.e., in killer whales) or group specific proportions of vocalization types (i.e., in sperm whales) to manage interactions within and among groups (Rendell and Whitehead, 2005; Deecke *et al.*, 2010). The functionality of sympatric dialects in killer and sperm whales has been interpreted as the enhancement of group cohesion, the advertisement of identity at different levels of the society and even the recognition of kin which facilitates outbreeding (Barrett-Lennard, 2000; Gero *et al.*, 2016). The resulting increased protection from predators (i.e., through group formation), cooperative hunting or caring for offspring (i.e., through task sharing), and/or improved genetic variation (i.e.,

through the avoidance of inbreeding) all warrant indirect fitness benefits (Alexander, 1974; Charlesworth and Willis, 2009; Pitman and Durban, 2012; Gero *et al.*, 2013).

Acoustic signals produced in the context of reproductive displays, in contrast, are thought to provide a more direct benefit to individual fitness by the attraction of potential mates and the mediation of intra-sexual reproductive competition (Mitoyen *et al.*, 2019). A widely known form of acoustic display are the songs in birds and baleen whales (Garland and McGregor, 2020).

Song in baleen whales

Among the 16 species of baleen whales (*Mysticeti*), only five species are known to produce songs: the blue whale (*Balaenoptera musculus*), fin whale (*Balaenoptera physalus*), humpback whale (*Megaptera novaeangliae*), minke whale (*Balaenoptera acutorostrata*), and bowhead whale (*Balaena mysticetus*) (Payne and Mcvay, 1971; Edds-Walton, 1997; Croll *et al.*, 2002; McDonald, 2006; Stafford *et al.*, 2008). Whale songs are thought to be a reproductive display, such as bird song, because only males sing and the main singing activity occurs during the breeding season (Janik, 2009). The level of complexity varies strongly between the different species with single vocalization repetitions in, for example, fin whales (Delarue *et al.*, 2009), the combination of a few vocalization types in, for example, blue whales (McDonald, 2006), and the multi-level hierarchically structured vocalization sequences in bowhead and humpback whales (Payne and Mcvay, 1971; Stafford *et al.*, 2008). This variability in the level of complexity is not yet well understood, but might be related to cognitive capacity or differences in mating systems (Herman, 2017; Garland and McGregor, 2020). In most baleen whale species, song characteristics and composition seem to be population-specific, most likely related to the geographic isolation of distinct breeding stocks (Payne and Guinee, 1983; McDonald, 2006; Delarue *et al.*, 2009). The monitoring and analysis of baleen whale song has resulted in many valuable insights into the distribution and ecology of these cryptic and highly mobile species (i.e., Clapham and Mattila, 1990; McDonald, 2006; Magnúsdóttir *et al.*, 2014; Herman, 2017; Buchan *et al.*, 2019).

The humpback whale – a vocal model species

Humpback whales – the songbirds of the sea

Among the baleen whales, the humpback whale is probably the most studied species due to its occurrence in high numbers in shallow tropical and sub-tropical waters during winter (Clapham, 2018). Already during early sudies in the mid-20th century, humpback whale vocalizations were recorded with the first submergeble recording systems and the first discovery of song in baleen whales was documented as the repetition of a series of sounds with considerbale precision (Payne and Mcvay, 1971; Darling, 2002). Payne and Mcvay (1971) described humpback whale songs as hierachically structured with units defined as the smallest entity building phrases, the repetition of phrases building themes, and the combination of themes composing a song (Figure 2). Songs may be repeated uninterupted for sevaral minutes to hours, which is termed a song session. Male humpback whales of a specific breeding population are known to converge closely on the same current rendition of song, termed song type (Winn and Winn, 1978a; Winn *et al.*, 1981; Payne and Guinee, 1983; Payne and Payne, 1985a; Herman, 2017). Each song type is characterized by a distict combination of themes (Payne and Mcvay, 1971; Cholewiak *et al.*, 2013).
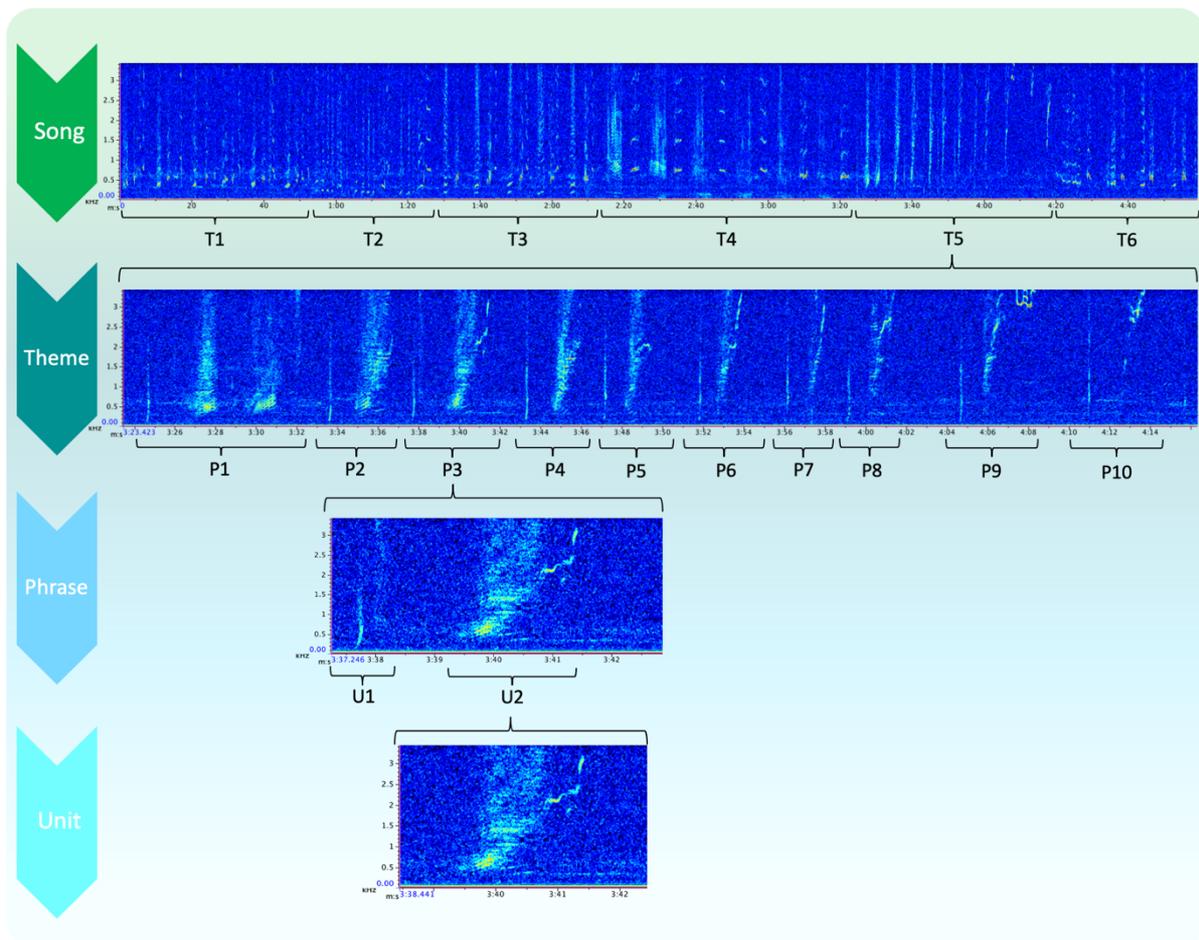
Figure 2. Hierarchical structure of humpback whale song with representations of song, themes, phrases and units as in Payne and Mcvay (1971). The upper panel shows the spectrogram representation of a song indicating start and end times of distinct themes (i.e., T1-T6). The second panel shows the spectrogram representation of a single theme (i.e., T5) indicating the start and end times of individual phrases (i.e., P1-P10). The third panel shows the spectrogram representation of one phrase (i.e., P3) illustrating the composition by two units (i.e., U1 and U2). The lower panel shows exemplary spectrogram representation of a single song unit (i.e., U2).

Humpback whale songs gradually change over time and song progression is most notable on an annual timescale (Payne and Mcvay, 1971; Darling, 2002). This song development is most likely a result of the humpback whale's ability to immitate sounds and to innovate new vocalizations and the neverending quest for novelty is probably driven by sexual selection (i.e., both inter- and intrasexual selection; Noad *et al.*, 2000; Cerchio *et al.*, 2001; Mercado *et al.*, 2005). Two different forms of song development can be differentiated in humpback whales, namely evolutions and revolutions (Garland *et al.*, 2011; Garland

et al., 2017; Allen *et al.*, 2018; Garland and McGregor, 2020). Evolution is the most observed form of song development in humpback whales, describing the progressive change of song, including the addition, deletion, and/or substitution of units, phrases and themes and all males within a population incorporate these changes into their own song (Winn and Winn, 1978a; Payne, 1983; Garland and McGregor, 2020). The continous evolution of song can lead to increasing complexity, notable in the number of distinct units or themes composing a song (Allen *et al.*, 2018). Song revolution, on the other hand, is less common and so far has only been described for the humpback whale populations of the western South Pacific and Indian Ocean (Noad *et al.*, 2000; Garland *et al.*, 2011; Garland *et al.*, 2013b; Garland *et al.*, 2015b; Garland *et al.*, 2017). Song revolutions are described as the rapid and complete replacement of a song by another distinct song from a different population which is usually accompanied by a reduction in song complexity (Allen *et al.*, 2018). Therefore song revolutions may be a result of the cognitive limit of humpback whales when learning complex song structures (Allen *et al.*, 2018). The continous process of learning new songs is most likely driven by cultural transmission, which is defined as the social sharing of information and learning of behaviors among conspecifics (Rendell and Whitehead, 2001; Garland *et al.*, 2011; Garland and McGregor, 2020). In contrast to, for example, migratory behavior, which is shaped by vertical (parent-offspring) cultural transmission, singing behavior in humpback whales is thought to be shaped by horizontal cultural transmission among unrelated conspecifics of similar age classes (Garland *et al.*, 2011). This horizontal cultural transmission also allows the exchange of song material among populations when singing males meet on the feeding grounds or during migration, or when single males visit multiple breeding grounds (Payne and Guinee, 1983; Helweg *et al.*, 1998; Darling and Sousa-Lima, 2005; Darling *et al.*, 2019). Therefore, the degrees of song similarity among populations can be indicative of population mixing (Garland *et al.*, 2015b).

To date, the functionality of humpback whale male song is not entirely understood, but songs are thought to increase the chances of reproduction for individual whales by mediating inter- and/or intrasexual interactions, similar as in songbirds (Herman, 2017). Song complexity potentially is a result of inter-sexual selection, driven by female preference for more complex or new vocal repertoires (Tyack, 1981; Cerchio *et al.*, 2001), whereas song convergence might be driven by intra-sexual vocal competition resulting in song copying (Mercado *et al.*, 2005). The presence and characteristics of a male humpback

whale's song might also convey fitness of the singer to the female or even stimulate the female's reciptivity (Winn and Winn, 1978a; Chu and Harcourt, 1986; Herman, 2017). Additionally, humpback whale song might mediate male-male interactions, such as aggression, dominance or cooperation (Darling *et al.*, 2006; Cholewiak, 2008). In an alternative scenario, the often parallel chorusing of multiple males on the breeding grounds could be a form of mutualism in the framework of a lekking system (i.e., aggregation of males that females visit for mating; Herman, 2017). Communal singing, in this scenrio, could be a broadly propagating spatial signal that is supposed to attract females to a lek instead of attracting females to individual singers (Herman, 2017). In the same context, songs could also serve as signals to attract other humpback whales to newly colonized wintering grounds (Clapham and Zerbini, 2015; Herman, 2017). The most likely scenario is that humpback whale song has a multi-purpose role in the humpback whale mating system. The majority of songs were therefore recorded on the low-latitude breeding grounds where breeding takes place, but evidence increases that singing is also common during migration and on the feeding grounds during different times of the year (Payne and Mcvay, 1971; McSweeney *et al.*, 1989; Noad and Cato, 2007; Smith *et al.*, 2008; Garland *et al.*, 2011; Stimpert *et al.*, 2012; Vu *et al.*, 2012; Kowarski *et al.*, 2018; Ross-Marsh *et al.*, 2020).

Migration and vocal behavior

Monitoring humpback whale acoustic presence and behavior, for example singing, can help to understand small-scale and large-scale movement patters, such as migration (e.g., Clapham and Mattila, 1990; Charif *et al.*, 2001; Dunlop *et al.*, 2008). Most baleen whale species migrate annually between winter and summer habitats (Stern, 2009). Usually, summer habitats are productive mid- to high-latitude waters, where baleen whales spent most of their time feeding, therefore termed summer feeding grounds (Clapham, 2018). For migratory baleen whale species, such as the humpback whale, winter habitats are located in unproductive low-latitude waters, where the whales usually fast, engage in reproductive activities and give birth (Clapham, 2018). Why baleen whales migrate has been discussed intensely. While it is clear, why baleen whales visit high-productivity areas during summer, the reason for visiting low-productivity areas close to the equator for breeding remains speculative. Experts, as of now, suggest a combination of two reasons being responsible for the annual migration of most baleen whales to their

tropical breeding grounds and great part of this theory is derived from observations of humpback whales. First, shallow tropical areas, which are usually preferred by pregnant females to give birth (Hindell, 2009), seem to provide shelter to minimize the risk of predation by killer whales or sharks on new-born calves (Stern, 2009; Derville *et al.*, 2018). Second, the migration to low-latitude areas could be an evolutionary holdover from the period of the glacial maximum, when cold and productive waters were located much closer to the equator (Stern, 2009). Except for one non-migratory humpback whale population in the Arabian Sea (Mikhalev, 1997), all humpback whale populations migrate between tropical breeding grounds and polar or sub-polar feeding grounds (Clapham, 2018) (Figure 1). Due to a maternally inherited site fidelity, humpback whales usually return every year to the breeding ground where they were born and often also show a clear preference for a specific feeding ground (most likely the one they first visited with their mothers (Clapham, 2018). In the Northern Hemisphere, at least six different breeding grounds are recognized by the International Whaling Commission (IWC): Asia and Northern Philippines, Hawaii, Mexico, Central America, West Indies, and Cape Verde Islands, from where whales migrate to the polar and subpolar waters of the North Pacific and North Atlantic (Figure 3) (Donovan, 1991; Calambokidis *et al.*, 2001; Stevick *et al.*, 2006; Cooke, 2018). In the Southern Hemisphere, at least 10 different breeding grounds are recognized by the IWC: Brazil, West Africa, East Africa, Madagascar, West Australia, East Australia, multiple smaller aggregations in Oceania, and Columbia/Ecuador, from where whales migrate to the Southern Ocean or southern subpolar waters (Figure 3) (International Whaling Commission, 2006; 2011). Connectivity among breeding grounds usually correlates with the geographical distance between these areas (Calambokidis *et al.*, 2001; Rosenbaum *et al.*, 2017). Especially in the Southern Hemisphere, the degree of longitudinal movements on the Antarctic feeding grounds most likely relates to the degree of connectivity between two respective breeding grounds (Calambokidis *et al.*, 2001; Stevick *et al.*, 2003; Rosenbaum *et al.*, 2017). In the Northern Hemisphere, extensive Photo-ID studies, both at breeding and feeding grounds, as well as along the migration routes, created a comprehensive picture of the Northern Hemisphere humpback whale stock structure (e.g., Calambokidis *et al.*, 2001; Stevick *et al.*, 2006), which can aid population and ecosystem management and conservation efforts. In the Southern Hemisphere, comparative results through Photo-ID studies are limited by the reduced availability of photos from the feeding grounds due

to the high logistic effort for studies in the Southern Ocean. The IWC divided the Southern Ocean and adjacent subpolar waters into six management areas (International Whaling Commission, 2006), but only humpback whales from management area I (60°W-120°W), around the Antarctic Peninsula have been studied over longer time scales (i.e., multiple years; e.g., Olavarria *et al.*, 2007; Dalla Rosa *et al.*, 2008; Friedlaender *et al.*, 2008; Acevedo *et al.*, 2017). The Antarctic management area I is frequented by humpback whales that mainly originate from the breeding stock off Columbia/Ecuador (stock G) and to some extent also by humpback whales from French Polynesia (stock F) (Acevedo *et al.*, 2017; Albertson *et al.*, 2018). From the other Antarctic management areas, the picture of feeding ground occupation by the different breeding stocks is much less clear, although the IWC assumes humpback whales to migrate to management areas within a similar longitudinal range as their respective breeding stocks (International Whaling Commission, 2006; 2011), a notion also supported by recent satellite tagging studies (e.g., Horton *et al.*, 2001; Zerbini *et al.*, 2011; Rosenbaum *et al.*, 2014). On the other hand, evidence exists that humpback whales from different breeding stocks mix on the feeding grounds in the Southern Ocean (Amaral *et al.*, 2016; Rosenbaum *et al.*, 2017; Riekkola *et al.*, 2018). Longitudinal movements of humpback whales in the Southern Ocean seem to be quite common and most likely are necessary to maximize feeding opportunities (Amaral *et al.*, 2016; Rosenbaum *et al.*, 2017; Riekkola *et al.*, 2019). While humpback whales feed and migrate, social interactions among group members, including mother-calf pairs, are common and individuals produce a great variety of vocalizations, termed social sounds (Dunlop *et al.*, 2008; Fournet *et al.*, 2014). Social sounds, especially when they are exchanged between mother and calf, do not reach high intensities and can, therefore, only be detected over short distances (Dunlop *et al.*, 2013; Videsen *et al.*, 2017). Humpback whale song, in contrast, is detectable over tens of kilometers (Au *et al.*, 2006) permitting monitoring of humpback whale presence over larger scales. Hence, the arrival and departure of humpback whales on breeding and feeding grounds or the spatio-temporal delineation of migration routes can be studied by analyzing continuous underwater sound recordings to detect the onset and cessation of singing behavior (e.g., Clapham and Mattila, 1990; Clark and Clapham, 2004a; Vu *et al.*, 2012; Cerchio *et al.*, 2016; Warren *et al.*, 2020).
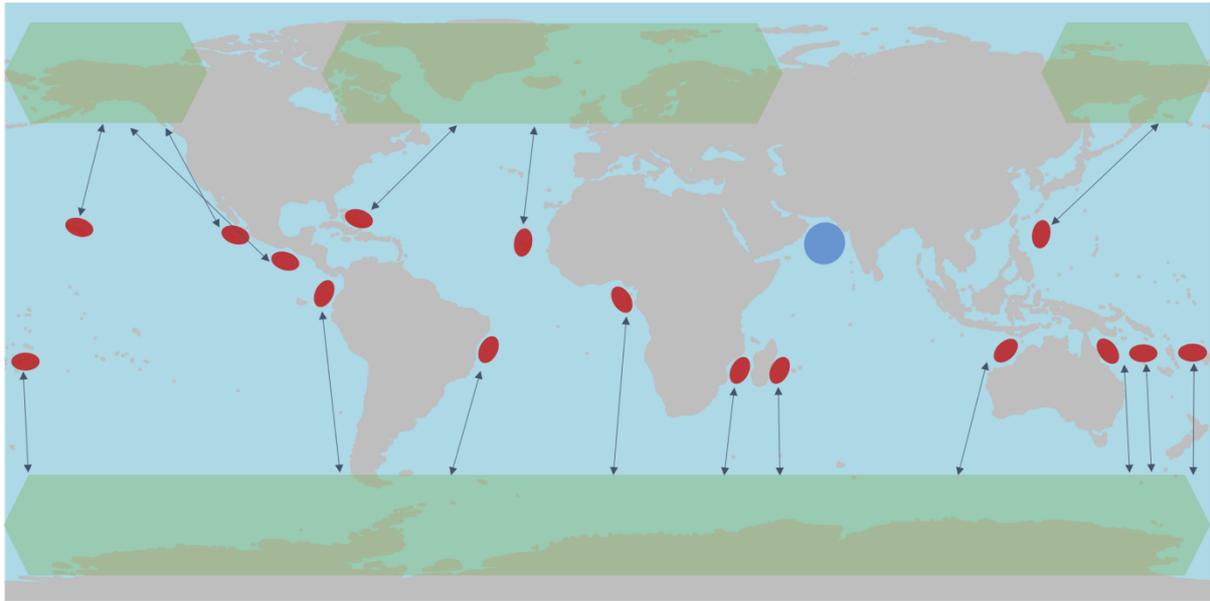
Figure 3. World map illustrating the approximate geographical locations of humpback whale breeding and feeding grounds. Red ovals represent known breeding grounds (10 for the Southern Hemisphere and six for the Northern Hemisphere), green shading represent the feeding areas and blue patch represents the area inhabited by the only non-migratory humpback whale population in the Arabian Sea. Arrows represent schematically migration routes between breeding and feeding grounds.

Song on the feeding grounds

Through the availability of long-term passive acoustic data from mid and high latitude areas, Northern Hemisphere humpback whales are known to sing primarily (excluding breeding ground singing) during the late autumn prior to migartion, during migration, and/or during the spring following migration, although year-round singing has also been registered for mid-latitude feeding grounds (Mattila *et al.*, 1987; McSweeney *et al.*, 1989; Clapham and Mattila, 1990; Clark and Clapham, 2004a; Vu *et al.*, 2012). Spring and autumn have therefore been defined as shoulder seasons directly following and preceding the breeding season (i.e., post- and pre-breeding shoulder seasons, respectively; Stimpert *et al.*, 2012; Vu *et al.*, 2012; Magnúsdóttir *et al.*, 2015). Songs recorded on feeding grounds were composed of the same hierarchical structure as on the breeding grounds, although in some cases, less complex song sequences or fragments of songs were registered (Mattila *et al.*, 1987; McSweeney *et al.*, 1989; Magnúsdóttir *et al.*, 2015; Kowarski *et al.*, 2019; Magnúsdóttir and Lim, 2019). For Northern Hemisphere humpback whales, the analysis of feeding ground songs suggests that immature males conduct "off-season" singing on the feeding grounds and during

migration to practice singing (Kowarski *et al.*, 2019). Opportunistic singing outside the breeding grounds and/or breeding season was also interpreted as low-cost reproductive advertisement by males, e.g., to access females that failed to conceive during the breeding season, although actual mating activities, too date, have never been observed outside the breeding grounds (Clark and Clapham, 2004a; Vu *et al.*, 2012). The fact that humpback whales sing on the feeding grounds is furthermore thought to facilitate cultural transmission of new songs within the breeding population and potentially also between different breeding stocks (Magnúsdóttir and Lim, 2019).

On Southern Hemisphere feeding grounds, the data on humpback whale song occurrence and dynamics are still limited both spatially and temporally. To date, two studies have presented recordings of song from Antarctic waters comprising four days from two sites (Stimpert *et al.*, 2012; Garland *et al.*, 2013a). One study collected acoustic data near a humpback whale 'super-group' off western South Africa and described the song that was recorded there (Gridley *et al.*, 2018) while another study reported on the migratory timing of singing humpback whales passing central New Zealand (Warren *et al.*, 2020).

Due to the annual population-wide convergence on one specific song type, humpack whale songs can be used to determine stock affilitation of singers (Payne and Guinee, 1983; McSweeney *et al.*, 1989; Gabriele and Frankel, 2002; Garland *et al.*, 2013a; Herman, 2017). In the Southern Hemisphere, humpback whales migrating through the Cook Strait in central New Zealand and feeding around the Balleny islands were identified by their song to originate from the breeding population of eastern Australia/New Caledonia (stock E; Garland *et al.*, 2013a; Warren *et al.*, 2020).

Thus, the identification and structural analysis of humpback whale songs from Southern Hemisphere feeding grounds can provide a unique source of information which can be used to close existing knowledge gaps on humpback whale behavioural ecology and migratory links, especially in remote regions, such as the Atlantic sector of the Southern Ocean (ASSO). At least two humpback whale populations are thought to migrate to the ASSO (stock A and B; International Whaling Commission, 2011), but information on distribution, movements, and behaviour of humpback whales in this area is largely unavailable (Zerbini *et al.*, 2011; Van Opzeeland *et al.*, 2013; Rosenbaum *et al.*, 2014).

The Atlantic sector of the Southern Ocean

Ecological importance

The ASSO is one of the most productive areas of the Southern Ocean and sustains a wide variety of predators including marine birds, mammals and bony fishes (Deacon, 1979; Knox, 2007). The ASSO ecosystem is dominated by dynamic sea ice, the eastward-flowing Antarctic Circumpolar Current (ACC) and its associated fronts, and the Weddell Sea Gyre (Figure 4) (Deacon, 1979; Orsi *et al.*, 1995; Nicol *et al.*, 2008). The Polar Front constitutes the northern limit of the Southern Ocean, located as far north as 50°S in the Atlantic sector (Orsi *et al.*, 1995). Various island groups uniquely characterize the northern part of the ASSO (Orsi *et al.*, 1995). The high concentration of nutrient-rich Upper Circumpolar Deep Water at the southern boundary of the ACC creates a number of productivity hotspots in the ASSO (Tynan, 1998). The Weddell Gyre acts as a isolating current system regulating temperature in the Weddell Sea and efficiently circulates nutrients, phytoplankton, and zooplankton throughout great parts of the ASSO (Deacon, 1979; Siegel, 2016). Both the Weddell Gyre and the ACC function as transport mechanisms for the recruitment of zooplankton larvae from, for example, the West Antarctic Peninsula (i.e., the 'conveyor belt' mechanism; Figure 4; Siegel, 2016). The formation of sea ice in winter is a major driver of ocean overturning circulation through the release of dense brine into the water column. Sea ice concentration and extent both during winter and summer have major effects on primary as well as secondary production (Nicol *et al.*, 2008). Sea ice serves as a colonization platform for sea ice algae which form an important food resource for pelagic herbivores in winter (Nicol, 2006; Nicol *et al.*, 2008; Flores *et al.*, 2012b). During the springtime sea ice melt, nutrients are released and communities of ice algae seed the surface waters with an initial population of algae, resulting in massive ice edge blooms (Nicol *et al.*, 2008).
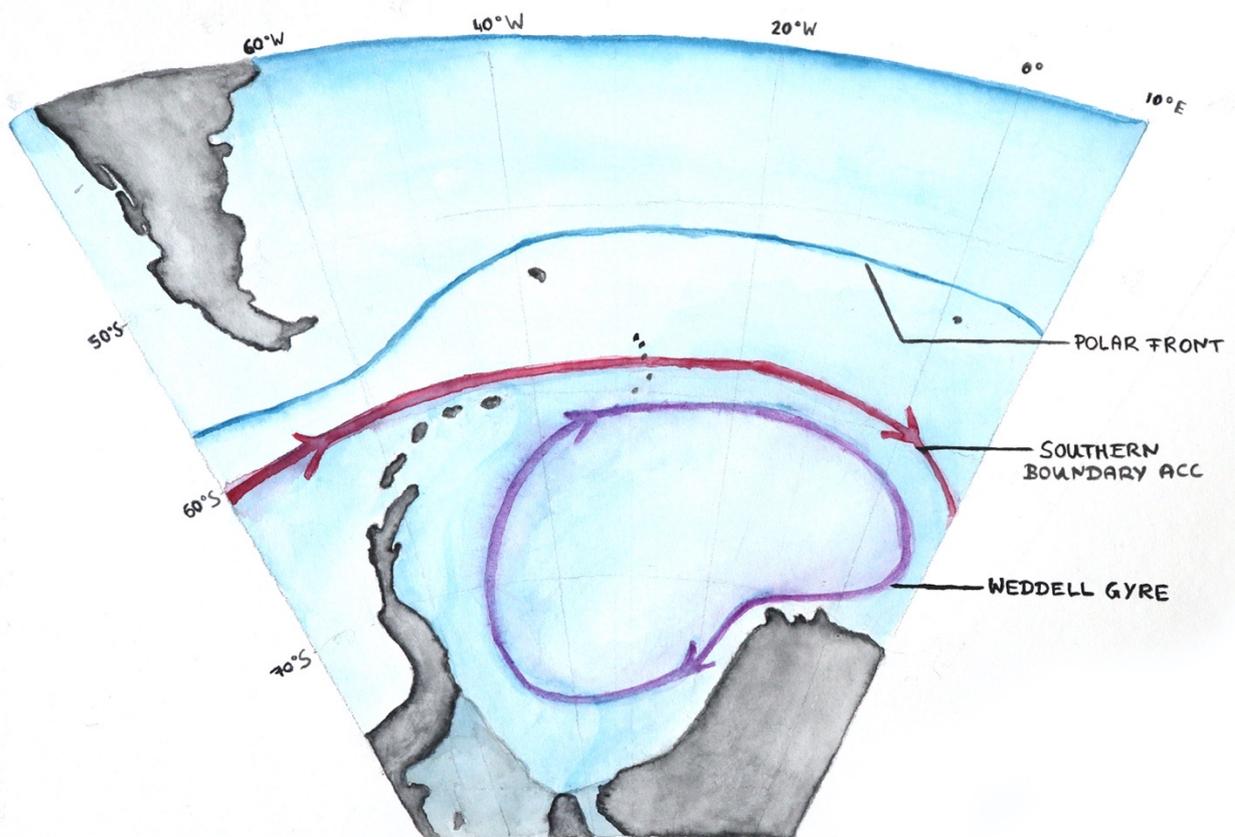
Figure 4. The Atlantic sector of the Southern Ocean (ASSO). The Polar Front defines the northern limit of the Southern Ocean. The southern boundary of the eastward flowing Antarctic Circumpolar Current (ACC) and the Weddell Gyre are key oceanographic features of the ASSO that affect ecological processes.

The ASSO, as well as many other parts of the Southern Ocean, is described as a 'krill-based-ecosystem', in which the Antarctic krill (*Euphausia superba*) acts as a keystone species (Siegel and Loeb, 1995; Nicol *et al.*, 2008). Antarctic krill occurs on a circumpolar scale in large concentrations and high densities, mainly associated with the continental shelf break (Nicol, 2006). The reproductive strategy and life cycle of the Antarctic krill is entirely adapted to the environmental conditions of the Southern Ocean including sea ice dynamics, ocean circulations and light availability, allowing for an optimized recruitment of krill populations (Nicol, 2006; Flores *et al.*, 2012b). In the ASSO, krill densities are highest were the Weddell Sea Gyre meets the ACC (see Figure 4) and the regional krill abundance in summer is positively correlated with the sea ice extent from the previous winter (Nicol, 2006). In

comparison to other sectors of the Southern Ocean (i.e., Indian Ocean sector and Pacific sector), the ASSO is colder, more productive (in terms of primary production), and sustaining greater densities of Antarctic krill (Deacon, 1979). The abundance of Antarctic krill, in the ASSO, is key to the subsistence of various Antarctic and seasonally visiting predator species, as crabeater seals (*Lobodon carcinophaga*), Adélie penguins (*Pygoscelis adeliae*), and multiple baleen whale species (Knox, 2007).

Humpback whales and other baleen whales in the Southern Ocean ecosystem

The Southern Ocean ecosystem sustains many thousand baleen whales in addition to many other smaller krill predator species, such as penguins and pinnipeds (Knox, 2007; Leaper *et al.*, 2008; Boyd, 2009). Eight different baleen whale species, namely the Antarctic blue whale (*Balaenoptera musculus intermedia*), the pygmy blue whale (*Balaenoptera musculus brevicauda*), the fin whale, the Antarctic minke whale (*Balaenoptera bonaerensis*), the dwarf minke whale (*Balaenoptera acutorostrata* subspecies), the Southern right whale (*Eubalaean australis*), the sei whale (*Balaenoptera borealis*), and the humpback whale, are considered *true* Antarctic baleen whales due to their dependence on the Southern Ocean as a habitat (Boyd, 2009). These baleen whale species are highly adapted to efficiently exploit Antarctic krill occurring in high densities and at predictable locales (Nicol *et al.*, 2008) with different baleen whale species usually occupying slightly distinct ecological niches (i.e., specializing on krill in different life-stages; Friedlaender *et al.*, 2006; Friedlaender *et al.*, 2009; Friedlaender *et al.*, 2011). The occurrence of Antarctic krill is dependent on the availability of phytoplankton and especially the availability of large diatoms (Nicol *et al.*, 2010; Siegel, 2016). In the Southern Ocean, the growth of phytoplankton and particularly large diatoms is limited by the availability of dissolved iron in surface waters (Boyd *et al.*, 2007). Baleen whales take an important part in the Southern Ocean iron cycle because these whales recycle iron in surface waters when defecating rapidly dispersing iron-rich feces which, in turn, fertilize phytoplankton blooms (Smetacek and Nicol, 2005; Nicol *et al.*, 2010).

Many baleen whales visit the Southern Ocean as seasonal visitors during the summer months when productivity rates are highest (Knox, 2007). Recent studies, however, also highlighted the importance of this area as an overwintering ground for multiple baleen whale species, such as the Antarctic blue whale, the Antarctic minke whale, and the humpback whale (Širović *et al.*, 2004; Širović *et al.*, 2009;

Van Opzeeland *et al.*, 2013; Thomisch *et al.*, 2016; Filun *et al.*, 2020). Overwintering whales are thought to exploit additional prey resources to fuel growth, pregnancy, or lactation (Craig *et al.*, 2003; Van Opzeeland *et al.*, 2013; Thomisch *et al.*, 2016; Filun *et al.*, 2020). For Antarctic blue whales and Antarctic minke whales, the acoustic recordings of song, moreover, suggested that overwintering individuals also spatially shift their reproductive behavior from low latitudes to the Southern Ocean (Thomisch *et al.*, 2016; Filun *et al.*, 2020).

Humpback whales are one of the most abundant whale species in the Southern Ocean (Branch and Butterworth, 2001). The ASSO is equivalent to management area II (0°-60°W) as defined by the International Whaling Commission (IWC) and at least two humpback whale breeding stocks from the South Atlantic are thought to visit this area during summer: breeding stock A from the southwest Atlantic and breeding stock B from the southeast Atlantic (International Whaling Commission, 2011). The breeding stocks G and C (from the south-eastern Pacific and the south-western Indian Ocean, respectively) are thought to migrate to feeding grounds in the direct vicinity of the ASSO (i.e., within management areas I and III; International Whaling Commission, 2011). Due to the logistical difficulties of data collection in the Southern Ocean, available information on, for example, humpback whale distribution, behavior, and habitat use is generally biased towards lower-latitude regions and/or the summer season (Gibbons *et al.*, 2003; Engel and Martin, 2009; Rosenbaum *et al.*, 2009; Zerbini *et al.*, 2011; Bombosch *et al.*, 2014; Rosenbaum *et al.*, 2014; Amaral *et al.*, 2016). Information on feeding ground occupation by the different humpback whale breeding stocks is lacking, but crucial to management decisions on ecosystem and population conservation (International Whaling Commission, 2011; 2016; Teschke *et al.*, 2016).

Passive acoustic monitoring to study humpback whales in the Southern Ocean

Passive acoustic monitoring (PAM) using autonomous recording systems is one of the most efficient tools to investigate large-scale and long-term patterns in baleen whale occurrence and behavior (e.g., Širović *et al.*, 2013; Risch *et al.*, 2014a; Van Opzeeland *et al.*, 2014; Davis *et al.*, 2017). In the case of the Southern Ocean, PAM is the only tool to study (vocalizing) whales year-round because these data can be collected independently of factors like weather, daylight, and sea ice concentration (Širović *et*

al., 2004; Širović *et al.*, 2009; Širović and Hildebrand, 2011; Van Opzeeland *et al.*, 2013; Thomisch *et al.*, 2016; Miller and Miller, 2018; Roca and Van Opzeeland, 2019; Filun *et al.*, 2020; Shabangu *et al.*, 2020). The implementation of a large-scale and long-term PAM system in the ASSO (Rettig *et al.*, 2013a) allows for the investigation of the acoustic ecology of multiple vocally active marine mammal species in parallel and the generation of baseline data to detect species' responses to environmental and anthropogenic impacts.

Humpback whales have been studied intensively with PAM because humpback whales are vocally active during most times of the year related to different types of behavior (e.g., D'Vincent *et al.*, 1985; Clark and Clapham, 2004a; Darling and Sousa-Lima, 2005; Van Opzeeland *et al.*, 2013; Magnúsdóttir *et al.*, 2014; Fournet *et al.*, 2015). A prerequisite for using PAM to study animal presence or behavior is the production of sounds by the respective animals, meaning that silent individuals will remain undetected. Not much is known about the rates of acoustic activity in humpback whales, except that vocalization rates are highly variable (i.e., 0.1-10 vocalizations per minute; Dunlop *et al.*, 2008; Indeck *et al.*, 2020). Consequently, the absence of humpback whale sound detections does not necessarily imply the physical absence of humpback whales, rather the acoustic activity of humpback whales can be interpreted as "presence-only" data (Moore *et al.*, 2012; Gregr *et al.*, 2013). Nevertheless, spatio-temporal patterns in presence and behavior, such as singing behavior, can be assessed with PAM and for humpback whales, this information is mostly lacking in the ASSO (Van Opzeeland *et al.*, 2013). The analysis of PAM data from the ASSO can help to approach central questions, such as 'How do humpback whales respond to environmental changes?' or 'Which humpback whale breeding stocks mix on the ASSO feeding grounds?'.

Objectives

This PhD thesis project aims at the investigation of humpback whale ecology using an extensive passive acoustic dataset from the ASSO.

The following objectives structured the work during the three-year project duration and shaped the results described in the four presented manuscripts as well as some preliminary results which are discussed in the synthesis:

1. Develop tools to efficiently detect and classify humpback whale vocalizations and song structures

2. Use the acoustic presence of humpback whales to infer spatio-temporal patterns in their distribution and relate these patterns to variabilities in the environment

3. Investigate the spatio-temporal pattern in humpback whale song occurrence and structure in the ASSO to fill knowledge gaps on humpback whale behavioral ecology in the Southern Ocean

4. Asses if the ASSO feeding ground is frequented by different humpback whale breeding populations by using song comparison analyses

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Chapter I

Large-scale spatial variabilities in the humpback whale acoustic presence in the Atlantic sector of the Southern Ocean

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Large-scale spatial variabilities in the humpback whale acoustic presence in the Atlantic sector of the Southern Ocean

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Southern Hemisphere humpback whales (*Megaptera novaeangliae*) inhabit a wide variety of ecosystems including both low- and high-latitude areas. Understanding the habitat selection of humpback whale populations is key for humpback whale stock management and general ecosystem management. In the Atlantic sector of the Southern Ocean (*ASSO*), the investigation of baleen whale distribution by sighting surveys is temporally restricted to the austral summer. The implementation of autonomous passive acoustic monitoring, in turn, allows the study of vocal baleen whales year-round. This study describes the results of analysing passive acoustic data spanning 12 recording positions throughout the *ASSO* applying a combination of automatic and manual analysis methods to register humpback whale acoustic activity. Humpback whales were present at nine recording positions with higher acoustic activities towards lower latitudes and the eastern and western edges of the *ASSO*. During all months, except December (the month with the fewest recordings), humpback whale acoustic activity was registered in the *ASSO*. The acoustic presence of humpback whales at various locations in the *ASSO* confirms previous observations that part of the population remains in high-latitude waters beyond austral summer, presumably to feed. The spatial and temporal extent

of humpback whale presence in the *ASSO* suggests that this area may be used by multiple humpback whale breeding populations as a feeding ground.

1. Introduction

Humpback whales (*Megaptera novaeangliae*) inhabit all major oceans and have adapted to diverse ecosystems, including polar and subpolar ecosystems mainly to feed during the summer months, and equatorial ecosystems almost exclusively to breed and calve throughout the winter months (e.g. [1–5]). To reach the most productive feeding areas, humpback whales undertake one of the longest mammalian migrations, stretching between their low-latitude breeding grounds and mid- to high-latitude feeding grounds [6,7]. As in other baleen whale species, migratory behaviour, in humpback whales, is characterized by population-specific spatio-temporal patterns, but is also flexible in terms of destinations and timing, including the omission or delay of migration or the spatial adaptation of migration routes [3,7–10]. Less extreme migratory deviations are very common in many baleen whale populations worldwide. Individuals or groups of baleen whales frequently extend their stay in productive feeding areas beyond the summer months in order to maximize energy uptake [9,11]. The Southern Ocean includes the most important feeding areas for baleen whales in the Southern Hemisphere [12], but knowledge on the year-round distribution of baleen whales in many regions of the Southern Ocean is still limited due to the restricted accessibility of these areas outside the summer months. Baseline information on baleen whale distribution and ecology is key for understanding their role as large predators in structuring the Southern Ocean ecosystem [13].

One presumed high-latitude feeding area for humpback whales is the Atlantic sector of the Southern Ocean (hereinafter referred to as *ASSO*). The *ASSO* is equivalent to the management area II defined by the International Whaling Commission (IWC) and is thought to serve as a feeding area for two humpback whale breeding stocks from the South Atlantic: breeding stock A from the southwest Atlantic and breeding stock B from the southeast Atlantic [14]. The *ASSO* is a typical Southern Ocean ecosystem dominated by sea ice dynamics, the Antarctic Circumpolar Current (ACC) and associated fronts and boundaries, and the Weddell Sea Gyre [15–17]. Sea ice concentration and extent both during winter and summer have major effects on primary as well as secondary production [15]. The Southern Boundary of the ACC creates various productivity hotspots around the Antarctic continent due to its high concentration of nutrient-rich Upper Circumpolar Deep Water [18]. The Weddell Gyre acts as an insulating current system which regulates temperature in the Weddell Sea and efficiently circulates nutrients, phytoplankton and zooplankton throughout great parts of the *ASSO* [16,19]. Both the Weddell Gyre and the ACC function as transport mechanisms (e.g. the 'conveyor belt') for the recruitment of zooplankton larvae from other Antarctic regions such as the West Antarctic Peninsula [19]. In comparison with the other sectors of the Southern Ocean (i.e. Indian Ocean sector and Pacific sector), the *ASSO* is colder, more productive (in terms of primary production), and therefore sustaining larger densities of Antarctic krill (*Euphausia superba*) [16]. The abundant availability of Antarctic krill is key to the subsistence of various Antarctic and seasonally visiting predator species, such as crabeater seals (*Lobodon carcinophaga*), Adélie penguins (*Pygoscelis adeliae*) and humpback whales [12].

Recent studies using passive acoustic monitoring (PAM) have discovered that at least parts of the Antarctic blue whale and humpback whale populations even remain in the *ASSO* during austral winter [11,20]. Large-scale trends of the humpback whale distribution, however, remain unexplored. Particularly, in the oceanic regions of the *ASSO*, the distribution patterns of humpback whales are to date largely unknown, although these regions are assumed to be the main migratory destinations of humpback whales from the South Atlantic [21–24].

Technological advances in the fishing industry and predicted climate change might open up new opportunities for the krill fishery shifting fishing grounds further south, where most favourable krill habitats are located [25,26]. Insights into spatio-temporal patterns in the distribution of humpback whales throughout the *ASSO* are therefore of crucial importance for effective management and conservation planning, e.g. by the International Whaling Commission [24]. Furthermore, the scientific community has also proposed the establishment of a Marine Protected Area (MPA) in the Weddell Sea, which aims to also include areas ecologically relevant to large marine predators [25]. Baseline data on the distribution and abundance of species that rely on the resources provided by the Weddell Sea area, such as humpback whales, are crucial for the planning and eventually also the approval of an MPA in the *ASSO*.

This study aims to investigate the year-round distribution of humpback whales over the full spatial range of the *ASSO* by analysing the passive acoustic data collected by a network of 12 simultaneously recording receivers. Humpback whales are a highly vocal species producing sounds on the breeding and feeding grounds as well as during migration, which makes them a suitable species for PAM-based studies [20,27,28]. Through the analysis of a spatially extensive dataset from the *ASSO*, we will explore the spatio-temporal variability in the occupancy of potential feeding areas in the *ASSO* by Southern Hemisphere humpback whales.

2. Material and methods

2.1. Passive acoustic data

Humpback whale acoustic behaviour was investigated using data from 12 recording positions throughout the *ASSO* (table 1 and figure 1), which recorded simultaneously in 2013 (figure 2). Passive acoustic recordings were obtained using SonoVaults (Develogic GmbH, Hamburg; Reson TC4037-3 hydrophone, -193 dB re1 V µPa^{-1} hydrophone sensitivity, 48 dB amplification gain, 24 bits resolution) operated on a continuous recording scheme and with a sampling rate of 5333 or 9600 Hz (table 1). The recorders were deployed as part of oceanographic moorings with multiple instruments installed on a vertical line which usually extended to 800 m as the shallowest depth (to avoid being damaged by drifting icebergs; except for the mooring position W12 off Elephant Island, where the water depth was only 300 m) (see also [29–31] for more information on the HAFOS moorings).

2.2. Automatic detection and classification of humpback whale vocalizations

All available passive acoustic data were processed by the 'low-frequency detection and classification system' (LFDCS) developed by Baumgartner & Mussoline [32] and a custom-made acoustic-context filter to detect humpback whale acoustic presence on an hourly basis. LFDCS was set up with a customized call library based on the most common vocalization types of humpback whales and other acoustically abundant Antarctic marine mammal species (i.e. Antarctic minke whale (*Balaenoptera bonaerensis*), killer whale (*Orcinus orca*), Weddell seal (*Leptonychotes weddellii*), crabeater seal, leopard seal (*Hydrurga leptonyx*) and Ross seal (*Ommatophoca rossii*)) [27,32–37]. Parameter settings and thresholds of LFDCS and the acoustic context filter were tuned employing multiple test datasets to optimize the automatic detection of humpback whale vocalizations to the requirements of this study. Detailed information on set-up and test runs of the automatic detection process are provided in the electronic supplementary material. Resulting detected hours with presumed humpback whale acoustic presence are termed *presumed Humpback Whale Presence* (*pHWP*) hereinafter.

2.3. Manual post-processing of detection results

To limit the temporal effort of manual post-processing, only even *pHWP* hours (i.e. hours starting at 00.00, 02.00, 04.00, 06.00, 08.00, 10.00, 12.00, 14.00, 16.00, 18.00, 20.00, 22.00) were included in the further analysis. We evaluated if subsampling only the even hours would not affect the results by performing comparative analyses for two recorders (from 2011) for which all hours were manually analysed. From this full dataset, only even hours were subsampled and the acoustic presence at odd hours was interpolated (condition: two consecutive even hours with acoustic presence determines acoustic presence in intermediate odd hour). When comparing the interpolated results with the original results, similarity between the subsampled-interpolated and full datasets was above 95%. Therefore, acoustic presence in consecutive even hours in the large majority of cases indicates acoustic presence in the intermediate odd hour. Given that the number of acoustic presence hours is underestimated, i.e. approximately halved, our results are all presented as proportions of hours per day or per month. Four human analysts revised even *pHWP* hours visually and aurally for the presence of humpback whale vocalizations by creating spectrograms in Raven Pro 1.5 (Hann Window, 1025–1790 window size, 80% overlap, 2048 DFT size; Bioacoustics Research Program 2014). Spectrograms were screened for humpback whale vocalizations by viewing windows of 60 s duration, spanning 0 to 1.80 kHz. Hours with confirmed humpback whale acoustic presence (herein referred to as *confirmed Humpback Whale Presence*; *cHWP*) could contain both humpback whale social calls and humpback whale song. The level of agreement in manually classifying *cHWP* and false-positive hours between the principal analyst and the other three analysts was calculated on
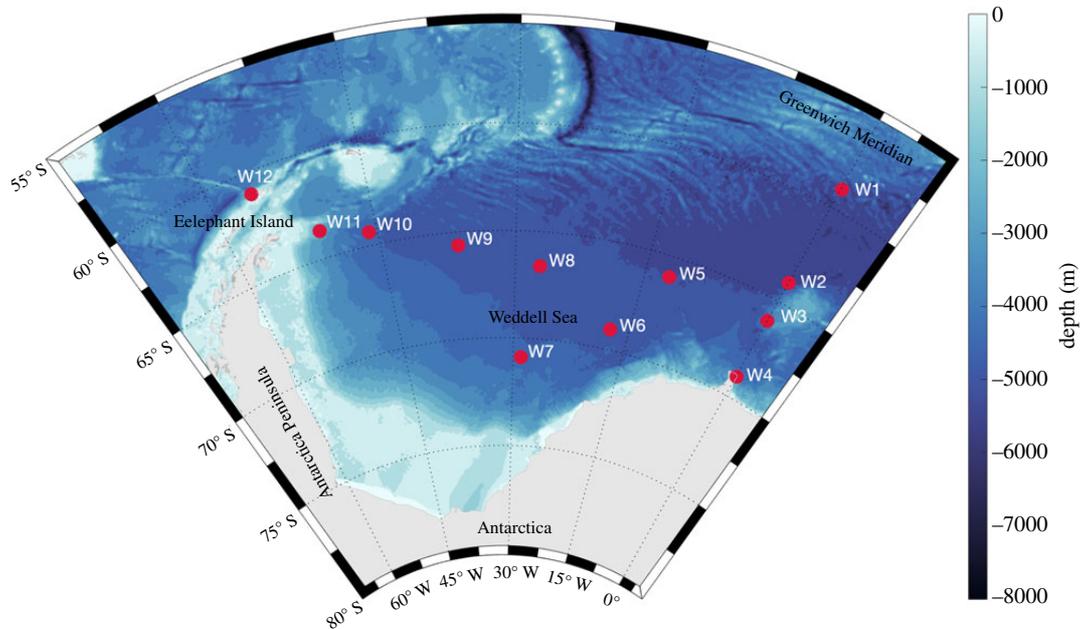
Figure 1. Bathymetric map of the *ASSO* and the geographical positions of the 12 bottom-moored recorders included in this study.

Table 1. Information on passive acoustic recordings included in the dataset. For reference to earlier publications, the original mooring ID is listed in brackets.

mooring ID	latitude	longitude	recorder ID	sampling frequency (Hz)	deployment depth (m)
W1 (AWI227)	59 2.82° S	000 5.78° E	SV1025	5333	1020
W2 (AWI229)	63 59.85° S	000 1.84° E	SV1010	5333	998
W3 (AWI230)	66 2.01° S	000 3.12° E	SV1009	5333	949
W4 (AWI232)	68 59.94° S	000 4.38° E	SV1011	5333	958
W5 (AWI248)	65 58.09° S	012 15.12° W	SV1013	5333	1081
W6 (AWI245)	69 3.480° S	017 23.32° W	SV1012	5333	1065
W7 (AWI249)	70 53.55° S	028 53.47° W	SV1014	5333	1085
W8 (AWI209)	66 36.45° S	027 7.26° W	SV1028	5333	1007
W9 (AWI208)	65 37.23° S	036 25.32° W	SV1030	5333	956
W10 (AWI217)	64 22.94° S	045 52.12° W	SV1020	5333	960
W11 (AWI207)	63 42.09° S	050 49.61° W	SV1033	9600	1012
W12 (AWI251)	61 1.07° S	055 58.67° W	SV1008	5333	212

varying test datasets of at least 150 *pHWP* hours (presented in Results). Hourly humpback whale acoustic presences were transformed into proportion of *cHWP* hours per day. Proportions of *cHWP* hours per day were averaged per month and respective standard deviations were calculated or the monthly acoustic presence was calculated as the number of *cHWP* hours per month divided by the total number of recording hours of the respective month.

2.4. Sea ice data

The sea ice concentration data used for this study were extracted from: a combination of satellite sensor data from the Nimbus-7 Scanning Multichannel Microwave Radiometer (SMMR), the Defense Meteorological Satellite Program (DMSP) -F8, -F11 and -F13 Special Sensor Microwave/Im rs (SSM/Is) and the DMSP-F17 Special Sensor Microwave Imager/Sounder (SSMIS), with a grid size of 25 km [38]. The data were used to calculate the daily sea ice concentration of the area within 50 km radius around each recording location, with the Daily Antarctic Sea Ice Concentration packages in Matlab
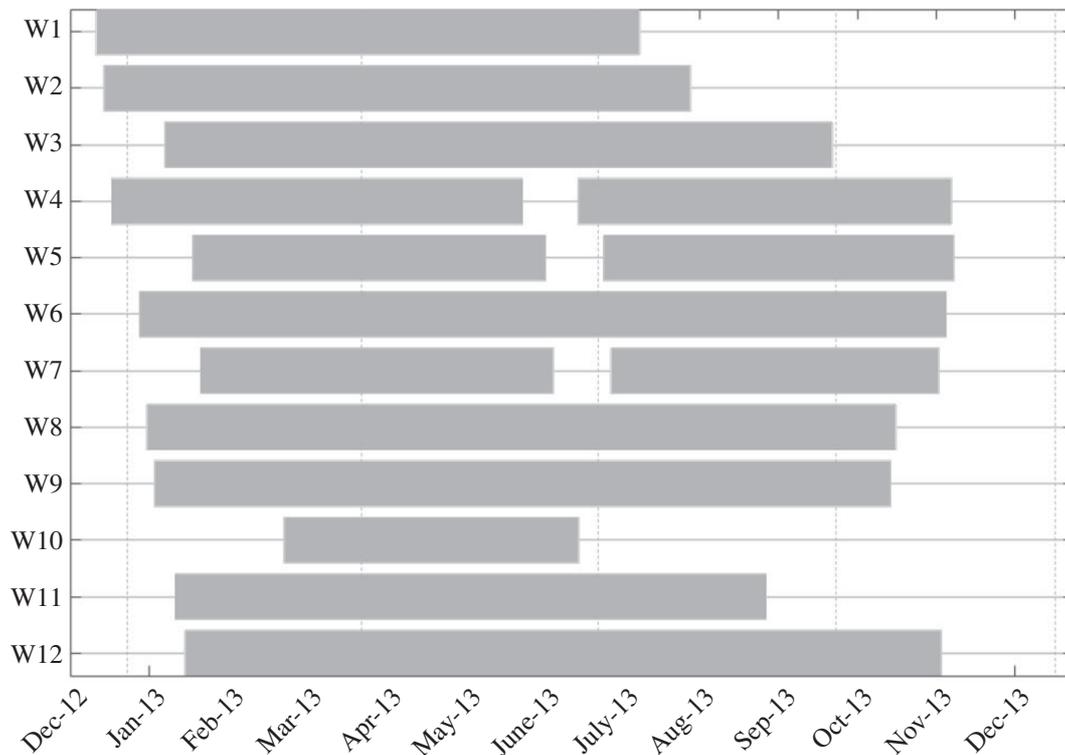
Figure 2. Timeline showing the availability of passive acoustic data collected throughout 2013 for the 12 recording positions in the *ASSO*.

[39]. The radius of 50 km was chosen because the acoustic range of humpback whales in the *ASSO* was estimated at 2–78 km [20]. Additionally, the data were used to calculate monthly averages of sea ice concentrations for the *ASSO* and plotted as maps with the Antarctic Mapping Tools and Daily Antarctic Sea Ice Concentration packages in Matlab [39,40]. In order to test for correlations between humpback whale acoustic presence and the local sea ice concentration, the Pearson correlation coefficient was calculated for four different temporal regimes: Comparing monthly averages, comparing three-monthly averages starting in January (i.e. JFM, AMJ, etc.), comparing three-monthly averages starting in February (i.e. FMA, MJJ, etc.), and comparing three-monthly averages starting in March (i.e. MAM, JJA, etc.).

3. Results

In total, 74 628 h of recordings were processed, of which 13 049 were *pHWP* hours. Roughly half of these hours were post-processed by human analysts and, summing all recording locations, 983 h were verified as *cHWP* hours (table 2). Among the four analysts, the level of agreement in classifying *cHWP* or false positive hours was between 93% and 97%.

3.1. Spatial pattern

During austral summer and autumn (January–June) in 2013, nine of the 12 recording positions recorded humpback whale vocalizations (table 2). At the positions W10, W11 and W7 humpback whale acoustic presence could not be confirmed in 2013 (i.e. considering only the even recording hours were included in the analyses; table 2 and figure 3). At most recording positions (W9, W8, W6 and W4), the monthly acoustic presence of humpback whales was not higher than 10% (figure 3). The recording positions W5 and W12 registered monthly humpback whale acoustic presences of up to 20% and at the recording position off Elephant Island (W12), humpback whales were acoustically active during all recorded months of the year 2013 (figure 3). The highest monthly acoustic presences of humpback whales (i.e. greater than 20%) were confirmed at the four recording positions W3, W2 and W1 on the Greenwich Meridian (figure 3). Monthly acoustic presences of more than 10% were only registered in areas without sea ice cover, and, in most cases, monthly acoustic presences of 0% were only registered in areas with a sea ice concentration of at least 50%. In the central Weddell Sea, humpback whales were only sporadically acoustically present (i.e. less than or equal to 10%), which presumably was
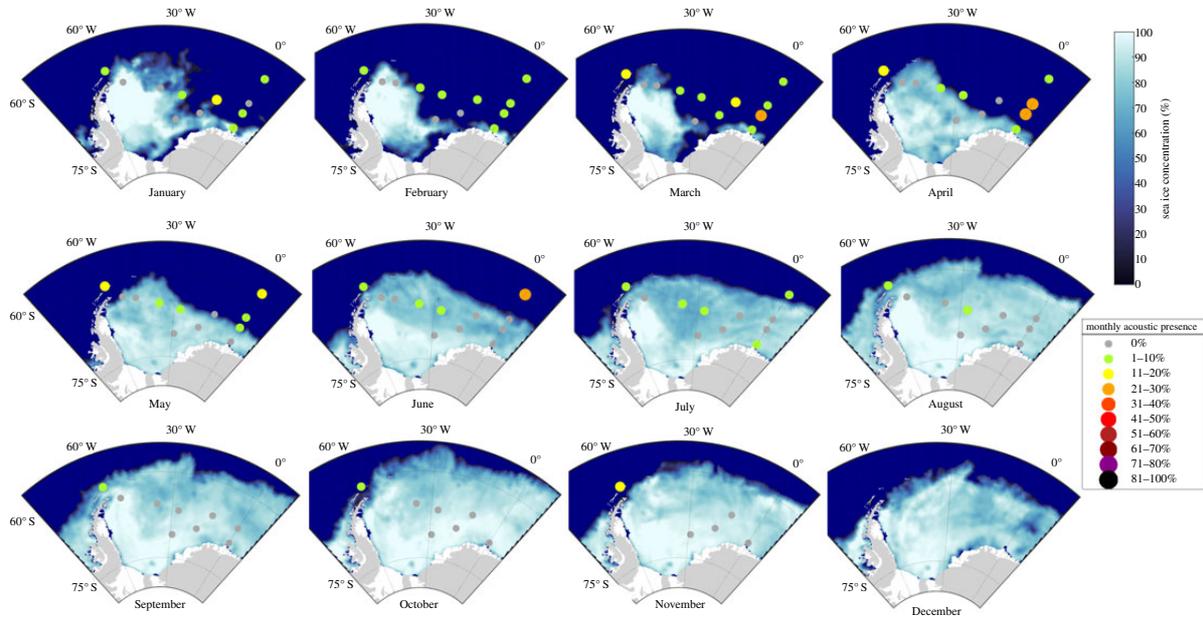
Figure 3. Percentage of acoustic presence of humpback whales in the *ASSO* averaged per recording location and month for the year 2013. Size and colour of dots indicates a respective range of percentage of hours per month with humpback whale acoustic presence. The monthly averaged sea ice concentrations are depicted at a 25 × 25 km resolution.

Table 2. Overview of recording hours, presumed humpback whale acoustic presence (*pHWP*) hours, post-processed hours and confirmed humpback whale acoustic presence (*cHWP*) hours per recording location and as an overall sum.

mooring ID	total hours	*pHWP* hours	hours post-processed	*cHWP* hours
W1	5140	584	284	200
W2	5538	628	306	157
W3	6316	826	428	203
W4	7386	1958	993	23
W5	6649	1440	739	77
W6	7630	163	85	10
W7	6424	312	157	0
W8	7077	1639	823	16
W9	6973	1159	594	46
W10	2767	452	230	0
W11	5558	923	460	0
W12	7170	2965	1476	251
total	74 628	13 049	6575	983

related to the fact that the area was covered with sea ice over extended periods (figure 3). At positions W11, W10 and W7, which were covered by sea ice almost year-round, humpback whales were acoustically absent throughout 2013.

3.2. Intra-annual temporal pattern

From January until May 2013, at least 50% of recording positions registered humpback whale acoustic presences (figures 3 and 4). In March 2013, humpback whales were acoustically present at the largest proportion of the recording positions (9 out of 12). At recording position W6, for example, humpback whales were acoustically present exclusively during a continuous period of 4 days, between 18 March 2013 and 21 March 2013. At the recording position W5, humpback whales were acoustically present in January, February and March 2013 (figure 4). April 2013 was the month with the highest
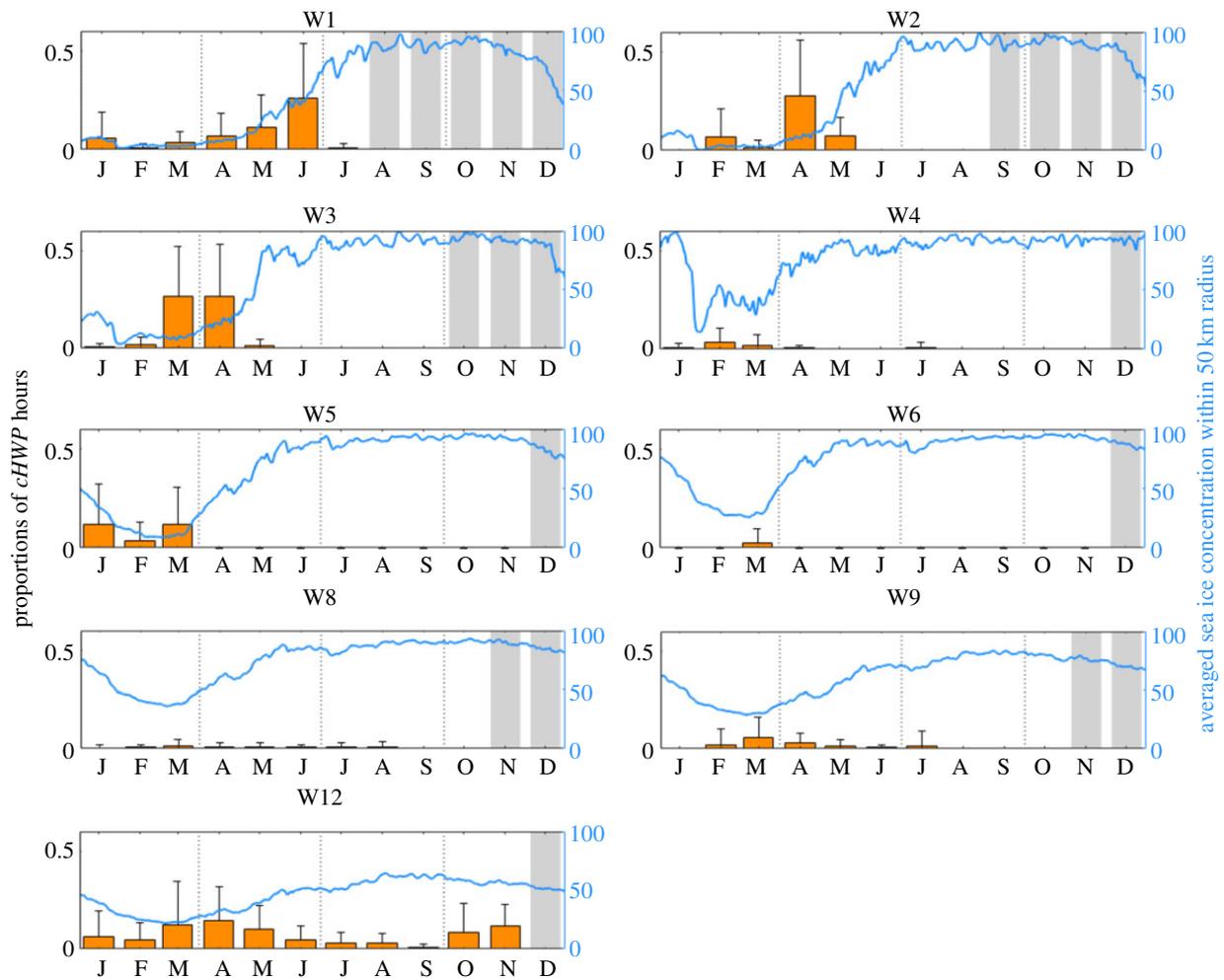
Figure 4. Average proportion of confirmed humpback whale presence (*cHWP*) hours per month at the nine recording positions, W1, W2, W3, W4, W5, W6, W8, W9 and W12 from January until December 2013 (orange bars). Vertical error bars show the respective standard deviations and continuous grey bars represent months without recording data. The blue solid lines and the right *y*-axis depict the daily averaged sea ice concentration per location within a 50 km radius (average sea ice concentration data for recording position W12 has to be interpreted with caution, as data pixels along the coast, covering both oceanic and ice shelf areas, remain masked in the dataset used, i.e. are biased towards high values). At three recording positions (W7, W10 and W11) humpback whales were acoustically absent, graphs are therefore not displayed.

proportion of *cHWP* hours summed over all recording positions. Off Elephant Island (W12) the peak periods for humpback whale acoustic presence were March until May and October and November (figure 4). During the months January and February and June until September only sporadic acoustic presence (i.e. only single hours) was confirmed at the recording position W12 (figure 4). Similarly, sporadic acoustic presence of humpback whales was registered for January/February until August/ July at recording positions W8 and W9, respectively (figure 3). At the recording positions W1 to W3 at the Greenwich Meridian the acoustic presence of humpback whales was strongly seasonal: humpback whales were acoustically present between January and July with peak periods in March until June (depending on the position; figure 4). By contrast, at the southernmost recording position at the Greenwich Meridian (W4), *cHWP* hours were confirmed sporadically in the months January, February, March, April and July (figure 4).

3.3. Diurnal pattern

The data of most recording positions did not show diurnal patterns in humpback whale acoustic presence when comparing the proportions of (even) hours of the day with confirmed humpback whale acoustic presence per month against each other. For example, at the recording position W12 off Elephant Island (figure 5), but also at the positions W3, W4, W5, W6, W8 and W9, humpback whales were acoustically present during seemingly random hours of the day (W7, W10 and W11 did not record humpback whale vocalizations at all). Only at the recording positions W1 and W2 a weak diurnal pattern can be detected during the months May and June (figure 5). During these months,
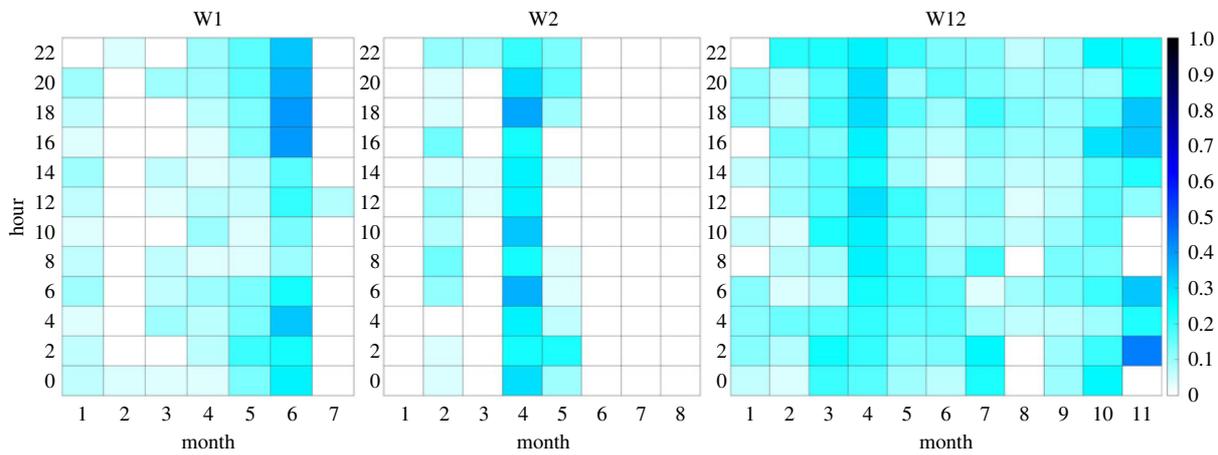
Figure 5. Diurnal pattern per month at the recording positions W1, W2 and W12. At the three recording positions W7, W10 and W11 humpback whales were acoustically absent, graphs are therefore not displayed. The diurnal pattern at W3, W4, W5, W6, W8 and W9 was similarly random as at W12, therefore these graphs are also not displayed. Proportions of confirmed humpback whale presence (*cHWP*) hours were calculated for each hour of the day and month of the year 2013. The *y*-axes only display even hours, because only even hours were analysed in this study.

humpback whales were less acoustically active in the morning and during midday (i.e. from 06.00/08.00 until 14.00/16.00; figure 5).

3.4. Spatio-temporal trends in relation to sea ice

The spatial pattern of humpback whale acoustic presence in the *ASSO* can be reduced to a longitudinal and a latitudinal trend. The longitudinal trend was characterized by minimal average proportions of *cHWP* hours at the central longitudes of the study area, while at the western and eastern edges of the study area the highest average proportions of *cHWP* hours were recorded. In turn, the latitudinal trend was clearly linear, with increasing average proportions of hourly acoustic presences at decreasing latitudes (i.e. from south to north). Both spatial trends are connected to the spatial extent of the sea ice cover which temporally opened up especially at the western, eastern and northern edges of the *ASSO*, but which was present year-round in the southern-central part of the Weddell Sea (figure 3).

The intra-annual temporal pattern of humpback whale acoustic presence in the *ASSO* was not clearly driven by sea ice concentration. Monthly and three-monthly averages of humpback whale acoustic presence were only weakly correlated with the local sea ice concentration (within a 50 km radius). The pronounced seasonal acoustic presence of humpback whales at the Greenwich Meridian (three oceanic recording positions W1–W3) nevertheless seems to be connected to the presence of sea ice. During the rapid decrease in sea ice concentration in the beginning of summer, humpback whale acoustic presence was generally low at the Greenwich Meridian (figure 4). The first acoustic activity of humpback whales in the season was within 1 day and 56 days after the sea ice concentration dropped below 15% (for definition sea ice edge, see [41]). At all three oceanic recording positions (i.e. W1–W3), the proportion of *cHWP* hours peaked simultaneously with the rapid increase of the sea ice concentration in late summer/autumn (figure 4). The last acoustic activity of humpback whales in the season was within 39 to 67 days after the sea ice concentration exceeded 15%. At all recording locations on the Greenwich Meridian, the proportion of *cHWP* hours declined when the sea ice concentration exceeded 50% (figure 4).

4. Discussion

4.1. Spatial distribution

Our results confirm earlier observations that the *ASSO* is likely to form an important feeding area for humpback whales from the South Atlantic (breeding stock A off the coast of Brazil and stock B off the coast of Angola/Gabon, see [14]). Humpback whales are known to migrate between ocean basins and migration from the eastern South Pacific and western Indian Ocean into the *ASSO* has been suggested as well [6,14,42]. The highest proportions of *cHWP* hours were recorded at the eastern and western edges of our study area, which are the direct longitudinal extensions of the South American and

African continents. In the Southern Hemisphere, migrating humpback whales are often observed to travel along or close to coastlines, where coastal fronts are thought to aid navigation and provide chances for opportunistic feeding [23,43–45]. The eastern and western acoustic hotspots in our data could therefore reflect humpback whale migratory routes along the eastern/western coastline of South America/South Africa extending south towards the Antarctic continent. Satellite tracking studies targeting humpback whales off Brazil, Gabon and South Africa revealed possible summer feeding destinations north of 60° S in the waters around South Georgia, the South Sandwich Islands and Bouvet Island, but did not register any movements inside the Southern Ocean [21–24]. Besides the favourable position in terms of distance to breeding areas, the eastern and western edges of the *ASSO* could also present areas of elevated food availability; the coastal areas around the northern part of the Western Antarctic Peninsula are known for high densities of Antarctic krill and smaller krill hotspots can also be found along the Greenwich Meridian [19,46].

Alternatively, the observed longitudinal trend could reflect an underlying latitudinal trend. At the eastern and western edges of the *ASSO*, data collection was biased towards lower latitudes, where generally more calls were recorded compared with the higher latitude recording sites. Our data show a clear latitudinal trend with the highest proportions of *cHWP* hours at the most northern recording positions. There are several possible explanations if this trend is real. First, it could be related to the trade-off between the cost of migration and the energetic gain of feeding in high-latitude waters [47,48]. Southern Hemisphere humpback whales migrate southward with the retreating sea ice edge to search for high densities of near-surface swarms of euphausiids in order to maximize their energy intake [47,48]. To minimize the energetic effort, they possibly only travel as far south as necessary to restore energy reserves. An alternative explanation for the observed latitudinal trend is that humpback whales decrease their vocal activity as they move south, e.g. determined by decreasing hormone levels in spring [49]. Humpback whales are sometimes sighted south of 70° S, indicating that single whales are roaming these waters, but might not be acoustically active during this time [50]. Further collection of passive acoustic data over a longer period of time (i.e. longer than one year) combined with visual data are underway and will make it possible to draw further conclusions on these observations.

4.2. Seasonal and diurnal patterns in humpback whale acoustic presence

Humpback whale movement strategies in the *ASSO* are probably optimized in terms of the energy gain and costs, most likely driving intra-annual and potentially even diurnal patterns of acoustic presence in the *ASSO*. Individual humpback whales are likely to adapt their habitat selection and migratory behaviour on the feeding grounds based on their life stage, reproductive status and body condition, as has been confirmed for many baleen whale species [7,51]. This diverse repertoire of migratory behaviour and the ability to adapt to the local environment probably explains the observed seasonal fluctuation in humpback whale acoustic absence and presence throughout the study area.

Summarizing all recording positions, our data indicate humpback whale presence in the *ASSO* during all months of the year, except December. However, for all locations, overall data coverage for December was poor (only a few days during December 2012) which could have affected detection probability of calls. In January and February, also only low proportions of *cHWP* hours were recorded at all recording locations, while overall data coverage was good for these months. These months could either be the time with the fewest or no humpback whales present in the *ASSO*, or represent a period during which whales do not or only rarely vocalize. From ship-based sighting surveys, it is known that humpback whales are regularly sighted in the *ASSO* from December to February [50,52–60], indicating that humpback whales are physically present in the area but may be less vocal during this time. This finding temporally matches the singing pause registered for Northern Hemisphere humpback whales from June to August, when humpback whales probably concentrate on feeding activities to rapidly restore their energy budgets [61].

The virtually basin-wide and near year-round acoustic presence of humpback whales reported in this study suggests that individuals frequenting this area may regularly deviate from the traditional migration model. During austral winter, at least some humpback whales seem to remain in areas of the *ASSO* without sea ice cover, e.g. the waters around Elephant Island or coastal polynyas close to the Antarctic continent (recording position W4 and also see [20]). Similar to what has been reported for humpback whales from other ocean basins, humpback whales migrating in and out of the *ASSO* are likely to exhibit diverse migration strategies [20], potentially including sex- and age-dependent differences in timing of migration, as well as the complete omission of migration during some years [7,9,51,62,63]. During March, humpback whales were acoustically present at the most recording locations

simultaneously (nine out of 12). March could be the time of the year, when most humpback whales, including all sex and age classes, are arriving at the feeding areas in the Southern Ocean, which in turn causes a higher spatial dispersal of feeding individuals or groups to avoid competition. April, May, June were the months with the highest proportions of cHWP hours recorded during this study. A high proportion of the acoustic activity during these months was attributed to singing humpback whale males (preliminary analyses show up to 50% of the vocal activity consists of song which is known to be exclusively produced by males; Schall *et al.* unpublished data). The austral fall forms part of the 'pre-breeding shoulder season', which is the period preceding the breeding season. During this time humpback whale males start singing before or while migrating to the breeding grounds, presumably to improve their chances of mating success [5]. During the months August/September generally low proportions of cHWP hours were recorded at all recording locations. August and September most likely represent the months during which fewest individual humpback whales are present in the *ASSO*, because most (vocally active) individuals spend this time at their low-latitude breeding grounds [10,64,65].

Our recordings did not exhibit any clear diurnal pattern for the acoustic activity of humpback whales in the *ASSO*, which suggests opportunistic sound production during random times of the day. During austral summer, humpback whales might prioritize restoring their energy reserves in a time-efficient manner and might be concentrating most of their activities on feeding and searching for prey. In the waters off the western Antarctic Peninsula, tagging studies have shown that humpback whales follow a diel feeding pattern, with most feeding dives occuring at night when krill swarms are closer to the surface [66]. This vertical migration in Antarctic krill has been described for various regions in the Southern Ocean, although the pattern is not consistent for all regions across the Southern Ocean (see [19] for overview). Humpback whales in the *ASSO* might therefore feed and vocalize rather opportunistically, adapting their behaviour to changes in local prey availability and the presence of conspecifics.

4.3. Spatio-temporal trends and sea ice

The estimated correlation between humpback whale acoustic presence and sea ice concentration was weak. It cannot be excluded that this weak correlation is a consequence of inaccuracies in the sea ice concentration data, which might be biased towards high values due to merging ice shelf areas with oceanic areas for pixels intersecting the coast [38]. The recordings from the Greenwich Meridian suggest that humpback whales moved south, following the retreating sea ice edge. Humpback whales generally seem to prefer open water or larger ice-free areas within the sea ice (i.e. polynyas), which is probably related to the easier access to ice-free space for breathing [20,67]. Along the sea ice edge, humpback whale feeding groups could also be exploiting the high densities of krill, characteristic for the marginal ice zone [19,68]. The dynamic interactions between nutrient supply by melting sea ice, open water fuelling primary production and sea ice as a key habitat for juvenile krill [69–71] influence prey availability for humpback whales in the *ASSO* in a complex spatio-temporal arrangement [72].

4.4. The *ASSO* humpback whale feeding ground

The *ASSO* is probably a feeding ground for at least two humpback whale breeding populations [6,14,42]. The distinct peaks of acoustic activity detected at the eastern and western edges and potentially even the differentiation of temporal patterns (i.e. the western edge with a rather continuous acoustic presence pattern and the eastern edge with a seasonal acoustic presence pattern) may be reflective of the presence of two distinct humpback whale populations. The spatial segmentation of the *ASSO* feeding ground for the distinct humpback whale breeding populations as well as the potential overlap in the occupied area among these populations represents baseline knowledge necessary for efficient stock management and deserves further investigation. Our study, among many others (e.g. [11,20,73]), has proven remote PAM as very effective for the study of highly mobile marine mammal species in the Southern Ocean. The more detailed analysis of humpback whale acoustic recordings can provide further information on male singing behaviour, which is thought to a be a population-specific reproductive display [74,75].

The attribution of specific feeding grounds to the humpback whale populations in the Southern Hemisphere, as well as the level of connectivity among these distinct breeding stocks are still largely unresolved [24]. Both the political difficulties of implementing dynamic conservation strategies for migratory species as well as the need to estimate the ecological capacity of the *ASSO* food web for krill fishery stock management, would profit from insights in the distribution range for individual humpback whale stocks. Ongoing investigations of humpback whale songs in the *ASSO* are therefore aimed at obtaining such fundamental insights into the population-specific distribution patterns within this important Southern Ocean feeding ground.

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Chapter II

Multi-year presence of humpback whales in the Atlantic sector of the Southern Ocean but not during El Niño

Multi-year presence of humpback whales in the Atlantic sector of the Southern Ocean but not during El Niño

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Abstract

Humpback whales are thought to undertake annual migrations between their low latitude breeding grounds and high latitude feeding grounds. However, under specific conditions, humpback whales sometimes change their migratory destination or skip migration overall. Here we document the surprising persistent presence of humpback whales in the Atlantic sector of the Southern Ocean during five years (2011, 2012, 2013, 2017, and 2018). However, in the El Niño years 2015 and 2016, humpback whales were virtually absent. Our data show for the first time that humpback whales are systematically present in the Atlantic sector of the Southern Ocean and suggest that these whales are particularly sensitive to climate oscillations which have profound effects on winds, sea ice extent, primary production, and especially krill productivity.

Introduction

Humpback whales (*Megaptera novaeangliae*) inhabit all major oceans but these iconic large predators were thought to extend their range to polar and subpolar ecosystems only to feed during the summer months (Clapham, 2018). To reach these high latitude productive feeding areas, humpback whales undertake one of the longest mammalian migrations (Stevick *et al.*, 2010). In the Atlantic sector of the Southern Ocean (ASSO), the investigation of humpback whale distribution by ship-based sighting surveys is only feasible during the austral summer and still limited due to necessary logistic effort. Therefore, systematic data on their (year-round) presence, abundance, and spatial distribution are missing for the ASSO. Insights on distribution are however vital for understanding their present and future role as large predators in structuring the Southern Ocean ecosystem (Smetacek and Nicol, 2005; Nicol *et al.*, 2010). A long-term autonomous passive acoustic monitoring (PAM) network was installed in 2010 to record humpback whales in their natural Antarctic environment year-round. Humpback whales are excellent candidates for PAM studies due to their year-round vocal activity of all sex and age classes (Stimpert *et al.*, 2011b; Van Opzeeland *et al.*, 2013; Dunlop, 2017). To improve the understanding of the ecological conditions under which humpback whales use the area as a feeding ground, we investigated the inter-annual changes in humpback whale acoustic presence in relation to three environmental parameters that are key to the Southern Ocean: 1) The Southern Annular Mode (SAM) which is the dominant pattern of natural climate variability in polar and subpolar regions of the Southern Hemisphere. 2) The El Niño Southern Oscillation (ENSO) causes periodic fluctuation of sea surface temperature and air pressure originating from the tropical Pacific. Both climate oscillations have large effects on the Southern Ocean productivity (Loeb *et al.*, 2009; Loeb and Santora, 2015; Siegel, 2016; Atkinson *et al.*, 2019). 3) Local sea ice concentration (SIC) directly affects whale access to open water areas which is necessary for breathing. Indirect effects of local sea ice concentration entail its impact on the distribution of primary productivity, which in turn drives the distribution of Antarctic krill (*Euphausia superba*), the humpback whale's key prey species (Brierley *et al.*, 2002; Van Opzeeland *et al.*, 2013; Bombosch *et al.*, 2014; Siegel, 2016). The large-scale mooring network in the ASSO that we have been maintaining for more than ten years(Rettig *et al.*, 2013a) allowed us to relate the long-term trend in humpback whale acoustic presence to long-term trends in SIC and climate oscillations.

Results and Discussion

We analyzed passive acoustic data of five recording positions (G1-G5) on the Greenwich Meridian from a mooring network throughout the ASSO from December 2010 to September 2018 (Figure 1).
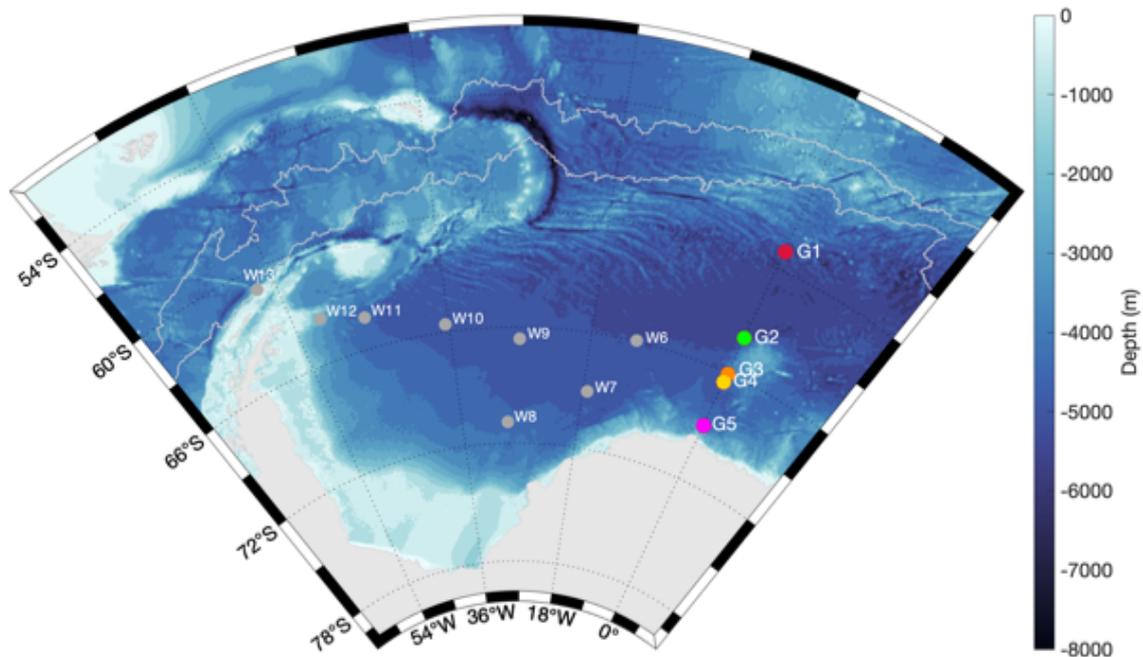
Figure 5. Bathymetric map of the Atlantic sector of the Southern Ocean (ASSO) including the geographic positions of the HAFOS (Hybrid Antarctic Float Observation System) mooring network in the ASSO (coastline and bathymetry data were obtained from (Wessel and Smith, 1996; Amante and Eakins, 2009)). The five mooring positions, G1-G5, visualized with colored dots (i.e., red, green, orange, yellow, magenta), represent the recording locations of the receivers (moored between 2010 and 2018) which were analyzed during this study. Positions G1-G5 form part of the HAFOS long-term mooring network (gray dots(Rettig *et al.*, 2013a)). The other recording positions (W6-13) were only active during 2013 and were therefore not included here (but see (Schall *et al.*, 2020) for details). Light grey lines represent the minimum and maximum of the annual wintertime (21 June -21 September) maximum sea ice extent during the of the study period (2011-2018)(Spreen *et al.*, 2008). Please note, that the lines shown do not delineate the sea ice extent of the specific years with the maximum and minimum wintertime maximum sea ice extent, but - calculated independently for each longitude - the multi-year composite of the maximum and minimum of the wintertime maximum sea ice extent during this period.

At the four oceanic recording locations (G1-G4), humpback whales were acoustically present during summer and autumn of the years 2011, 2012, 2013, 2017, and 2018 (i.e., times at which data were available for each recording position), coinciding with periods of low SIC (Figure 2A, Supplementary material S2, S3). The high proportion of hours with humpback whale acoustic presence during autumn at G1-G4 coincided with the known timing of onset of singing behavior in Southern Hemisphere humpback whale males in lower latitude waters (Stimpert *et al.*, 2012; Garland *et al.*, 2013a). During this period, two or more individuals

often were vocalizing at the same time in our recordings and acoustic activity was registered at all four locations in parallel, indicating the presence of multiple animals. Close to the coastal recording location (G5) where high sea ice concentrations were common during most months, humpback whales were acoustically absent or appeared only at low rates (e.g., during the years 2011-2013; Supplementary material S2, S3). At the same position (G5) and one of the oceanic locations (G3), humpback whales were acoustically present also during winter months, when SIC reached almost 100% (Figure 2A, Supplementary material S2, S3). Although humpback whale winter acoustic presence was limited compared to the summer months, the occurrence of calls in winter was persistent between years occurring at multiple sites (Supplementary material S3).

In contrast to previous and following years, only very low numbers of humpback whale vocalizations were detected in 2015 and 2016 at all locations (Figure 2A, Supplementary material S2, S3), whereas vocalizations of other species, e.g., the Antarctic minke whale (*Balaenoptera bonaerensis*), were detected during this time (see (Filun *et al.*, 2020)), excluding a technical artifact. Our findings are supported by the absence of opportunistic visual observations of humpback whales in the ASSO during the summer seasons 2014/2015 and 2015/2016 and only a few sightings during systematic ship-based and aerial surveys during January 2015 (Boebel, 2015; Herr *et al.*, 2018a; b; Burkhardt, 2020). During the same years, 2015 and 2016, when humpback whales were virtually absent, SAM and ENSO (represented by the Oceanic Niño Index, ONI) both simultaneously were in strong positive phases and one of the strongest El Niño phases since the beginning of measurements was registered (National Oceanic and Atmospheric Administration and Department of Commerce, 2019) (Figure 2B).
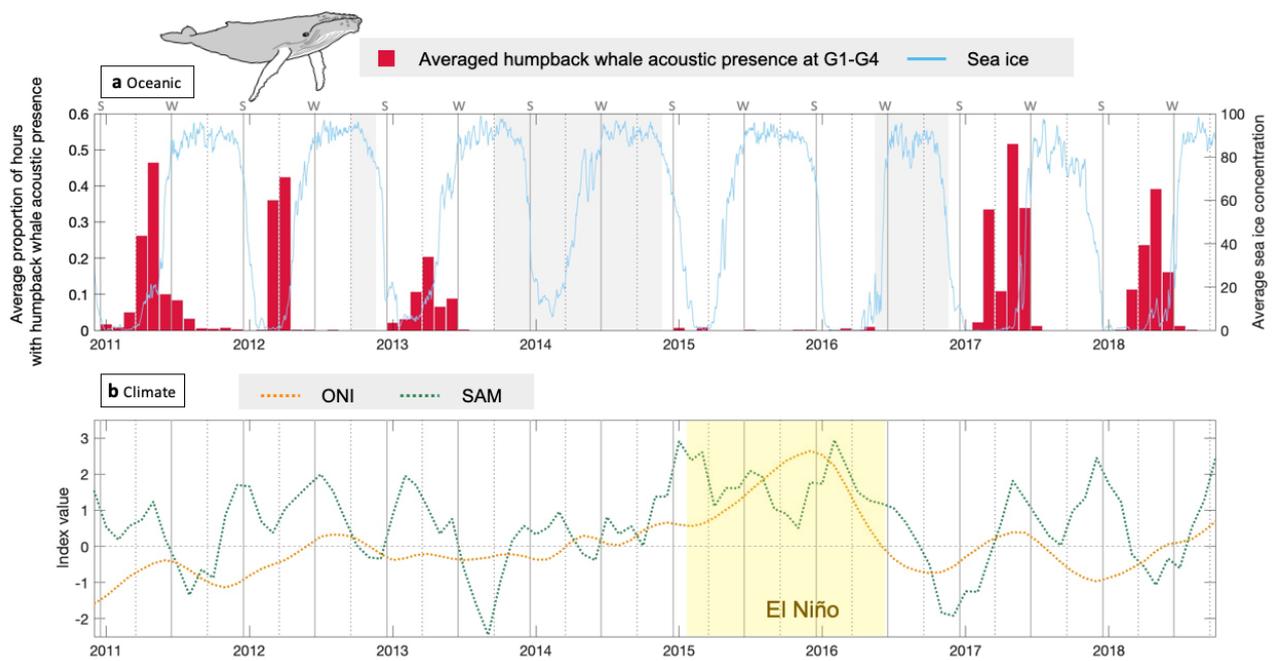
*Figure 2. **A**: Average proportion of hours with humpback whale acoustic presence per month from the four oceanic recording locations (G1-G4) on the Greenwich Meridian from December 2010 until September 2018 (red bars). Gray-shaded areas represent months without recording data. The blue solid line and the right y-axis depict the daily averaged sea ice concentration within a 50 km radius around recording locations. **B**: Climatic variations from 2011 until 2018 indicated by three-month running means of the Southern Annular Mode index (SAM) as a dominant pattern of natural climate variability in polar and subpolar regions of the Southern Hemisphere and the Oceanic Niño Index (ONI) representing the periodic fluctuation of sea surface temperature and air pressure originating from the tropical Pacific. Time span of strong El Niño phase in 2015/16 is indicated by the yellow rectangle. Vertical gray lines indicate the onset of summer (S) and winter (W) and vertical dotted lines indicate the onset of spring and autumn (based on equinoxes and solstices). Horizontal dashed line represents zero-orientation line.*

Modeling the effect of SIC, SAM, and ONI on the acoustic presence of humpback whales at the study location revealed that mainly SIC and ONI explain the observed pattern of humpback whale acoustic presence in the ASSO. The smoothed effects of month and SIC were highly significant because these variables explain seasonality in humpback whale presence on the feeding ground (Table 1, Figure 3; (Van Opzeeland *et al.*, 2013; Bombosch *et al.*, 2014)) in five out of seven years. The model showed that the ONI in the positive phase predicts a significantly lower probability of humpback whale acoustic presence than ONI in neutral or negative phases (Table 1, Figure 3). The smoothed effect of the SAM index was not statistically significant (Table 1, Figure 3). The model prediction for the SAM index showed lower predicted values at negative and high positive index values, although with higher uncertainties (Figure 3). This appears reasonable when looking at the original time-series. The negative phases of SAM were usually registered during winter when acoustic presences are naturally low, and extreme positive phases were only registered during summer 2015 and 2016 (Figure 2). Uncertainties at extreme index values (also for ONI) are high because these

values are rare in the analyzed time-series, which potentially also explains the resulting non-significant effect of SAM. To quantify the relationship between humpback whale presence and climate indices with higher certainty, much longer time-series than presented here would be required.

Table 1. Summary of the best-fit model for the acoustic presence of humpback whales at stations G3/G4, including sea ice concentrations (SIC), SAM, and month as smooth terms, as well as ONI as a categorical predictor. Note that the factor levels of ONI as a categorical predictor are listed under the parametric coefficients.

Formula: PA ~ s(SIC) + ONI + s(SAM) + s(Month)				
Parametric coefficients:				
	Estimate	Std. Error	t value	Pr(>|t|)
ONI $_{Positive}$	− 5.8490	0.9888	− 5.915	3.87e−09 ***
ONI $_{Positive}$ − ONI $_{Neutral}$	3.6750	0.9682	3.796	0.000151 ***
ONI $_{Positive}$ − ONI $_{Negative}$	3.7672	1.0207	3.691	0.000229 ***
Approximate significance of smooth terms:				
	edf	Ref.df	F	p-value
s(SIC)	3.381	3.381	9.576	1.34e−06 ***
s(SAM)	2.103	2.103	1.561	0.167
s(Month)	4.635	8.000	4.387	7.23e-07 ***
R-sq.(adj) = 0.485				
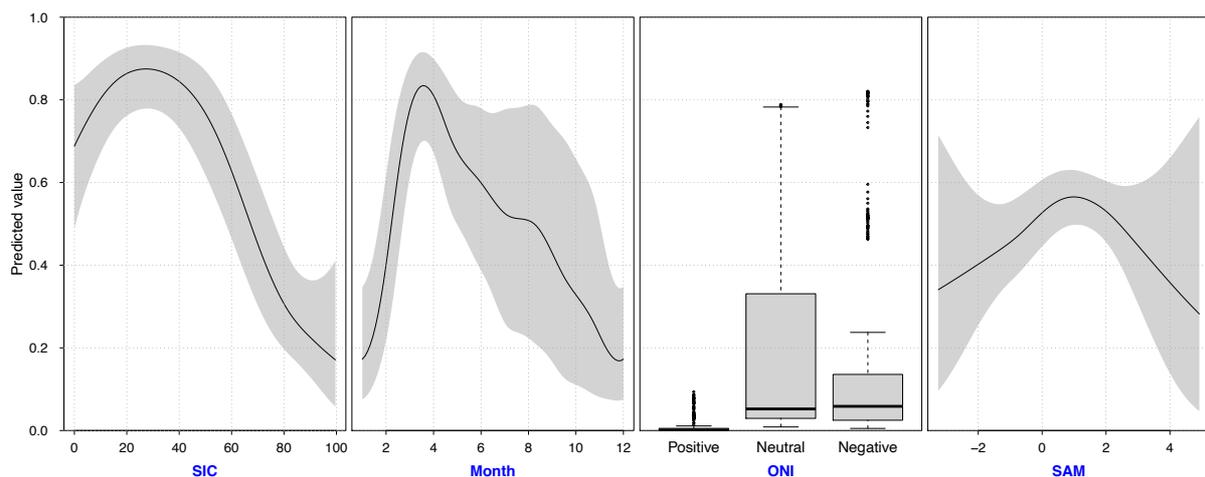
Figure 3. Model predictions of the best-fit model for the acoustic presence of humpback whales at stations G3/G4, including the smooth terms sea ice concentration (SIC), month, and SAM as well as ONI as a categorical predictor (see methods for further explanation of categories). Gray-shaded areas in line plots depict 95%-confidence intervals.

Local sea ice concentration is one of the most important environmental factors explaining the spatio-temporal distribution of baleen whales in the Southern Ocean (Širović *et al.*, 2004; Bombosch *et al.*, 2014; Thomisch *et al.*, 2016; Filun *et al.*, 2020). Similarly, sea ice dynamics play an important role in the intra-annual timing of humpback whale presence in the ASSO, showing that they move out of the area when SIC increases and that humpback whales are rarely present at SIC >80% (see also (Van Opzeeland *et al.*, 2013; Schall *et al.*, 2020)). Additionally, our new data indicate that large-scale climate variabilities drive the major inter-annual variability in the acoustic presence of humpback whales on a Southern Ocean feeding ground. The most likely pathway by which climate variabilities such as ENSO and SAM could affect humpback whale presence in the Southern Ocean is through their influence on Antarctic krill (*Euphausia superba*) (Loeb and Santora, 2015), since the availability and distribution of this primary prey species most likely is the main driver behind the spatio-temporal distribution of humpback whales in the *ASSO*.

Both SAM and ENSO are factors influencing the spatial distribution and biomass of Antarctic krill by affecting winds, cloud cover, currents, sea surface temperature, and sea ice extent (Yuan, 2004; Loeb *et al.*, 2009; Loeb *et al.*, 2010; Sallée *et al.*, 2010; Kim and Orsi, 2014; Siegel, 2016; Atkinson *et al.*, 2019). During the positive phase of SAM, the westerly wind belt surrounding the Antarctic continent contracts towards the continental shelf and climatic conditions north of the wind belt change to warmer, windier, and cloudier weather. During positive values of SAM, the oceanic feeding areas of humpback whales in the ASSO show signs of reduced sea ice extent, reduced primary production, and, in turn, also reduced krill densities (Siegel, 2016; Atkinson *et al.*, 2019). Especially north of the Antarctic Polar Front, sea surface temperature increases and chlorophyll concentration decreases during positive SAM (Lovenduski and Gruber, 2005; Meredith *et al.*, 2008). ENSO has the strongest effects on the Pacific sector of the Southern Ocean, including the Western Antarctic Peninsula [8,35]. The Western Antarctic Peninsula is a key habitat for Antarctic krill as a spawning and nursery ground, from which krill is transported with the Antarctic Circumpolar Current (ACC) 'conveyor belt' into north-eastern areas of the ASSO (Siegel, 2016). During or after the positive phase of ENSO, El Niño caused warming and the reduction of sea ice at the Western Antarctic Peninsula. Due to these climate conditions, less krill might be recruited from the Antarctic Peninsula towards the oceanic regions of the ASSO, although this process is probably delayed by multiple months considering the estimated transport speed of the ACC (Hofmann *et al.*, 1998; Loeb *et al.*, 2009; Loeb and Santora, 2015; Siegel, 2016). Also, during years of El Niño, a manifestation of negative sea surface temperature anomalies in the

southwest Atlantic, termed the Antarctic dipole, is common which probably affects productivity in this area (Meredith *et al.*, 2008; Loeb *et al.*, 2009; Loeb and Santora, 2015). We therefore hypothesize that during the years 2015 and 2016, positive phases of both SAM and ENSO led to reduced densities of krill on the oceanic feeding grounds of humpback whales in the ASSO while potentially creating alternative prey resources in other areas. Among baleen whale species, the humpback whale is probably the most flexible when it comes to ecological requirements, being able to adapt to wide-ranging changes in the environment with alternative migration and feeding strategies (Witteveen *et al.*, 2008; Barendse *et al.*, 2010). This adaptivity is probably also the reason for the continued presence of at least some humpback whales in the ASSO during austral winter. Especially female and juvenile humpback whales tend to prolong their stay on the feeding grounds or even skip migration entirely in order to fuel growth, pregnancy, or lactation with additional winter feeding (Brown *et al.*, 1995; Craig *et al.*, 2003). During 2015 and 2016, the main part of the South Atlantic humpback whales (probably individuals from breeding stocks from South America and Africa(International Whaling Commission, 2011)) might have adapted their migration routes to exploit areas of high productivity elsewhere than in the ASSO (Barendse *et al.*, 2010). For example, an unusual assemblage of humpback whale 'super groups' was documented in 2015 and 2016 in the southern Benguela upwelling system off South Africa (Findlay *et al.*, 2017; Gridley *et al.*, 2018). Furthermore, in 2016, exceptional recordings of humpback whale song were made close to the west coast of South Africa (Gridley *et al.*, 2018; Ross-Marsh *et al.*, 2020) which indicates not only the displacement of the feeding area but also multifaceted habitat use (i.e., also including reproductive activities) along this displacement. Humpback whales acoustically and physically absent from the ASSO during 2015 and 2016 might have been exploiting alternative habitats and prey resources along the west coast of South Africa (Barendse *et al.*, 2010; Findlay *et al.*, 2017) or other yet undiscovered high productivity areas in the South Atlantic or adjacent waters. To date, the current knowledge on spatio-temporal trends in productivity hotspots in the Southern Hemisphere is nevertheless too sparse to explain trends in migratory predator distribution with certainty. In this context, the maintenance and implementation of further long-term observation systems such as the HAFOS mooring network from which the analyzed recordings originate (see Figure 1 and (Rettig *et al.*, 2013a)) are essential to detect and understand changes in this ecosystem and its functions.

Future climate change could cause the shift of ENSO and SAM towards higher frequencies of positive phases (Cai *et al.*, 2014; Atkinson *et al.*, 2019), which in turn might change the

overall occupancy of certain feeding areas or prey resources by humpback whales on a hemisphere-wide spatial scale. Our results clearly show that acoustic detection of whales can shed new light on biophysical interactions within the fascinating Southern Ocean ecosystem. Interannual trends in the distribution or health status (e.g.,(Bengtson Nash *et al.*, 2018)) of humpback whales and other baleen whales from the South Atlantic, but also other areas, warrant further investigation to provide information to whale stock and fishery management. Evaluating the sensitivity of keystone species to climate variabilities is essential to our understanding of the effects of climate-induced changes on the Southern Ocean ecosystem.

Methods

Passive acoustic data

Humpback whale acoustic behavior throughout the ASSO was investigated by analyzing a multi-year passive acoustic dataset (2010-2018) from five recording positions along the Greenwich Meridian (Table 2, Figure 1). Passive acoustic recordings were obtained using SonoVaults (Develogic GmbH, Hamburg) operated on a continuous recording scheme and with a sampling rate of 5,333 or 6,857 Hz (Table 2).

Table 2. Information on passive acoustic recordings included in this study. The different recording periods at the five mooring positions were covered by different SonoVault recording units. For reference to earlier publications, the original mooring ID is listed in brackets.

Mooring ID	Latitude	Longitude	Recorder ID	Sampling Frequency (Hz)	Deployment Depth (m)	Recording Period
G1 (AWI227)	59 2.82 °S	000 5.78 °E	SV0002	5333	1007	2010-12-11 - 2011-05-21 2011-05-30 2011-06-14 - 2011-08-22 2012-12-11 - 2013-07-13 2016-12-22 - 2018-09-18
			SV1025	5333	1020	
			SV1004	6857	1070	
G2 (AWI229)	63 59.85 °S	000 1.84 °E	SV1000	5333	1007	2010-12-15 - 2011-06-18 2012-12-14 - 2013-08-02 2014-12-16 - 2016-05-19
			SV1010	5333	998	
			SV1057	6857	970	
G3 (AWI230)	66 2.01 °S	000 3.12 °E	SV1001	5333	934	2010-12-16 - 2012-04-13 2012-05-06 - 2012-09-17 2013-01-07 - 2013-09-27
			SV1009	5333	949	
G4 (AWI231)	66 30.71 °S	000 1.51 °E	SV1002	5333	1083	2010-12-17 - 2012-02-05 2012-02-28 - 2012-07-30 2012-08-04 - 2012-08-09 2012-08-11 - 2012-08-14 2014-12-18 - 2016-05-28 2016-12-26 - 2018-10-28
			SV1058	6857	973	
			SV1023	6857	859	
G5 (AWI232)	68 59.94 °S	000 4.38 °E	SV1003	5333	987	2010-12-18 - 2012-05-09 2012-06-01 - 2012-08-10 2012-12-17 - 2013-05-28 2013-06-19 - 2013-11-13 2015-01-08 - 2015-01-26 2015-02-14 - 2015-02-21 2015-03-04 - 2015-08-24
			SV1011	5333	958	
			SV1059	6857	999	

Automatic detection and classification of humpback whale vocalizations

All available passive acoustic data were processed by the 'Low Frequency Detection and Classification System' (LFDCS) developed by (Baumgartner and Mussoline, 2011a) and a custom-made acoustic-context filter to detect humpback whale acoustic presence at an hourly basis (humpback whales which did not produce any sounds remained undetected). LFDCS was set up with a customized call library based on the most common vocalization types of humpback whales and other acoustically abundant Antarctic marine mammal species (i.e., Antarctic minke whale, killer whale (*Orcinus orca*), Weddell seal (*Leptonychotes weddellii*), crabeater seal (*Lobodon carcinophaga*), leopard seal (*Hydrurga leptonyx*), and Ross seal (*Ommatophoca rossii*)) (Dunlop *et al.*, 2008; Klinck *et al.*, 2010; Van Opzeeland *et al.*, 2010; Stimpert *et al.*, 2011b; Risch *et al.*, 2014c; Schall and Van Opzeeland, 2017). Parameter settings and thresholds of LFDCS and the acoustic context filter were tuned employing multiple test datasets to optimize the automatic detection of humpback whale vocalizations to the requirements of this study. Detailed information on set up and test runs of the automatic detection process is provided in the Supplementary material (S1).

Manual post-processing of detection results

In order to limit the temporal effort of manual post-processing, only even hours (i.e., hours starting at 00:00, 02:00, 04:00, 06:00, 08:00, 10:00, 12:00, 14:00, 16:00, 18:00, 20:00, 22:00) were included in the further analysis. Four human analysts revised even hours with presumed humpback whale acoustic presence visually and aurally for the presence of humpback whale vocalizations by creating spectrograms in Raven Pro 1.5 (Hann Window, 1025-1790 window size, 80% overlap, 2048 DFT size (Bioacoustics *et al.*, 2014)). Spectrograms were screened for humpback whale vocalizations by viewing windows of 60 s duration, spanning 0 to 1.80 kHz. Hours with confirmed humpback whale acoustic presence could contain both humpback whale social calls and humpback whale song.

Environmental data

The SIC data used for this study were extracted from a combination of satellite sensor data from the Nimbus-7 Scanning Multichannel Microwave Radiometer (SMMR), the Defense Meteorological Satellite Program (DMSP) -F8, -F11, and -F13 Special Sensor Microwave/Imrs (SSM/Is), and the DMSP-F17 Special Sensor Microwave Imager/Sounder (SSMIS), with a grid size of 25 km (Cavalieri *et al.*, 1996). The data were used to calculate the daily SIC of the area within a 50 km radius around each recording location, with the Daily Antarctic Sea Ice Concentration packages in MATLAB (Greene, 2020). The radius of 50 km was chosen because the acoustic range of humpback whales in the ASSO was estimated at 2-78 km (Van Opzeeland *et al.*, 2013).

The two most common climate indices for the Southern Hemisphere, the Southern Annular Mode (SAM) (Marshall, 2003a) and the Oceanic Niño Index (ONI, representing ENSO variabilities) (National Oceanic and Atmospheric Administration and Department of Commerce, 2019) were used in this study. SAM data was downloaded from the Climate Data Guide (Marshall and National Center for Atmospheric Research Staff (Eds), 2019) as monthly averages. ONI data was downloaded from the Climate Prediction Centre (National Oceanic and Atmospheric Administration and Department of Commerce, 2019) as three-month running means.

Statistics and Reproducibility

To assess the impact of the three climate variables, SIC, ONI, and SAM on the acoustic presence of humpback whales in the ASSO, generalized additive mixed models (GAMMs) were applied in R (R Core Team, 2018). To model the effects of the three climate variables on the presence of humpback whales in the ASSO, the data from G3 and G4 were combined into a single time series (i.e., averaged daily SIC and daily averaged proportion of hours with humpback whale acoustic presence) because these recording positions were less than 50 km apart and provided the most complete time series (see Table 2 and Supplementary material S2). SAM and ONI were also converted into categorical variables with negative, neutral, and positive phases (index value < −0.5 = negative; index value between −0.5 and 0.5 = neutral; index value > 0.5 = positive; see (National Oceanic and Atmospheric Administration (NOAA) and Climate Prediction Centre (CPC), 2019) for details on ONI categories. The same standard was applied for SAM to create a neutral buffer between positive and negative phases). Binomial GAMMs were applied to model the daily acoustic presence/absence of humpback whales at G3/4 as a function of Month, SIC, ONI (either continuous or categorical variable), and SAM (either continuous or categorical variable), including a model to account for temporal autocorrelation (functions *gamm* of the package *mgcv* (Wood, 2017) and *corARMA* of the package *nlme* (Pinheiro *et al.*, 2020) for an auto-regressive moving average (ARMA) model for the residuals). The optimal setup of starting values and orders for the implemented correlation structure was estimated in two ways: (1) with the function *auto.arima* (package *forecast* (Hyndman *et al.*, 2020)), (2) by allowing the corARMA function to estimate its parameters directly from our data. Model selection was performed using the Akaike Information Criterion (AIC), adjusted r-squared values, and the analyses of residuals.

Data availability

The hourly humpback whale acoustic presence data that support the findings of this study are available on Dryad (https://datadryad.org/stash/dataset/doi:10.5061/dryad.ncjsxkss0) with the identifier https://doi.org/10.5061/dryad.ncjsxkss0.

Author contributions

E.S. analyzed the data and wrote the manuscript. K.T. participated in some data collection and helped draft the manuscript. O.B. coordinated the study and collected the majority of the data. G.B. guided the analysis and helped draft the manuscript. S.MW. helped with data analysis. A.E-G. supervised the statistical analysis. I.V.O. coordinated the study, collected part of the data, and helped draft the manuscript. All the authors reviewed and contributed to the final document edits. All the authors gave the final approval for publication.

Competing interests

The authors declare no competing interests.

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Chapter III

Acoustic metrics to asses humpback whale song unit structure from the Atlantic sector of the Southern Ocean

Acoustic metrics to asses humpback whale song unit structure from the Atlantic sector of the Southern Ocean

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ABSTRACT

Acoustic metrics aggregate the acoustic information of a complex signal into a unique number, assisting our interpretation of acoustic environments and providing a rapid and intuitive solution to analyze large passive acoustic datasets. Manual identification and characterization of intraspecific call trait variation has been largely used in a variety of sonic taxa. However, it is time consuming, relatively subjective, and measurements can suffer of low replicability. This study assesses the potential of using a combination of standardized and automatically computed acoustic metrics (AM) to train a supervised classification model, as an alternative to discrimination protocols and manual measurements to categorize humpback whale (*Megaptera novaeangliae*) song units from the Southern Ocean. Our random forest model successfully discriminated between the 12 humpback whale unit types (UT), achieving an average classification accuracy of 84%. UTs were further described and discussed in the context of the hierarchical structure of humpback whale song in the Southern Ocean. We show that accurate discriminant models based on relevant AM combinations, provide an interesting automated solution to use for simple, rapid and highly reproducible identification and comparison of vocalization types in humpback whale populations, with potential to be applied to both aquatic and terrestrial contexts, on other vocal species and over different acoustic scales.

I.   INTRODUCTION

Assessing the intraspecific variation of call traits in vocal species is vital to understand communication systems, its behavioral implications and the mechanisms by which evolutionary forces shape communicative processes (e.g., Slabbekoorn and Smith, 2002; Ladich, 2015). Qualitative and quantitative analyses of call trait variation are necessary to define passive acoustic markers to reliably detect species or population presence (e.g., Brandes, 2008; Stimpert *et al.*, 2011a; Schall and Van Opzeeland, 2017) and asses repertoire differences among populations which may be indicators for speciation processes (e.g., Slabbekoorn and Smith, 2002; Riesch *et al.*, 2012). The analysis of highly structured acoustic displays, such as the songs of whales and songbirds, is of particular interest to study cultural processes in non-human animals (Baker *et al.*, 1984; Garland *et al.*, 2011; Fayet *et al.*, 2014; Allen *et al.*, 2018). Reliable and reproducible parametrization and classification of call traits, however, is a prerequisite to explore such higher-level patterns in animals' acoustic displays. The manual identification and characterization of intraspecific call types by means of visually screening spectrographic images of sound has been widely used in a variety of taxa, including cetaceans, seals, birds and primates (e.g., Fischer and Hammerschmidt, 2002; Catchpole and Slater, 2003; Ballentine *et al.*, 2004; Van Opzeeland *et al.*, 2010; Schall and Van Opzeeland, 2017). However, it also has particular drawbacks (but see Janik, 1999) as it is time consuming, can be relatively subjective, and hence measurements can suffer of low replicability (e.g., Janik, 1999; Baumgartner and Mussoline, 2011a). Here we use automatically computed acoustic metrics as an alternative standardized method to characterize acoustic signals, thereby circumventing the hurdles and drawbacks of manual parametrization and classification of species' call traits.

Humpback whales (*Megaptera novaeangliae*) represent an ideal model to explore the effectiveness of acoustic metrics to discriminate between discrete call type categories; the vocalizations of humpback whales cover a broad frequency range, they present intraspecific

variability both spectrally and temporally and comprise sounds used in different behavioral contexts. Humpback whale song (vocalizations produced exclusively by males in the context of breeding) is a strictly hierarchically structured acoustic display, which can be decrypted by the analysis of the smallest entity, termed unit, and the combination of units, termed phrases (Payne and Mcvay, 1971; Cholewiak *et al.*, 2013). The qualitative differentiation of vocalization types is common for both social and song vocalizations (Payne and Mcvay, 1971; Dunlop *et al.*, 2008). In most recent studies, manual measurements of vocalization parameters (e.g., duration, maximum frequency) or a combination of manual and automatic measurements are supplied to machine learning algorithms to validate the manual classification (Mercado and Kuh, 1998; Dunlop *et al.*, 2007; Green *et al.*, 2011; Garland *et al.*, 2013b; Allen *et al.*, 2017; Warren *et al.*, 2020). This reduces, to some extent, the subjectivity of the categorization and increases the replicability of results, yet it does not remove the uncertainty related to the manual parametrization of call types.

Acoustic metrics assist our interpretation of acoustic environments by aggregating the acoustic information of a complex signal into a unique number. They are designed to, e.g., capture the distribution of acoustic energy across time and/or frequency bands and can function as statistical summaries of sound recordings. The various acoustic metrics capture very different characteristics of the acoustic environment since they are based on different mathematical principles and are used to address diverse research questions (Sueur *et al.*, 2014). Standardized and automatically computed acoustic metrics (we will hereinafter refer to these as AM) provide a rapid, objective and intuitive solution to analyze large passive acoustic datasets. So far, AMs have been successfully used for different purposes in marine ecosystems, including: as proxies for biodiversity (Harris *et al.*, 2016; Desiderà *et al.*, 2019), to assess temporal or spatial variation in biotic acoustic activity (Parks *et al.*, 2014; Pieretti *et al.*, 2017), to describe habitat type and quality (Bertucci *et al.*, 2016; Butler *et al.*, 2016;

Ceraulo *et al.*, 2018), and to identify key ecosystem functions (Elise *et al.*, 2019). While most of this research has used a single AM to describe general acoustic diversity patterns, there is some evidence showing that a combination of AMs can be very efficient in discriminating species-specific vocalizations from natural marine acoustic environments (Roca and Van Opzeeland, 2019). However, to our knowledge, AMs to date have not been applied to discriminate between intraspecific call traits.

In this study we will explore the potential of a combination of AMs to characterize and discriminate between the intraspecific variation in song unit types from humpback whale songs from the Atlantic sector of the Southern Ocean (ASSO) over five years. In addition, we describe and discuss the resulting discrete unit type categories in the context of the observed hierarchical structure (i.e., phrases) of the humpback whale songs visually characterized in a multi-year passive acoustic data set. With this we provide a robust framework that has the potential to be generalized to other ecological systems, allowing to categorize animal vocal traits in a more automated, rapid and reproducible manner.

II.   MATERIAL AND METHODS

A. Data and data processing

Humpback whale acoustic behavior was investigated using data from 13 recording positions throughout the *ASSO* (Figure 1), which recorded in different periods between 2010 and 2018 (Figure S1). Passive acoustic recordings were obtained using SonoVaults (Develogic GmbH, Hamburg) operated on a continuous recording scheme and with sampling rates that differed between instruments being either 5,333, 6,857 or 9,600 Hz (Rettig *et al.*, 2013c).
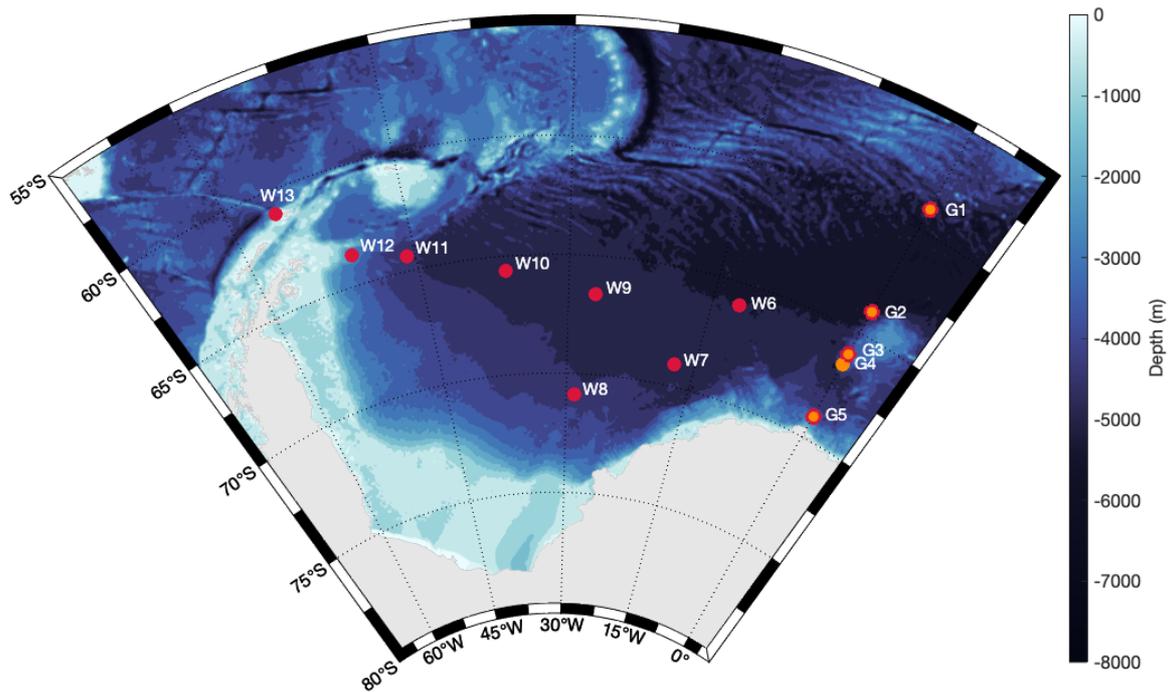
Figure 1. Mooring positions included in this study. Mooring positions marked in orange and labelled with the prefix 'G' in the name are part of the multi-year Greenwich dataset (2010-2018). Mooring positions in red and labelled with the prefix 'W' in the name are part of the single-year Weddell dataset (2013). Mooring positions which are marked in orange and red are part of both datasets.

All available passive acoustic data (in total 186,074 hours) were processed by the 'Low Frequency Detection and Classification System' (LFDCS) developed by Baumgartner and Mussoline (2011a) and a custom-made acoustic-context filter to detect humpback whale acoustic presence at an hourly basis. LFDCS was set up with a customized call library based on the most common vocalization types of humpback whales and other acoustically abundant Antarctic marine mammal species (i.e., Antarctic minke whale (*Balaenoptera bonaerensis*), killer whale (*Orcinus orca*), Weddell seal (*Leptonychotes weddellii*), crabeater seal (*Lobodon carcinophaga*), leopard seal (*Hydrurga leptonyx*), and Ross seal (*Ommatophoca rossii*)) (Dunlop *et al.*, 2008; Klinck *et al.*, 2010; Van Opzeeland *et al.*, 2010; Stimpert *et al.*, 2011a;

Risch *et al.*, 2014c; Schall and Van Opzeeland, 2017). Parameter settings and thresholds of LFDCS and the acoustic context filter were tuned employing multiple test datasets to optimize the automatic detection of humpback whale vocalizations to the requirements of this study. Detailed information on set up and test runs of the automatic detection process are provided in Schall *et al.* (2020).

B. Song presence

To avoid including false-positives, hours with detected humpback whale acoustic presence were revised visually and aurally from spectrograms created in Raven Pro 1.5 (Hann window, 1025-1790 window size, 80% overlap, 2048 DFT size) (Center for Conservation Bioacoustics, 2014). Preliminary analyses comparing humpback whale presence patterns between hourly and bi-hourly data showed no substantial differences (Schall *et al.*, 2020). Therefore, to reduce processing time, only even hours were post-processed and included in further analyses. Spectrograms were scanned for humpback whale vocalizations by viewing 60 s windows from 0 to 1.80 kHz. Humpback whale vocalizations that were organized in at least two different themes (i.e., a theme is defined as the repetition of one phrase type, see Cholewiak *et al.* (2013)) were manually classified as song. Remaining vocalizations, identified as humpback whale social calls, were not considered in this study.

C. Vocal repertoire within songs

The song repertoire of humpback whales in the ASSO was investigated and catalogued by analyzing all even hours with high quality song sequences (i.e., SNR $\geq$ 10 dB and at least to distinct themes discernible). Both the preceding and succeeding odd hours relative to the analyzed hour were also included in the analysis if those also contained high quality song sequences. Humpback whale vocalizations were manually logged within the spectrograms in Raven Pro (same spectrogram settings as above) and manually classified into distinct unit

types (hereinafter referred to as UT) according to the following criteria: differentiation of tonal or broadband characteristics, duration, frequency range and time-frequency slope. Within a humpback whale song sequence phrases were logged and classified according to the rules of unit repetition from Cholewiak *et al.* (2013). Phrases were identified with an uppercase letter (indicating the 1st UT), a lowercase letter (indicating the combination of following UTs) and a sequence of numbers (indicating the number of repetitions of each UT) in order to be able to breakdown to the original unit sequence (e.g., Aa13 indicates one repetition of UT1 and three repetitions of UT4a). The combination of letters essentially represents the phrase type, whereas the sequence of numbers only indicated UT usage for the downstream analysis process.

D. AMs to characterize humpback whale song units

We selected > 20 acoustic clips per UT from the high-quality song recordings throughout the ASSO to include in the classification model, for a complete subset of 436 clips (Table 1). We sampled as many different years, months and locations as possible (Figure 1; and see Figure S1) in order to capture as much temporal, spatial, and individual variation as possible. All acoustic clips had a 3s length and were decimated to 5,000 Hz sampling frequency in MATLAB R2020b, to ensure processing consistency across the sampled data.

We computed 21 different AMs (see detailed list in Table S1) for every acoustic clip in the subset. These AMs can be classified in three categories: (1) indices based on different algorithms to compute acoustic complexity, entropy or diversity (acoustic indices); (2) metrics measuring amplitude or background patterns (energy metrics); and (3) metrics computing ratios between acoustic activity over time and frequency bands (ratio metrics). To account for the complexity and variability in the spectral patterns between the different UTs, we additionally computed AEI, ADI, ACI, BI and NP metrics (see Table S1) on five relevant bandwidths: 0.01–0.25 kHz; 0.25–0.5 kHz; 0.5–1 kHz; 1–2.5 kHz; and the full bandwidth 0–

2.5 kHz, for a total of 44 AMs computed per acoustic clip. All AMs were computed using R (R Core Team, 2018). We used functions from the R package seewave (Sueur *et al.*, 2008) to calculate H, th, sh, ACI, NP and M, and from the R package soundecology (Villanueva-Rivera *et al.*, 2018) to calculate AEI, ADI, BI and NDSI.

E. *Automatic classification of song units*

We used a random forest classification model (Breiman, 2001) as supervised machine learning algorithm to assess the robustness of the manual classification of humpback whale UTs and evaluate the discrimination potential of the AMs. Random forest models are widely-used tools that show high predictive accuracy and can cope with high-dimensional problems, complex interactions and even highly correlated predictor variables.

We applied the Boruta algorithm (Kursa and Rudnicki, 2010) to select relevant AMs to include as predictor variables in the random forest classification model. The Boruta algorithm iteratively removes the variables that are statistically less relevant than random probes. A random probe is a 'shadow' variable, whose values are obtained by shuffling values of the original variable across objects. The algorithm then performs a classification using all attributes (original variables and random probes) and computes their importance based on their contribution to the classification accuracy. The set of importance of shadow attributes is used as a reference to decide which original variable is truly important (shadow attributes' importance can be nonzero only due to random fluctuations). We used the Boruta function from the Boruta package (Kursa and Rudnicki, 2010) in R.

We used the randomForest function in the R randomForest package (Liaw and Wiener, 2002) to develop the random forest classification model. We ran an hyperparameter grid search using the R package ranger (Wright and Ziegler, 2015) on values for the total number of trees necessary to stabilize prediction error rates, the number of predictor variables to randomly sample from at each node, the minimum number of samples within the terminal nodes and the

maximum number of nodes (both define the degree of model complexity) and finally, the sizes of training and test data subsets to find the best model parameterization according to the above mentioned criteria. We grew 4,001 trees with a node size of 1 and tested 6 predictor variables at each split. For each tree constructed in the random forest, 2/3 of the data were subsampled with replacement to train the classification model and 1/3 was left out as a test set (i.e., Out-of-bag or OOB cases). The general misclassification rate of the model (general OOB estimate) is computed as the average across all OOB cases and trees. We used a conditional permutation scheme (Strobl *et al.*, 2008) to assess variable importance, in order to account for correlations that occurred between some of the AMs. We used the permimp function from the permimp package in R (Debeer and Strobl, 2020) with a 0.90 threshold value.

III. RESULTS

We analyzed the humpback whale song composition from the ASSO between 2010 and 2018 by evaluating 302 song sessions (see Payne and Mcvay, 1971 for definition of song sessions) from 78 recording days (i.e., probably representative of individual singers due to a minimum pause of 24 hours between song recordings at the same recording position). In total we classified 29,304 units and 7,247 phrases from 5 years (i.e., 2011, 2012, 2013, 2017, 2018; remaining years had no high-quality song recordings).

A. Humpback whale vocal repertoire in the ASSO

Humpback whale males in the ASSO feeding area produced ten unique UTs and two subtypes (in total 12 categories; i.e., UT1, UT3, UT4a, UT4b, UT5a, UT5b, UT6, UT8, UT10, UT12, UT18, UT19) to form their songs between the years 2011 and 2018. Missing numbers in the

list of unit types occur because these call types (e.g., UT2 or UT7) were only found in non-song vocalization sequences, which were rarely found with acceptable signal-to-noise ratios and were therefore not included in this study. Ten of the 12 unit (sub-) types were tonal sounds (i.e., UT1, UT3, UT4a/b, UT5a/b, UT6, UT10, UT18, UT19) and two were broadband sounds (i.e., UT8 and UT12) (Figure 2). The ten tonal unit types were mainly characterized by differences in the slope of the time-frequency contour and their frequency range (Figure 2). The two broadband unit types were mainly different in their duration and frequency range. Nine out of the 12 types had most of their energy below 600 Hz (i.e., UT1, UT3, UT4a, UT5a, UT6, UT10, UT12, UT18, UT19) (Figure 2). Two of these unit types were characteristically below 120 Hz (i.e., UT18 and UT19). UT4b, UT5b, and UT8 had most of their energy above 600 Hz (Figure 2).
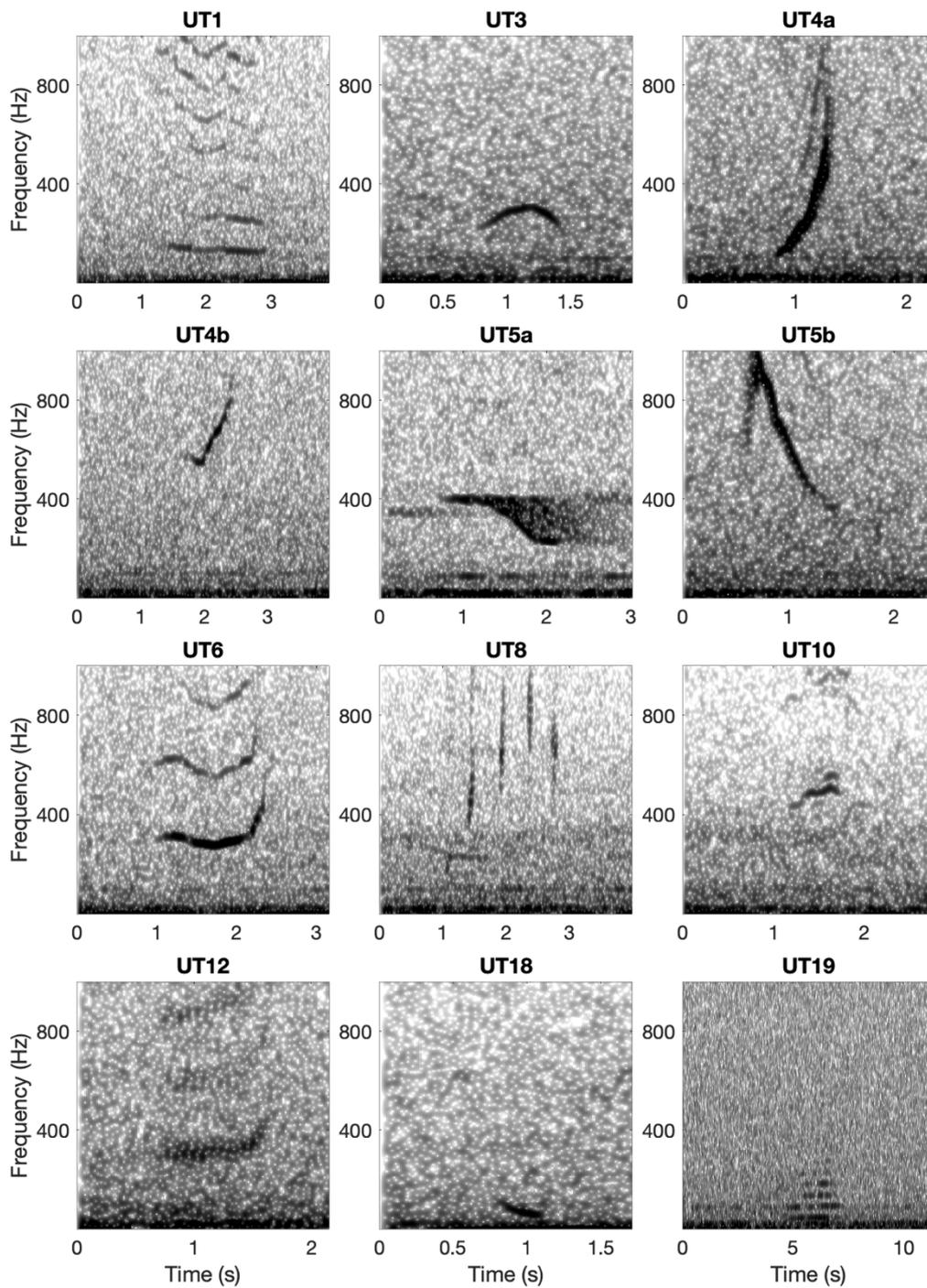
Figure 2. Example spectrograms to each humpback whale unit type (i.e., UT1-UT19).

Spectrograms were created with a hamming window, a FFT size of 1800, a window size of

80ms, and a window overlap of 10ms.

Combinations of the 12 unit (sub-) types formed 62 distinct phrase types (i.e., Aa – Ib), organized in nine groups depending on the starting UT (e.g., group A starts with UT1 and group B starts with UT6). Only UT8 was never encountered at the beginning of a phrase. Phrase types were composed of one to four distinct UTs (see Figure 3 for three of the most common phrase types). Some unit and phrase types were only used in a single year and some were used over multiple years (Figure 4). Each year, humpback whales used between five and nine UTs to form the songs and the overlap among the unit repertoire from the different years was high (i.e., on average 43%; Figure 4). The average per-year phrase repertoire was 18.8 phrase types per year with a range between 10 and 28 phrase types (Figure 4). Among years, overlap in phrase repertoire was smaller than for the unit repertoire (i.e., on average 7%).
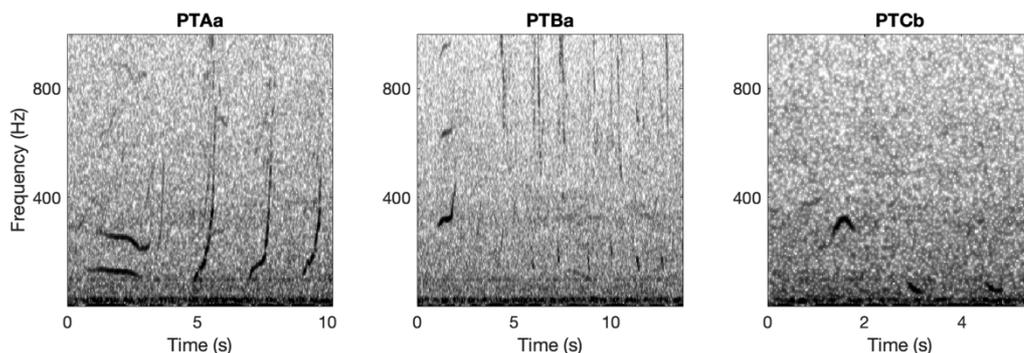
Figure 3. Spectrogram representations of three of the most common humpback whale phrase types (i.e., PTAa, PTBa, and PTCb) from the ASSO. Spectrograms were created with a hamming window, a FFT size of 1800, a window size of 120ms, and a window overlap of 30ms.
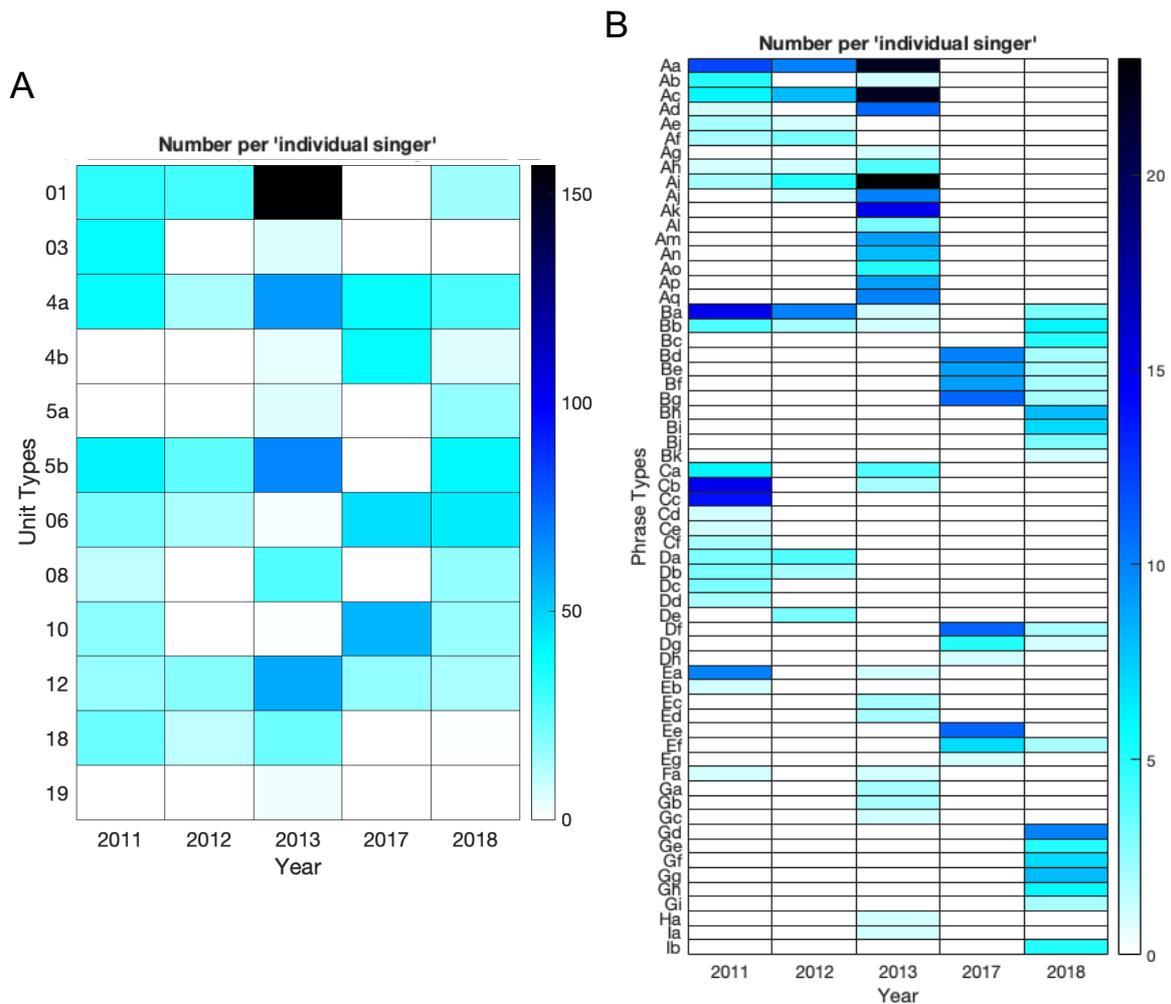
*Figure 4. Heatmaps of unit and phrase repertoires per year with song recordings. **A** illustrates repertoire changes for unit types (e.g., unit types 01, 4a, and 19) between the years (i.e., 2011-2018). **B** illustrates the repertoire changes for phrase types (e.g., Aa, Ab, and Ib) between years. Color represents number of units or phrases per type and individual singer.*

B. Automatic classification of song units

The random forest model using a combination of AMs successfully discriminated between all 12 humpback whale UTs (see Figure S2 for detailed classification tree). Average model OOB error estimation was 16%. UT5b and UT4b had the highest missed detection rate (32% and 30% respectively), while UT5a and UT19 showed the lowest miss rate (3% and 0%

respectively; Table 1). The most important AM to discriminate between UTs were ACI and

BI computed on the lower frequency bands (0.01–0.5 kHz). They were closely followed by

AR, low frequency NDSI, and 0.01–0.25 kHz band computed ADI and AEI (Figure S3). Yet,

the Boruta algorithm considered 43 out of the 44 metrics relevant for the classification.

Table 1. Random Forest confusion matrix and classification error for the 12-humpback whale UTs identified in the ASSO. The overall classification error (OOB) was 16%. First column contains the true UT categories, second column the number of samples (N) per UT and the subsequent columns comprise the classification output of the model for each UT category and the corresponding UT (class) error rate.

	N	UT1	UT3	UT6	UT8	UT10	UT12	UT18	UT19	UT4a	UT4b	UT5a	UT5b	Class error
UT1	57	49	0	0	1	0	3	1	3	0	0	0	0	0.14
UT3	20	0	18	0	0	0	0	1	0	1	0	0	0	0.10
UT6	42	3	0	34	0	0	1	0	0	3	1	0	0	0.19
UT8	38	0	0	0	28	1	0	0	0	5	0	0	4	0.26
UT10	32	0	1	1	2	26	0	2	0	0	0	0	0	0.19
UT12	62	2	0	1	0	0	57	0	0	1	0	0	1	0.08
UT18	27	1	2	0	0	0	0	24	0	0	0	0	0	0.11
UT19	28	0	0	0	0	0	0	0	28	0	0	0	0	0.00
UT4a	53	3	0	0	1	1	0	0	4	41	0	2	1	0.23
UT4b	20	1	0	0	3	0	1	0	0	0	14	0	1	0.30
UT5a	29	0	0	1	0	0	0	0	0	0	0	28	0	0.03
UT5b	28	0	0	1	1	2	0	0	0	5	0	0	19	0.32

IV. DISCUSSION

Here, we show for the first time that a combination of mathematically-derived AMs can be used to characterize and accurately discriminate between humpback whale UTs and complement the qualitative classification of a complex acoustic display. This study provides a practical application and robust framework to validate the qualitative categorization of humpback whale song units and highlights the potential of this method for more general applications exploring acoustic trait variation.

In this study, we identified 12 different UTs from the song repertoire of humpback whales in the ASSO. Other studies assessing humpback whale song repertoire in the Southern and Northern Hemisphere have reported a higher number of UTs (e.g., Pace *et al.*, 2010; Magnúsdóttir *et al.*, 2015; Allen *et al.*, 2017; Rekdahl *et al.*, 2018). The small number of UTs reported here, with 10 unit types and two additional sub-types, can either reflect less complexity in the repertoire of humpback whales on the ASSO feeding ground or a classification tendency to divide the repertoire into a small number of categories (Allen *et al.*, 2017). Less complexity in a feeding ground song repertoire may be typical and be caused by the production of songs which are still under development in the process of annual song evolutions and revolutions (Magnúsdóttir *et al.*, 2015; Allen *et al.*, 2018; Kowarski *et al.*, 2019; Magnúsdóttir and Lim, 2019). The coarse differentiation of a smaller number of UTs is valuable to increase robustness of the classification and to generate generalized sound categories (Mercado and Kuh, 1998; Zsebők *et al.*, 2018). The overlap among acoustic characteristics for this small number of UTs is already high, especially within a song sequence, when a singer gradually changes from one UT to another (Cholewiak *et al.*, 2013), therefore the differentiation into more UTs would only increase this overlap. The consistency in the presented qualitative and quantitative classification of 12 UTs and their temporal stability over multiple years (see Figure 4), however, shows the potential of these UTs to

serve as passive acoustic markers to reliably (automatically) detect humpback whale acoustic presence in large datasets. Indeed, all 12 UTs are common in social and song repertoires of humpback whales from both the Southern and the Northern Hemisphere (e.g., Stimpert *et al.*, 2011a; Magnúsdóttir *et al.*, 2015; Rekdahl *et al.*, 2017; Fournet *et al.*, 2018a) and could, therefore, be potentially used as standardized humpback whale vocalization templates for studies worldwide.

Despite the relatively small number of UTs, the ASSO repertoire size is comparatively large in terms of number of phrase types (i.e., 62) for a 5 year period (Garland *et al.*, 2011; Magnúsdóttir *et al.*, 2015; Allen *et al.*, 2018; Rekdahl *et al.*, 2018). This large number of phrase types in the repertoire could be an indicator of multi-population singing activity in the ASSO, which is reflected in the recordings of multiple song types (hence a larger number of phrase types) per year originating from different breeding stocks (Payne and Guinee, 1983; Garland *et al.*, 2011). The comparison of phrase repertoires among populations or areas is complex due to the evolutionary nature of song (Cholewiak *et al.*, 2013) and shall not be addressed in this study. The constant development of song (also see Figure 4 for the visualization of phrase repertoire changes over multiple years) makes phrase types unideal candidates for reliable passive acoustic markers to detect humpback whale presence in PAM data.

The resulting repertoire of song units and phrases for humpback whales roaming in the ASSO may, however, be used in a number of applications including comparative analyses on temporal and spatial scales and exploring patterns in sound usage (e.g., Green *et al.*, 2011). Spatio-temporal patterns in humpback whale distribution and movements can be investigated on a large scale by using the described UTs as passive acoustic markers to detect humpback whale acoustic presence (Schall *et al.*, 2020). Repertoire stability and sharing within and

among populations can be assessed using reliable marker vocalizations (Fournet *et al.*, 2018a; Fournet *et al.*, 2018b). Furthermore, the results of this study may now facilitate a more standardized investigation of the complex processes of cultural transmission and cultural development of songs (i.e., evolutions and revolutions) on a temporal scale and among humpback whales on feeding grounds, migration routes, and breeding grounds, which previously was largely based on manual data processing (Darling and Sousa-Lima, 2005; Garland *et al.*, 2011; Garland *et al.*, 2013a; Allen *et al.*, 2018; Rekdahl *et al.*, 2018; Magnúsdóttir and Lim, 2019; Warren *et al.*, 2020).

While AMs have already shown their relevance in describing acoustic diversity patterns in different acoustic contexts, we show for the first time that a combination of AMs, rather than a single AM (also see Roca and Van Opzeeland (2019) for evidence on the discrimination of marine species identities), can be used to accurately categorize complex vocalization units in a supervised machine learning context. Our random forest model was able to accurately (84%) discriminate between the 12 UTs of humpback whales from the ASSO over a large range of years and sites. Other studies feeding manual (more subjective) measurements of vocalization parameters (e.g., min, max, peak frequency, duration) to machine learning algorithms to classify humpback whales and other marine mammal's vocalizations showed very similar, in some cases even higher, error rates. For example, random forest analysis also yielded relatively low average error rates when discriminating between 36 call types of beluga whales (*Delphinapterus leucas*) from the Beaufort Sea (83.2% accuracy; Garland *et al.* (2015a)), 11 call types of humpback whale from west coast of southern Africa (85%; Rekdahl *et al.* (2017)) and 16 call types of humpback whales from southeast Alaska (73%; Fournet *et al.* (2018a)). Higher average accuracy values have been shown when discriminating between call types of Bigg's killer whales (*Orcinus orca*) across three different regions in western Alaska (36 call types and 95% accuracy; Sharpe *et al.* (2019)). However, the manual

measurements used to generate the predictor variables in the latter study were complex and highly elaborated (i.e., including time consuming acoustic measurements) supporting the discrimination abilities of the model.

Model results on individual UT's misclassification rate showed relatively low values for all 12 humpback whale UTs described in this study (<30%; Table 2). We found the highest misclassification rates among the UT categories with the lowest sample sizes (i.e., UT4b and UT5b). However, other UTs with the same low sample sizes showed, in turn, very high accuracy scores (e.g., UT19 and UT03). This result, together with the general low error rates, firstly may reflect that, in our case, > 20 samples per UT were enough to obtain high accuracy results from the AM discrimination model. Secondly, AMs were successful to capture the variation in the spectral pattern of humpback whale UTs in our study. Other studies reporting a similar number of humpback whale UTs and using models constructed based on partial (manual) measurements, showed higher error rates for several of the categorized UTs (e.g., Rekdahl et al., 2017; Fournet et al., 2018a; Fournet et al., 2018b). Future research on the application of humpback whale UT models could further and quantitatively assess the optimal sample size per UT category to potentially increase the classification model's precision and estimate's robustness.

One advantage of including acoustic indices over other automated metrics used for classification is that acoustic indices provide integrative information about the spectral and temporal patterns characterizing each UT. This allows for a more intuitive and direct comparison between UTs. 43 out of 44 AMs were judged relevant according to the Boruta algorithm and included in the classification model. However, the conditional variable importance results showed interesting patterns in which some AMs, mainly computed in the 0-0.5kHz band, were of particular importance for the accurate discrimination between

humpback whale UTs in the ASSO. ACI and BI were in general the most important AMs, followed by acoustic indices NDSI, ADI and AEI. These results suggest that the variation in acoustic complexity and in the heterogeneity of the spectral and temporal patterns, mainly of the lower frequency band of the UT samples, played a major role in the discrimination between the 12 UTs identified for the humpback whales roaming the ASSO.

The selection and optimal combination of AM to use in predictive models to characterize UTs of any marine animal species will probably affect the model's efficiency and vary according to the acoustic context. It is of critical importance to choose relevant AMs to the ecological situation; that is, AMs of which the mathematical principle or algorithm is well suited to reflect and capture the spectral and temporal patterns of the target vocalizations. While automatically computed AMs palliate to some extent the relative subjectivity of manual measurements to construct the classification models, they still have some drawbacks. As manual measurements may be biased by background levels, background noise patterns have also shown to affect AMs to some extent (e.g., Gasc et al., 2015) and therefore, can introduce some error when, e.g., using classification models to assess UTs in new acoustic environments. However, the importance of this caveat may be lessened when controlling for the acoustic quality of the newly selected UT samples and when the misclassification error rate of each UTs is checked to remain very low.

Accurate discriminant models trained with a combination of relevant AMs, as the one presented in this study, may provide an interesting automated solution to use for simple and rapid identification of specific humpback whale UTs in large datasets. Furthermore, suitable models could be trained with AMs – to characterize the acoustic patterns of UTs, and used to compare, in a quantitative and highly reproducible manner, UT repertoire composition between different humpback whale populations or across multiple years in a particular

population of interest. It still remains to be investigated, whether a suitable combination of AMs (as an alternative or complement to more complex, specific and manually computed metrics) in the context of other supervised learning algorithms, such as regression models, could successfully capture gradual changes in the temporal or spectral structure of humpback whale UTs.

The application of AMs and supervised classification models also have further potential for the analysis of humpback whale song composition. In future studies simple automatic segmentation algorithms based on signal-to-noise ratios can be applied to song sequences to identify sound snippets containing units (Pace *et al.*, 2010). Measured AMs and supervised classification models would translate song sequences (i.e., sequences of sound snippets) into strings of unit succession, which in turn can be supplied to string comparison methods for decoding the hierarchical structures of song (Garland *et al.*, 2012; Malige *et al.*, 2020). In addition, AMs might also provide valuable information for the differentiation of themes and song types by describing energy content and entropy in different frequency bands when directly applied to these higher-level song structures. We conclude that AMs exhibit high potential to provide useful tools for multiple applications that are far beyond the scope of their original purpose.

V. ACKNOWLEDGMENTS

VI.   ENDNOTE

See supplementary material at [URL will be inserted by AIP] for additional tables and figures.

VII.   LITERATURE

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Chapter IV

Humpback whale song recordings suggest common feeding ground occupation by multiple populations

Humpback whale song recordings suggest common feeding ground occupation by multiple populations

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100

Abstract

Humpback whale males are known to sing on their low-latitude breeding grounds, but evidence is increasing that songs are also commonly produced 'off-season' on the feeding grounds or during migration. This opens exciting opportunities to investigate migratory aggregations, study humpback whale behavioral plasticity and potentially even assign individual singers to specific breeding grounds. In this study, we analyzed passive acoustic data from 13 recording positions and multiple years (2011-2018) within the Atlantic sector of the Southern Ocean (ASSO). Humpback whale song was detected at nine recording positions in five years. Most songs were recorded in May coinciding with the rapid increase in sea ice concentration at most recording positions. The spatio-temporal pattern in humpback whale singing activity on Southern Ocean feeding grounds is most likely shaped by local prey availability and humpback whale migratory strategies. Furthermore, the comparative analyses of song structures clearly show a differentiation of two song groups, of which one was solely recorded at the western edge of the ASSO and the other song group was recorded throughout the ASSO. This new finding suggests a common feeding ground occupation by multiple humpback whale populations in the ASSO, allowing for cultural and potentially even genetic exchange among populations.

Introduction

Humpback whales annually undertake one of the longest mammalian migrations between their mid to high latitude feeding areas and low latitude breeding areas (Clapham, 2018). Various hypotheses on what drives baleen whale migration between such extremely spatially separated habitats have been put forward (Corkeron and Connor, 1999; Geijer *et al.*, 2016), but to date, the reasons have not been understood entirely. On the breeding grounds, humpback whale sexual selection, copulation and parturition take place (Baker and Herman, 1984; Palsbøll *et al.*, 1992; Herman, 2017). Besides physical advertisement and intra/intersexual competition strategies (i.e., escorting of females and physical aggression among males)(Baker and Herman, 1984; Palsbøll *et al.*, 1992), humpback whale males also perform acoustic displays in the form of songs (Payne and Mcvay, 1971; Herman, 2017). Humpback whale song is thought to fulfil a multi-purpose role within the species' mating system, in many aspects comparable to bird song (Kroodsma and Byers, 1991; Herman, 2017). Male humpback whale song production is thought to increase the chances of reproduction for individual males by mediating inter- and intrasexual interactions (Herman, 2017). The majority of songs are therefore produced on the low-latitude breeding grounds, but 'off-season' song has also repeatedly been recorded along migration routes and on feeding grounds during different times of the year (Payne and Mcvay, 1971; McSweeney *et al.*, 1989; Noad and Cato, 2007; Smith *et al.*, 2008; Garland *et al.*, 2011; Stimpert *et al.*, 2012; Vu *et al.*, 2012; Kowarski *et al.*, 2018; Ross-Marsh *et al.*, 2020). Opportunistic singing outside the breeding grounds and/or season is interpreted as low-cost reproductive advertisement by males, e.g., to access females that failed to conceive during the breeding season, although to date copulation has never been visually observed outside the breeding grounds (Clark and Clapham, 2004b; Vu *et al.*, 2012).

Not much is known on which humpback whale stocks use which areas for feeding in the Southern Hemisphere (International Whaling Commission, 2011; 2016). Given that songs are breeding population-specific, the presence of song on the feeding grounds opens the possibility to assess breeding stock affiliation by comparative analyses of songs (McSweeney *et al.*, 1989; Garland *et al.*, 2013a). As in many other baleen whale species, song in humpback whales can be used to determine stock affiliation, also on the feeding grounds (Payne and Mcvay, 1971; Payne and Guinee, 1983; McSweeney *et al.*, 1989; Gabriele and Frankel, 2002; McDonald *et al.*, 2006; Delarue *et al.*, 2009; Garland *et al.*, 2013a; Herman, 2017). Male humpback whales on a specific breeding ground are known to converge closely on the same

current rendition of song, termed song type (Winn and Winn, 1978a; Winn *et al.*, 1981; Payne and Guinee, 1983; Payne and Payne, 1985a; Herman, 2017). Each song type is characterized by a distinct combination of themes, which in turn are built by the repetition of specific phrase types and each phrase type is composed of a unique combination of units (Payne and Mcvay, 1971; Cholewiak *et al.*, 2013). Songs recorded on feeding grounds are composed of the same hierarchical structure as on the breeding grounds, although in some cases less complex song sequences or fragments of songs were registered (Mattila *et al.*, 1987; McSweeney *et al.*, 1989; Stimpert *et al.*, 2012; Magnúsdóttir *et al.*, 2015; Kowarski *et al.*, 2019; Magnúsdóttir and Lim, 2019). For Northern Hemisphere humpback whales, the analysis of feeding ground songs suggests that these mainly stem from immature males conducting "off-season" singing on the feeding grounds and during migration to practice singing (Kowarski *et al.*, 2019). The fact that humpback whales sing on the feeding grounds is furthermore thought to facilitate cultural transmission of new songs within the breeding population, but potentially also between different stocks (Magnúsdóttir and Lim, 2019). On Southern Hemisphere feeding grounds, the data on humpback whale song occurrence and dynamics are still limited both spatially and temporally. At the same time, information on stock distributions while on the feeding grounds is lacking, but crucial to management decisions on ecosystem and population conservation (International Whaling Commission, 2011; 2016; Teschke *et al.*, 2016). To date, two studies have presented song recordings from Antarctic waters comprising four days from two sites (Stimpert *et al.*, 2012; Garland *et al.*, 2013a). One further study collected acoustic data near a humpback whale 'super-group' off western South Africa and describes the song that was recorded there (Gridley *et al.*, 2018). These studies showed that the identification and structural analysis of humpback whale song from austral feeding grounds can provide valuable information on humpback whale behavioural ecology and potentially even offer insight into the breeding stock origin of humpback whale males present in the feeding areas.

By analysing a passive acoustic data set spanning 13 recording positions deployed throughout the Atlantic sector of the Southern Ocean (ASSO) covering multiple years between 2011 and 2018, this study is the first to investigate the large-scale spatio-temporal patterns in humpback whale song presence and structure in the Southern Ocean. By assessing how humpback whale song evolves over time, latitude, and longitude, we explore the comparability of feeding ground song with songs on the breeding grounds, the role of the ASSO as an alternative mating ground, and the potential multi-population use of the ASSO feeding area.

Results

Humpback whale song and non-song presence

In total, 186,074 hours of recordings were processed, of which 4,796 hours were verified to contain humpback whale vocalizations. The preliminary song category, HWS2 was found in 430 hours and the complex song category, HWS1 was found in 1,127 hours. The remaining 3,239 hours contained exclusively humpback whale social calls.

Spatio-temporal pattern in the song presence

At most of the recording locations, the acoustic presence of humpback whales (i.e., detection of any humpback whale vocalizations including social calls) was dominated by the occurrence of humpback whale song. For almost all recording positions with records of humpback whale acoustic presence, humpback whale song also was identified in the recordings (Figure 3). The preliminary HWS2 was found in a similar spatio-temporal pattern as the complex HWS1, only in lower numbers (Figure 3). The earliest song of the year was detected at the recording position G1 on January 24, 2013 and the latest song of the year was detected at the same recording position on August 3, 2011 (Figure 7). Song recordings were seasonally restricted to the summer and autumn months (Figure 7). Most songs were detected at the recording locations G1, G1, G3, and G4 on the Greenwich Meridian in the months April, May, and June (Figure 3, Figure 7). During these months, songs were recorded continuously throughout the day or during random (even) hours of the day. March was the month when (complex) song was recorded at the most recording positions (i.e., five positions; Figure 3) Summarizing all song recordings over years and positions, the number of hours containing humpback whale song is highest in May. This peak coincides with the rapid increase in sea ice concentration in late summer/autumn (Figure 7). The first song recordings of the season were within 54 and 143 days after the sea ice concentration dropped below 15% (definition sea ice edge)(Tynan and Thiele, 2003). The last song recordings of the season were maximally 12 days after the sea ice concentration exceeded 15%.
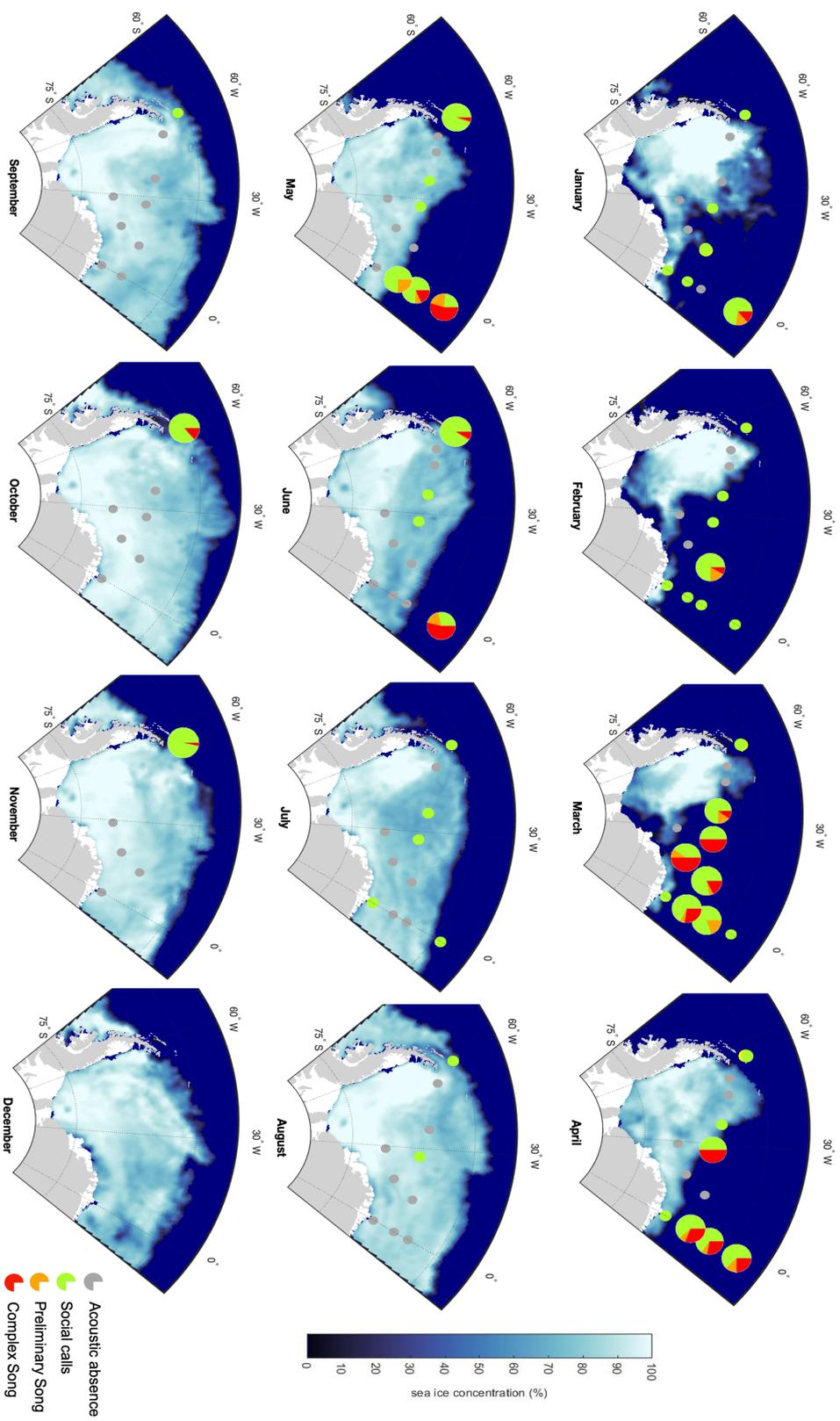
Figure 6. Proportion of social calls, preliminary song and complex song of humpback whales in the ASSO averaged per recording location and month for the year 2013. The monthly averaged sea ice concentrations are depicted at a 25x25km resolution. (See Schall et al. 2020 for details on acoustic presence)
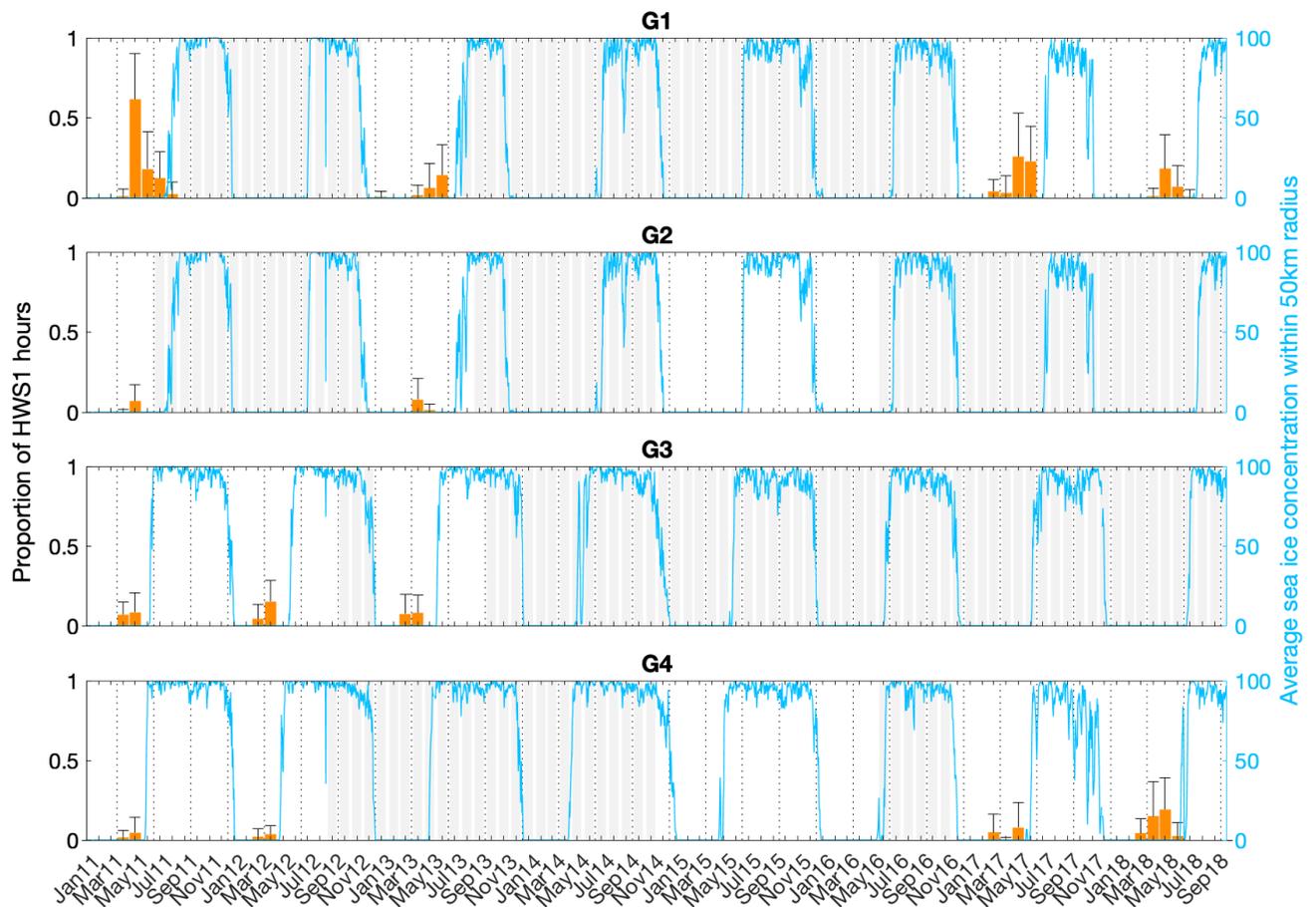
Figure 7. Proportion of HWS1 hours at the Greenwich Meridian averaged per month and recording location (G1-G4) from January 2011 until October 2018 (orange bars). Vertical error bars show the respective standard deviations and continuous grey bars represent months without recording data. The blue solid lines and the right y-axis depict the daily averaged sea ice concentration per location within a 50km radius.

Effects of latitude and time of the year on song length and complexity

Measures of song session and song length did not show a clear trend in the course of the year and did not show any trend along a latitude gradient (Supplementary Material 1: Table S1, Figure S2). A slight increase of song session and song length could be observed from calendar day 120 to calendar day 182, with a maximum mean song session length of 1603 units and a maximum mean song length of 400.75 units on calendar day 182 (Supplementary Material 1: Figure S2).

The level of agreement between the manual unit classification and the result of the supervised machine learning approach was high with a OOB misclassification rate of 16% indicating a robust differentiation of units, phrases, themes and songs (i.e., 62 phrase types; see Supplementary Material 1: Table S2 and Supplementary Material 2). Resulting measures of unit, phrase and song complexity did not show a trend in the course of the year or along a latitude gradient (Supplementary Material 1: Table S1, Figure S2). Different levels of complexity were almost equally distributed throughout time and across latitude.

Effects of longitude and year on song structure

The phrase repertoires of individual singers were strongly differentiated between the eastern and western edges of the ASSO. Two individuals (based on prior assumptions) recorded off Elephant Island (i.e., W1305/06/13 and W1305/10/13; Figure 6) used a phrase repertoire which was completely different to all other phrase repertoires, whereas one individual recorded off Elephant Island did use a phrase repertoire which was similar to the phrase repertoires recorded on the eastern edge of the ASSO (i.e., W1316/06/13; Figure 6; Supplementary Material 1: Table S2). All repertoires of the recording positions from the eastern edge of the ASSO (i.e., Greenwich Meridian) and the central Weddell Sea (i.e., all Weddell Sea recorders except the recorder close to Elephant Island) were highly similar to each other depending on the year of recording (Figure 6; Supplementary Material 1: Table S2). Phrase repertoires from the years 2011-2013 had the highest similarities to each other and repertoires from 2017 and 2018 had variable similarities between 30 and 80%. The phrase repertoires from 2011-2013 and 2017/18 were at least 50% different (Figure 6). Some individual singers within the same recording year shared the phrase repertoire to a 100% (Figure 6).

Similarity of phrase repertoires
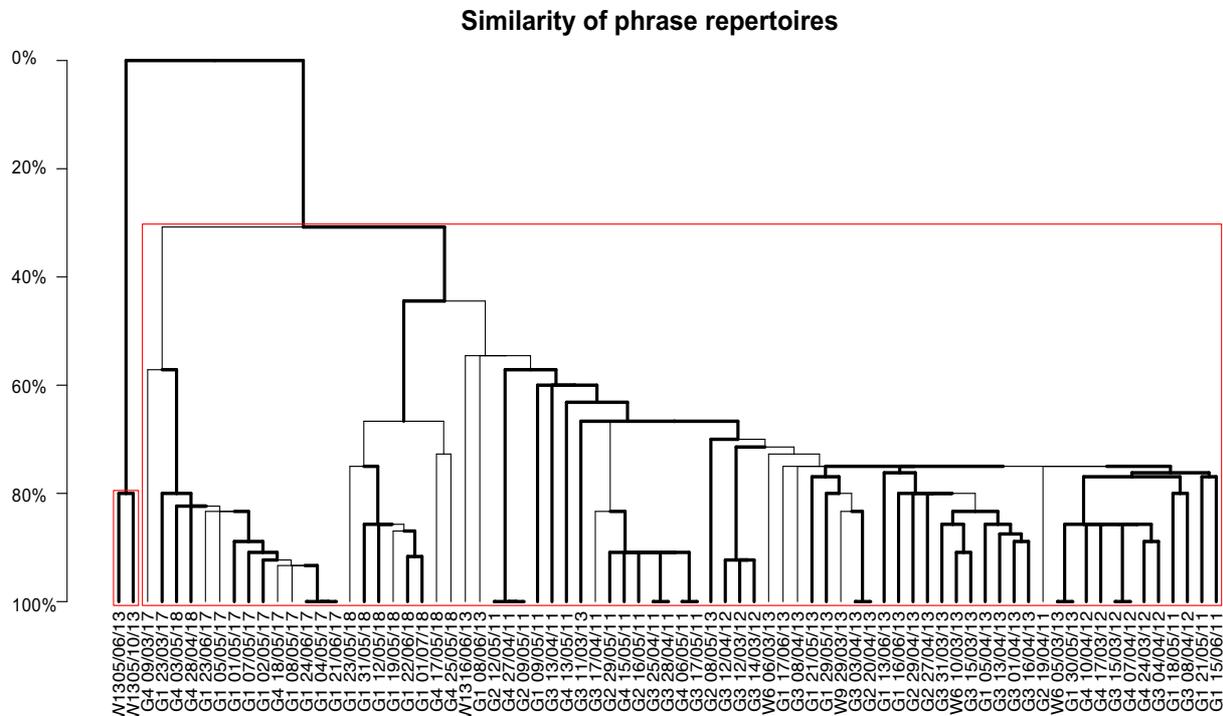
Figure 8. Bootstrapped dendrogram from hierachical clustering of set median song strings recorded at different locations and years, based on DCI analysis. Names on each branch belong to individual singers encoded with the name of the recording position (first 2-3 symbols, i.e., 'W13', 'G4',...) and the date of the recording (last 8 symbols, i.e., '05/06/13', '05/10/13',...). Bold lines indicate divisions that were likely to occur (i.e., AU >95%) and red boxes indicate clusters which are strongly supported by the data.

The song structure in terms of theme order was again highly differentiated between the eastern and western edges of the ASSO. Two individual singers recorded of Elephant Island sang song sequences which had 0% similarity with all other song sequences recorded in this study (i.e., W1305/06/13 and W1305/10/13; Figure 7), while one individual singer recorded also off Elephant island sang a song sequence which was similar to the song sequences recorded at the eastern edge of the ASSO (i.e., W1316/06/13; Figure 7; Supplementary Material 1: Table S2). Except for these two distinct individual singers from 2013 off Elephant Island, all other recorded song sequences from the years 2011, 2012, and 2013 were similar in structure, i.e., with similarities between 30% and 70% (Figure 7; Supplementary Material 1: Table S2). Song sequences from 2017 and 2018 were only 20% similar to the song sequences from the other

years and between the years 2017 and 2018 similarity was also low (i.e., 20%), except for two individual singers from 2018 which were recorded early in the season (i.e., G403/05/18 and G428/04/18; Figure 7; Supplementary Material 1: Table S2).

Similarity of theme sequences
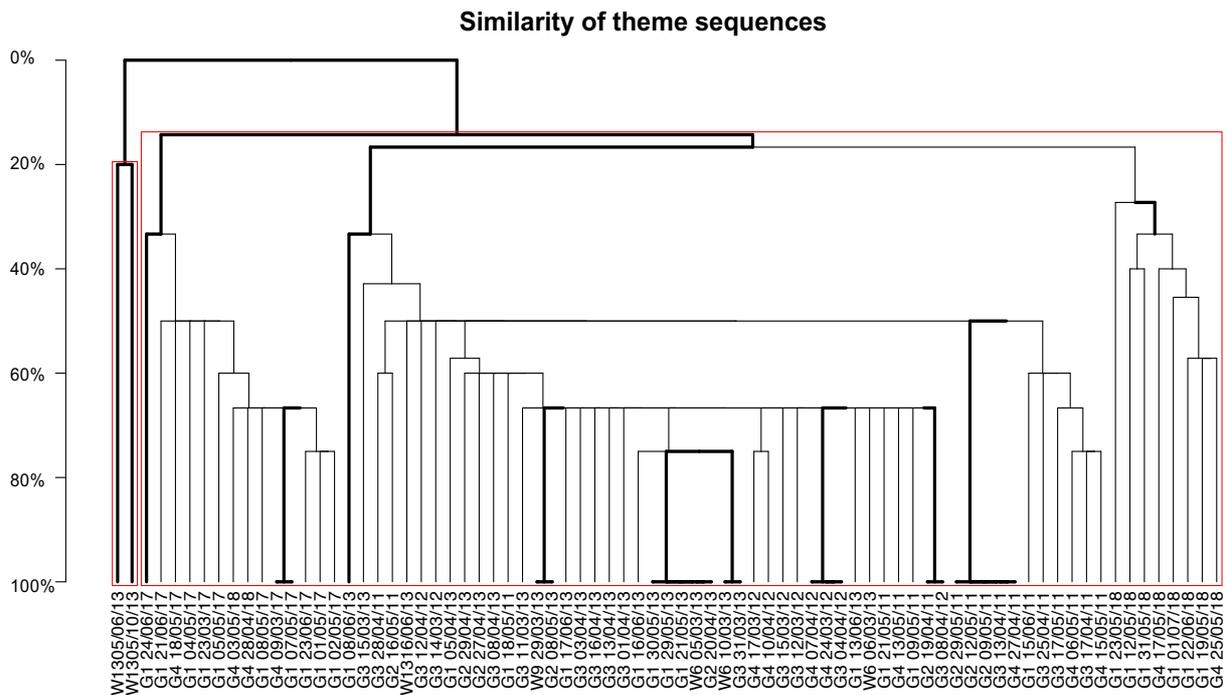
Figure 9. Bootstrapped dendrogram from hierachical clustering of set median song strings recorded at different locations and years, based on LSI analysis. Names on each branch belong to individual singers encoded with the name of the recording position (first 2-3 symbols, i.e., 'W13', 'G4',…) and the date of the recording (last 8 symbols, i.e., '05/06/13', '05/10/13',…). Bold lines indicate divisions that were likely to occur (i.e., AU >95%) and red boxes indicate clusters which are strongly supported by the data.

Discussion

Spatio-temporal pattern

The present study is the first record of the large-scale occurrence of humpback whale song in the ASSO. Humpback whale song was recorded at nine of the 13 recording positions and multiple years of song recordings were registered in the course of this study. Our data was able to show for the first time that reproductive activities are likely to occur over a large spatio-temporal scale on the feeding grounds in the Southern Ocean. 2015 and 2016 were the only years with no

humpback whale song recordings, which is probably related to the physical absence of humpback whales from the area in these years due to unfavourable environmental conditions (E Schall, submitted manuscript).

The presence and absence of humpback whale song on the feeding ground might be directly determined by local prey availability, as whales might be spending more time searching for food when local prey abundance is low, negatively affecting the likelihood of displaying singing behaviour. In zebra finches (*Taeniopygia guttata*), experiments showed that singing rates decreased when the prey availability was reduced (Ritschard and Brumm, 2012). Both changes in body condition and time budget available for acoustic displays were suggested as two possible connections between the availability of food and singing behaviour. It can therefore not be ruled out that humpback whales were present in the area around the Greenwich Meridian in 2015 and 2016, but that individuals produced no or very little calls, possibly due to climate oscillations negatively affecting krill productivity, and therefore whales needing to spend more time foraging to fulfil their energetic needs (E Schall, submitted manuscript). The reduction of singing behaviour in humpback whales due to environmental changes could also explain the small inter-annual differences in the amount of song recorded among the years 2011, 2012, 2013, 2017, and 2018.

Spatially, humpback whale song was found at all recording positions where acoustic presence was registered except the southernmost recording position at the Greenwich Meridian (G5, Schall *et al.* (2020)). This recording position is the closest to the Antarctic continent among all analysed recording positions and most of the time of the year it is covered by sea ice. The environmental conditions at this recording position are very similar to the conditions at the coastal recording station PALAOA, where similarly only humpback whale social calls were recorded during many months of the years 2008 and 2009, but no humpback whale songs were registered (Van Opzeeland *et al.*, 2013). These combined results potentially support previous suggestions that the habitat close to the continent with an often dense ice cover might only be used by females and/or immature whales residing here throughout winter to presumably improve body condition (Craig *et al.*, 2003; Van Opzeeland *et al.*, 2013). This migratory-segregation depending on sex, age, and reproductive status in humpback whales (Dawbin, 1997) possibly also explains the detection of social calls at other recording positions during the winter months when at the same time no humpback whale songs were recorded.

The detections of humpback whale songs were in general strongly seasonal. Male song production increased with the end of the summer/beginning of autumn alongside with rapidly increasing sea ice concentrations. Humpback whale males seem to travel as far south as the sea ice retreats in summer and also adapt their northward migration to the expansion of the sea ice in autumn (Thiele et al., 2004; Van Opzeeland et al., 2013; Bombosch et al., 2014). To optimize access to females, sexually mature males may not travel as far into the ice compared to females or immature males, to ensure their in-time arrival at the breeding grounds which may have reproductive advantages (Brown et al., 1995; Craig et al., 2003). While the males still roam on the feeding grounds, they already commence the so-called (pre-breeding) shoulder season with the start of song production (Stimpert et al., 2012; Vu et al., 2012; Garland et al., 2013a; Kowarski et al., 2018). In other baleen whale species, song production has also been documented to occur outside the breeding area and season (McDonald et al., 2006; Simon et al., 2010; Stafford et al., 2012; Risch et al., 2013; Oleson et al., 2014; Thomisch et al., 2016), but the precise functionality of "off-season" song remains unknown. Similarly, some humpback whale males still sing when they arrive at the feeding ground in spring (during the post-breeding shoulder season) (Vu et al., 2012; Magnúsdóttir et al., 2014; Kowarski et al., 2019), which in the case of the ASSO was only observed at Elephant island (W13). In tropical birds, the year-round production of song is related to territorial defense and is thought to play a role in interspecific communication (Brenowitz et al., 1997; Tobias et al., 2011). Singing activities in humpback whale males are thought to be triggered by elevated testosterone levels which slowly increase during the end of summer and decreases in spring (Vu et al., 2015; Herman, 2017). Additionally, sexually mature males might also start singing when nutritional status allows singing activities during breaks from feeding. In song birds, the nutritional status has been shown to be a crucial factor affecting the amount of singing (Casagrande et al., 2016; Yamada and Soma, 2016). For example, male Bengalese finches showed higher song output including higher rates of singing and longer songs when receiving a high-nutrition diet compared with males receiving a moderate-nutrition diet (Yamada and Soma, 2016). The length of the pre-breeding shoulder season in our data (up to 5 months) indicates that humpback whale males during this time mix feeding and reproductive behaviours on a regular basis (Weinrich, 1995; Stimpert et al., 2012). Early whaling studies showed that the timing of conception in Southern Hemisphere humpback whales ranged between June and October (Chittleborough, 1954; 1958). Consequently, the

ASSO might serve as an alternative breeding ground for the part of the population which skips migration.

Song development on the feeding ground

Feeding grounds and pre-breeding shoulder seasons have been suggested to be the place and the time for the annual events of humpback whale song innovation (McSweeney *et al.*, 1989; Cerchio *et al.*, 2001; Garland *et al.*, 2013b). Our data do not suggest a clear sign of song development on the feeding ground. The less complex preliminary song category (HWS2) was detected in lower numbers than the complex song category (HWS1) during almost all months when humpback whale songs were recorded. Additionally, the analysis on song complexity and length suggests that songs recorded on the ASSO feeding ground do not get more elaborate in the course of the season, only a slight increase in song and session length was detected. McSweeney *et al.* (1989) discovered that songs on the feeding ground were shorter than the comparable songs on the breeding ground. However, the sample size in this study was very small and thus the increase in session/song length in the course of the season on the feeding ground potentially remained undetected. Vu *et al.* (2012) also detected an increase in session length in autumn and suggested a connection between the amount of singing activity and the testosterone level. Our results indicate that this connection could also be true for singing activity on Southern Ocean feeding grounds. Song complexity and the process of developing the complex breeding ground song on the feeding ground, in contrast, seems not to be connected with the elevation of testosterone levels. Instead, humpback whale males might start singing the song from the previous breeding season and change or adapt random themes in the course of the season until the new song is formed (McSweeney *et al.*, 1989; Garland *et al.*, 2013a). However, it cannot be ruled out that other measures for song complexity as a condensed 'complexity score' or phrase transition patterns may have shown trends over the course of a season (Allen *et al.*, 2018; Magnúsdóttir and Lim, 2019). The change or adaptation of themes is probably a product of cultural transmission of songs among and within different breeding populations while whales visit common feeding areas (Cerchio *et al.*, 2001; Garland *et al.*, 2011; Garland *et al.*, 2013a). The production of song on the ASSO feeding grounds could therefore serve the facilitation of this cultural transmission to increase the chances of reproduction on the breeding grounds by

singing a newly innovated version of song and/or could have direct benefits to the reproductive success of males in place.

Song differentiation in the ASSO

Although humpback whale males might not sing the fully developed breeding ground song on the feeding ground, our data suggest a clear differentiation of two distinct song groups, which most likely belong to (at least) two distinct humpback whale breeding stocks. The parallel presence of two distinct song groups in the ASSO demonstrates its ecological significance for cultural and maybe even genetic exchange among humpback whale breeding stocks in this area. One song group was recorded in 2013 exclusively at the western edge of the ASSO, north of the Antarctic Peninsula, and close to the coast of Elephant island. The other song group was recorded throughout the ASSO from 2011 to 2018. These two song groups were completely different both in phrase repertoire and theme sequence. The clear result of higher differentiation between these two groups than among years indicates that at least two different breeding populations visit the ASSO as a feeding area. The fact that song sequences of both song groups were recorded off Elephant islands additionally indicates that the distinct breeding populations spatially overlap in their distribution on the feeding ground. At least four distinct breeding stocks are in spatial vicinity to the ASSO on the longitude scale: Breeding stock G in the eastern South Pacific, breeding stock A in the western South Atlantic, breeding stock B in the eastern South Atlantic, and breeding stock C in the western Indian Ocean (International Whaling Commission, 2011). Humpback whales from the breeding stock G are thought to occupy the Antarctic management area I (120–60°W) as a feeding ground, which has been proven by genetic and Photo-ID studies (Stevick *et al.*, 2004; Engel *et al.*, 2008). A circumpolar study on humpback whale genetics has shown that humpback whales from the Antarctic management area I are highly differentiated from all other management areas (except for samples collected close to management area I in management area II; 60°W–0) (Amaral *et al.*, 2016). The two song sequences that were strongly different from the rest of the song sequences recorded during this study were recorded on the border between management area I and II, which makes it likely that this song group stems from a South Pacific breeding stock. The second song group including the majority of the song sequences recorded during this study probably stems from a South Atlantic breeding stock or could also be related to an Indian Ocean breeding stock. Previous studies have

shown that songs from breeding stocks A, B, and C often show similarities both in repertoire as well as structure (Darling and Sousa-Lima, 2005; Razafindrakoto *et al.*, 2009; Rekdahl *et al.*, 2018). Satellite tagging studies have shown that humpback whales from breeding stock A and B both migrate to the eastern part of the South Atlantic (Zerbini *et al.*, 2011; Rosenbaum *et al.*, 2014) and might therefore both contribute to the songs recorded in this study. Single song phrases detected in this study were also documented for song sequences recorded off the Western Cape of South Africa (Gridley *et al.*, 2018; Ross-Marsh *et al.*, 2020). In order to fully understand the eventual sharing of common feeding areas among humpback whales from different breeding stocks and the cultural transmission of song among them, further comparative analyses of songs from the breeding grounds and the ASSO are necessary.

Conclusions and Outlook

The ASSO forms an important summer feeding habitat for various baleen whale species and different studies have also shown its importance as an overwintering ground (Van Opzeeland *et al.*, 2013; Thomisch *et al.*, 2016; Filun *et al.*, 2020; Schall *et al.*, 2020). The first evidence of humpback whale song over a large spatio-temporal scale furthermore proves the additional importance of the ASSO for reproductive activities. The distinct timing of song occurrence at the eastern and western edges of the ASSO together with the identification of two different song groups in these two regions indicates that at least two different breeding stocks of humpback whales use the ASSO for feeding and reproduction. Comparative song analyses including songs from the ASSO as well as songs from the different breeding stocks are planned to gather more detailed information on how the occupation of this large feeding area in the Southern Ocean connects to the acoustic recordings of humpback whale songs from lower latitudes. The identification of crucial habitats for migratory baleen whales, as well as, the linkages between breeding and feeding grounds is of key importance for stock management and the planning of large-scale marine protected areas (International Whaling Commission, 2016; Teschke *et al.*, 2016).

Methods

Data and processing

We investigated humpback whale acoustic behaviour using data from 13 recording positions throughout the *ASSO* (Figure 10) which recorded in different periods between 2011 and 2018 (five recording positions form the multi-year Greenwich dataset and eight recording positions form the single-year Weddell dataset; Supplementary Material 1: Figure S1). Passive acoustic recordings were obtained using SonoVaults (Develogic GmbH, Hamburg) operated on a continuous recording scheme and with a sampling rate of 5,333 to 9,600 Hz (Rettig *et al.*, 2013b).
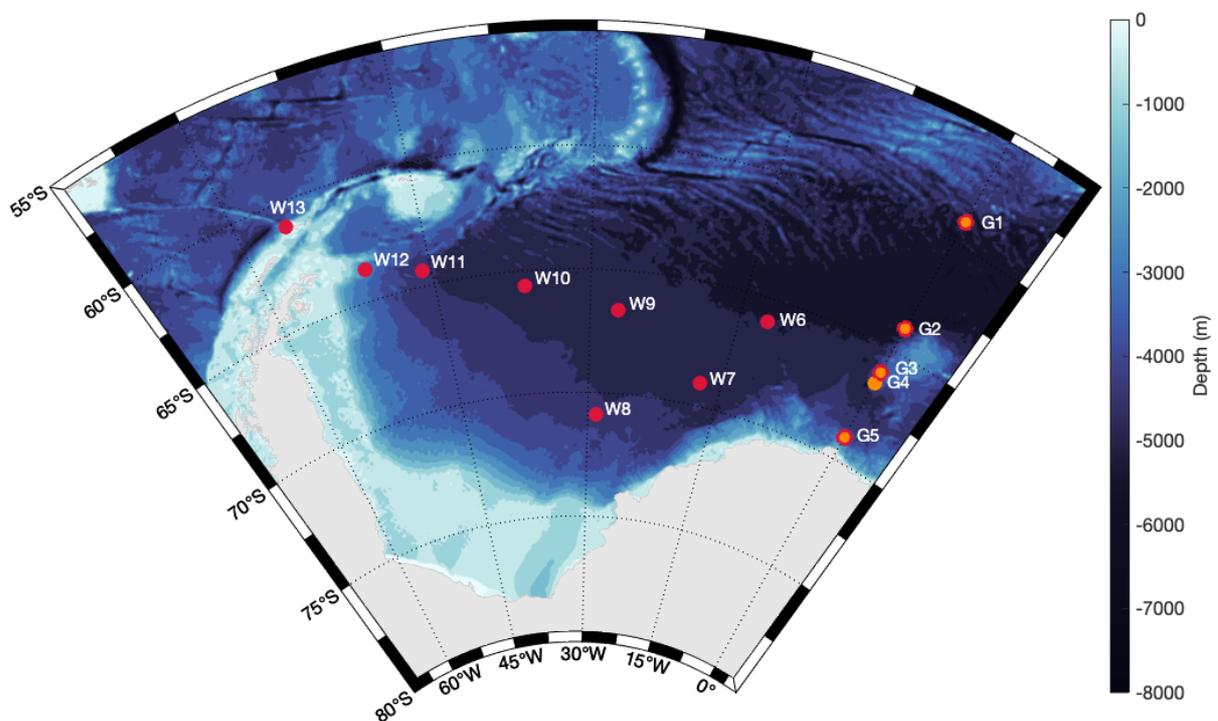
Figure 10. Mooring positions included in this study. Mooring positions marked in orange and labelled with the prefix 'G' in the name are part of the multi-year Greenwich dataset (2010-2018). Mooring positions in red and labelled with the prefix 'W' in the name are part of the single-year Weddell dataset (2013). Mooring positions which are marked in orange and red are part of both datasets.

All available passive acoustic data were processed by the 'Low Frequency Detection and Classification System' (LFDCS) developed by Baumgartner and Mussoline (2011b) and a

custom-made acoustic-context filter to detect humpback whale acoustic presence at an hourly basis. LFDCS was set up with a customized call library based on the most common vocalization types of humpback whales and other acoustically abundant Antarctic marine mammal species (i.e., Antarctic minke whale (*Balaenoptera bonaerensis*), killer whale (*Orcinus orca*), Weddell seal (*Leptonychotes weddellii*), crabeater seal (*Lobodon carcinophaga*), leopard seal (*Hydrurga leptonyx*), and Ross seal (*Ommatophoca rossii*)) (Dunlop *et al.*, 2008; Klinck *et al.*, 2010; Van Opzeeland *et al.*, 2010; Stimpert *et al.*, 2011a; Risch *et al.*, 2014c; Schall and Van Opzeeland, 2017). Parameter settings and thresholds of LFDCS and the acoustic context filter were tuned employing multiple test datasets to optimize the automatic detection of humpback whale vocalizations to the requirements of this study. Detailed information on set up and test runs of the automatic detection process are provided in Schall *et al.* (2020).

The sea ice concentration data used for this study were extracted from: a combination of satellite sensor data from the Nimbus-7 Scanning Multichannel Microwave Radiometer (SMMR), the Defense Meteorological Satellite Program (DMSP) -F8, -F11 and -F13 Special Sensor Microwave/Im rs (SSM/Is), and the DMSP-F17 Special Sensor Microwave Imager/Sounder (SSMIS), with a grid size of 25 km (Cavalieri *et al.*, 1996) and the satellite images from the Advanced Microwave Scanning Radiometer for EOS (AMSR-E) satellite sensor with a grid size of 6.25 km (Spreen *et al.*, 2008). The data were used to calculate the daily sea-ice concentration of the area within 50 km radius around each recording location of the *Greenwich* dataset in MATLAB. Additionally, the data were used to calculate monthly averages of sea-ice concentrations for the *ASSO* and plotted as maps with the Antarctic Mapping Tools and Daily Antarctic Sea Ice Concentration packages in MATLAB (Greene *et al.*, 2017; Greene, 2020).

Song presence

Even hours with presumed humpback whale acoustic presence (i.e., hours 0, 2, 4, 6, 8, 10, 12, 14, 16, 18, 20, 22 indicated by the automatic detector) were revised visually and aurally for the presence of humpback whale vocalizations by creating spectrograms in Raven Pro 1.5 (Hann Window, 1025-1790 window size, 80% overlap, 2048 DFT size; Bioacoustics Research Program 2014). Spectrograms were scanned for humpback whale vocalizations by viewing 60 s windows from 0 to 1.80 kHz. Hours with confirmed humpback whale acoustic presence were separated in hours with humpback whale social calls and hours with humpback whale song, applying

guidelines from Cholewiak *et al.* (2013). Hours with humpback whale song were further divided into two song categories: the preliminary song category and the complex song category. Humpback whale vocalizations that were organized in at least two different themes were classified as the complex song category 1 (*humpback whale song 1*; HWS1; Figure 11). If humpback whale vocalization bouts did not conform to the rule of the complex song category, but still formed at least three repeated, similar phrases, the respective hour was classified as the preliminary song category 2 (*humpback whale song 2*; HWS2; Figure 11).
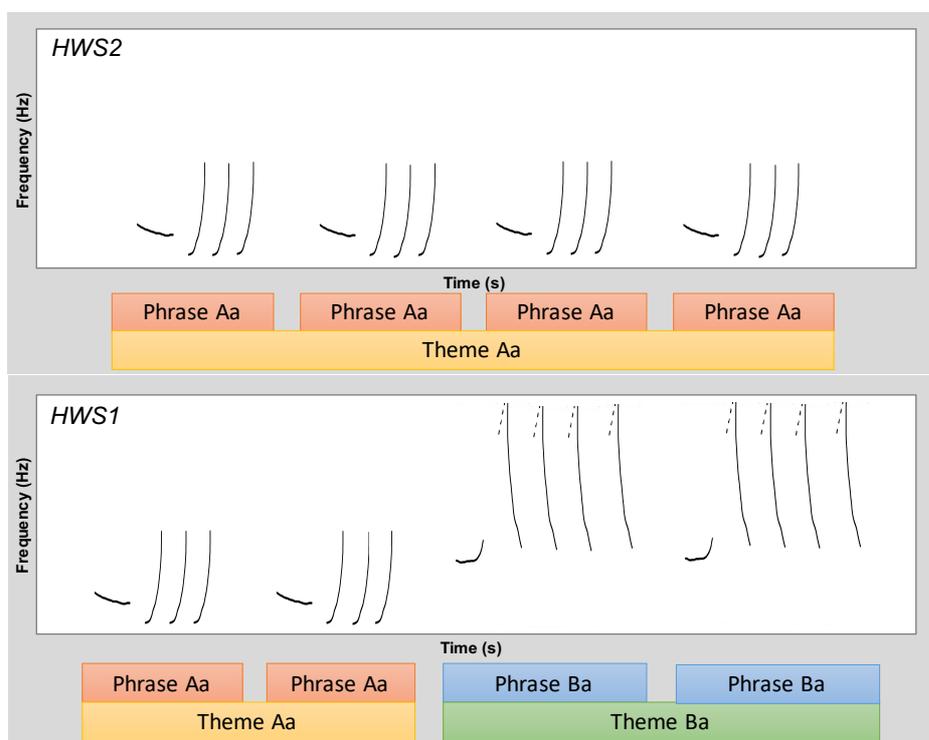
Figure 11. Schematic illustration of spectrogram visualizations of the preliminary humpback whale song 2 (HWS2) and complex humpback whale song 1 (HWS1) categories. HWS2 is defined as a vocalization sequence organized in at least three repeated, similar phrases and HWS1 is defined as a vocalization sequence organized in at least two different themes (see (Cholewiak et al., 2013) for details on phrase and theme delineation).

Song sequence analysis

Song sequences of humpback whales in the ASSO were investigated and catalogued by analysing all even hours with high quality complex songs (i.e., SNR $\geq$ 10 dB and at least two distinct themes discernible). Both the preceding and succeeding odd hours to the respective

analysed hour were also included in the analysis if those also contained high quality song sequences. Humpback whale vocalizations were manually logged within the spectrograms in Raven Pro (with identical spectrogram settings). Logged calls were manually classified into distinct unit types (call types: CT followed by a number) according to the following criteria: 1) differentiation of tonal or broadband characteristics, 2) duration, 3) frequency range and 4) time-frequency slope. Within a humpback whale song sequence, phrases were logged and classified according to unit repetition following Cholewiak *et al.* (2013) recommendations. Phrase types were identified with an uppercase letter (indicating the 1st unit type), a lowercase letter (indicating the combination of following unit types) and a sequence of numbers (indicating the number of repetitions of each unit) in order to be able to breakdown to the original unit sequence in the downstream analysis process.

The manual subjective analysis of unit and phrase repertoire was tested in terms of robustness by applying an automated classification approach to a subset of units (i.e., 436 exemplar units with at least 20 exemplars per unit type). We computed 44 different acoustic metrics for every extracted unit (i.e., 3s sound file decimated to 5,000 Hz to ensure comparability). The 44 metrics can be described as belonging to either of these three categories: (1) indices based on different algorithms to compute acoustic complexity, entropy or diversity (acoustic indices); (2) metrics measuring amplitude or background patterns (energy metrics); and (3) metrics computing ratios between acoustic activity over time and frequency bands (ratio metrics). Details on the acoustic metrices used and the process of computation for the 436 sound examples can be found in Schall et al. 2021 (submitted manuscript attached for review purposes only). The 44 acoustic metrics for each extracted unit were used in a supervised machine learning approach (i.e., random forest, see Schall et al 2021 for details, submitted manuscript attached for review purposes only) to discriminate between manually classified unit types and the automatic classification accuracy was assessed with the general 'Out-of-bag' (OOB) misclassification rate.

Song structure, length and complexity

Registered song sequences were allocated to presumed individual singers in order to assess inter-individual variation in song sequences. Due to the nature of our single sensor autonomous recordings, song sequences cannot be attributed to individual calling males. Therefore, the following assumptions were made to differentiate among individual singers. Firstly, recordings

of humpback whales at the distinct recording positions, at a specific point in time were assumed to be distinct humpback whale individuals due to the geographic distances of more than 200 km among recording positions, except for the recording positions G3 and G4, between which a humpback whale with an average swimming speed of 4 km/h (Noad and Cato, 2007) could travel within 24 hours. Second, recordings of humpback whale song, between which more than 24 hours had passed were assumed to belong to different individual singers due to the estimated travel rates of 17 to 75 km/day in humpback whales on an Antarctic feeding ground (Dalla Rosa *et al.*, 2008).

Furthermore, for the following quantitative comparisons of song length, complexity, repertoire and structure, song sequences of individual singers were separated into song sessions and songs. Song sessions are commonly defined as all song elements sung until a gap of silence of more than one minute occurs (Payne and Mcvay, 1971; Cholewiak *et al.*, 2013). The definition of the start and end of an explicit song can however be problematic due to the numerous distinct attempts defining a song in different studies (Cholewiak *et al.*, 2013). Inspecting our song sequence data for common patterns, the most sensible definition for song in the ASSO seemed to be the complete rendition of all unique theme types per song sequence to form an explicit humpback whale song (Cholewiak *et al.*, 2013).

To quantitatively compare the elaborateness (including complexity and length) of song per time of the year and latitude, two measures of length and three measures of complexity were included in the analyses. The length of song sessions and songs was measured as the number of vocalization units per sequence. Session and song length were averaged per individual singer and standard deviations were calculated. Furthermore, three measures of unit and phrase complexity were adapted from studies on bird song (Boogert *et al.*, 2008; Zann and Cash, 2008; Woodgate *et al.*, 2012; Templeton *et al.*, 2014). Unit complexity was defined as the number of unique unit types divided by the total number of units per song. Phrase complexity was defined as the number of unique phrase types divided by the total number of phrases per song. To adapt an overall measure of song complexity (Boogert *et al.*, 2008; Templeton *et al.*, 2014; Allen *et al.*, 2018), the unit complexity was multiplied by phrase complexity.

Song repertoire and structure comparison

119

The phrase repertoire of all individual singers was compared by applying the Dice Coincidence Index (DCI) with a custom-written script in R (Dice, 1945; R Core Team, 2018):

$$DCI = 2A/(B + C),$$

with *A* being the number of shared phrase types between a pair of singers, *B* and *C* being the number of phrase types of each singer, respectively. The resulting similarity matrix was supplied to a hierarchical cluster analysis in R (R Core Team, 2018) using the "nearest neighbour" method and the output was visualized in a dendrogram. Hierarchical clustering was bootstrapped (1000 times) with the R function 'pvclust' (Suzuki *et al.*, 2019) to generate approximate unbiased (AU) values with AU values exceeding 95% indicating dendrogram divisions that are likely to occur.

To compare the song structure among individual singers the sequences of phrases were transcribed to sequences of themes (i.e., ignoring the repetition of phrases) and a set median string was chosen for each individual singer. The set median string was defined as the sequence of themes which had the highest similarity to all sequences of themes of a given set, in this case, all songs recorded within a single 24-hour window at one recording position. The similarity between sequences was calculated by applying the Levenshtein Distance Similarity Index (LSI) in MATLAB (Kohonen, 1985; Garland *et al.*, 2012):

$$LSI(a, b) = 1 - \min (I + D + S)/\max [L(a), L(b)],$$

with *a* and *b* being the two theme sequences, *I* being insertions, *D* being deletions, *S* being substitutions and *L* being the length of the respective sequence. In the following, the set median strings of all individual singers were compared by applying the LSI to pairs of individuals with the R function 'stringdist' (Van der Loo, 2014). The resulting similarity matrix was supplied to a hierarchical cluster analysis using the "nearest neighbour" method, the output was visualized in a dendrogram, and hierarchical clustering was bootstrapped (1000 times)(R Core Team, 2018; Suzuki *et al.*, 2019).

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Data Availability

Analyses reported in this article can be reproduced using the data provided by Schall (2021) at Data Dryad: https://datadryad.org/stash/share/tCp5x14Xl3xGdFHS36eonq7ENNXyVT832_jv5-n_xxA.

Synthesis

In the following synthesis, I will discuss the outcomes and most important results of the four presented chapters in the context of methodological achievements, defining important areas within the ASSO, the effects of climate oscillations and climate change, conservation of ecosystems and humpback whale populations and recommendations for management. Furthermore, I will present additional preliminary results revealing further evidence of the simultaneous presence of multiple humpback whale populations in the ASSO. Through connecting these and earlier findings, I will evaluate the role of population mixing in the ASSO. Finally, I will discuss open questions and potential future research directions including specific applications for prospective research projects.

Methodological achievements

The long-term PAM network as part of the Hybrid Float Observing System (HAFOS; see Rettig *et al.*, 2013c) maintained by the Ocean Acoustics Laboratory of the Alfred-Wegener-Institute for Polar and Marine Research in the ASSO, has yielded so far - and continues to generate to date - a unique dataset facilitating the year-round investigation of Antarctic marine mammals in their natural environment. In the light of my PhD thesis and on account of the HAFOS dataset, it was possible to obtain new insights into the habitat preferences and acoustic ecology of humpback whales in the Southern Ocean. The size of the HAFOS dataset included in this thesis (> 10 recorder positions and five years) required the implementation of powerful tools for data processing. The first objective of my PhD project therefore was the development of a set of tools to detect and classify humpback whale vocalizations in the extensive HAFOS dataset in an efficient and standardized way. It is widely recognized that computer-based tools or algorithms help to reduce data-processing time as well as to increase reproducibility by decreasing the bias through human subjectivity (Janik, 1999; Baumgartner and Mussoline, 2011a; Bergler *et al.*, 2019). For the analysis of the HAFOS dataset which formed the basis for Chapters *I-IV* of this thesis, I therefore implemented a combination of existing and custom-developed algorithms to detect humpback whale

vocalizations. The development of new algorithms is usually very time-consuming and the final performance on the full data set is often unpredictable. For my analyses, I was able to achieve good reliability and efficiency in detecting the highly variable and large repertoire of humpback whale vocalizations by adapting an existing algorithm ('Low Frequency Detection and Classification System' (LFDCS) developed by Baumgartner and Mussoline (2011a)). LFDCS was adapted to specifically detect humpback whale vocalizations in the HAFOS dataset while ignoring vocalizations of other Antarctic marine mammal species using a self-compiled, dataset-specific vocalization library (i.e., including all vocalization types of humpback whales and other species' vocalizations frequently encountered in the HAFOS data). I furthermore combined LFDCS with simple custom-made logical filters for detected vocalizations and carried out a thorough testing procedure, which resulted in an effective tool to reliably detect and classify humpback whale vocalizations with a reasonably high accuracy for the HAFOS dataset (*Chapter I, II, III, IV*). In *Chapter III*, I additionally describe a promising alternative approach for the automated and standardized characterization and classification of vocalization types which proved to be effective for the application to humpback whale song units. All tools and procedures that I developed in the light of this thesis can easily be extended or applied to remaining and future HAFOS datasets or even passive acoustic data from other regions which allows to generate standardized results for future research questions.

Year-round habitat preferences of humpback whales in the ASSO

The results of my PhD project highlight the relevance of the ASSO as a humpback whale feeding area. The importance of the ASSO for humpback whales was reflected in the discovery of two humpback whale hotspots at the northeastern and northwestern edges of the ASSO, most likely coinciding with high densities of Antarctic krill in these areas (*Chapter I*; Atkinson *et al.*, 2008; Siegel, 2016). The most pronounced humpback whale acoustic presence in these areas occurred in late summer until late autumn, during which period the acoustic presence was dominated by male singing (*Chapter IV*). The length of the

singing period indicates that humpback whales regularly mix feeding and reproductive activities in the ASSO, potentially even including opportunistic breeding. Furthermore, the HAFOS data confirmed occasional humpback whale acoustic presence during austral winter, through the occurrence of social vocalizations (no songs, *Chapter I*). Most likely, every year, some females and/or juvenile whales remain in the Southern Ocean also during austral winter to fuel growth, lactation, or pregnancy with the exploitation of additional prey resources. The ecological relevance of these findings is further elaborated in *Chapter II*, where I evaluate their implications in the light of climate variations, including both regular climate oscillations and potential present and future effects of climate change.

In the light of climate variations
One of the most crucial questions in the conservation and management of baleen whales and polar ecosystems is how these respond to future changes in their environment (e.g., Davis *et al.*, 2020). The ability of baleen whales to cope with long-term changes in, for example, the sea ice habitat and the corresponding changes in prey availability, is still largely unknown. To date, most research efforts on this issue concentrate on the Arctic (see Moore *et al.*, 2019 for a review). Although less pronounced than for the Arctic, the Southern Ocean is prone to be affected by climate change. Predictive studies suggest a 24-33% decline in annual average total sea ice cover until 2100 and the largest effect is predicted for the Weddell Sea in late summer (Arzel *et al.*, 2006; Bracegirdle *et al.*, 2008). A decrease in sea ice cover will most likely result in a decrease in primary production both within the sea ice and the marginal ice zones, yet it will also result in an increase of primary production in the open ocean areas of the Southern Ocean (Arrigo and Thomas, 2004). To what extent this shift is likely to affect secondary productivity, mainly the abundance and distribution of Antarctic krill, remains speculative at this time. Although the open ocean population of adult krill may benefit from the increased availability of open ocean habitat and prey resources, the recruitment of young krill from the marginal sea ice zone or the under-ice habitat might be severely reduced under a global warming scenario (Flores *et al.*, 2012a; Siegel, 2016). The impacts of climate change on higher trophic levels, such as baleen whales and pinnipeds in the Southern Ocean are

even less understood due to their known ability to adapt to changes making use of phenotypic plasticity (Silber *et al.*, 2017; Meynecke *et al.*, 2020).

In *Chapter II* of this thesis, I describe the recurring multi-year presence of humpback whales in the ASSO, with the exception of El Niño years, which suggests that these whales are particularly responsive to changes to their environment caused by climate oscillations. Recurring climate oscillations, such as the El-Niño-Southern-Oscillation (ENSO) or the Southern Annular Mode (SAM)[1] (Philander, 1983; Marshall, 2003b; Yuan, 2004; Lovenduski and Gruber, 2005; Meredith *et al.*, 2008; Loeb *et al.*, 2009; Loeb *et al.*, 2010; Sallée *et al.*, 2010; Kim and Orsi, 2014; Siegel, 2016; Atkinson *et al.*, 2019) provide the opportunity to investigate the responses of baleen whales to climate variability within a relatively short time span (i.e., less than a decade). Furthermore, climate change is thought to cause frequency shifts in the modes of various climate oscillations (e.g., more frequent El-Niño phases; Gille, 2002; Cai *et al.*, 2014). Understanding the impacts of climate oscillations on baleen whales and the Southern Ocean ecosystems, therefore, is crucial to our efforts in anticipating the intricate effects of climate change. The most likely pathway by which climate variations could affect baleen whale distribution during most of the year (i.e., except during the breeding season) is through their influence on spatio-temporal patterns of prey availability (followed by indirect effects, such as changes in resource competition or predation pressure; Kovacs and Lydersen, 2008; Moore *et al.*, 2019), in case of the Southern Ocean, the availability of Antarctic krill (Loeb and Santora, 2015). Unfortunately, the knowledge on climate change impacts on krill and especially the interactions between krill and other key ecosystem processes is still scarce (Flores

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[1] SAM is the dominant pattern of natural climate variability in polar and subpolar regions of the Southern Hemisphere (Marshall, 2003). During the positive phase of SAM, the westerly wind belt surrounding the Antarctic continent contracts towards the continental shelf and climatic conditions north of the wind belt change to warmer, windier, and cloudier weather. Especially north of the Antarctic Polar Front, sea surface temperature increases and chlorophyll concentration decreases during positive SAM (Lovenduski and Gruber, 2005; Meredith et al., 2008). ENSO causes periodic fluctuation of sea surface temperature and air pressure originating from the tropical Pacific and therefore has the strongest effects on the Pacific sector of the Southern Ocean, including the Western Antarctic Peninsula (Philander, 1983). Both SAM and ENSO affect winds, cloud cover, currents, sea surface temperature, and sea ice extent in the Southern Ocean (Yuan, 2004; Loeb et al., 2009; Loeb et al., 2010; Sallée et al., 2010; Kim and Orsi, 2014; Siegel, 2016; Atkinson et al., 2019).

et al., 2012a), which hampers the interpretation of results based on a single species, such as in the context of this thesis, humpback whales. In *Chapter II*, all available information on climate variation impact on krill and the Southern Ocean ecosystems was considered to interpret the absence of humpback whales from the ASSO during El-Niño years, which still left considerable room for speculation. To successfully unravel the intricate effects of climate variations on Antarctic baleen whales, interdisciplinary studies integrating biological (e.g., spatio-temporal patterns in primary and secondary productivity), oceanographic (e.g., upwelling), biogeochemical (e.g., the role of micronutrients), and behavioral (e.g., degree of phenotypic plasticity) seem indispensable.

A perspective for a Marine Protected Area (MPA) in the Weddell Sea
The Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) aims for an ecosystem-based management approach to avoid irreversible changes to the Antarctic ecosystem due to anthropogenic harvesting (CCAMLR, 1982). CCAMLR consists of 24 member countries and the European Union and all parties have an interest in conserving Antarctic marine live while allowing for rational use of marine living resources (CCAMLR, 1982). The species on which harvesting focuses in the Southern Ocean is Antarctic krill, which at the same time is a keystone species for the 'krill-based Antarctic ecosystem' (Siegel and Loeb, 1995; Nicol *et al.*, 2008). The cumulative effects of future climate change are likely to have a negative effect on krill populations, consequently potentially increasing the vulnerability of krill and krill-dependent predator populations (Flores *et al.*, 2012a; Hill *et al.*, 2013; Klein *et al.*, 2018; Melbourne-Thomas, 2020). Germany (i.a., researchers from the Alfred-Wegener-Institute for Polar and Marine Research), therefore, proposed the establishment of a Marine Protected Area (MPA) in the Weddell Sea aiming at the conservation of representative examples of biodiversity, habitats, and ecosystem processes as well as the protection of an area maintaining the ability to adapt to the effects of climate change (Teschke *et al.*, 2016). Baleen whales play a crucial role in ecosystem processes (Smetacek, 2008; Nicol *et al.*, 2010) and baseline data on, for example, the distribution and abundance of the different species is key to the development of effective management strategies. The results presented

in *Chapters I, II*, and *IV* contribute to this baseline understanding by identifying humpback whale presence hotspots, recurring presences in both hotspots also during winter, migratory adaptations during extreme climatic events, and the flexibility in habitat use combining both feeding and breeding activities. One direct recommendation derived from the outcomes of my PhD project would be the northward extension of the proposed MPA area to 60°S (i.e., instead of 64°S) in order to include the two identified humpback whale hotspots at the northeastern and northwestern edges of the ASSO. Since the spatio-temporal distribution of humpback whales in the ASSO is most likely mainly driven by the availability and distribution of their primary prey species (Santora *et al.*, 2010), it is safe to assume that these humpback whale hotspots reflect areas with high krill densities, bearing in mind that whales may target specific age and size classes representing only part of the population (Friedlaender *et al.*, 2009). Long-term distribution data for Antarctic krill is lacking (Atkinson *et al.*, 2008; Flores *et al.*, 2012a; Atkinson *et al.*, 2017) and knowledge gaps could potentially be bridged with information on baleen whale distributions, implying that baleen whale presence could act as a proxy for krill presence (i.e., at least representing part of the krill distribution). Future MPA planning, evaluation, and approval could benefit from the incorporation of available information on year-round baleen whale distribution, improving the comprehensive representation of keystone species and processes.

Feeding ground sharing in humpback whales

Baleen whale populations and particularly their recovery from past whaling depletion are managed by the International Whaling Commission (IWC). The IWC lists the identification of breeding/feeding ground migratory linkages and connections as a priority research topic to improve conservation and management efforts for Southern Hemisphere humpback whales (International Whaling Commission, 2016). The results presented in *Chapter IV* indicate the presence of humpback whales from at least two distinct breeding populations in the ASSO with overlapping distributions. To gather more detailed information on which breeding stocks frequent the ASSO during summer, I conducted further comparative song analyses

including songs from the ASSO as well as songs from different breeding stocks. Through international collaborators I obtained song recordings from the Ecuadorian and Brazilian breeding stocks and from the South African migration route. A prerequisite for comparative song analyses is the temporal proximity of the song recordings to be compared (i.e., songs from the same years or from previous or following seasons) due to the evolutionary nature of humpback whale songs (Winn and Winn, 1978b; Payne and Payne, 1985b). Therefore, I was able to include breeding ground/migration route song recordings from 2011, 2012, 2013, 2014, 2016, 2017, 2018, and 2019 in the analysis. From each year and location, I analyzed multiple songs (from three, or the minimum available individual singers per location) and extracted a summarized phrase repertoire and one representative theme sequence (based on a Levensthein similarity measure) per location and year (see methods *Chapter IV* for detailed processes of song analyses). One exception were the song recordings from the South African migration route, where three representative theme sequences from the 2018 data were selected for analysis, because recordings were made both during the northward and southward migration. The songs recorded in the ASSO (presented in *Chapter IV*) were all included in the comparative analyses (i.e., without reduction to a representative theme sequence per year) due to the unknown number of breeding stocks that potentially contributed to the recordings. Comparative song analyses were conducted for each year of ASSO song recordings, including breeding ground/migration route song recordings from the previous, same, and following year, and song similarity was quantified with the Dice Coincidence Index (Dice, 1945) and the Levenshtein Distance Similarity Index (Kohonen, 1985; Garland *et al.*, 2012) and the bootstrapped hierarchical clustering of the resulting index values (see *Chapter IV* for details).

Overall, the comparative song analyses showed that humpback whales from the Ecuadorian, Brazilian and Angolan breeding stock (represented by the animals recorded during migration off South Africa) had acoustic contact to humpback whales recorded in the ASSO, most likely because at least parts of these breeding stocks migrate to a shared feeding ground in the ASSO.

The comparison of phrase repertoires, for example, revealed a high overlap (i.e., ~80%) between the ASSO and Ecuadorian repertoires in 2013 (i.e., 'ASSO_2_2013' and 'E_1_2013'), the ASSO and the

Brazilian repertoires in 2016 and 2017 (i.e., ~50%), and the ASSO and the South African repertoires in 2018 (i.e., ~70%) (Figure 12).
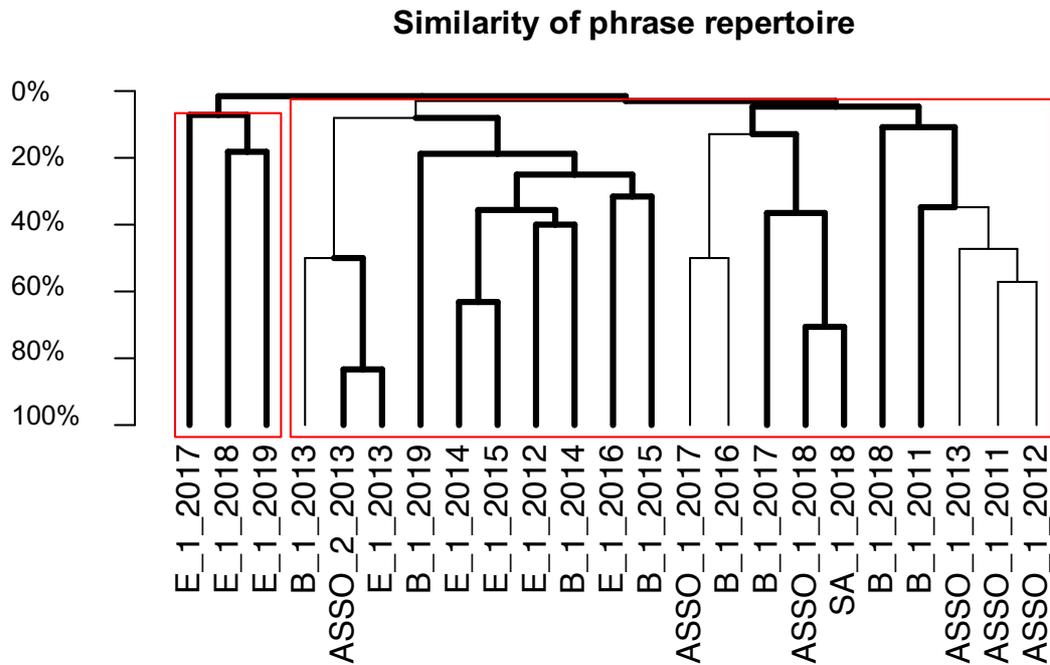
Figure 12. Bootstrapped dendrogram from hierarchical clustering of the similarity of phrase repertoires (Dice coincidence index) from the ASSO, the Ecuadorian breeding stock, the Brazilian breeding stock, and the South African migration route for all recording years. Phrase repertoires were compared as summarized repertoires per location and year. ASSO recordings from 2013 are represented as two repertoires, due to absence of common phrases in these both repertoires (see Chapter IV). The names on each branch indicate the location (i.e., 'E' for Ecuador, 'B' for Brazil, and 'SA' for South Africa), the repertoire ID (i.e., '1', '2'), and the year (i.e., '2017') to identify the respective phrase repertoire. Bold lines indicate divisions that were likely to occur (i.e., AU >95%) and red rectangles clusters of significant probability.

In 2011, songs recorded in the ASSO were partly similar to the songs recorded off Brazil in the same year, but did not show any similarity with the Ecuadorian song from the following year (Figure 13). Most likely, humpback whales from the Brazilian breeding stock migrated to the ASSO feeding area, more

specifically to the area around the Greenwich Meridian, and returned to the waters off Brazil in winter (Figure 14). This is also evident from the comparative analyses of the 2012 data, where the degree of song similarity between the Greenwich recordings and the Brazilian recordings from 2011 indicates acoustic contact in the previous year (Figure 13, Figure 14). Additionally, the hierarchical cluster of the 2012 data shows a connection between Ecuadorian and Brazilian song with a higher similarity between the Brazilian and Ecuadorian song from 2013 than between the Ecuadorian song from 2012 and 2013 (Figure 13), which suggests an event of acoustic contact between these populations in 2012 (Figure 14). The 2013 data shows that songs recorded off Elephant Island (i.e., 'W13_05-Jun-2013' and 'W13_05-Oct-2013') were the most similar to the songs recorded off Ecuador in the same year, indicating that humpback whales from the Ecuadorian breeding stock visited the area around Elephant Island, at least during this particular year (Figure 13, Figure 14). Songs recorded in the ASSO during 2017 and 2018 were partly similar to Brazilian songs from 2016 and 2019 and to Ecuadorian songs from 2017 (Figure 13) suggesting migrations from these breeding stocks to the ASSO during these years (Figure 14). Furthermore, the absence of similarity also can be indicative. For example, the verification that the biggest part of the ASSO songs from 2013 were not similar to the songs from the Ecuadorian or Brazilian breeding stock suggests that these 2013 ASSO songs originate from another population, most likely the Angolan breeding stock due to its geographical proximity to the ASSO.
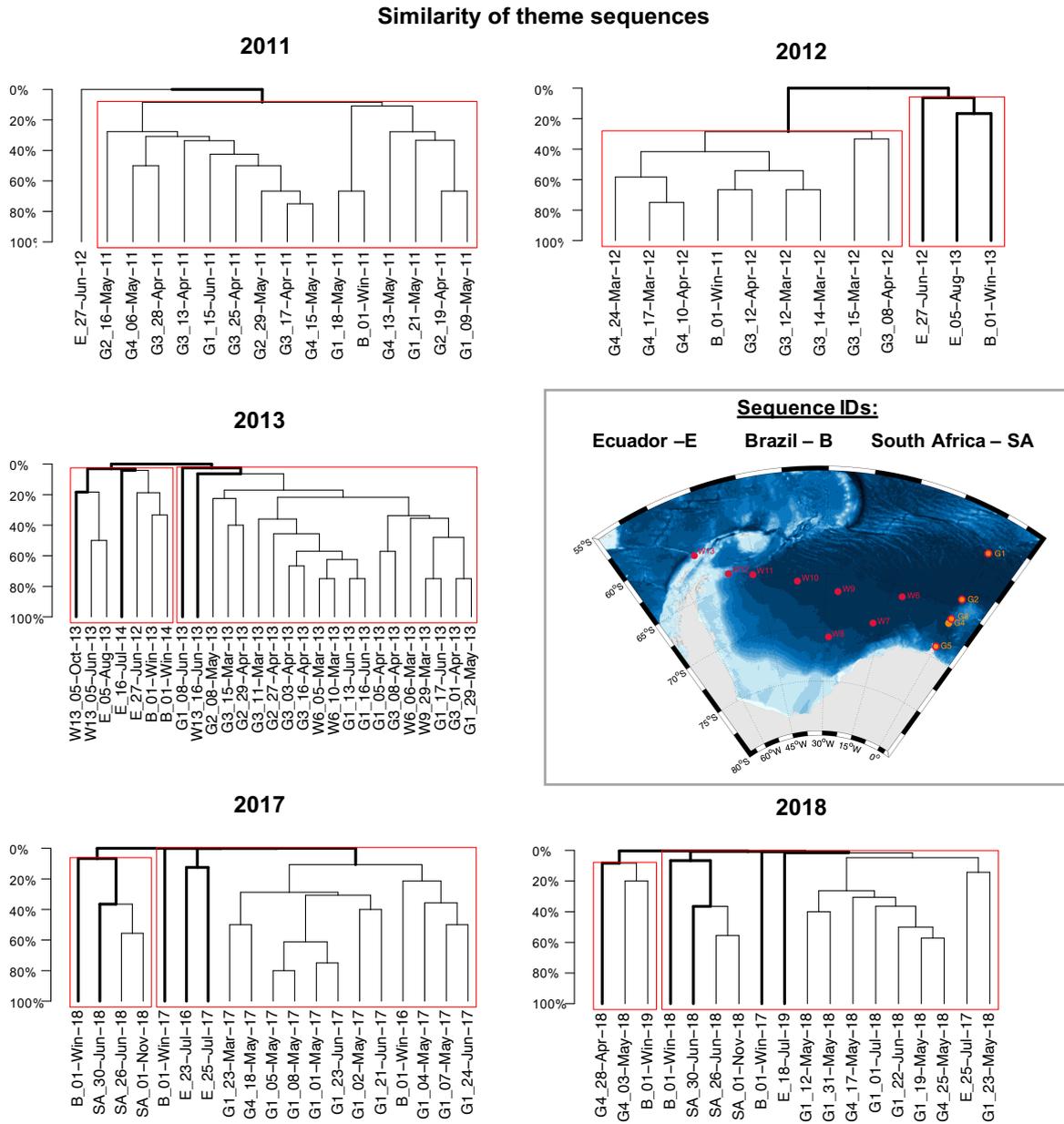
Figure 13. Bootstrapped dendrograms from hierachical clustering of similarity of theme sequences (Levensthein distance similarity index) from the ASSO, the Ecuadorian breeding stock, the Barzilian breeding stock, and the South African migration route for the five different years of song recordings from the ASSO. Names on each branch belong to individual singers (in case of the ASSO) or representative theme sequence (in case of breeding stock or migration route recordings) encoded with the name of the recording position (first 2-3 symbols, i.e., 'W13', 'G4', 'SA',…) and the date of the recording when known (last 9 symbols, i.e., '28-Apr-18', '01-Nov-18',…). Bold lines indicate divisions that were likely to occur (i.e., AU >95%) and red rectangles clusters of significant probability.
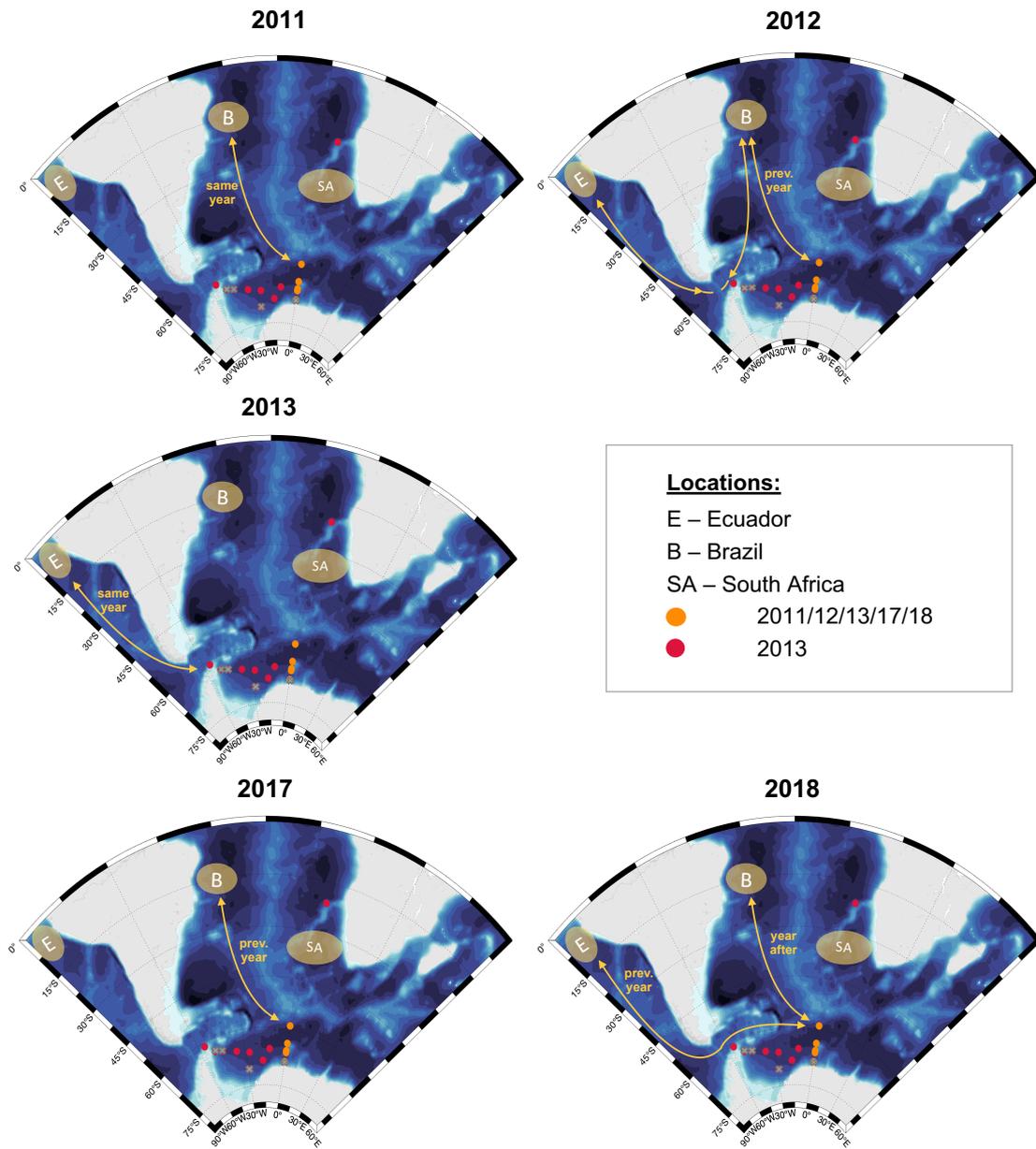
Figure 14. Schematic illustration of potential song transmission pathways between the ASSO and the Ecuadorian breeding stock, the Brazilian breeding stock, and the South African migration route indicated by comparative song analyses. Red dots indicate recording positions with data for 2013, organge dots represent recording positions with data for 2011, 2012, 2013, 2017, and 2018 and crossed dots represent recording positions without song recordings. Approximate recording positions for the Ecuadorian breeding stock, the Brazilian breeding stock, and the South African migration route are indicated by yellow ellipses. Recording data from off Namibia were not included in the current analyses due to the low

quality of song recordings. Arrows illustrate the likely pathways of acoustic contact between humpback whales recorded at the different locations for the previous, the same or the year after.

These preliminary results confirm the findings presented in *Chapter IV* and even present evidence for the migration of at least three breeding stocks to the ASSO feeding area. Humpback whales of these breeding stocks seem to mix in the ASSO repeatedly and mixing patterns seem to be variable on a temporal scale, meaning that most likely whales from different populations mix at different times (i.e., years) at feeding hotspots of variable locations. The flexibility of these mixing processes is most likely connected to variations in migratory patterns driven by spatio-temporal changes in prey availability. Optimizing their energy budgets, humpback whales of the different breeding populations are likely to migrate to those areas with sufficient prey availability that lie closest to the respective breeding ground. Baleen whales are thought to employ a multi-modal sensory system combining magnetoreception, somatosensory perception of oceanographic conditions, chemosensory cues as well as acoustic perception of conspecifics or other marine animals to find prey hotspots (Torres, 2017a). Humpback whales can detect and localize social vocalizations and songs of conspecific over tens of kilometers (Au *et al.*, 2006; Dunlop *et al.*, 2013) which allows migrating humpback whales to navigate to temporary prey hotspots following acoustic waymarkers. Prey availability seems to be variable in time and space and is most likely driven by climatic variations (see *Chapter II*) which, consequently, also drive humpback whale migration patterns and the flexible mixing of different populations at feeding hotspots. On average, the polar and subpolar regions of the South Atlantic Ocean (i.e., including the ASSO) have the highest densities of Antarctic krill on a circumpolar scale (Atkinson *et al.*, 2004; Nicol, 2006). This supports the outcome of the comparative song analyses and suggests that the high prey availability in the ASSO attracts humpback whales from different breeding populations and favors mixing among these (Amaral *et al.*, 2016). In this context, it is possible that also humpback whales from other breeding populations than those included in the comparative song analyses (e.g., humpback whales breeding around Madagascar), travel to the ASSO, contribute to the encountered variabilities in song recordings, and mix with whales stemming from the different populations (see also Amaral *et al.*, 2016).

Implications for breeding stock management

Confirmed by the results presented in this thesis, as many as three breeding stocks rely at least partly on resources encountered in the ASSO. For humpback whales from the South Atlantic breeding stocks, the ASSO has been assumed to be the primary feeding ground, however, to date, this assumption has never been confirmed (Zerbini *et al.*, 2011; Rosenbaum *et al.*, 2014). Additionally, the results present new evidence that humpback whales from the Ecuadorian breeding stock also migrate to the western part of the ASSO. Two important factors which ensure the prosperity of a population, therefore, are linked to the ASSO: (1) the ASSO provides (still) sufficient prey resources to allow population growth (Bortolotto *et al.*, 2016; Félix *et al.*, 2020; Ward *et al.*, 2020), and (2) the ASSO is an important area for both cultural and maybe even genetic exchange between populations supporting the maintenance of large gene pools which increase the populations' resilience to environmental change (Amaral *et al.*, 2016).

The combined results of my PhD project highlight the ecological relevance of the ASSO for humpback whales from multiple populations. The importance of this area should be considered in future management decisions by the IWC. Additionally, migration routes from the distinct breeding stock locations to the ASSO (e.g., the coastal areas along the South American continent; Felix and Guzman, 2014) have to be managed temporally (i.e., during the migration period) to allow for the movements of whales without biologically relevant disturbance. Based on the outcomes of this PhD project, I recommend that the joint forces of the IWC and CCAMLR create a management and conservation plan for MPA(s) including important humpback whale feeding hotspots in the ASSO (most likely overlapping with krill hotspots and potentially also important for other baleen whales). On the migration routes outside the ASSO, anthropogenic impacts (e.g., ship traffic) should be restricted (e.g., deceleration and/or rerouting of ship traffic) during sensitive periods of the year to reduce disturbance of whales while migrating. If such measures would be taken, humpback whales would most likely continue to recuperate from the effects of past overexploitation through industrial whaling and recover their role as abundant large pelagic predators structuring the Southern Ocean ecosystem (Nicol *et al.*, 2010).

Outlook

As most PhD projects, this project leaves open and generates new questions creating opportunities for future studies. The ongoing operation of the HAFOS recorder network will allow for studies encompassing comparisons over larger spatial and temporal scales than were possible with the dataset analyzed during this PhD project. The temporal extension of the dataset will support further investigation regarding the impact of climate oscillations and climate change and will allow for more robust correlations and interpretations of statistical results. The spatial extension of the HAFOS dataset by adding additional recording locations would aid in defining the spatial limits of feeding hotspots, as the identified hotspots for humpback whales in the ASSO were located at the northern boundaries of the area covered by HAFOS. Interesting additional recording positions for addressing this question would be, for example, the waters around the numerous islands in the ASSO, such as Bouvet Island, South Georgia, the South Orkney Islands, and the South Sandwich Islands or the Straits of Magellan (Chile), because sighting and satellite tagging studies suggest a crucial importance of these areas for humpback whales (Moore *et al.*, 1999; Gibbons *et al.*, 2003; Stevick *et al.*, 2004; Engel and Martin, 2009; Zerbini *et al.*, 2011; Rosenbaum *et al.*, 2014). Combining acoustic presence data with further environmental variables, for example, productivity measures, krill densities, measures of carbon flux and micronutrients would be an interesting approach to understand the underlying processes explaining the response of whales to climate variabilities. The oceanographic moorings of HAFOS could in the future be extended with biological and biogeochemical sensors which generate data to bridge the gap between physical patterns in the ocean and a predator at the very top of the food chain, such as the humpback whale. Furthermore, the combination of physical, biological, and biogeochemical datasets would assist in the interpretation of habitat preferences, species interactions and the niche partitioning among krill predators, presenting fundamental information for the management of the 'krill-based Antarctic ecosystem'. Finally, the preliminary comparative song analyses presented here can be extended with additional data, for example, from the breeding stock inhabiting the waters around Madagascar. The results of these complete

comparative analyses are planned to be published as a separate manuscript in the near future. All in all, the findings of this PhD project provide information on Southern Ocean humpback whale ecology that is likely to be of interest for scientists as well as management and conservation bodies, and highlight the promising possibilities for future research including multiple lines of interdisciplinary investigation.

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Publications and Author contributions

Chapter I
Schall, E., Thomisch, K., Boebel, O., Gerlach, G., Spiesecke, S., & Van Opzeeland, I. (2020). Large-scale spatial variabilities in the humpback whale acoustic presence in the Atlantic sector of the Southern Ocean. Royal Society Open Science, 7(12), 201347.

Statement of authorship: E.S. analysed the data and wrote the manuscript. K.T. participated in some data collection and helped draft the manuscript. O.B. participated in collecting data and coordinated the study. G.G. guided the analysis and helped draft the manuscript. S.S. collected all the data. I.V.O. coordinated the study, collected part of the data and helped draft the manuscript. All the authors reviewed and contributed to the final document edits. All the authors gave the final approval for publication.

Chapter II
Schall, E., Thomisch, K., Boebel, O., Gerlach, G., Mangia Woods, S., El-Gabbas, A., & Van Opzeeland, I. (2021). Multi-year presence of humpback whales in the Atlantic sector of the Southern Ocean but not during El Niño. Under review in Nature Communications Biology.

Statement of authorship: E.S. analyzed the data and wrote the manuscript. K.T. participated in some data collection and helped draft the manuscript. O.B. coordinated the study and collected the majority of the data. G.B. guided the analysis and helped draft the manuscript. S.M.W. helped with data analysis. A.E-G. supervised the statistical analysis. I.V.O. coordinated the study, collected part of the data, and helped draft the manuscript. All the authors reviewed and contributed to the final document edits. All the authors gave the final approval for publication.

Chapter III
Schall, E., Roca, I., & Van Opzeeland, I. (2021). Acoustic metrics to asses humpback whale song unit structure from the Atlantic sector of the Southern Ocean. Under review in the Journal of the Acoustical Society of America, Special Issue 'Machine Learning in Acoustics'.

Statement of authorship: E.S. analyzed part of the data and wrote part of the manuscript. I.R. analyzed part of the data and wrote part of the manuscript. I.V.O. coordinated the study, collected part of the data, and helped draft the manuscript. All the authors reviewed and contributed to the final document edits. All the authors gave the final approval for publication.

Chapter IV
Schall, E., Thomisch, K., Boebel, O., Gerlach, G., Mangia Woods, S., Roca, I., & Van Opzeeland, I. (2021). Humpback whale song recordings suggest common feeding ground occupation by multiple populations. Under review in Nature Scientific Reports.

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Die von mir vorgelegte Dissertation ist von Prof. Dr. Gabriele Gerlach und Dr. Ilse Van Opzeeland betreut worden.

Elena Schall

Bremen, May 2021

Supplementary Material – Chapter I & II

Material and Methods

Automatic detection and classification of humpback whale vocalizations

All available passive acoustic data were processed by the 'Low frequency detection and classification system' (LFDCS) developed by Baumgartner and Mussoline (2011b) in order to automatically detect and classify humpback whale vocalizations. A call library for humpback whale call types from the Atlantic sector of the Southern Ocean was constructed using data from two recording periods with confirmed humpback whale acoustic presence: May 2011 and June 2013 from recorders deployed at 59°S 0°E, 64°S 0°E, and 61°S 55°W. In total seven common humpback whale call types were included in the call library, comprising between 153 and 332 selected exemplars (Table *3*). To avoid the miss-classification of vocalizations from other marine mammal species (inhabiting the wider Weddell Sea area and occupying a similar frequency range as humpback whales) as a humpback whale vocalization, at least one common call type per species was determined to be included in the call library. In total seven additional call types from other vocal marine mammal species were included in the call library with between 160 and 321 selected exemplars per call type (Table *3*; (Klinck *et al.*, 2010; Van Opzeeland *et al.*, 2010; Risch *et al.*, 2014b; Schall and Van Opzeeland, 2017)). The humpback whale call type 18, a low frequency downsweep (*LF DS*), has acoustic characteristics that were very similar to those of the common low frequency downsweeps of other baleen whale species (Edds-Walton, 1997; Baumgartner *et al.*, 2008; Ou *et al.*, 2015). For this reason, the automatic detections of this particular call type cannot be considered as a reliable sign for humpback whale acoustic presence and corresponding detections were therefore only considered in combination with other humpback whale call type detections.

Table 3. LFDCS call library of all tonal sounds which serve as choices for the classification algorithm. Call type numbers were assigned arbitrarily (Humpback whale call type numbers were chosen to match the call type number given in catalogue for manual analysis). Call type names were assigned, based on the visual and aural appearance of the call types during analysis (e.g., 'LF' = low frequency; 'DS' = downsweep).

Species	Call Type	Name	N exemplars
	1	*Moan*	200

	3	Roof	192
Humpback whale	4	J	270
	5	L	191
	6	MoanUp	166
	18	LF DS	153
	19	LF Moan	332
Minke whale	30	Bioduck call	213
Killer whale	31	Excited DS	268
Weddell seal	32	Long DS	173
Crabeater seal	33	Low Moan	160
Leopard Seal	34	Low trill	275
Leopard Seal	35	High trill	139
Ross Seal	36	Sirene call	321
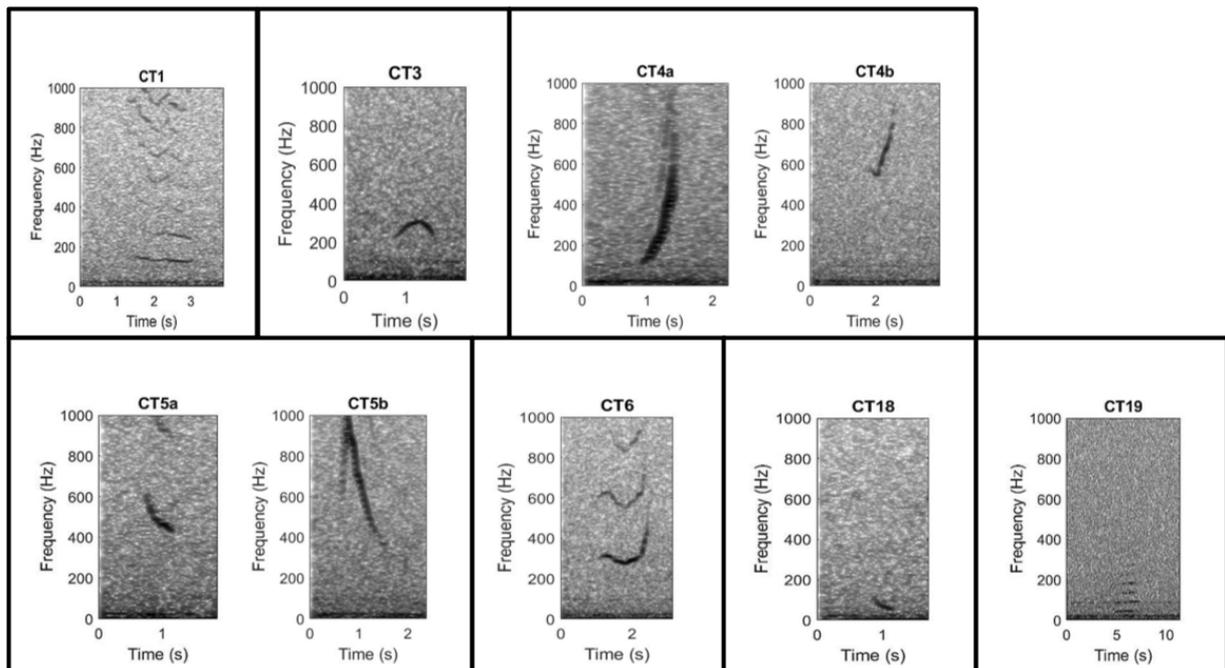
Figure 15. Exemplary humpback whale vocalizations of the call library.
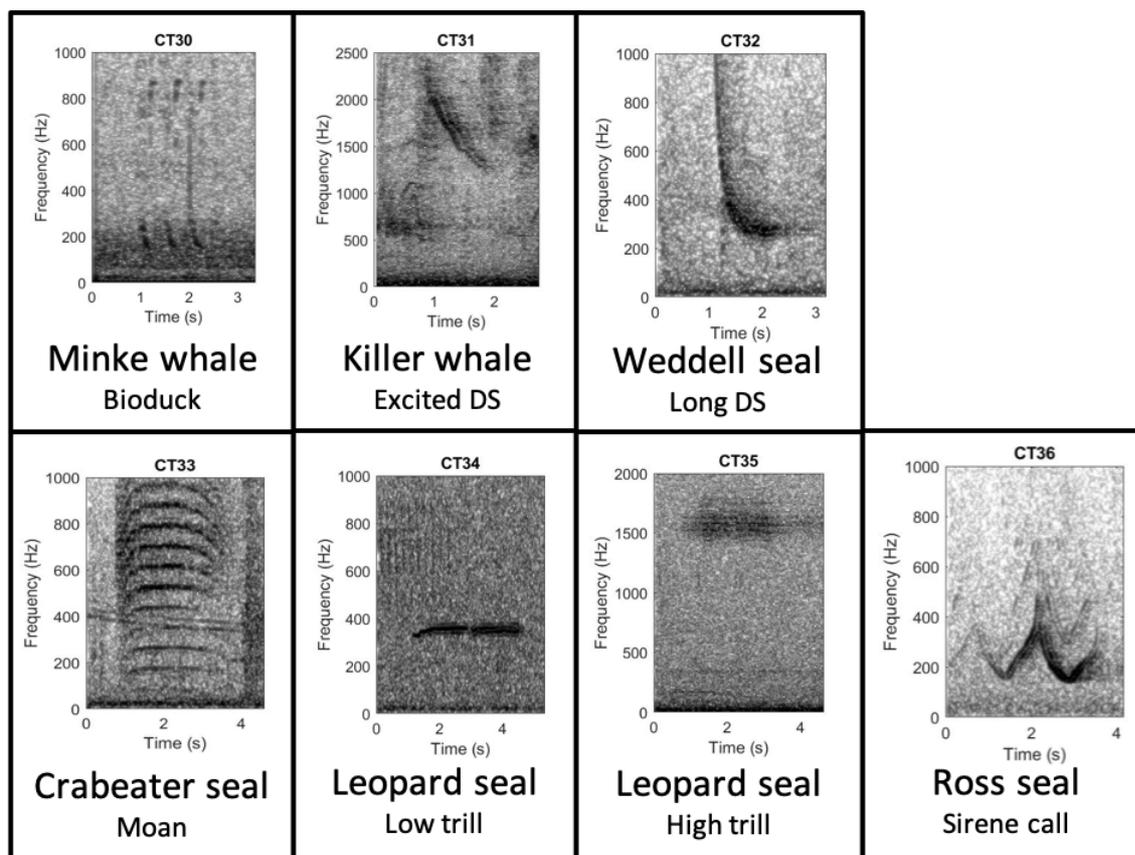
Figure 16. Exemplary marine mammal vocalizations of the call library. Call type names were chosen, based on the visual and aural appearance of the call types during analysis ('DS' = downsweep).

In order to tune the LFDCS detection and classification parameters to yield the best possible detector/classifier performance, a two-step evaluation analysis was applied to selected subsets of acoustic recordings. The first evaluation step was performed on a subset of the passive acoustic data summing up to 30 recording hours (30h-dataset). The 30h-dataset was selected in order to contain different quality humpback whale social calls and songs in different noise conditions (i.e., environmental, anthropogenic and electronic), silent periods, periods with only noise and periods with vocalizations from other marine mammals (i.e., Antarctic blue whale, fin whale, Antarctic minke whale, sperm whale, killer whale, leopard seal, Ross seal, crabeater seal and Weddell seal). This 30h-dataset was compiled from six different recording locations, three different years and all four different seasons. The 30h-dataset was manually screened in Raven Pro 1.5 (Hann Window, 1025 window size, 80% overlap, 2048 DFT size; Bioacoustics Research Program 2014) by marking the start-time of each clearly assignable humpback whale

vocalization. Manually detected vocalizations were manually classified into the seven tonal humpback whale call types included in the LFDCS call library. Further, the 30h-dataset was repeatedly automatically processed in LFDCS using the above mentioned customized call library with detection and classification parameters changing between single LFDCS runs in order to determine the optimal parameter settings (23 adjustable parameters; see Baumgartner and Mussoline (2011b) for parameter descriptions). Parameter settings were optimized in a parameter optimization cycle, which cycled through 2400 LFDCS runs with randomly chosen parameter combinations. For each run, automatic humpback whale call detections were compared against manual humpback whale call detections with a start-time buffer of 1.8 s (validated via manual comparison of detection start-times in the LFDCS browse mode). The number of true positive, false positive and false negative detections was determined and used to calculate recall, precision and ultimately F1 score (Powers, 2011).

The second evaluation step was designed to evaluate detection efficiency on an hourly basis. For this purpose, ten different parameter settings were chosen from the optimization cycle runs based on their step one performance results, i.e. the balance between recall, precision and F1 score (Figure *17*). Step two of the evaluation procedure was performed on a subset of the passive acoustic data summing up to 150 recording hours (150h-dataset) compiled from the same six locations, three years and four seasons as the 30h-dataset. Likewise, the 150h-dataset was composed of recordings with similar variable acoustic conditions as the 30h-dataset (i.e., including different noise conditions and vocalizations of the different marine mammal species). The 150h-dataset was manually screened in Raven Pro 1.5 (Hann Window, 1025 window size, 80% overlap, 2048 DFT size; Bioacoustics Research Program 2014) by detecting humpback whale acoustic presence on an hourly basis. In LFDCS, the 150h-dataset was processed in ten runs, each with one of the parameter settings chosen from the first evaluation step. For each run, automatic humpback whale detections were compared against manual detections of humpback whale acoustic presence per hour. To minimize false positive hours due to confusion with other species' vocalizations an additional acoustic-context filter was applied before evaluating the results. This acoustic-context filter was based on two conditions: (1) When the number of good quality detections (i.e., Mahalanobis distance (MD) ≤ 2 and signal-to-noise ratio (SNR) ≥ 14) of another species' call type similar to a humpback whale call type (Table *4*) within a respective hour exceeds an hourly call rate (CR) threshold (i.e., 4 calls per hour), and (2) when the number

of humpback whale good quality detections (i.e., MD ≤ 2 and SNR ≥ 14; summing over all call types), within a respective hour is lower than an hourly CR threshold (i.e., 6 calls per hour). In case these two conditions were met, all detections of the humpback whale call type similar to the respective other species' call type were deleted from the respective hour.
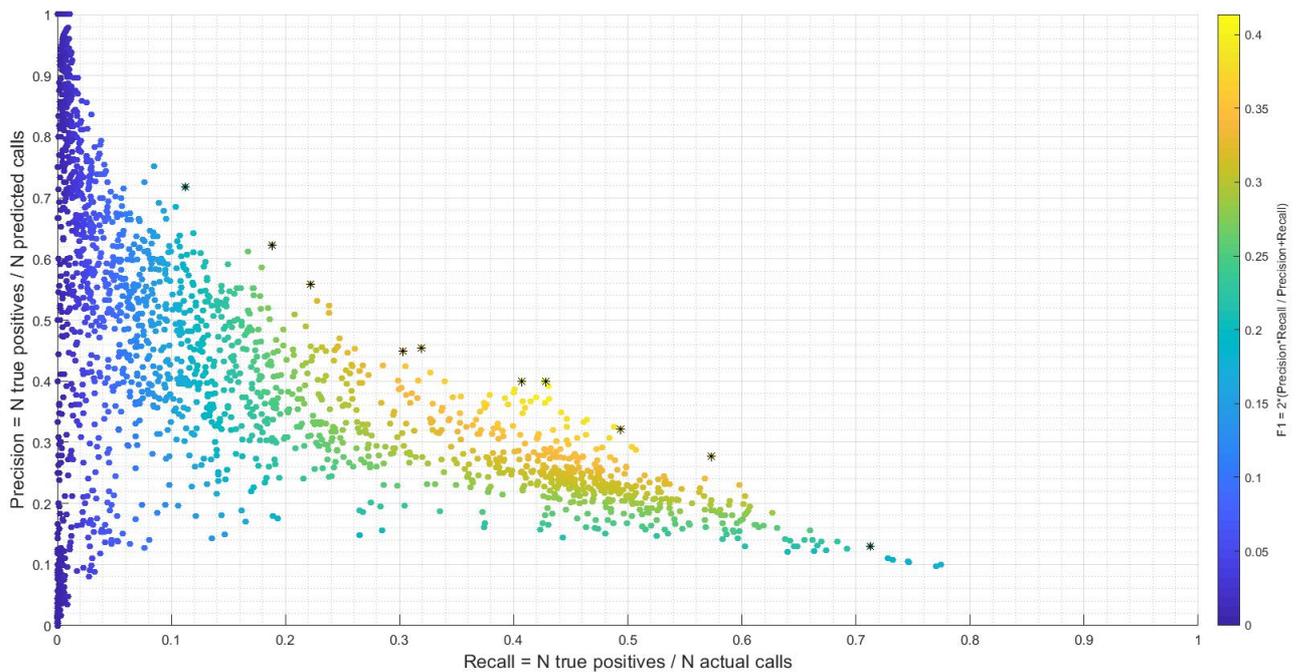
Figure 17. Performance evaluation of 2400 LFDCS runs on the 30h-dataset during step one of the performance evaluation. Ten distinct parameter settings with differently balanced performances (marked with black stars) were chosen for the second evaluation step.

Table 4. Potential sources of miss-identification of humpback whale calls with other species' call types. Humpback whale call types in the first column were frequently mistaken (by LFDCS) for call types of other species as listed in the second column ('CT' = call type).

Humpback whale call type	Similar call type from other species
CT1	leopard seal *Low trill* (CT34), Crabeater seal *Low Moan* (CT33)
CT3	Ross seal *Sirene call* (CT36)
CT5	killer whale *Excited DS* (CT31), Weddell seal *Long DS* (CT32)
CT6	Leopard seal *Low trill* (CT34)
CT18	Antarctic minke whale *Bioduck* call (CT30)

Remaining humpback whale call detections were the basis for step two of the evaluation procedure, where hourly detection efficiency of LFDCS and the acoustic context filter was estimated applying different detection quality and hourly CR thresholds. In total seven MD (i.e., 1.5-4.5), seven SNR (i.e., 8-14dB) and 30 CR thresholds (i.e., 1-30) were tested, summing up to 1470 threshold combinations. For each threshold combination the probability of HW hourly presence ($Prob_{Pres}$) and the probability of false negative hours ($Prob_{FN}$) were calculated:

$$Prob_{Pres} = \frac{n_{HW\ TP\ hours}}{n_{HW\ predicted\ hours}},$$

$$Prob_{FN} = \frac{n_{HWFN\ hours}}{n_{HW\ negative\ predicted\ hours}},$$

with the number of humpback whale true positive hours ($n_{HW\ TP\ hours}$), the number of humpback whale false negative hours ($n_{HWFN\ hours}$), the number of humpback whale positive predicted hours ($n_{HW\ predicted\ hours}$), and the number of humpback whale negative predicted hours ($n_{HW\ negative\ predicted\ hours}$). The parameter setting and MD/SNR/CR threshold combination of the run with the highest respective $Prob_{Pres}$ at a $Prob_{FN}$ lower than 20% was finally selected to process the full dataset (Table 5; see Baumgartner and Mussoline (2011b) for parameter descriptions). Resulting automatically detected hours with presumed humpback whale acoustic presence will be termed presumed *humpback whale presence* (pHWP) hours in the following.

Table 5. Final LFDCS parameter settings and Mahalanobis Distance (MD)/Signal-to-Noise Ratio (SNR)/Call Rate (CR) threshold combination. For parameter descriptions see Baumgartner and Mussoline (2011b).

Parameter	Value	Parameter	Value
Frame	1700 samples	BB_DetectionThreshold	75dB
Overlap	95%	BB_MinSegmentSpan	10Hz
SpectrogramDuration	20s	BB_MinTotalSpan	400Hz
PitchTrackingWindow	15s	BB_MinBroadbandDuration	0.2s
NoiseReductionsWindow	45s	DetectionThreshold	8dB
AvgFFTLowThreshold	-999dB	CostGradientThreshold	15dB
AvgFFTHighThreshold	79dB	DistanceWeighting	30dB
AvgFFTDurationLimit	110s	MinCallDuration	0.3s
BBP_InThreshold	13.5dB	MinAvgAmplitude	8dB
BBP_InDuration	5s	BlankingTime	0.2s

BBP_OutThreshold	5dB		BlankingFreq	2Hz
BBP_OutDuration	0.6s		MD	≤ 2.5
BBP_MaxDuration	25s		SNR	$\geq 13dB$
			CR	≥ 10

Comparative SNR measurements

In order to evaluate the influence of the missed humpback whale detections for the resulting acoustic presence data of humpback whales in the wider Weddell Sea area, comparative SNR measurements were conducted. Both detected and missed humpback whale calls of the 150h-dataset from the LFDCS run using the final chosen parameter settings (chosen by the highest $Prob_{Pres}$ and a $Prob_{FN}$ lower than 20%) were identified to measure their SNR. In all false negative hours, humpback whale calls were manually identified in Raven Pro 1.5 and their SNRs were measured by comparing the average power (dB re 1µPa) of the spectrum with the call's duration and bandwidth with the average power of two spectra with the same dimensions, one before and one after the call, respectively. From all true positive hours, a number of hours was randomly chosen in order to match the number of false negative hours. Three detected calls were randomly chosen from each of these selected true positive hours and SNRs of these calls were measured applying the same method as described above.

Results

Detector/classifier performance evaluation

In the 30h-dataset, 5274 humpback whale vocalizations were manually detected and classified into the seven humpback whale call types included in the LFDCS call library, with 357 manual detections of call type 1, 439 of call type 3, 2471 of call type 4, 1056 of call type 5, 508 of call type 6, 338 of call type 18, and 100 of call type 19. Different parameter settings in LFDCS yielded different performance results in terms of recall, precision and F1-score (*Figure 17*). The selected parameter setting resulted in a recall of 22%, a precision of 56%, and a F1-score of 0.32. In the present study, for the detection of humpback whale presence on an hourly basis, it was considered more important to aim for a higher precision of the automated detector at the cost of a lower recall (because it was not necessary to detect all vocalizations in order to capture hourly acoustic presence). The final parameter setting in combination with the acoustic-context filter and specific

MD, SNR and CR thresholds resulted in a good detection performance in terms of hourly humpback whale presence (Figure *18*). At an hourly CR threshold of at least 10 calls/hour the automatic detection process yielded a $Prob_{Pres}$ of 75% and a $Prob_{FN}$ of only 18%. Because it is common practice to exclude vocalizations with a SNR below 10 dB from the analysis (Dunlop *et al.*, 2008; Magnúsdóttir and Lim, 2019), the quality of missed vocalizations in these 18% of false negative hours was checked. In comparison to the sampled humpback whale vocalizations in the detected hours, the vocalizations in the false negative hours had SNRs which were mainly below 10 dB (Figure *19*).
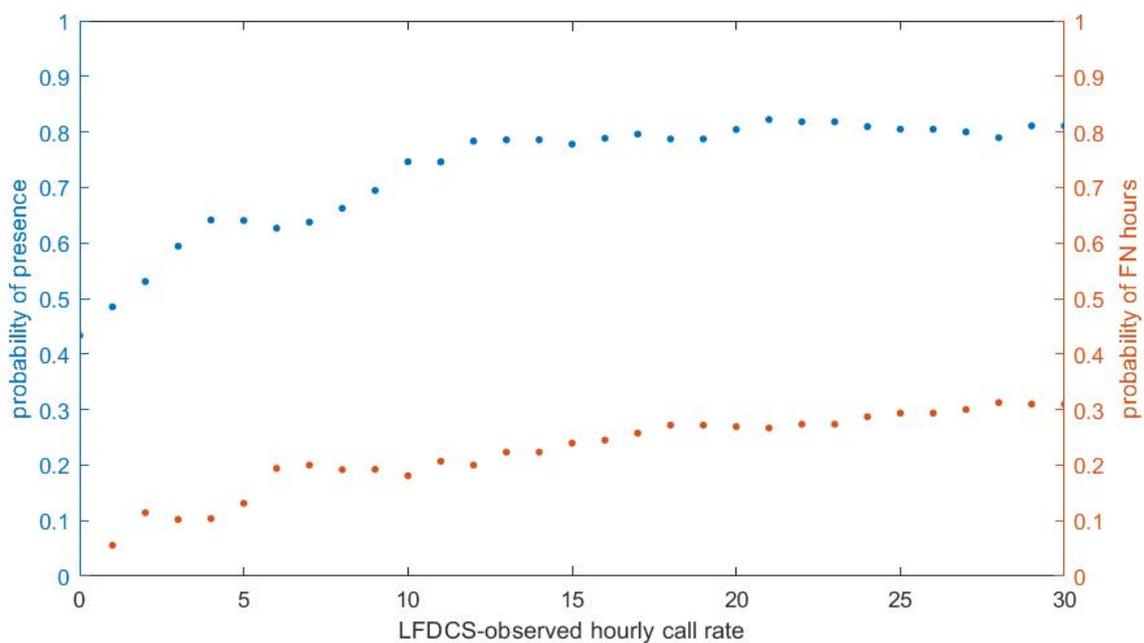
Figure 18. Final detection performance of hourly humpback whale acoustic presence in the 150h-dataset. The probability of humpback whale acoustic presence in the recording hours is depicted in blue on the left y-axis and the probability of false negative hours is depicted in orange on the right y-axis. The x-axis represents the hourly call rate observed by the detector after applying the acoustic-context filter.
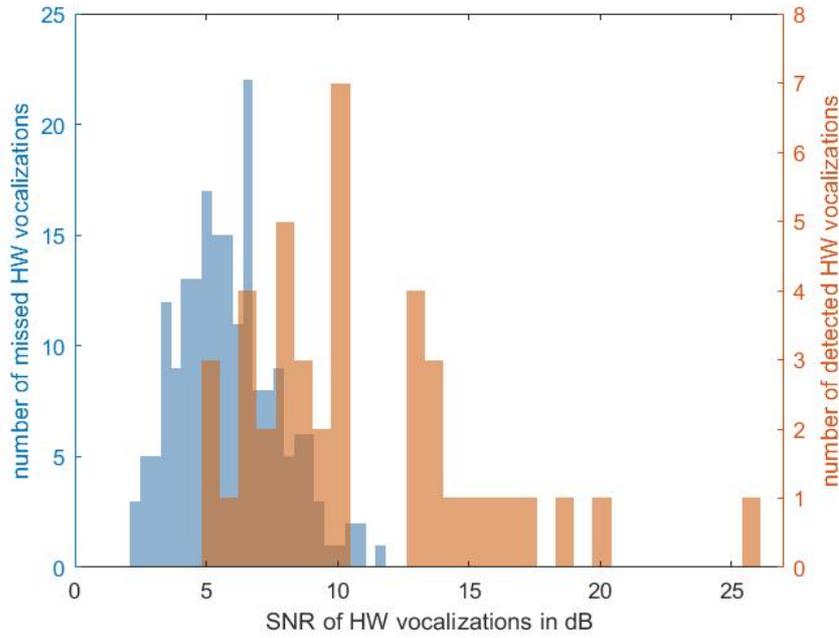
Figure 19. Measured signal-to-noise ratios (SNR) of humpback whale (HW) vocalizations. Blue bars (left y-axis) represent SNRs of vocalizations in false negative (missed) hours and orange bars (right y-axis) represent SNRs of vocalizations in detected hours.
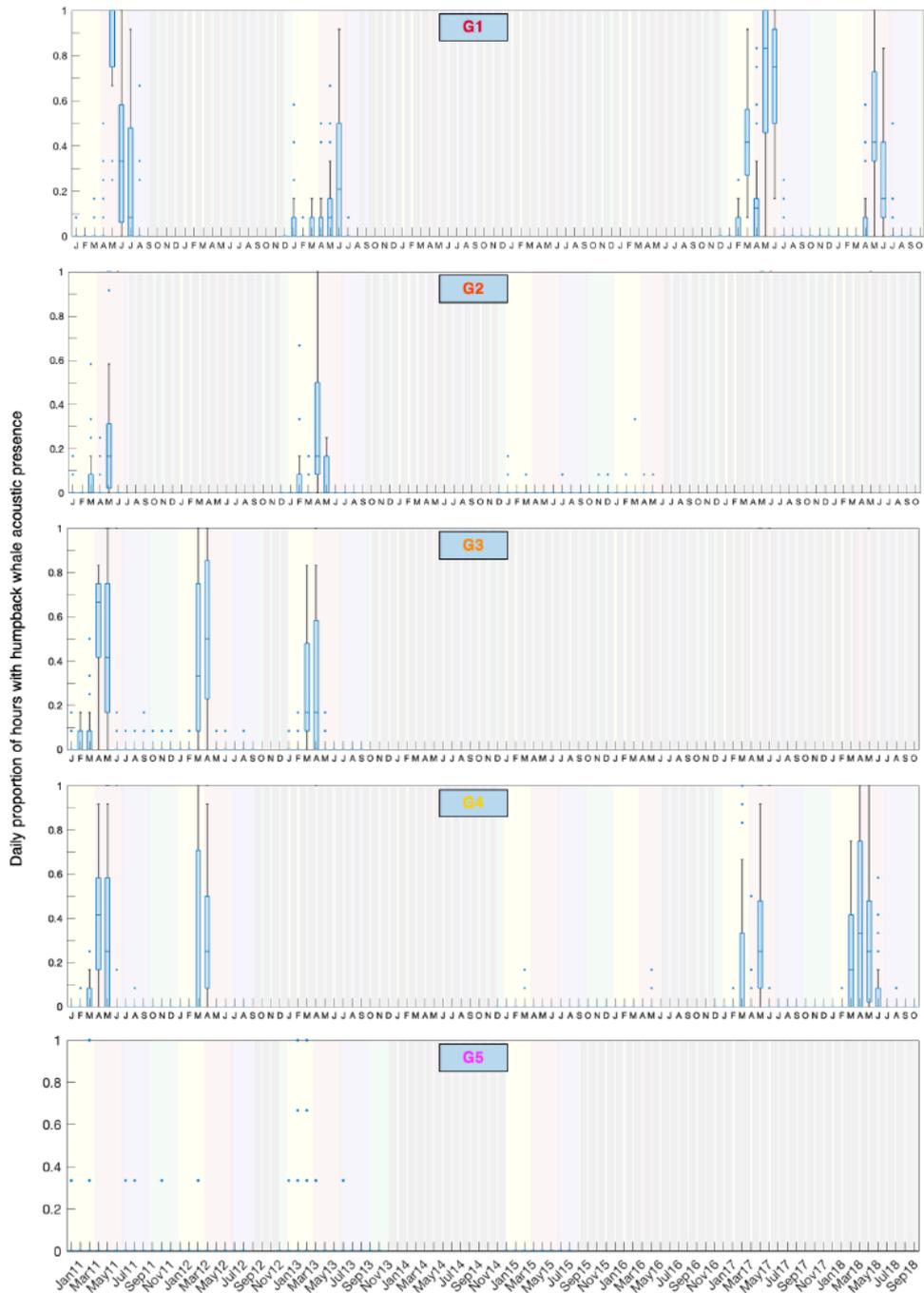
Figure 20. Boxplots of daily proportions of hours with humpback whale acoustic presence from the five recording positions (G1-G5) on the Greenwich Meridian displayed per month from December 2010 until September 2018 (center line, median; box limits, upper and lower quartiles; whiskers, 1.5x interquartile range; points, outliers). Grey bars represent months without recording data, yellow, red, blue and green shades indicate summer, fall, winter and spring seasons, respectively. *S*ingle points indicate single daily observations of humpback whale acoustic presence.
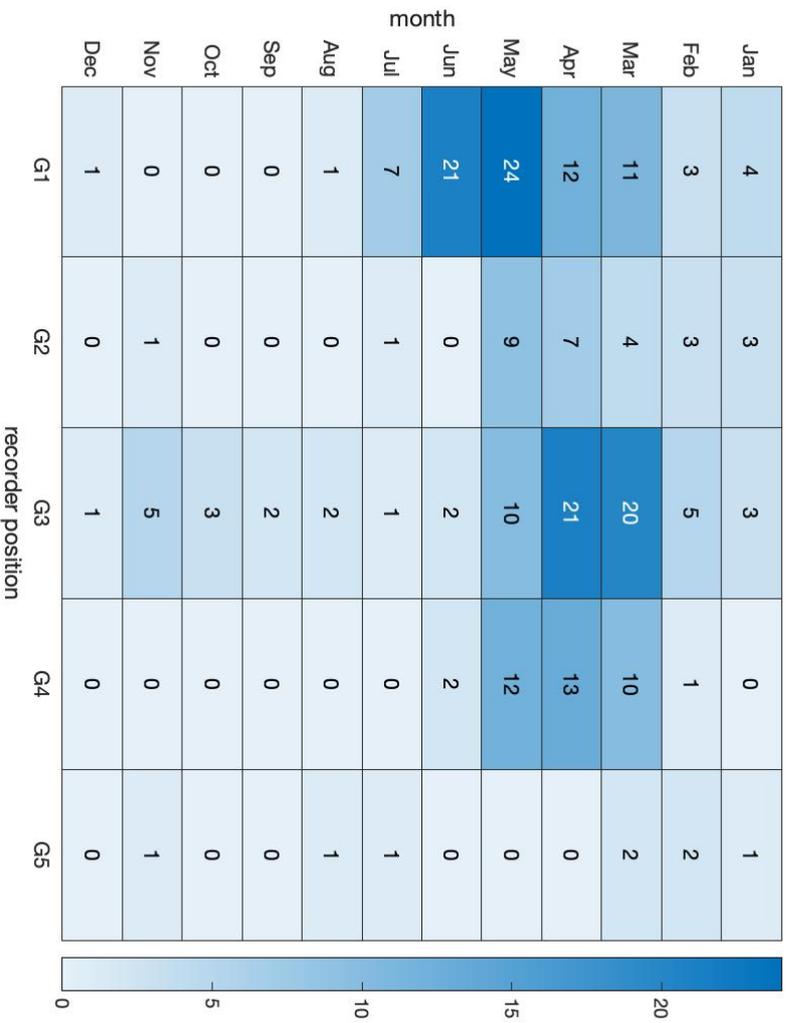
Figure 7. Heatmap showing the average number of days with humpback whale acoustic presence for all months for recording stations G1-5. Darker colors indicate higher presence, numbers in cells represent the average number of days with presence per month per recording station.

month	G1	G2	G3	G4	G5
Jan	4	3	3	0	1
Feb	3	3	5	1	2
Mar	11	4	20	10	2
Apr	12	7	21	13	0
May	24	9	10	12	0
Jun	21	0	2	2	0
Jul	7	1	1	0	1
Aug	1	0	2	0	1
Sep	0	0	2	0	0
Oct	0	0	3	0	0
Nov	0	1	5	0	1
Dec	1	0	1	0	0

recorder position

S3

Literature

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Supplementary Material – Chapter III
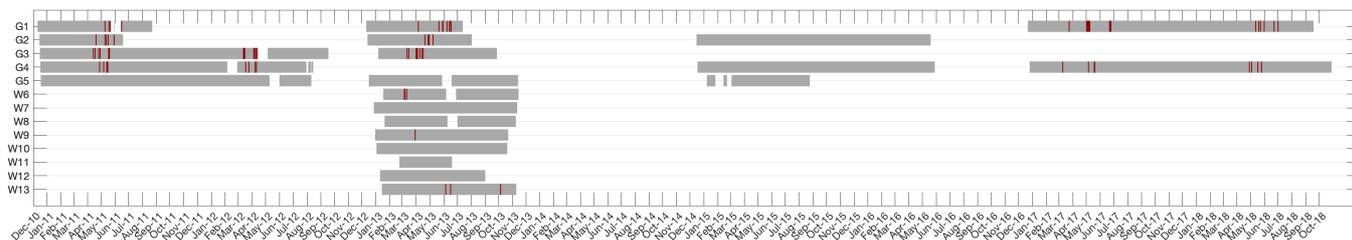
Figure S1. Timeline of acoustic recordings taken at the 13 recording locations of the Greenwich (e.g., 'G1') and Weddell datasets (e.g., 'W6') between 2010 and 2018. Temporal data coverage is indicated by gray bars and red lines indicate days with high quality humpback whale song recordings (i.e., SNR ≥ 10 dB and at least to distinct themes discernible) from which units were extracted for the analysis.

Table S1. Acoustic metrics (AM) used to discriminate between humpback whale unit types. AMs are divided in three categories. AMs marked with (5) indicate those that were computed on five bandwidths: 0.01–0.25 kHz; 0.25–0.5 kHz; 0.5–1 kHz; 1–2.5 kHz; and the full bandwidth 0–2.5 kHz. To compute the AM, where it applies, we used a window length of 512 samples and 50% overlap.

Category	AM	Description
Acoustic Indices	Hs	Spectral entropy: obtained by applying the Shannon evenness equation to the average frequency spectrum scaled by is integral.
	Ht	Temporal entropy: obtained by applying the Shannon evenness equation to the amplitude envelope obtained with the Hilbert transform of the signal, scaled by its integral.
	H	Acoustic entropy index (Sueur et al. 2008): obtained by the multiplication of Hs and Ht, it integrates both the spectral and temporal components of an acoustic signal. H varies between 0 and 1, where 1 indicates a highly heterogeneous signal.
	Ht_hist	Temporal entropy computed on the distribution obtained from a histogram: here we used the Sturges algorithm to define the histogram breaks. Ht_hist will not show a high temporal entropy value for a sustained sound with an almost flat envelope.
	ADI (5)	Acoustic diversity index (Peking et al. 2012): obtained by applying the Shannon diversity equation to the average frequency spectrum.

	AEI (5)	Acoustic evenness index (Villanueva-Rivera et al. 2011): obtained by dividing the spectrogram into bins and taking the proportion of the signals in each bin above the threshold (-50dBFS) and applying the Gini index to these bins.
	AR	Acoustic richness (Depraetere et al. 2012): obtained through the multiplication of the rank of the M and Ht indices scaled by the squared number of entries in the dataset. AR varies between 0 and 1, where 1 indicates a highly rich signal within that particular dataset.
	ACI (5)	Acoustic complexity index (Pieretti et al. 2011): computed as the average absolute fractional change in spectral amplitude for each frequency bin in consecutive spectrums.
	BI (5)	Bioacoustic Index (Boelman, *et al.* 2007): calculated as the area under the curve of the mean amplitude spectrum between two frequency limits, is a function of both the sound level and the number of frequency bands.
	ENS	Effective number of species (Chase and Knight 2013): the number of equally-common species required to give a particular value of a diversity index (e.g., Shannon diversity index). We obtained this index by computing the exponential of the acoustic diversity index (ADI).
Energy Metrics	NP (5)	Number of peaks (Gasc et al. 2013): number of peaks in the frequency spectrum with an amplitude slope parameter = 0.01.

	AMP	Amplitude value of the local maximum frequency peak computed on four bandwidths: 0.015–0.1 kHz; 0.1–0.5 kHz; 0.5–1 kHz; 1–2.5 kHz; and the full bandwidth 0–2.5 kHz.
	M	Median amplitude standardized. M varies between 0 and 1.
	SPL	Average amplitude value of the recording, computed as the mean of the amplitude envelope.
	NDSI_high	Sum of energy in the high frequency range (350-2500 Hz) of the recording.
	NDSI_low	Sum of energy in the low frequency range (10-350 Hz) of the recording.
	BL	Background noise level: average intensity from the mode intensity computed for each frequency bin. Computed following the background noise index calculation method (Towsey 2017).
	BP	Background noise level percentile: is the % of values in the amplitude distribution below the noise level value.
Ratio Metrics	RPS	Relative proportion of signal: ratio between the intensity counts above noise level and all sound.
	Anisotropy	Anisotropy is a measure used to determine if heterogeneity patterns are more heterogeneous along a particular direction. It characterizes the relative increase in the temporal heterogeneity of the soundscape and it is obtained as the temporal and spectral entropy ratio.

	NDSI	Normalized difference soundscape index (Kasten et al. 2012): developed to compare the acoustic signal of soundscapes with different relative contributions of anthrophony and biophony. In this paper we computed NDSI as the normalized difference in the absolute amplitude of a high frequency band (200–2500 Hz) minus a low frequency band (10–200 Hz). NDSI varies between -1 and +1, where +1 indicates a signal dominated by high frequency sounds.

Figure S2. Classification tree of the final random forest model including 43 AMs.
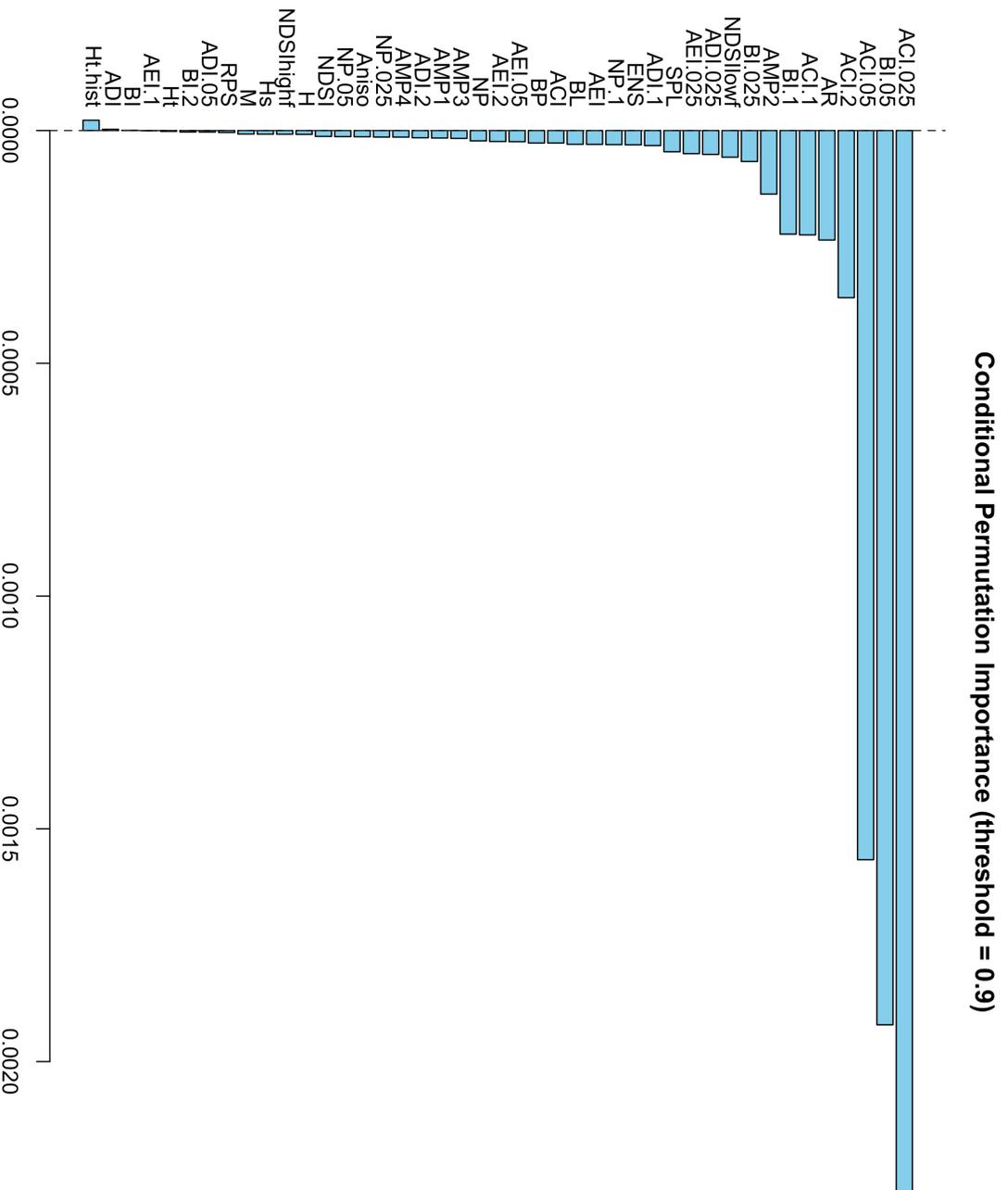
Figure S3. Conditional Variable Importance (CVI) for each AM (i.e., 43) included in the final random forest model.

Supplementary Material – Chapter IV

Table S1. Average (+/- standard deviation) session length, song length, unit complexity, phrase complexity, and song complexity per latitude of the recording location.

Latitude	Session length	Song length	Unit complexity	Phrase complexity	Song complexity
-59.05	107.36 +/- 100.90	71.65 +/- 74.83	0.12 +/- 0.08	0.32 +/- 0.17	0.05 +/- 0.05
-61.02	50.22 +/- 22.81	40.50 +/- 22.67	0.15 +/- 0.06	0.43 +/- 0.21	0.07 +/- 0.06
-64.00	85.04 +/- 101.56	49.63 +/- 81.44	0.23 +/- 0.18	0.49 +/- 0.16	0.13 +/- 0.12
-65.97	66.67 +/- 28.78	46.15 +/- 26.87	0.12 +/- 0.09	0.43 +/- 0.19	0.06 +/- 0.06
-66.03	69.64 +/- 40.45	40.97 +/- 31.04	0.17 +/- 0.11	0.43 +/- 0.16	0.08 +/- 0.07
-66.51	84.71 +/- 74.18	56.07 +/- 49.05	0.13 +/- 0.08	0.33 +/- 0.13	0.05 +/- 0.05
-66.61	42.88 +/- 14.12	36.44 +/- 19.19	0.14 +/- 0.06	0.50 +/- 0.16	0.08 +/- 0.05

Table S2. Set median song strings recorded at different locations and years in the Atlantic sector of the Southern Ocean. 'SessionIDs' correspond to individual singers encoded with the name of the recording position (first 2-3 symbols, i.e., 'W13', 'G4',…) and the date of the recording (last 8 symbols, i.e., '05/06/13', '05/10/13',…). Theme sequence is encoded with phrase type names (see Supplementary Material 2 for phrase type catalogue).

SessionIDs	Theme sequence
G3 13/04/11	Cb Cc
G3 17/04/11	Ea Cb Ba Aa
G2 19/04/11	Ba Aa
G3 25/04/11	Ea Cb Ca Cc Ba
G4 27/04/11	Cb Cc
G3 28/04/11	Cb Cc Ca Ba Ea
G4 06/05/11	Ea Cb Cc Ca
G2 09/05/11	Cb Cc
G1 09/05/11	Ba Ac Aa
G2 12/05/11	Cb Cc
G4 13/05/11	Ba Ac
G4 15/05/11	Ea Cb Cc Aa
G2 16/05/11	Cb Cc Ba Aa
G3 17/05/11	Aa Ea Cb Cc Ca Ba
G1 18/05/11	Ba Aa Ac Bb Ab
G1 21/05/11	Ba Aa Ac
G2 29/05/11	Cb Cc
G1 15/06/11	Cc Cb Ba Aa Ea
G3 12/03/12	Aa Ba
G3 14/03/12	Ac Aa Af Da De Ba

G3 15/03/12	Ac Aa Ba
G4 17/03/12	Aa Ai Ba
G4 24/03/12	Aa Ac Ba
G3 04/04/12	Aa Ac Ba
G4 07/04/12	Aa Ac Ba
G3 08/04/12	Ba Aa
G4 10/04/12	Aa Ai Aj Ba
G3 12/04/12	Ba Aa Af Da
W6 05/03/13	Aa Ai Ac
W6 06/03/13	Ad Aa Ac
W6 10/03/13	Aa Ai Ak Ac
G3 11/03/13	Ai Ac
G3 15/03/13	Ac An Ak
W9 29/03/13	Ap Aa
G3 31/03/13	Aa Ai Ak Ac
G3 01/04/13	Ac Aa Ai
G3 03/04/13	Aa Ai Aj Ac Ad
G1 05/04/13	Ac Aq Aa Am Ai An Ak
G3 08/04/13	Aq Aa Am Ai Ac
G3 13/04/13	Aa Ai
G3 16/04/13	Aa Ai An Ak Ac Ad
G2 20/04/13	Aa Ai Ac
G2 27/04/13	Aa Ap Ai Aq Ac
G2 29/04/13	Aa Ac Ai Ak Ap
G2 08/05/13	Ap Aa
G1 21/05/13	Aa Ai Ac
G1 29/05/13	Aa Ai Ac
G1 30/05/13	Aa Ai Ac
W1305/06/13	Ga Ha Ec Ed Gb
G1 08/06/13	Cb Fa Ba Ca Aj Ak
G1 13/06/13	Aa Ac
G1 16/06/13	Aa Ai Ac Aq
W1316/06/13	Ai Ap
G1 17/06/13	Ap Aa Ai
W1305/10/13	Ed Gb Ga
G4 09/03/17	Df Ee
G1 23/03/17	Bf Bd Bg Ee
G1 01/05/17	Bd Be Df Ee
G1 02/05/17	Bd Df Ee
G1 04/05/17	Be Df Ee Bf
G1 05/05/17	Bd Bg Df Ef Ee
G1 07/05/17	Df Ee

G1 08/05/17	Bg Df Ee
G4 18/05/17	Df Bd Be Ee
G1 21/06/17	Bf Be Df
G1 23/06/17	Bd Be Df Ef
G1 24/06/17	Df Dg Bg
G4 28/04/18	Bg Bd Be Df Ef Gd
G4 03/05/18	Bd Df
G1 12/05/18	Gd Ge Gg Gh Ib
G4 17/05/18	Bh Bi
G1 19/05/18	Gd Gf Gg Ge Bi Bb Bj
G1 23/05/18	Bi Bb Ib Bh Bc Gd Gh
G4 25/05/18	Gd Gf Gg Bh Bb Ba
G1 31/05/18	Gd Ge
G1 22/06/18	Gd Gg Bh Bi Bb
G1 01/07/18	Gd Gg Bh Bi Gh Bb Ge Gf Bc Bj Ib
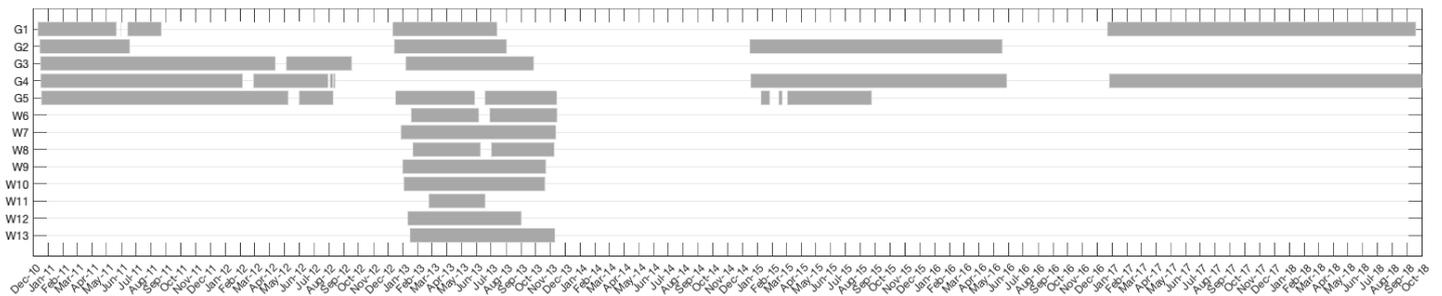
Figure S1. Timeline of acoustic recordings taken at the 13 recording locations of the Greenwich and Weddell datasets between 2010 and 2018. Mooring positions with the prefix 'G' in the name are assigned to the Greenwich dataset. Mooring positions with the prefix 'W' in the name are assigned to the Weddell dataset.
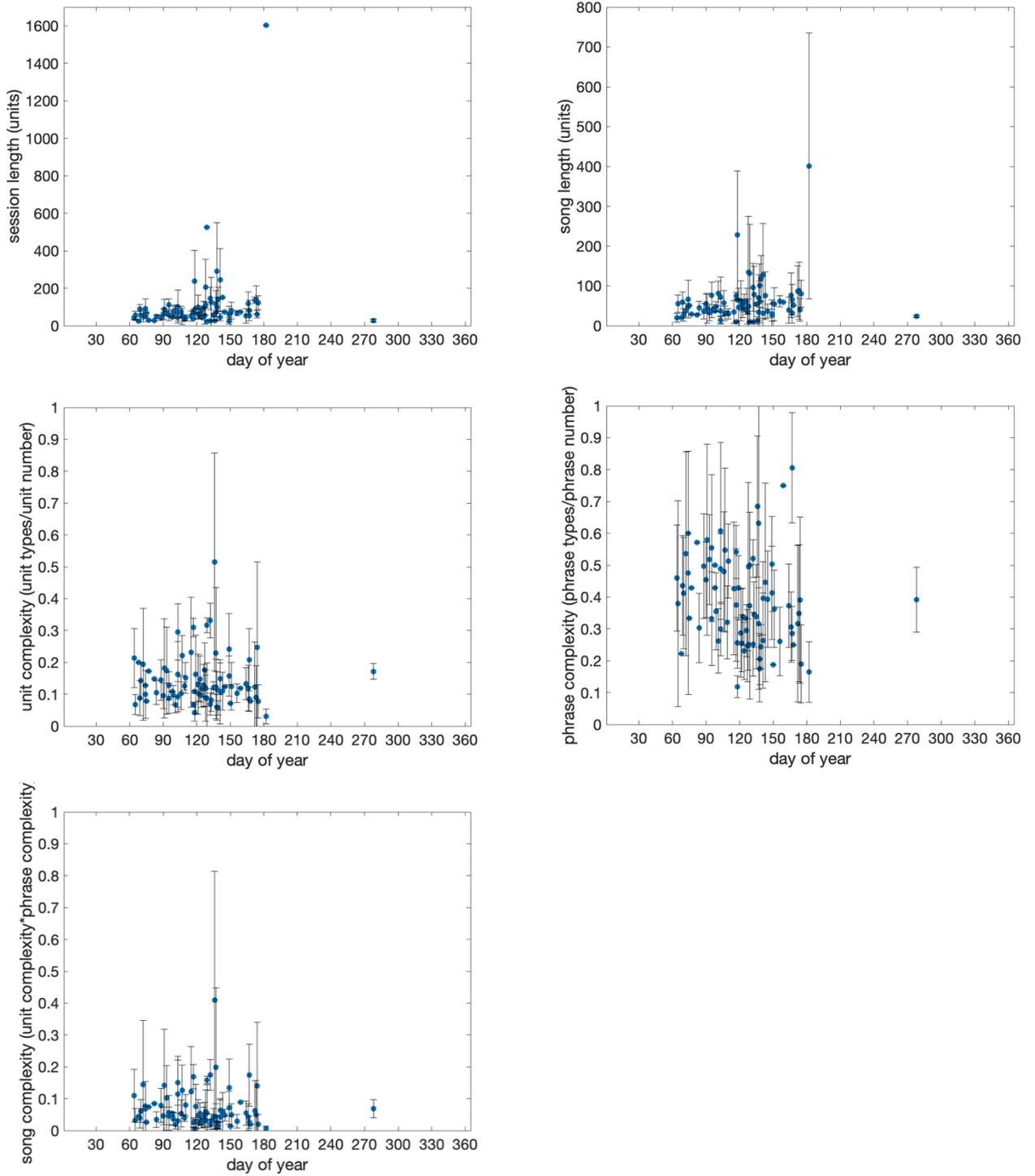
Figure S2. The five measures of song elaborateness (two for length and three for complexity) were plotted against day of the year pooled for all recording locations and years. Dots represent averages and error bars represent standard deviations.

170

Humpback whale call and phrase type catalogue – ASSO/Breeding grounds

➔ Atlantic sector of the Southern Ocean - **ASSO**
➔ Ecuador – **E**
➔ Brazil – **B**
➔ South Africa – **A**

- Call Types –

Representation of the call types used as song units.

Name	Example	Description
CT1		- tonal - Fundamental 100-300Hz - 1-2s - Constant frequency contour - Slightly downswept
CT3		- tonal - Fundamental 100-300Hz - 0.5-1s - Up-downsweep - Sometimes up- or downsweep dominates
CT4a		- tonal - Fundamental (a) 80-800Hz - Fundamental (b) 500-1200Hz - 0.3-0.7s - Upsweep - Sometimes almost pulsed
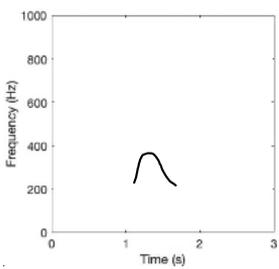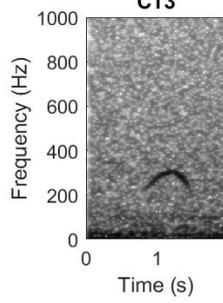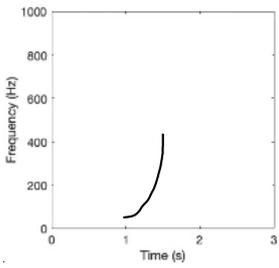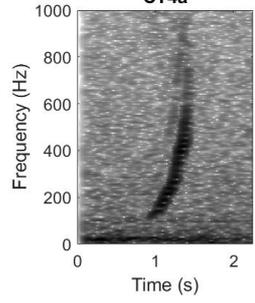
CT5b		- tonal - Fundamental (a)100-500Hz - Fundamental (b)300-1200Hz - 0.3-1.2s - Downsweep - Sometimes up-downsweep, sometimes upsweep, sometimes almost pulsed
CT6		- tonal - Fundamental 200-600Hz - 1-2s - Constant-upsweep - Sometimes almost upsweep
CT7		- Pulsed & tonal - 40-1500Hz - 0.3-0.8s - Amplitude modulated - Final upsweep as CT4a
CT8		- Pulsed - 300->2500Hz - 0.1-0.3s - Amplitude modulated - Sometimes almost upsweep
CT10		- tonal - Fundamental 400-600Hz - 0.5-2s - Irregular frequency modulations - Sometimes almost broadband
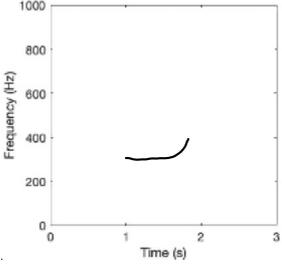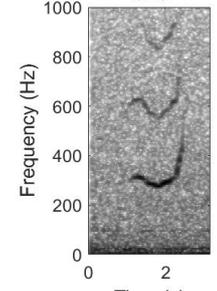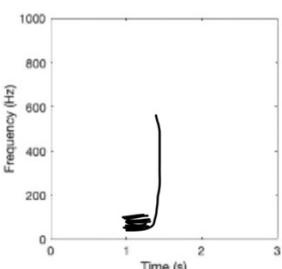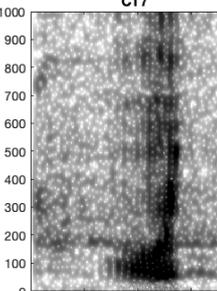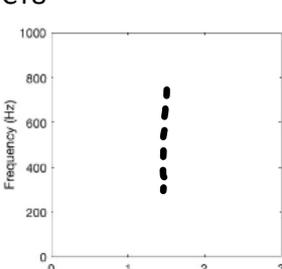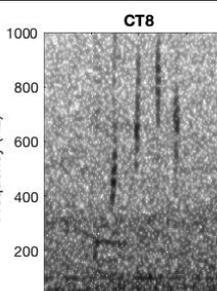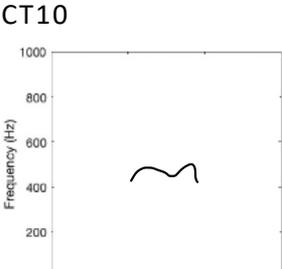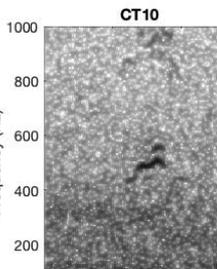
CT12		- Pulsed - 200-500Hz - 0.5-2s - Broadband with increasing frequency - Sometimes with 'harmonics' (Amplitude modulated)
CT13b		- Tonal - Fundamental (a) 50-300Hz - Fundamental (b) 200-700Hz - Fundamental (c) 500-1500Hz - 0.5-2s - Stepwise increase in frequency
CT15		- Pulsed & tonal - 40-1500Hz - 1-3s - Amplitude and frequency modulated - Final downsweep
CT16		- Pulsed & tonal - 40-1500Hz - 1-3s - Amplitude and frequency modulated - Final upsweep
CT17		- Pulsed & tonal - 40-1500Hz - 2-5s - Amplitude and frequency modulated - Final high frequency upsweep
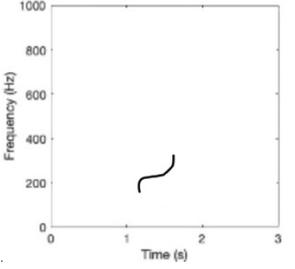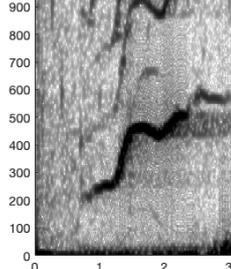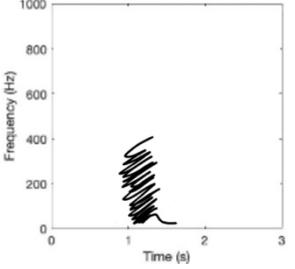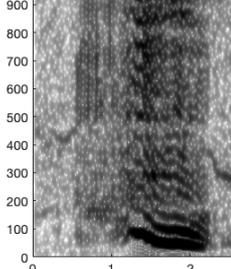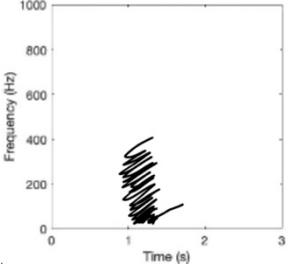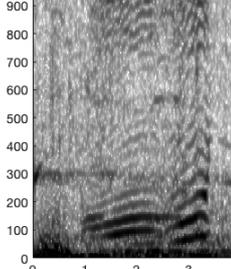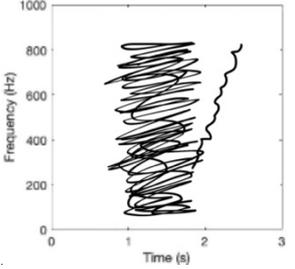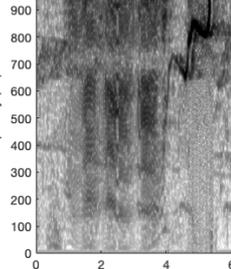
CT18		- tonal - Fundamental 20-120Hz - 0.2-1s - Downsweep - Sometimes up-downsweep
CT19		- tonal - Fundamental 20-100Hz - 1-4s - Constant frequency - Sometimes rather up-downsweep, down-upsweep, downsweep or upsweep
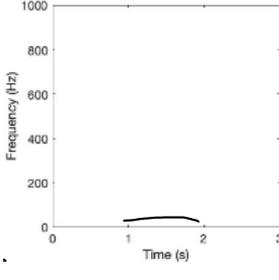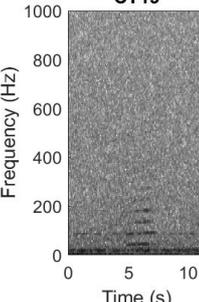
- ➔ Each phrase type is characterized by a distinct combination of units.
- ➔ Each phrase type is named by a capital letter and a lowercase letter, where the capital letter is an indicator for the first unit of the phrase type: i.e., Aa and Ab both start with call type (CT) 1.
- ➔ A phrase type is divided into phrase subtypes, when the number of repetitions of respective units differs: i.e., 1x CT1 and 3x CT4 translate into Aa13.

Type Aa
The combination of units CT1 & CT4a

Example of Aa13

ASSO, B
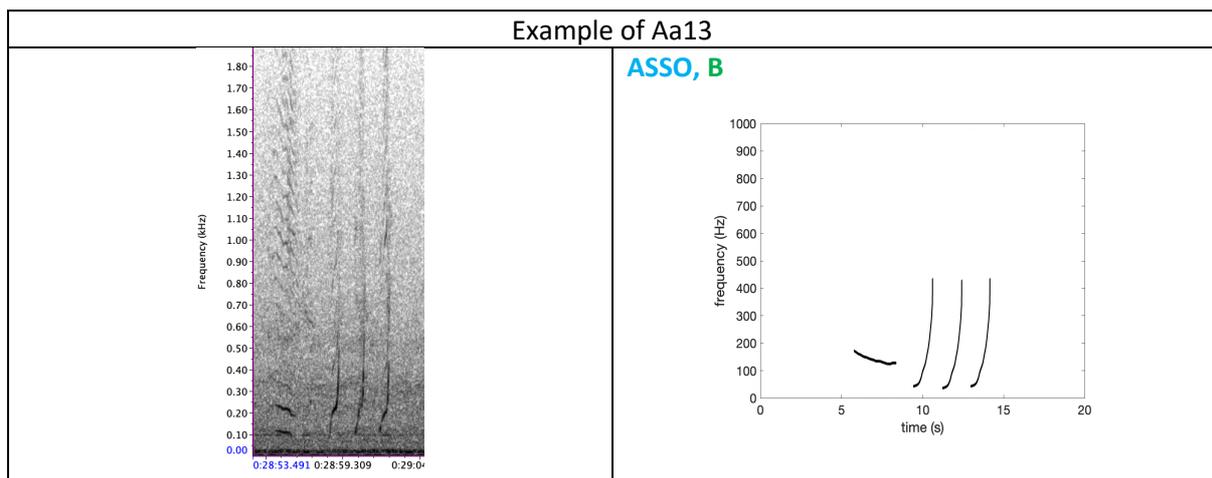
Type Ab
Combination CT1, CT4a & CT5b

Example of Ab123
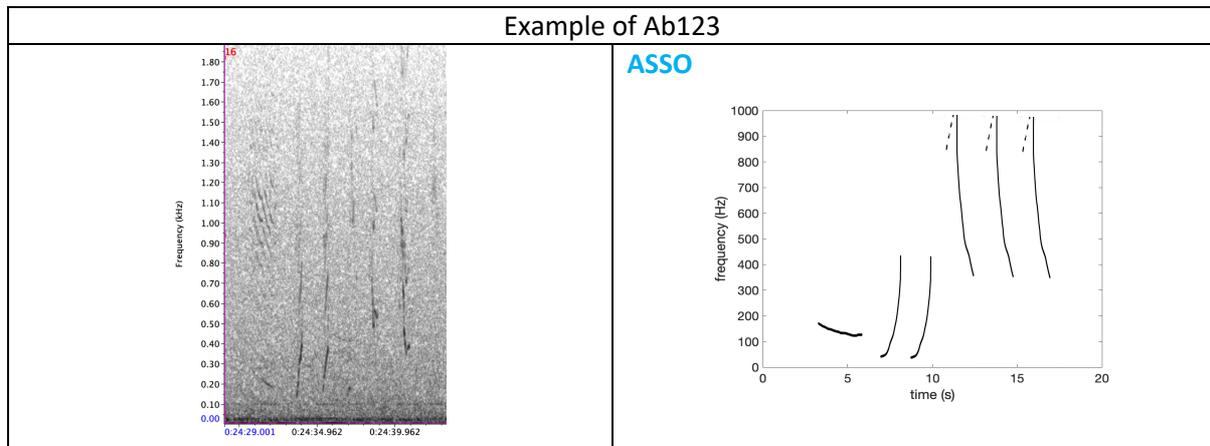
Type Ac
Combination of units CT1 & CT5b

Example of Ac13
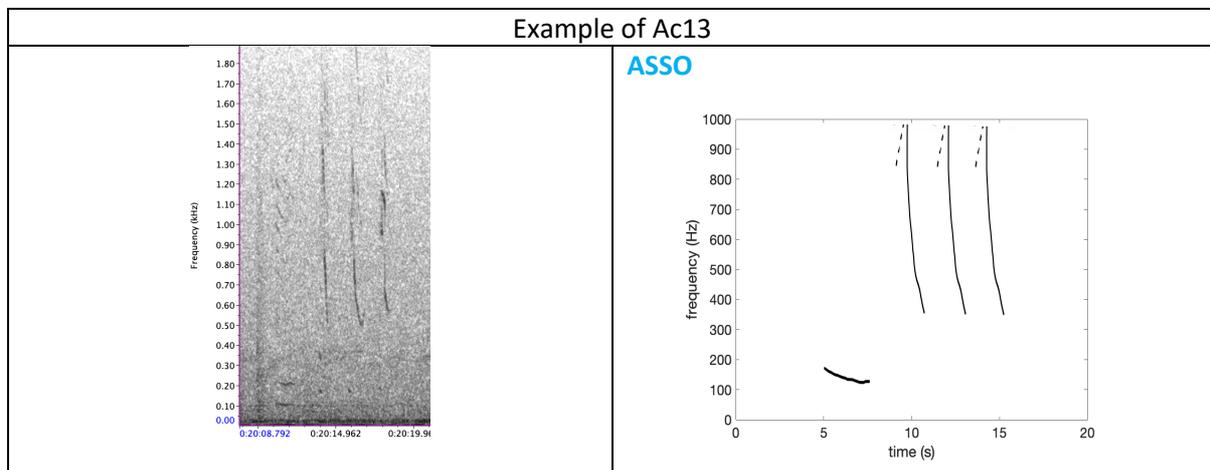
Type Ad

Combination of units CT1, CT5b, CT4a

Example of Ad123
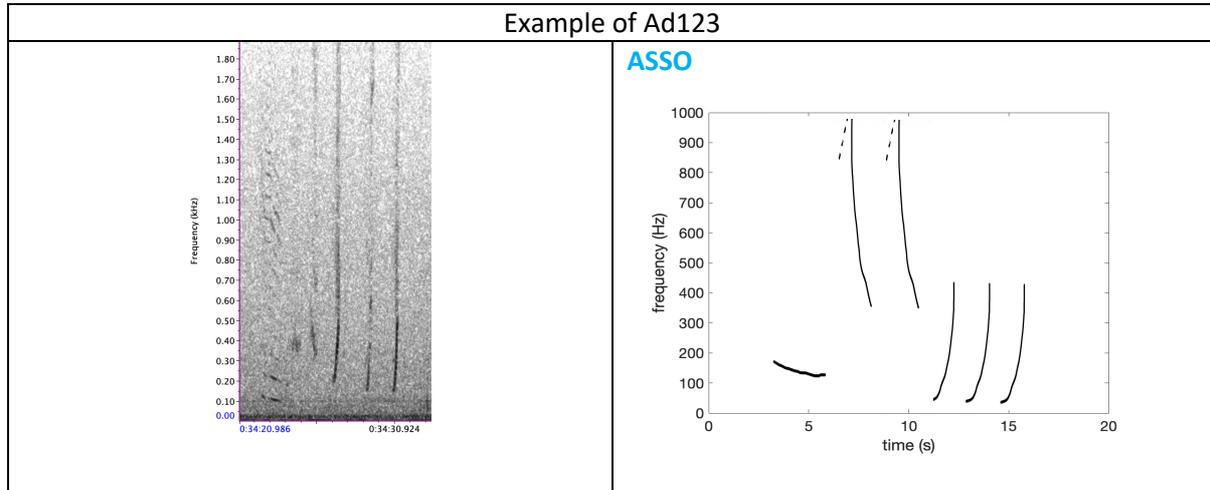
Type Ae

Combination of units CT1, CT6, CT5b

Example of Ae114
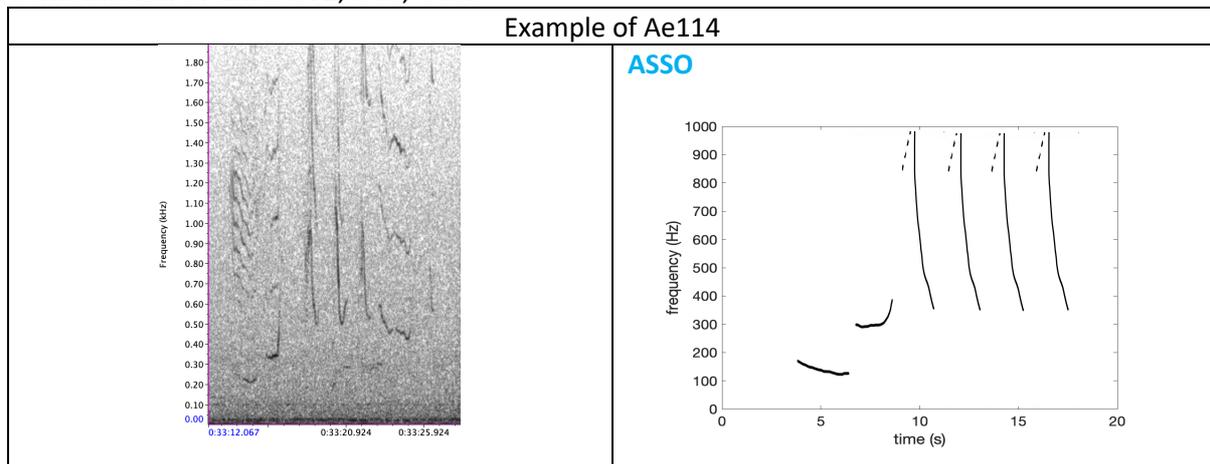
Type Af

Combination of units CT1, CT12, CT18

Example of Af112

ASSO, B
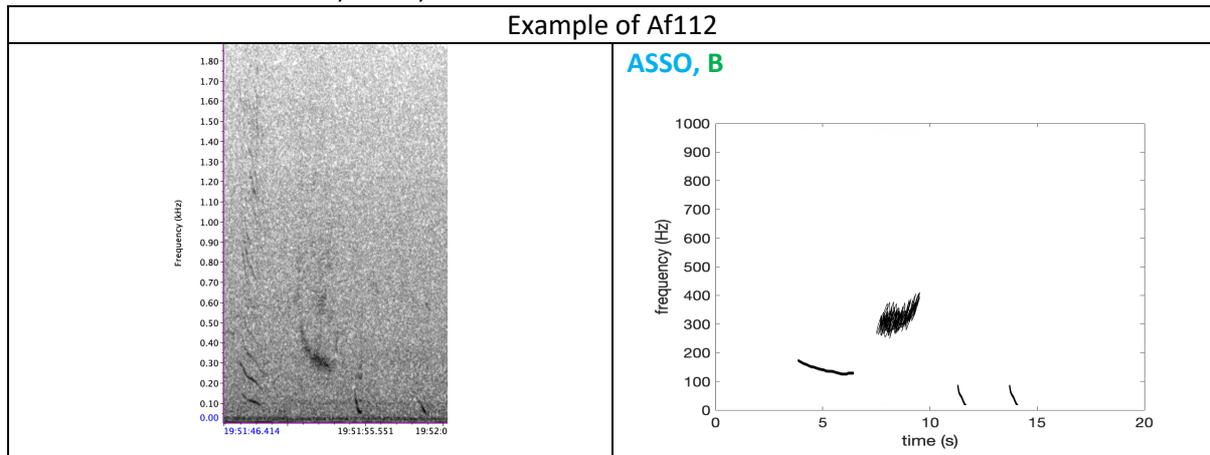
Type Ag

Combination of units CT1 and CT18

Example of Ag11

ASSO
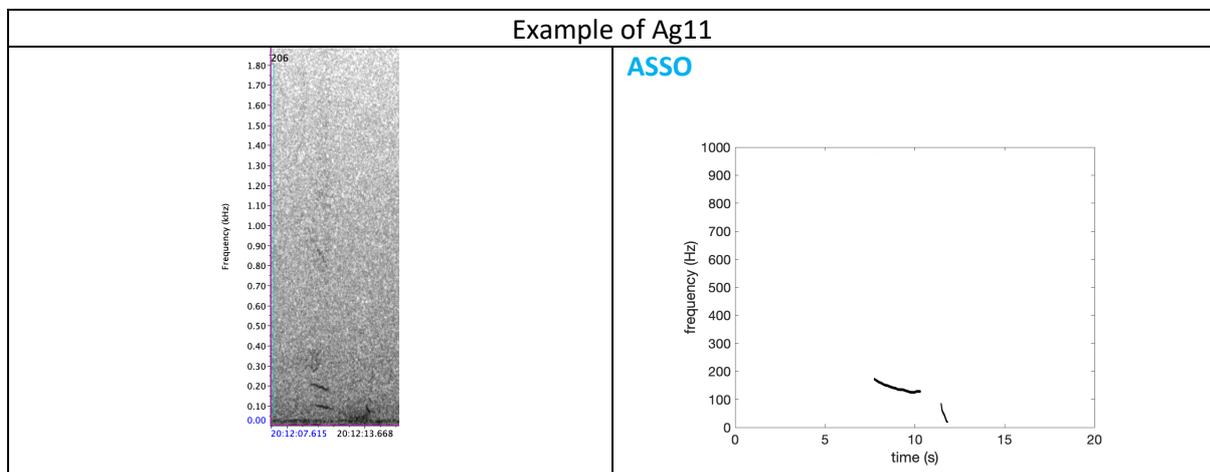
Type Ah

Combination of units CT1, CT12, CT4a

Example of Ah112
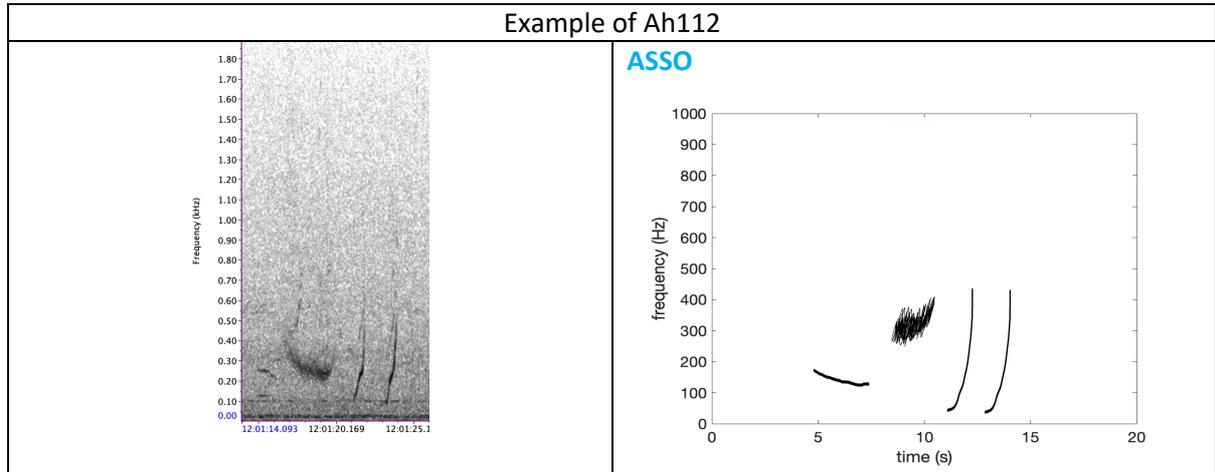
Type Ai

Combination of units CT1 and CT12

Example of Ai11
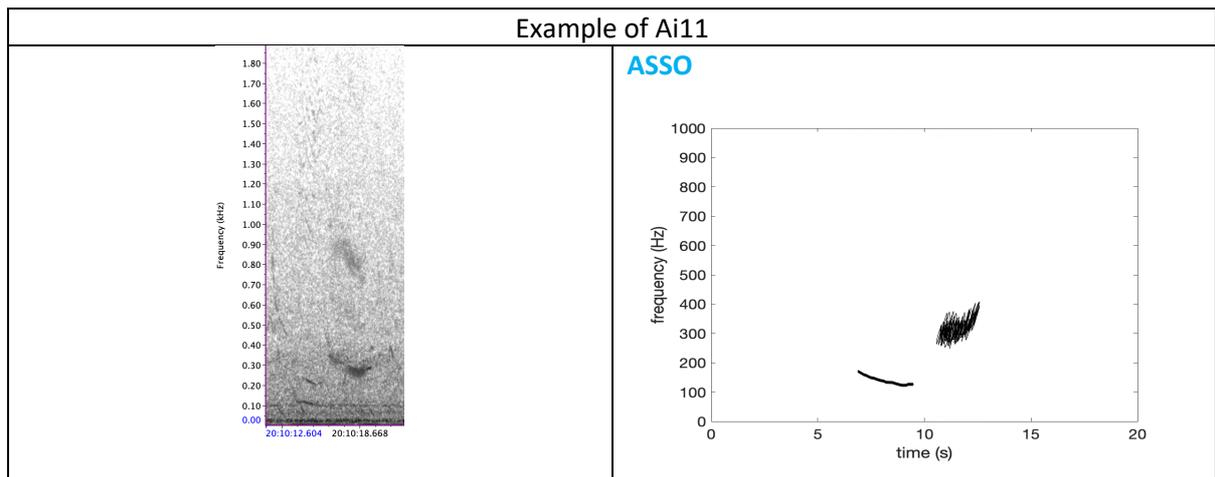
Type Aj

Combination of units CT1, CT12, CT5b

Example of Af114
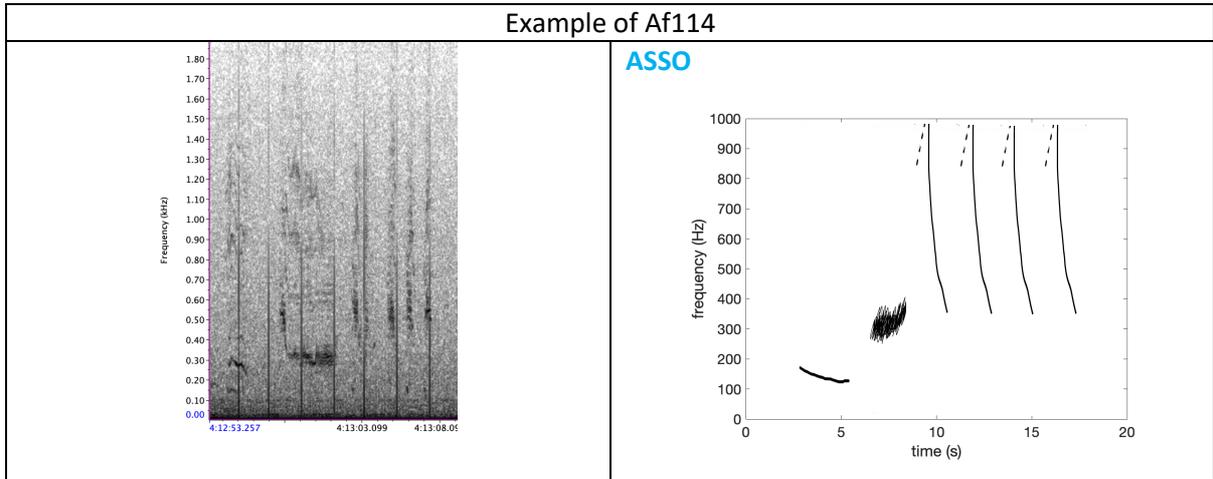
Type Ak

Combination of units CT1 & CT8

Example of Ak120
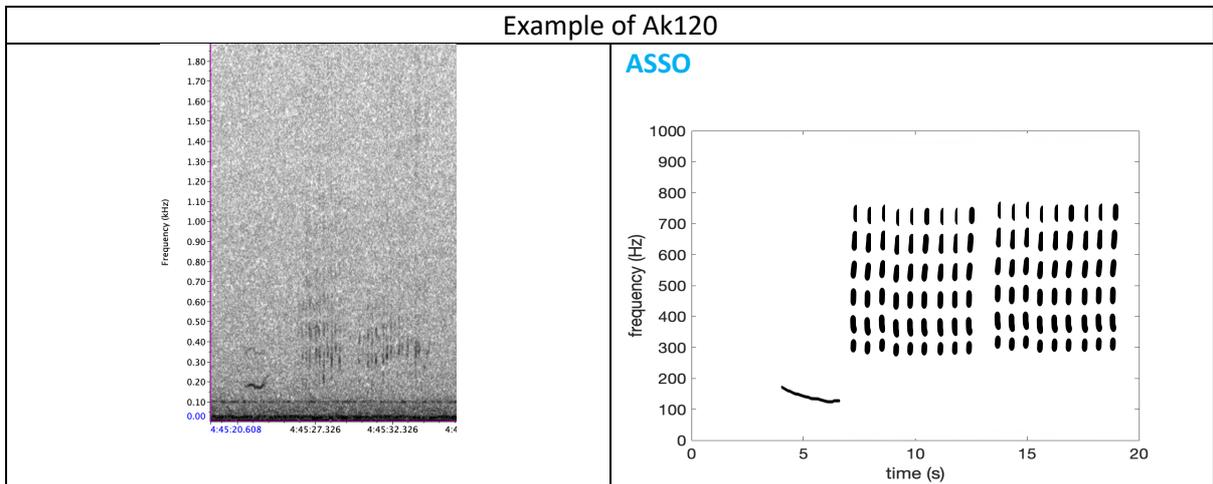
Type Al

Combination of units CT1, CT8, CT4a

Example of Al1171

ASSO
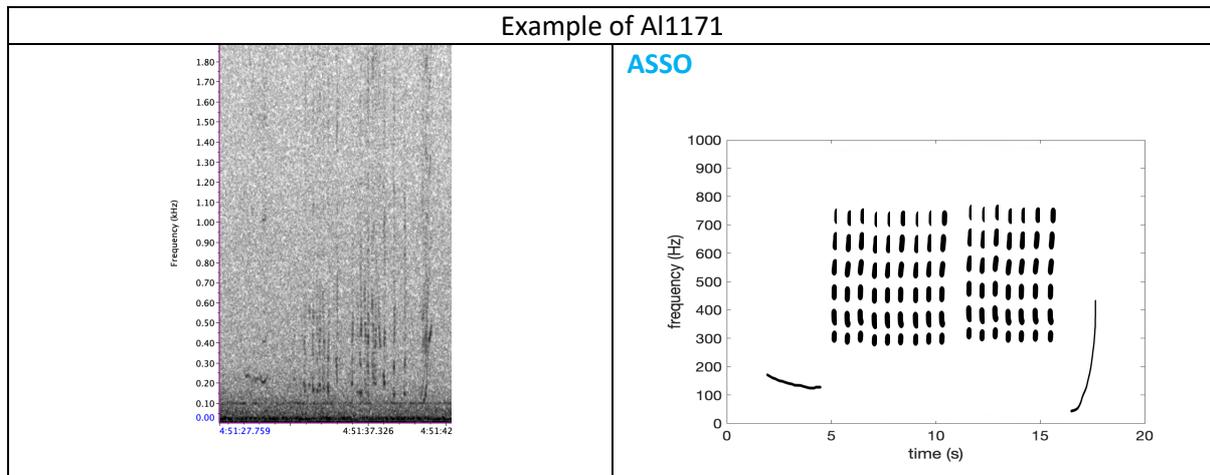
Type Am

Combination of units CT1, CT4a, CT12

Example of Am122

ASSO
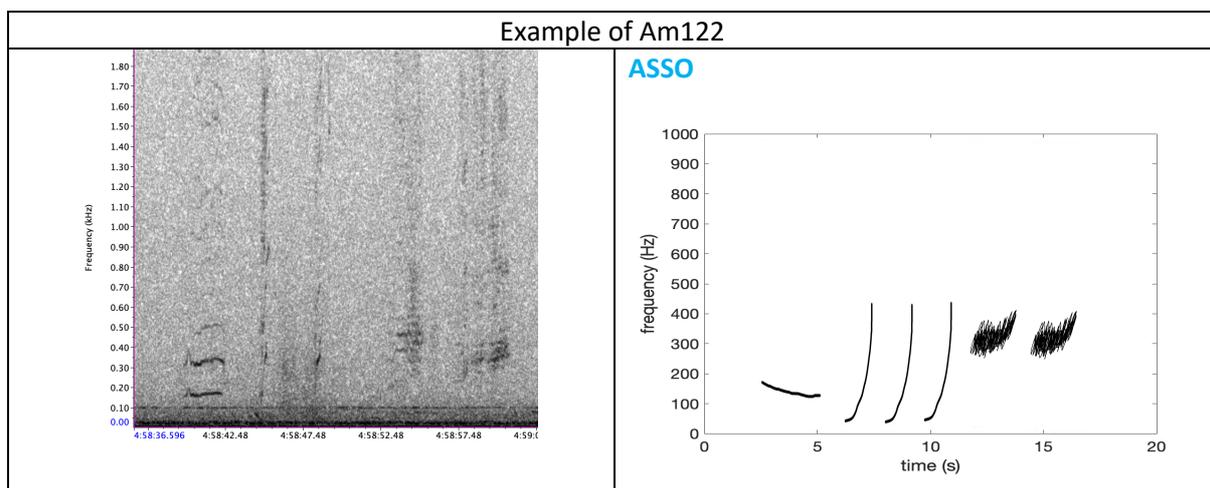
Type An

Combination of units CT1, CT12, CT8

Example of An1116
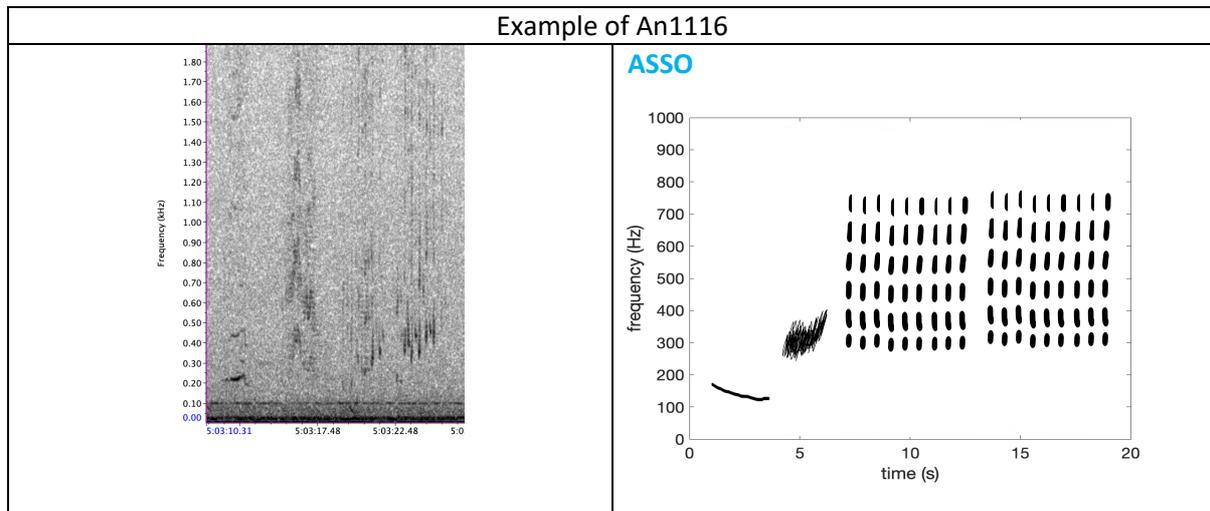
Type Ao

Combination of units CT1, CT5b/a & CT12

Example of Ao111
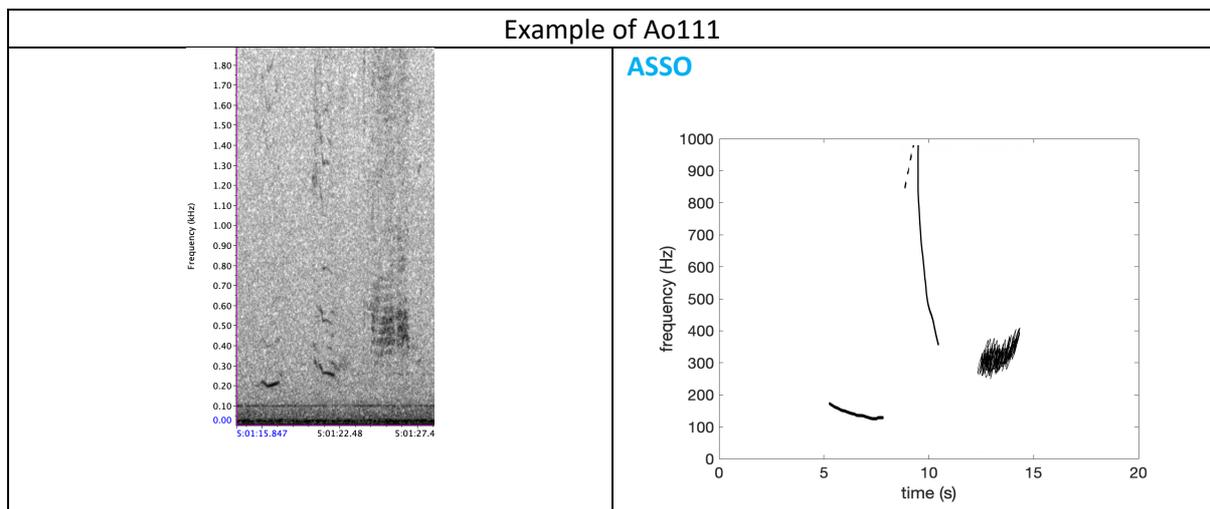
Type Ap

Combination of units CT1, CT4a & CT18

Example of Ap11214
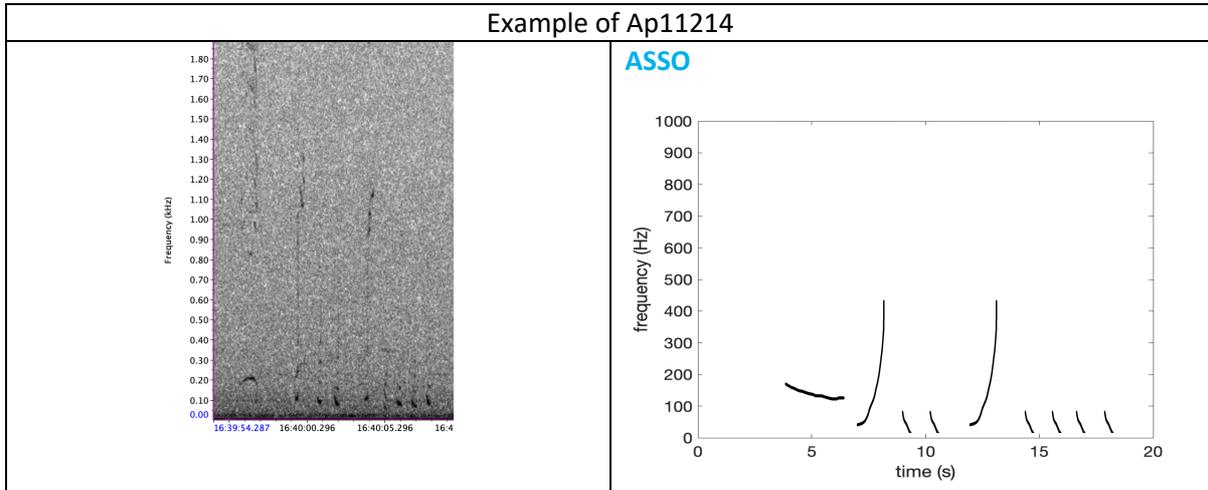
Type Aq

Combination of units CT1, CT5b & CT18

Example of Aq112121211
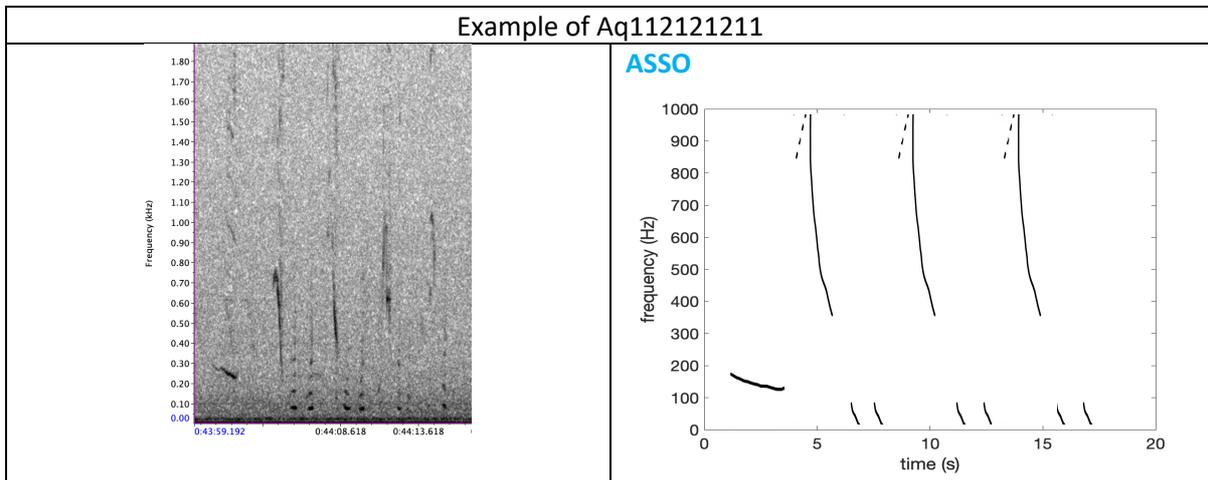
Type Ar

Combination of units CT1, CT10

Example of Ar11
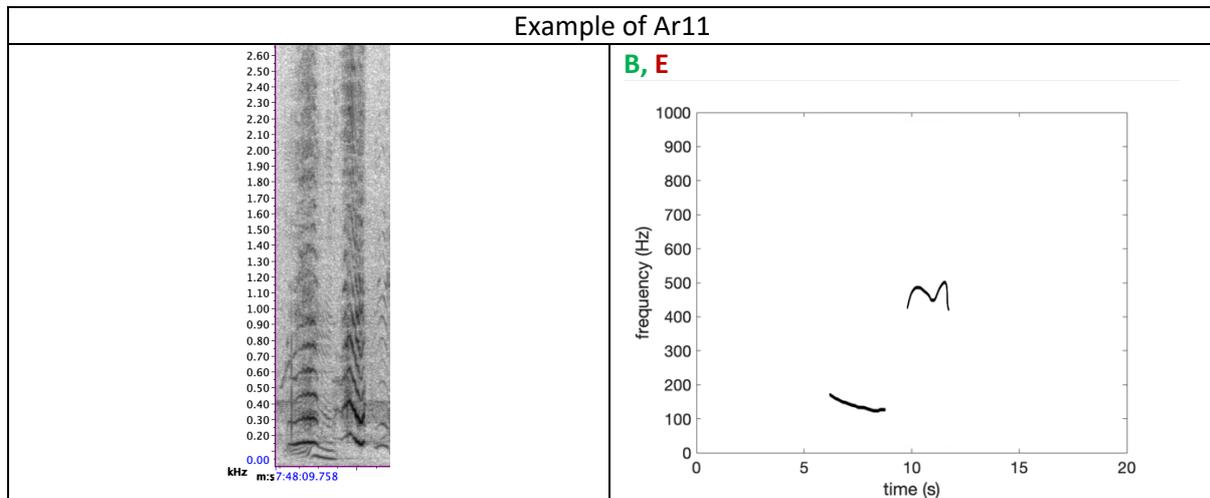
Type As

Combination of units CT1, CT15

Example of As11
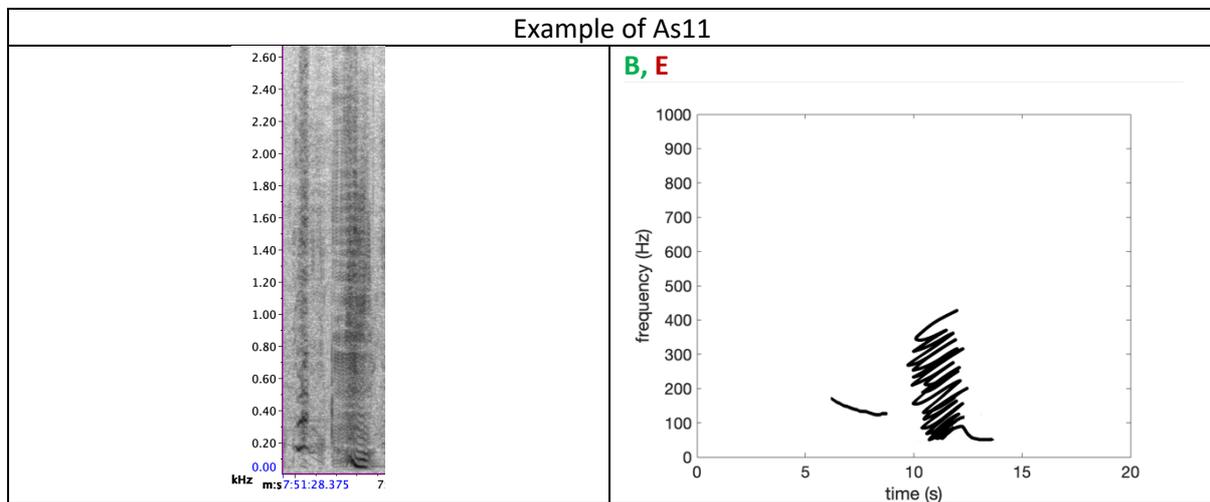
Type At

Combination of units CT1, CT5a

Example of At12
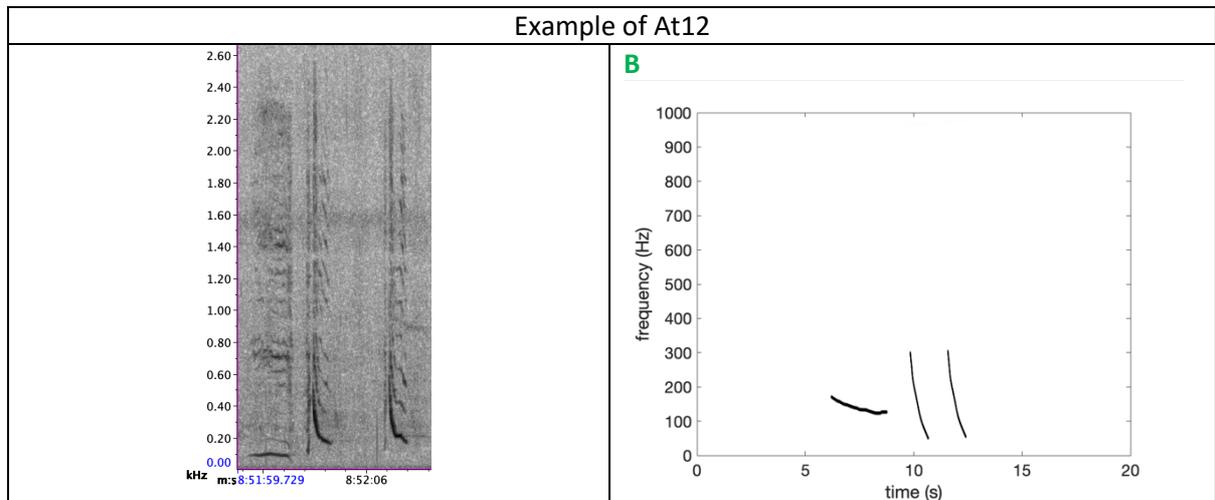
Type Au

Combination of units CT1, CT15, CT4a, CT19

Example of Au1112
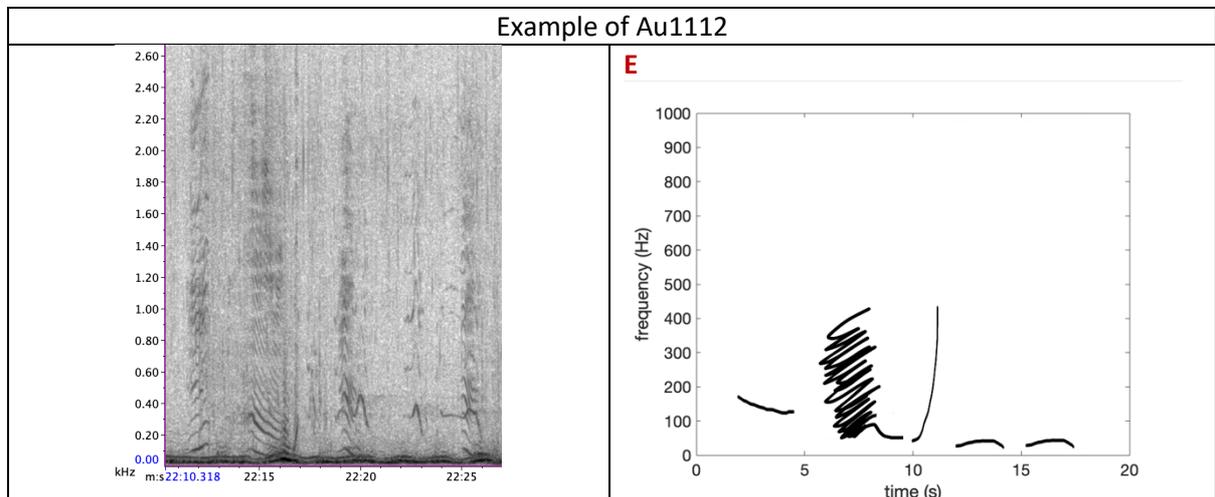
Type Av

Combination of units CT1, CT16, CT10

Example of Av211
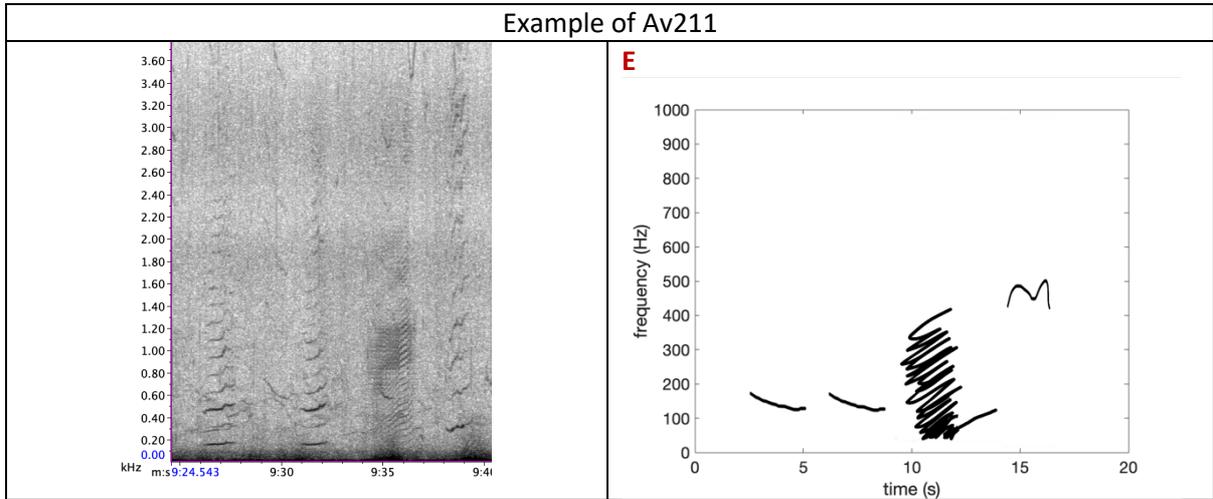
Type Aw

Combination of units CT1, CT13b

Example of Aw31
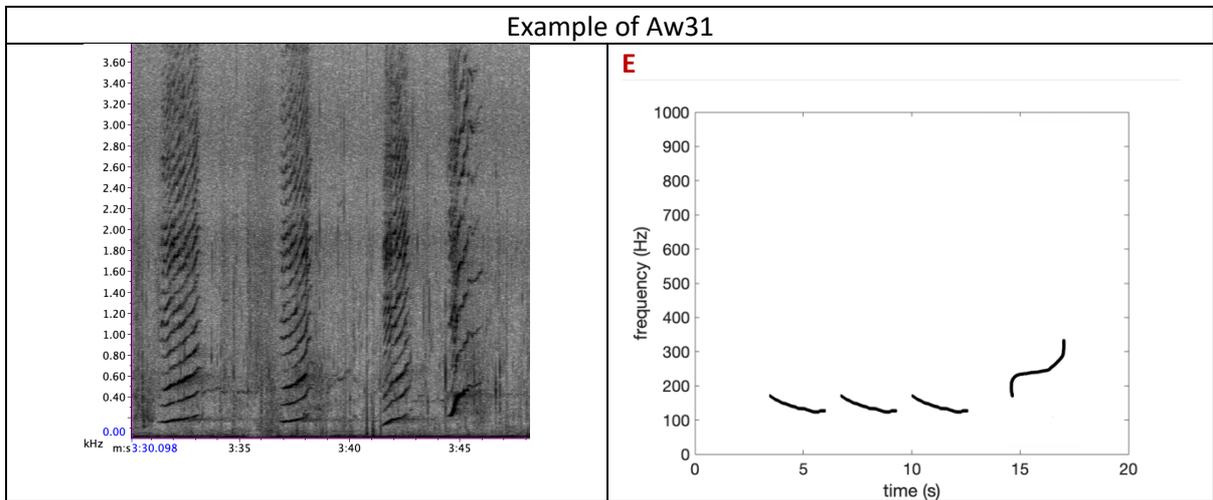
Type Ax

Combination of units CT1, CT16, CT13b

Example of Ax211
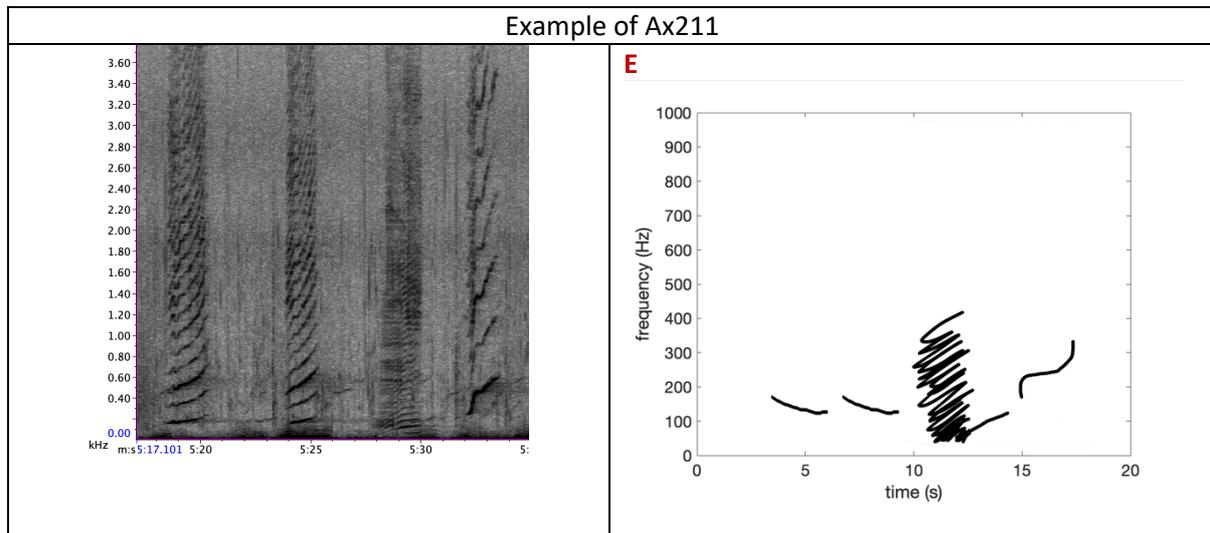
Type Ay

Combination of units CT1, CT15, CT10

Example of Ay211
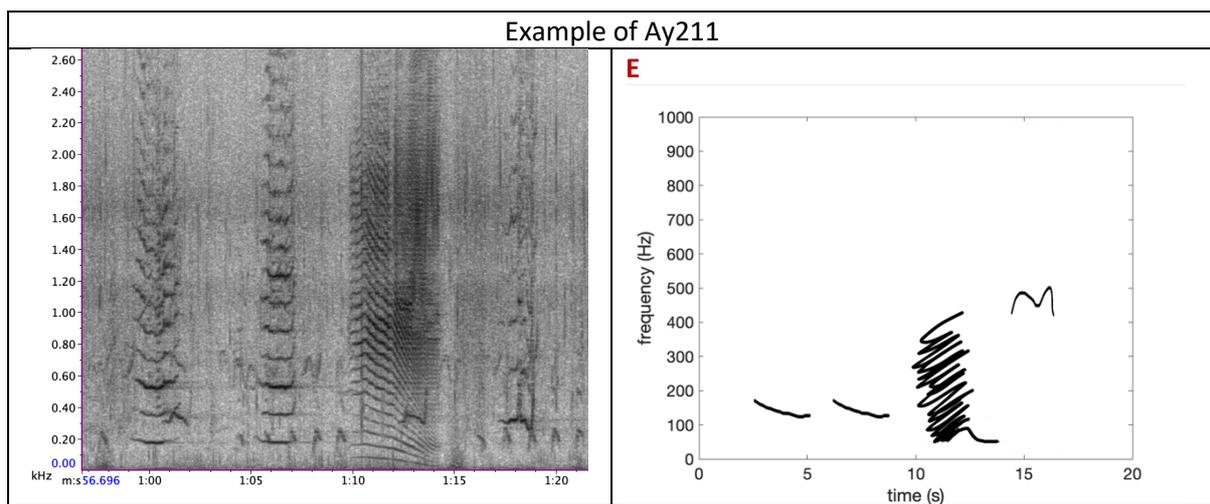
Type Ba

The combination of units CT6 & CT5b

Example of Ba17

ASSO, B
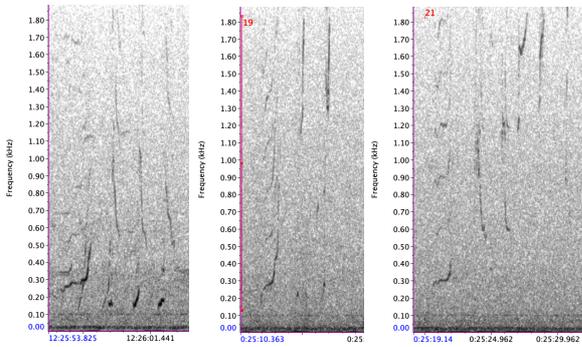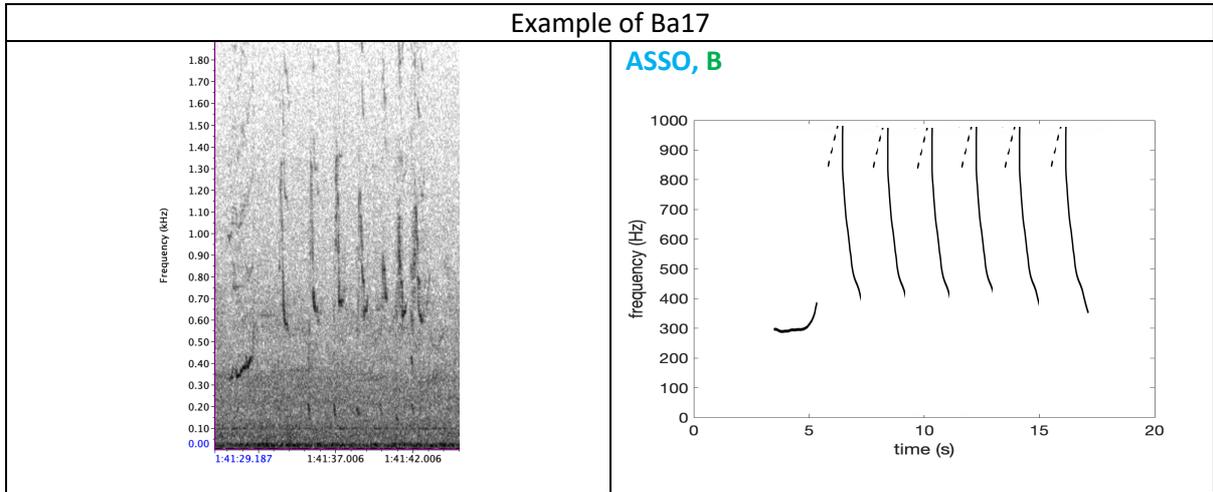
Type Bb

Combination of units CT6 & CT4a

Example of Bb12

ASSO, B, A
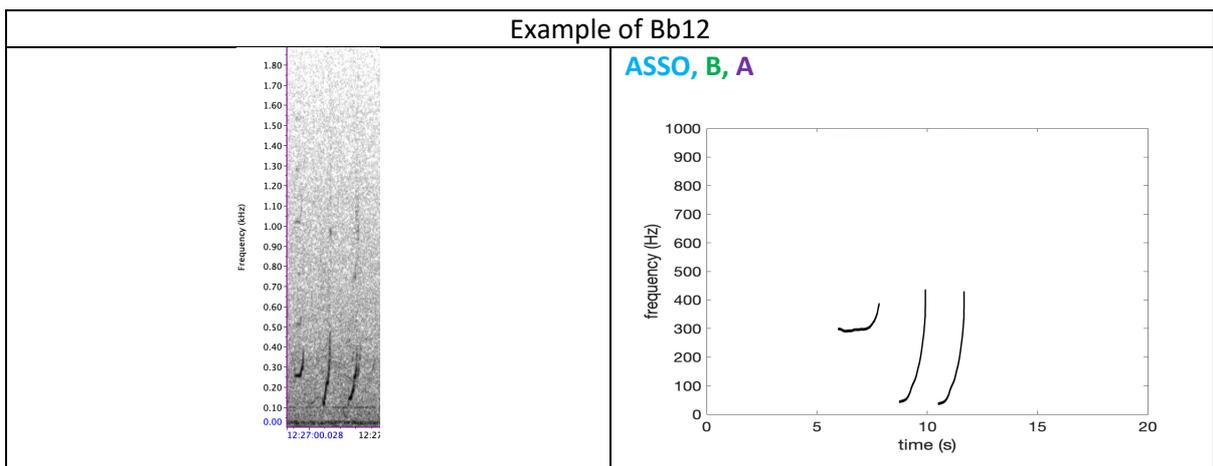
Type Bc

Combination of units CT6 & CT12

Example of Bc12
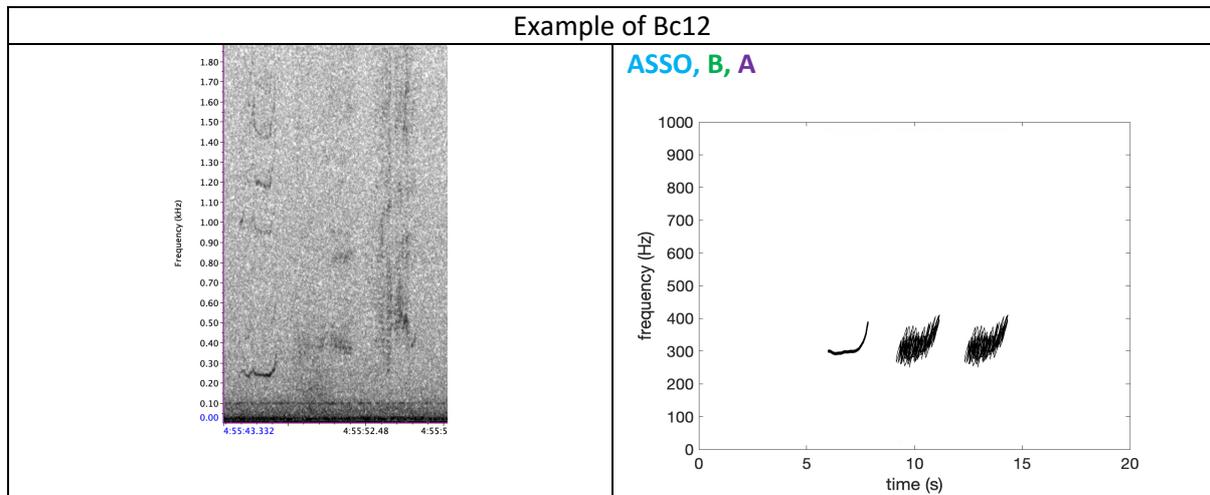
Type Bd

Combination of units CT6, CT4a, CT10 & CT4b

Example of Bd2111
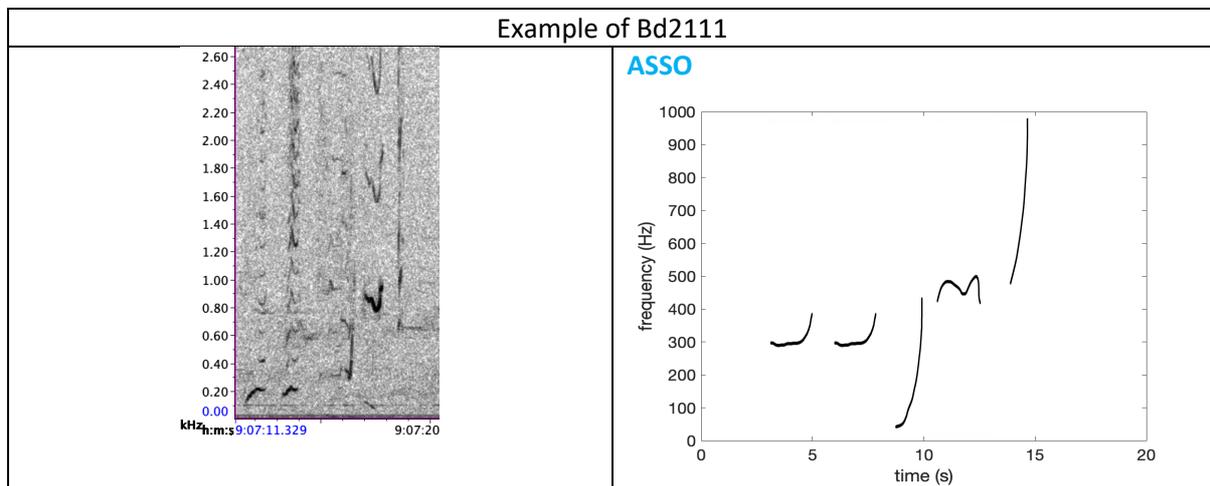
Type Be

Combination of units CT6, CT10

Example of Be11

ASSO, B
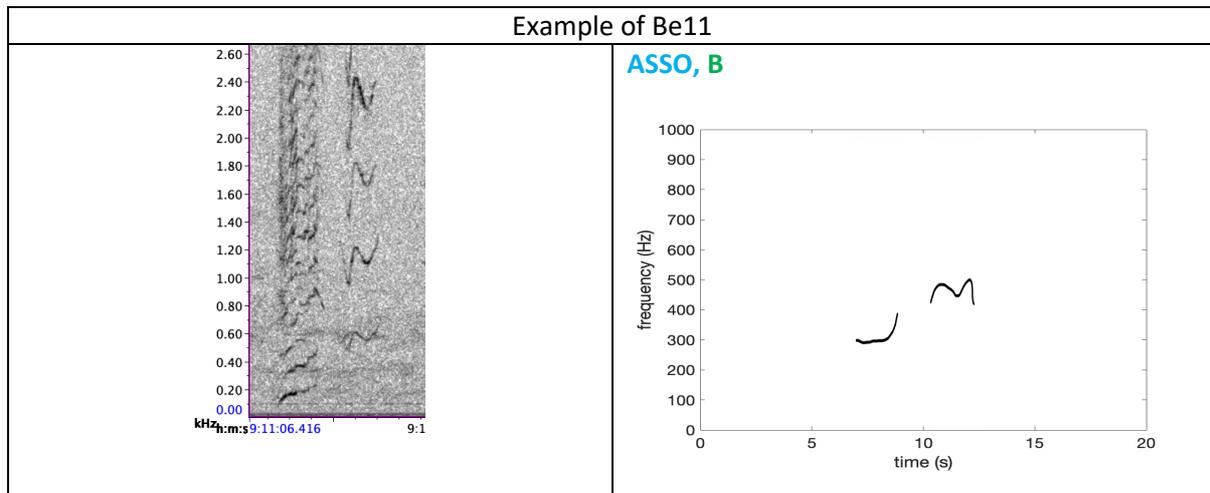
Type Bf

Combination of units CT6, CT4a, CT10

Example of Bf211

ASSO
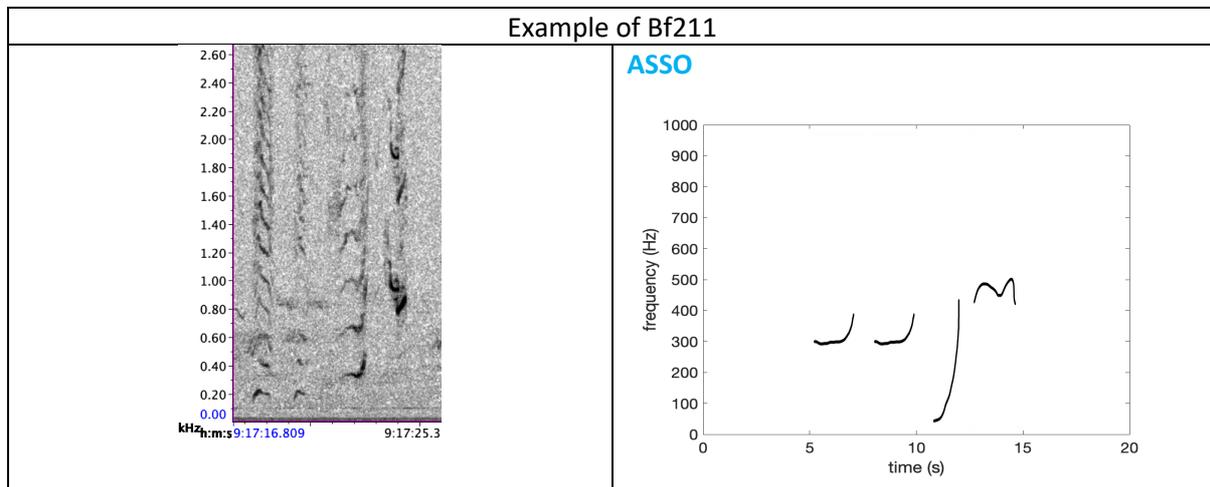
Type Bg

Combination of units CT6, CT10, CT4b

Example of Bg111
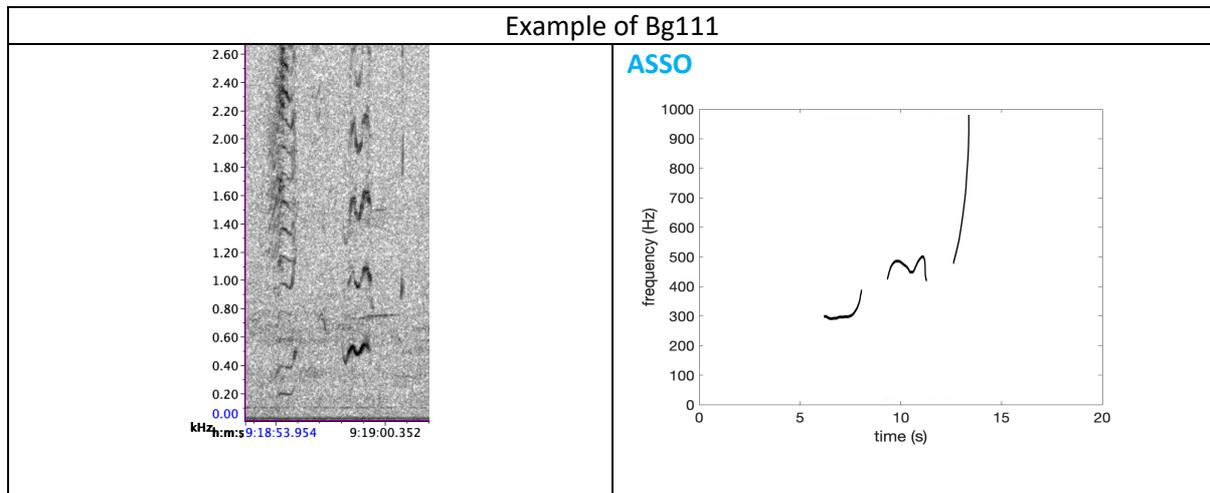
Type Bh

Combination of units CT6, CT1

Example of Bh13
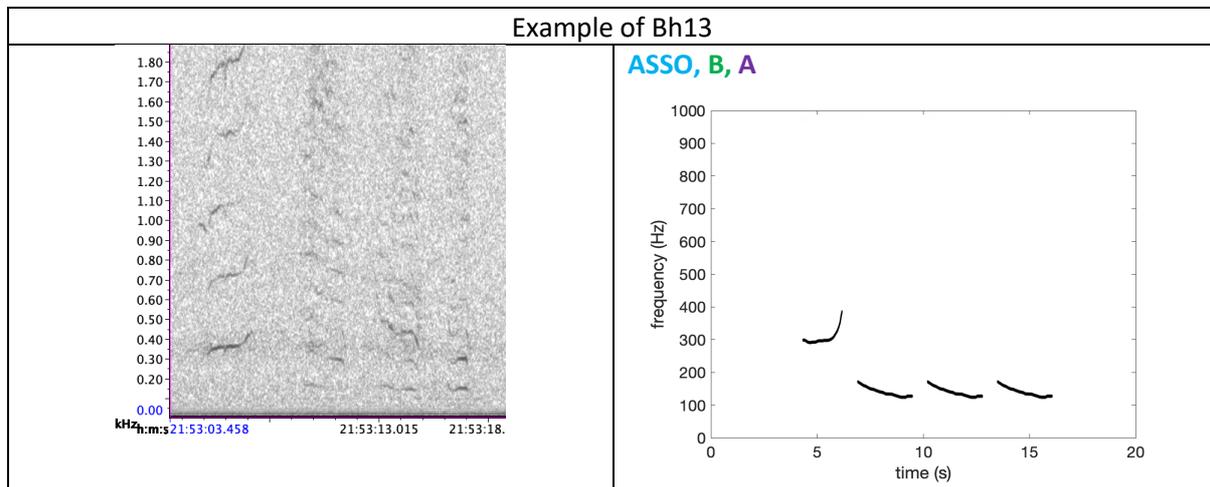
Type Bi

Combination of units CT6, CT1, CT4a

Example of Bi143

ASSO, B, A
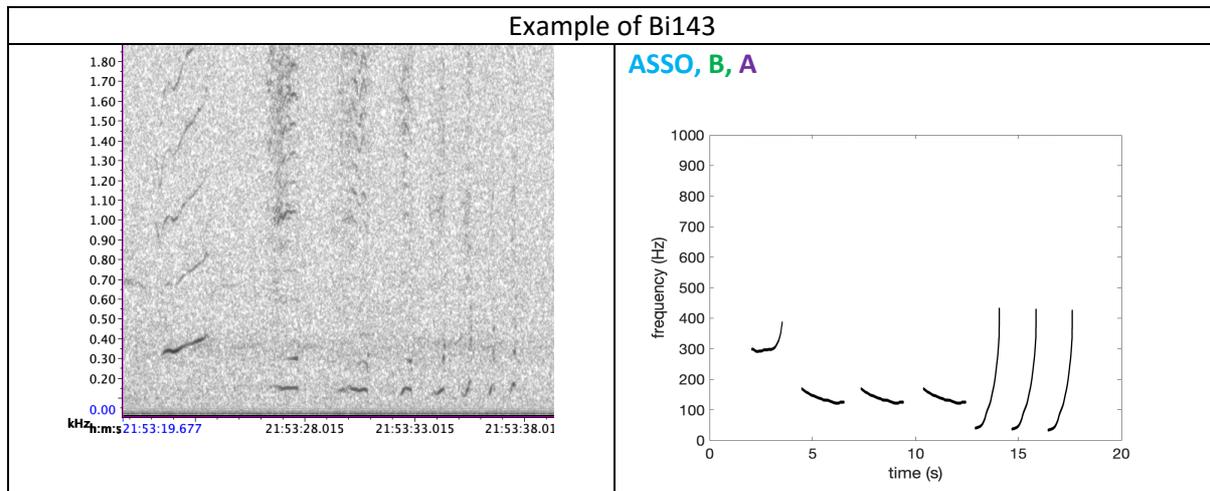
Type Bj

Combination of units CT6, CT12, CT4a

Example of Bj123

ASSO, A
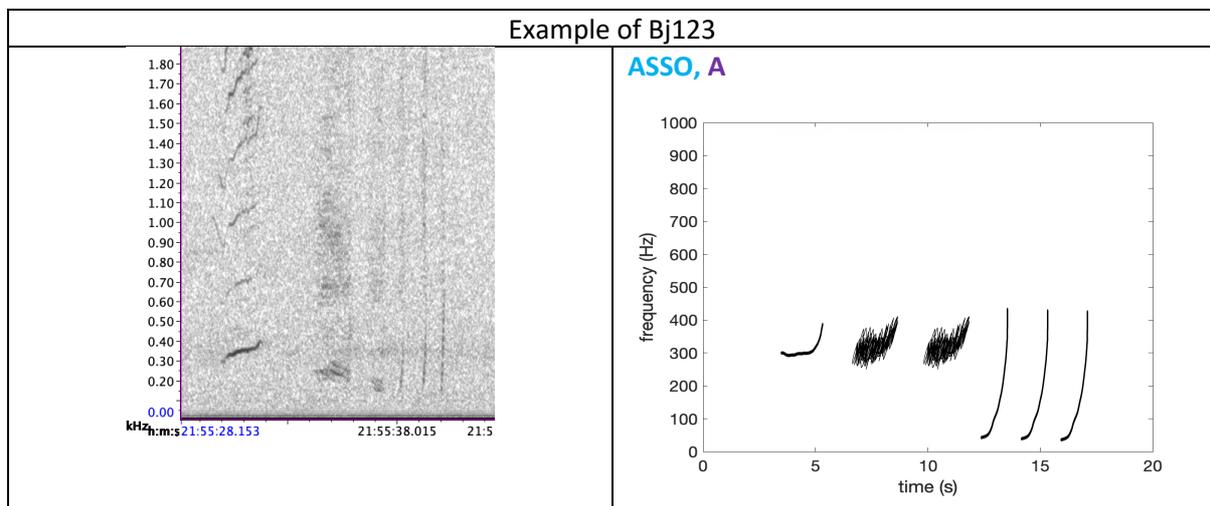
Type Bk

Combination of units CT6, CT18

Example of Bk15

ASSO, B, A
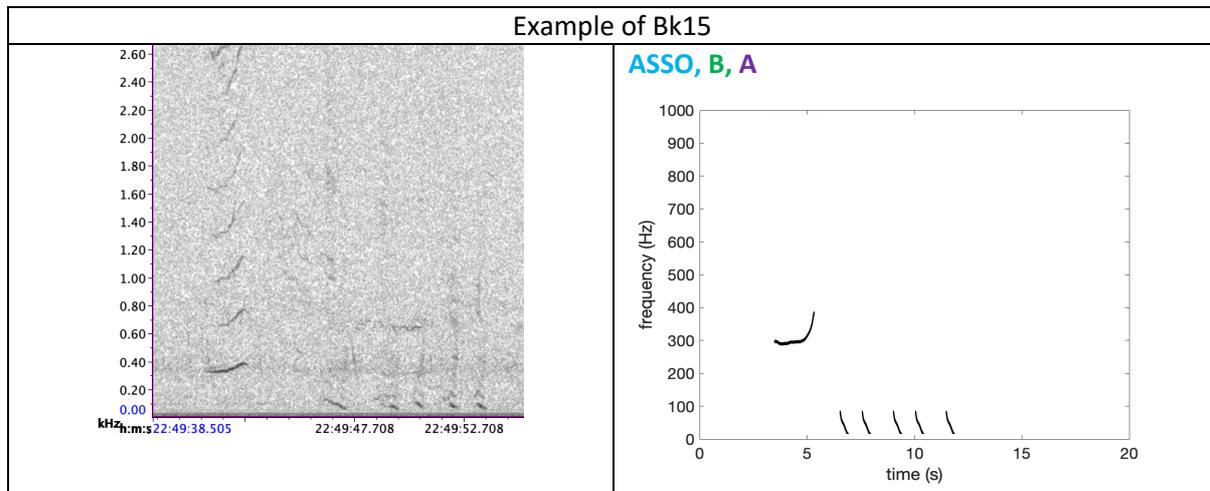
Type Bl

Combination of units CT6, CT5a, CT10

Example of Bk15

B
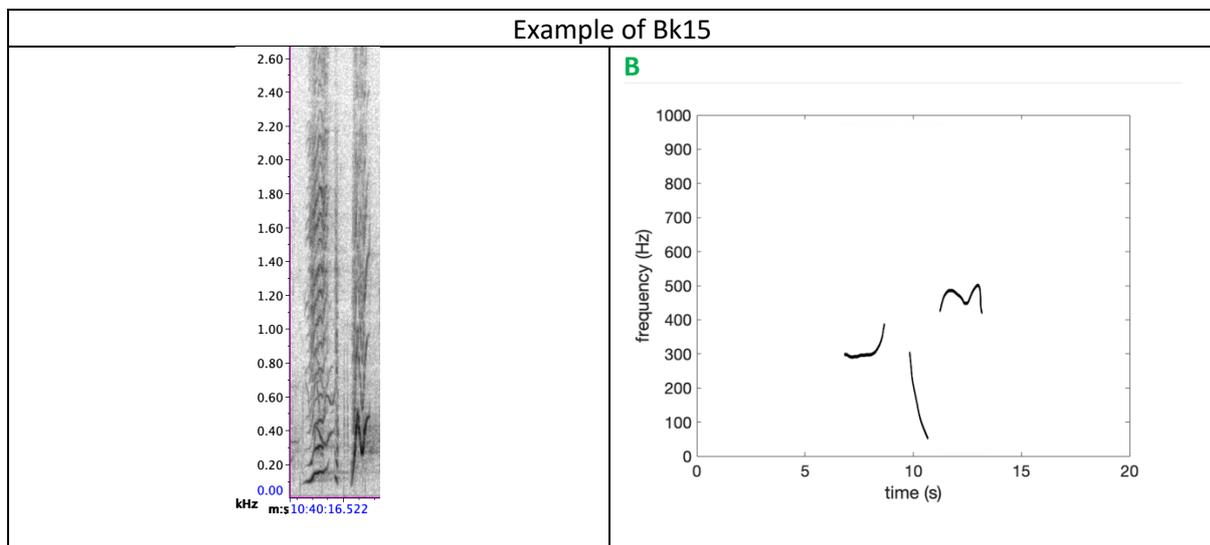
Type Bm

Combination of units CT6, CT7

Example of Bm13

B, A
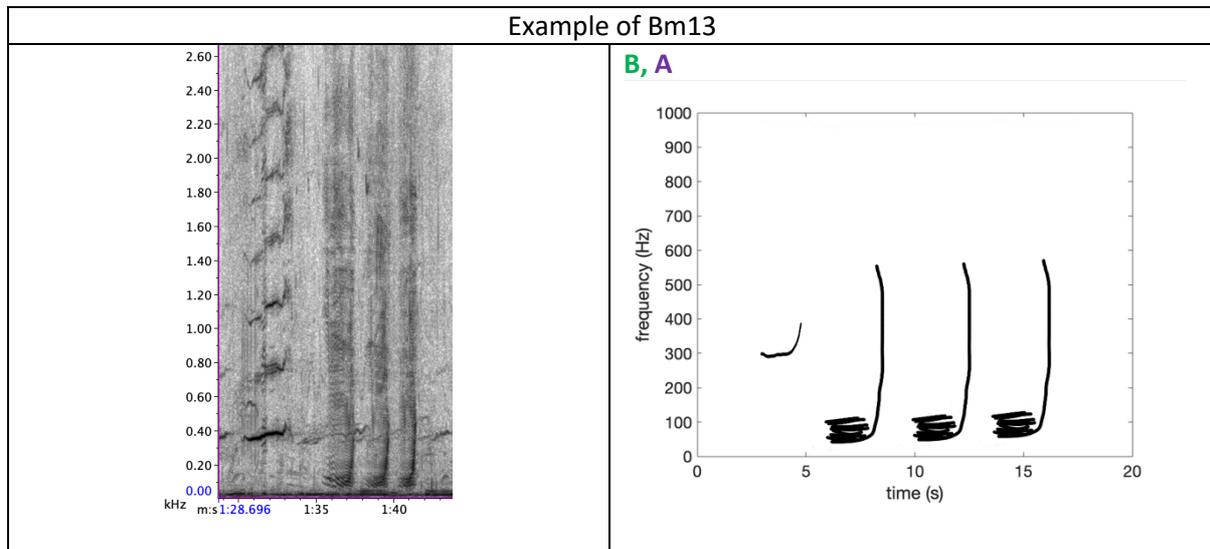
Type Bn

Combination of units CT6, CT19

Example of Bn12

B
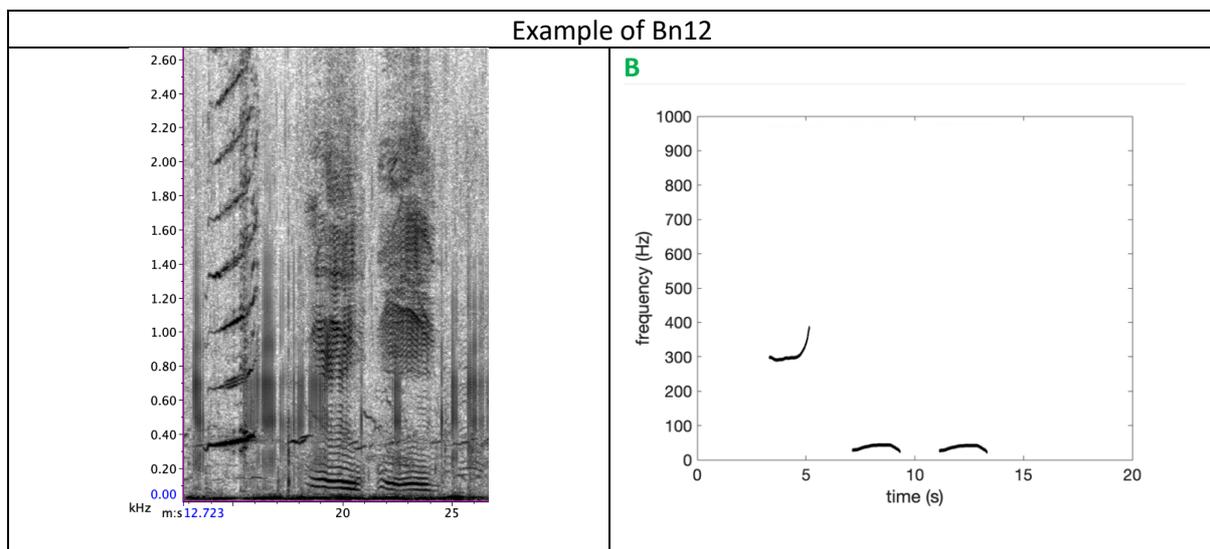
Type Bo

Combination of units CT6, CT8

Example of Bo14
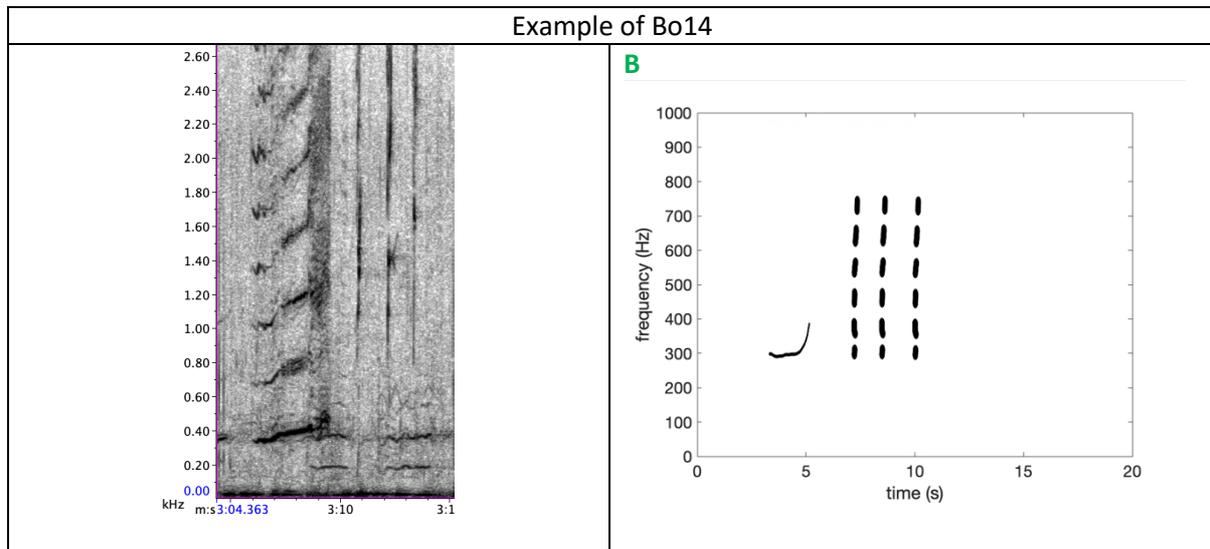
Type Bp

Combination of units CT6, CT8, CT10

Example of Bp171
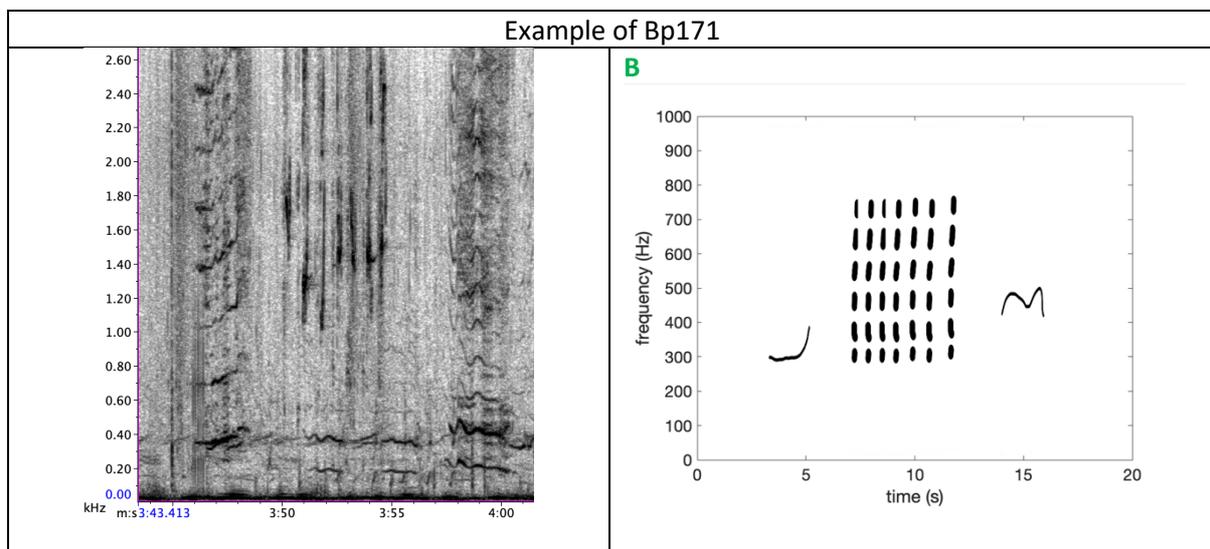
Type Bq

Combination of units CT6, CT4a, CT10, CT5b

Example of Bq1111
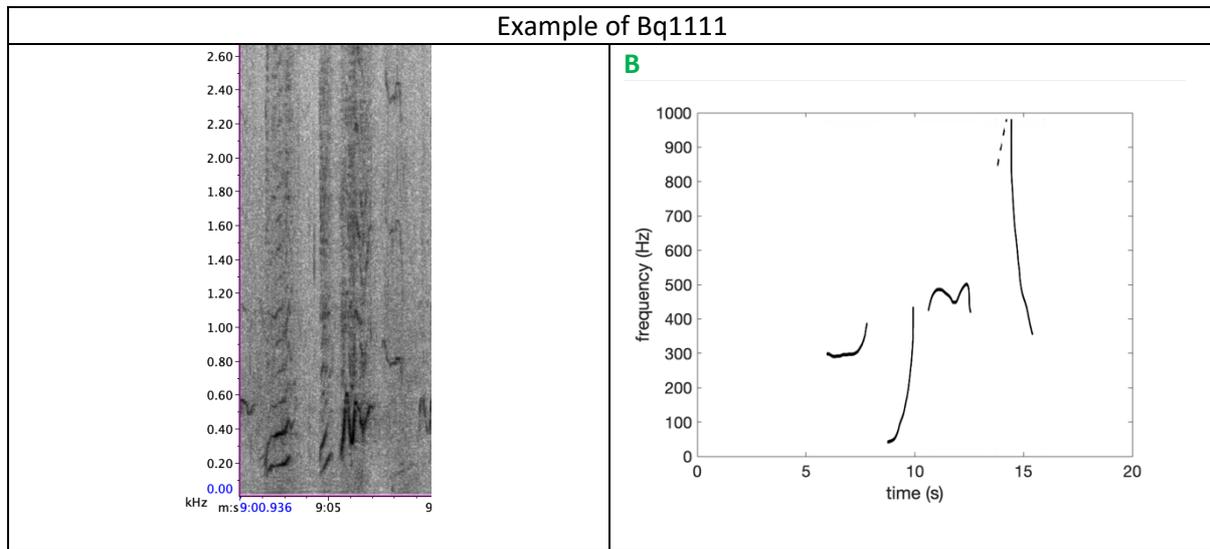
Type Ca

Combination of units CT3 & CT5b

Example of Ca13
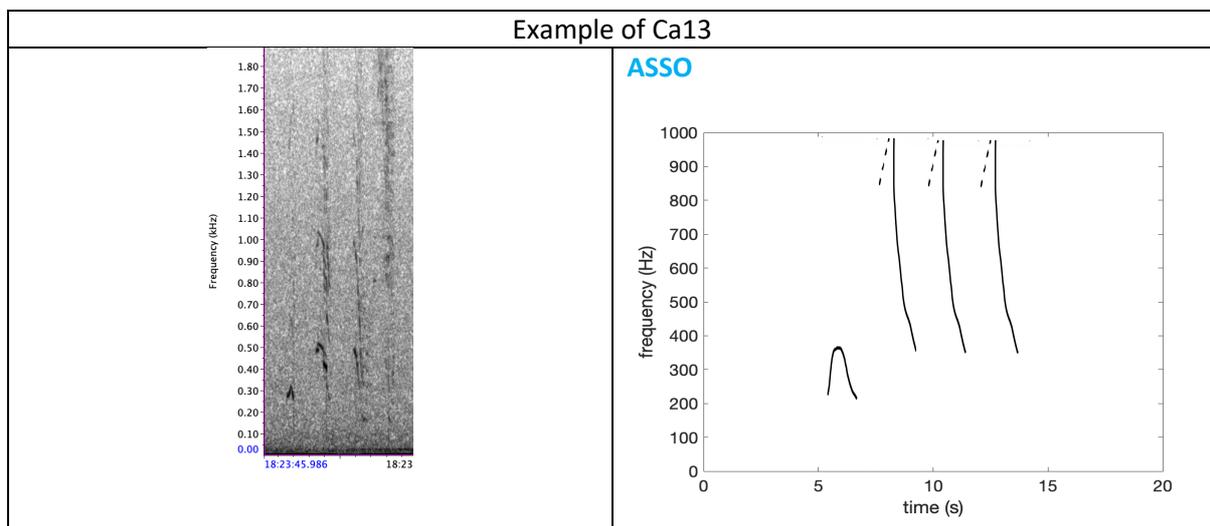
Type Cb

Combination of units CT3, CT18

Example of Cb11
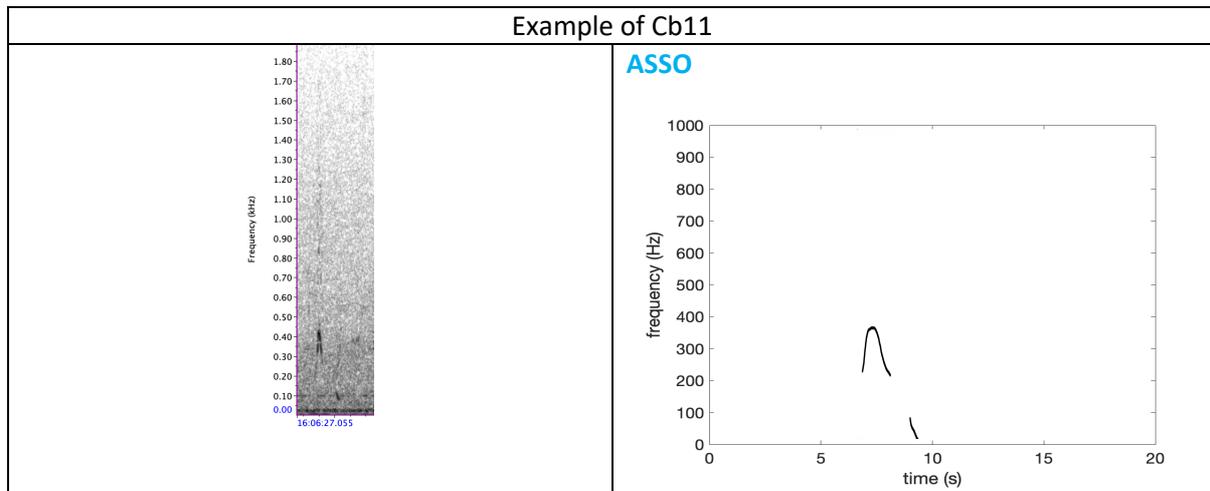
Type Cc

Combination of units CT3 and CT10

Example of Cc12
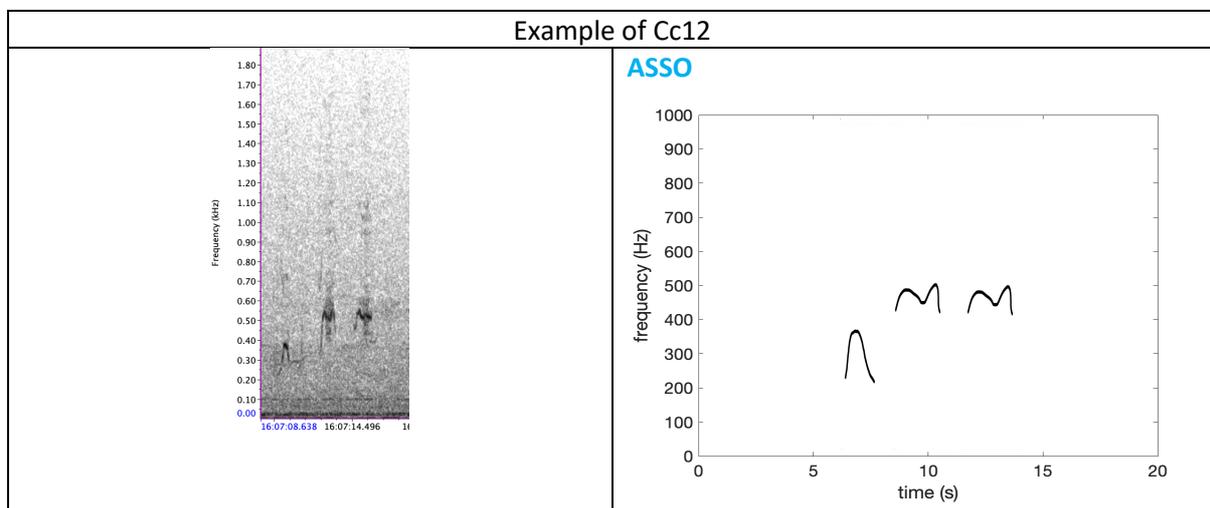
Type Cd

Combination of units CT3, CT18, CT10

Example of Cd111
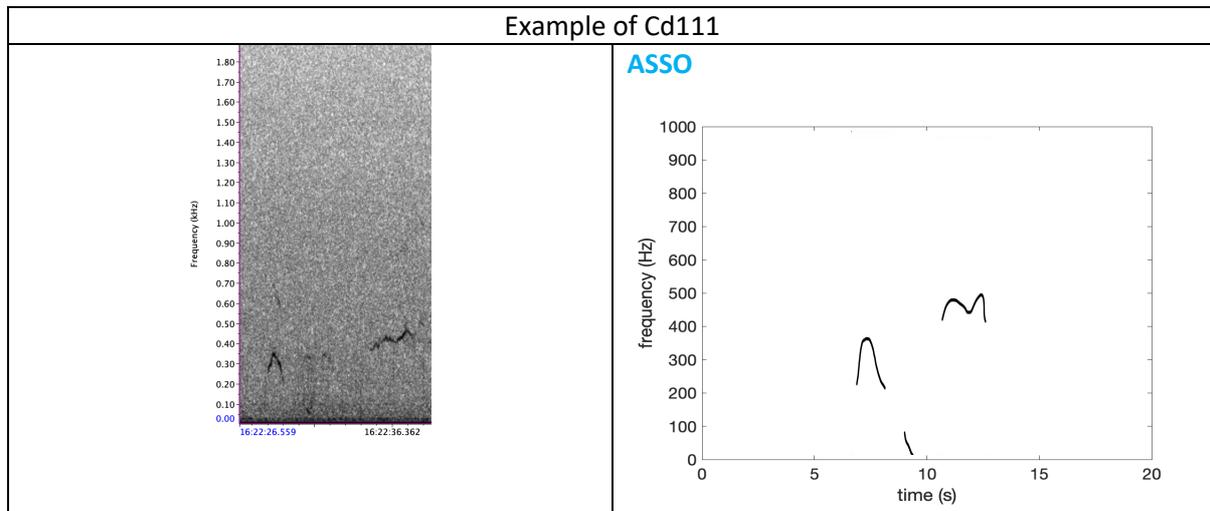
Type Ce

Combination of units CT3, CT10, CT18

Example of Ce111
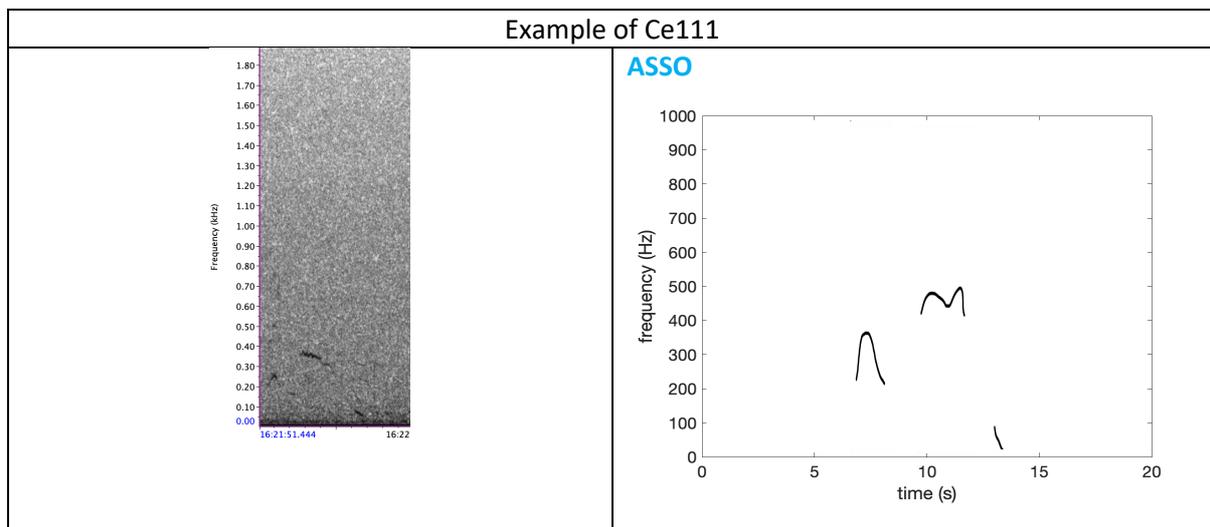
Type Cf

Combination of units CT3, CT10, CT5b

Example of Cf115
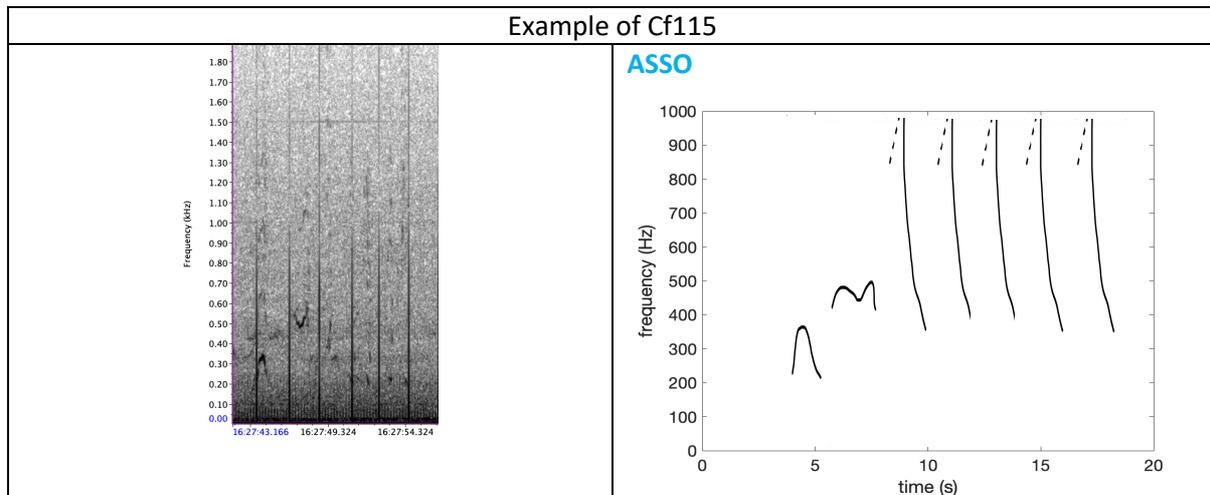
Type Cg

Combination of units CT3, CT10

Example of Cg32
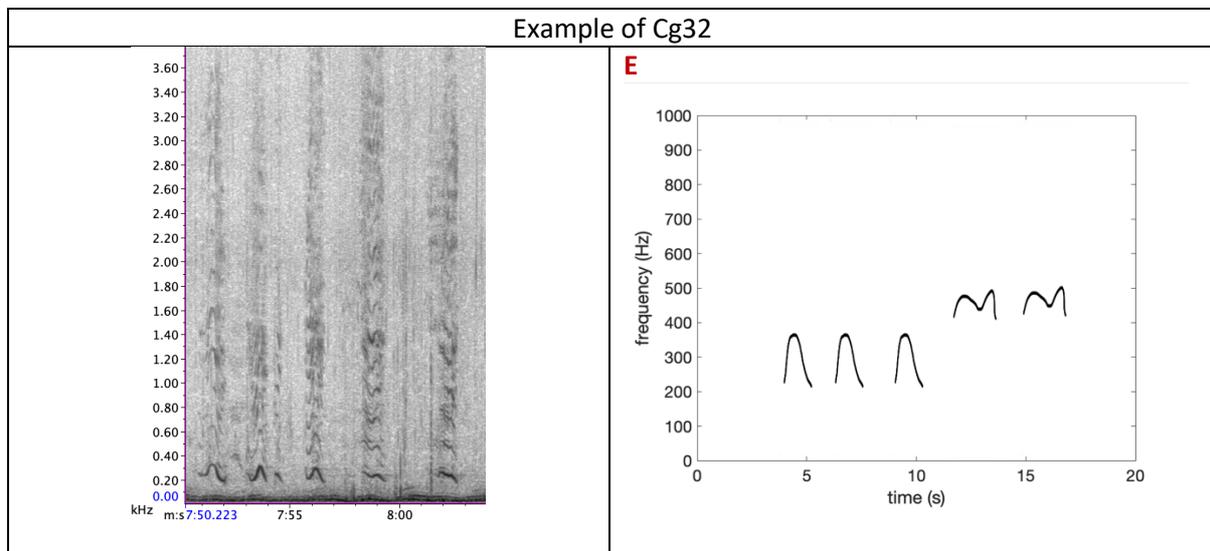
Type Da

Combination of units CT12 and CT18

Example of Da12
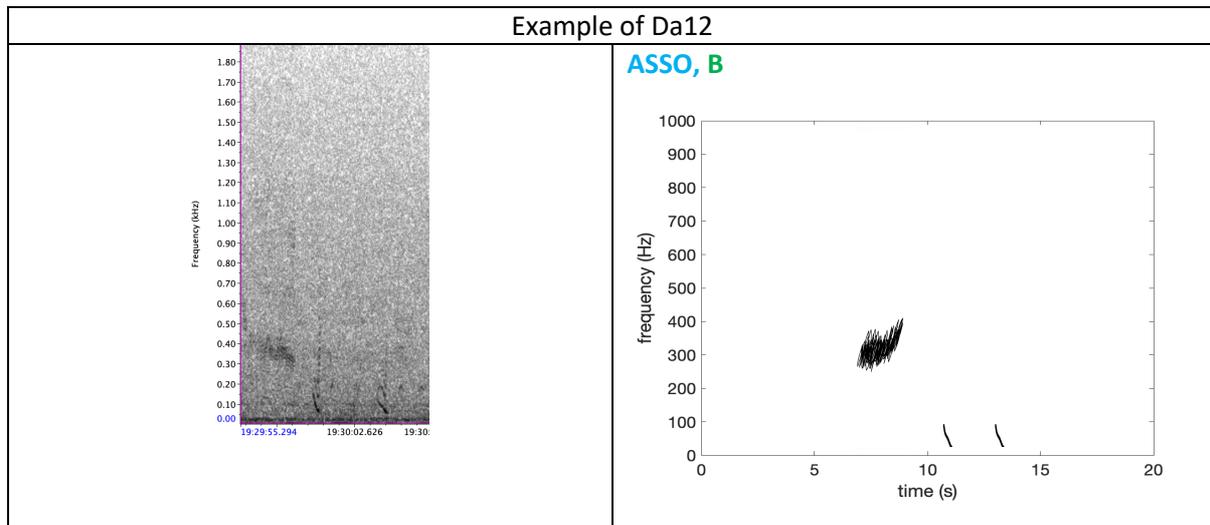
Type Db

Combination of units CT12 and CT5b

Example of Db13
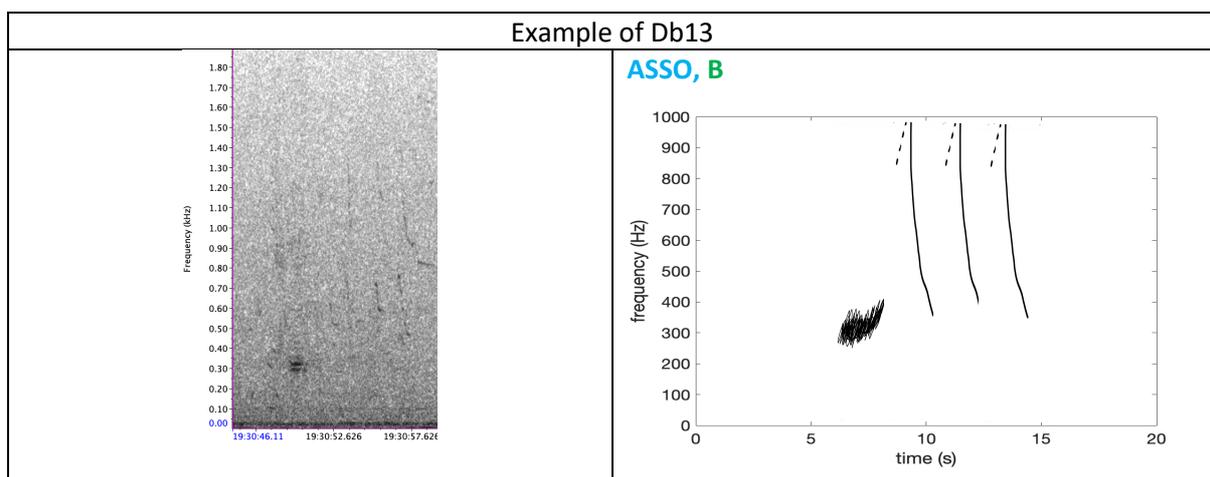
Type Dc

Combination of units CT12, CT4a

Example of Dc13
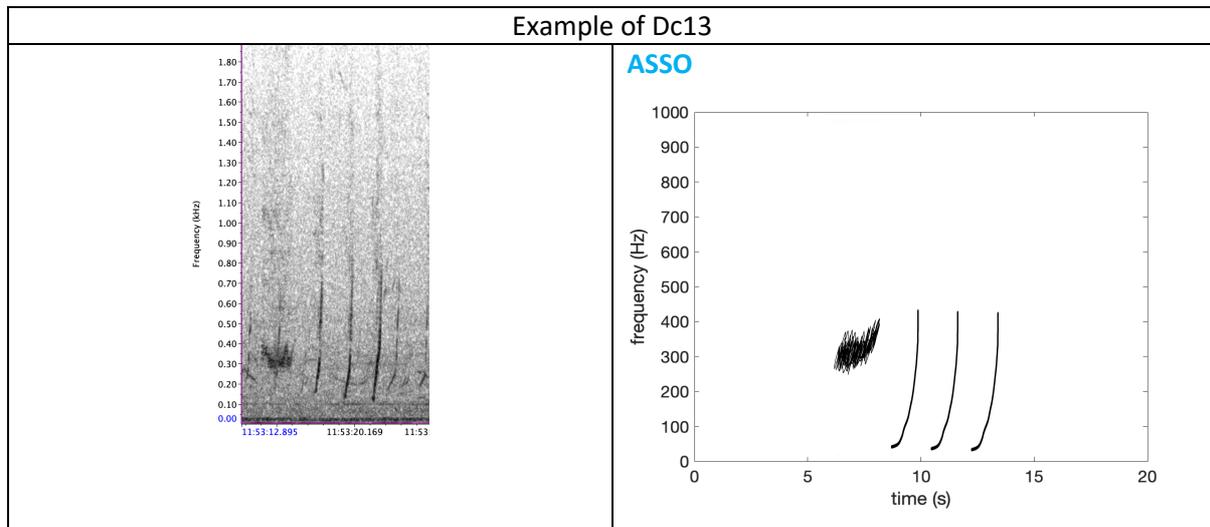
Type Dd

Combination of units CT12, CT1, CT4a

Example of Dd112
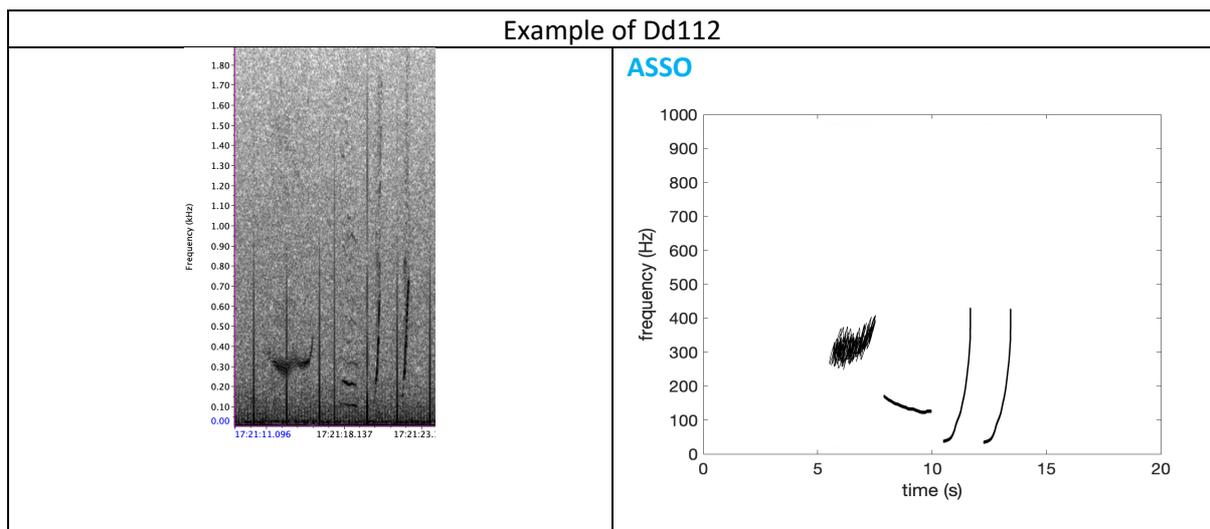
Type De

Combination of units CT12, CT18, CT5b

Example of De116

ASSO
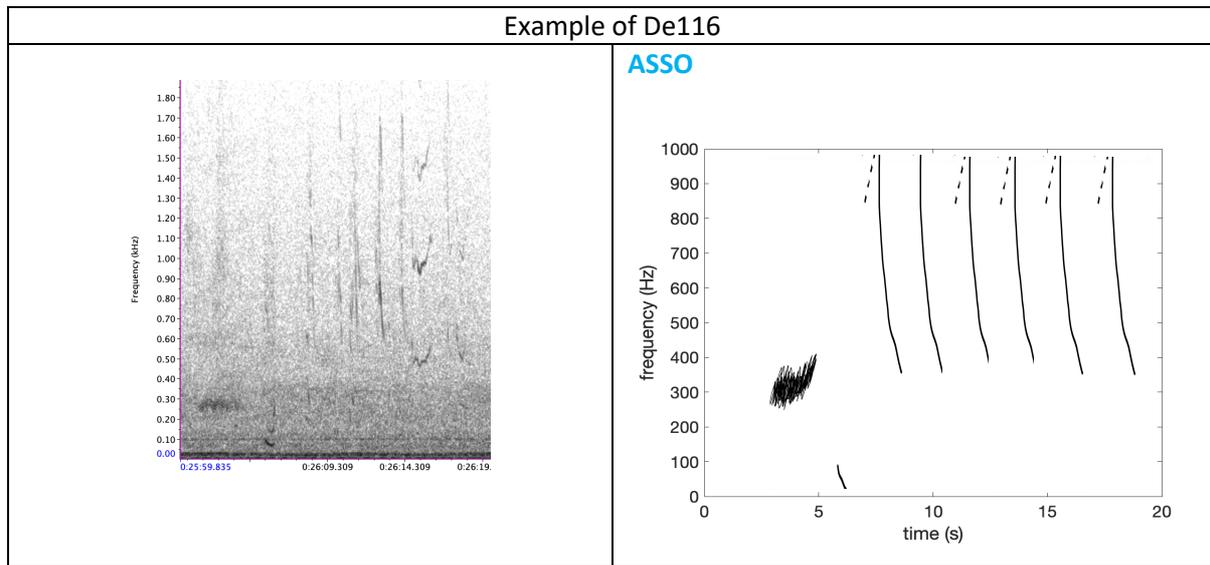
Type Df

Combination of units CT12, CT10

Example of Df11

ASSO, B
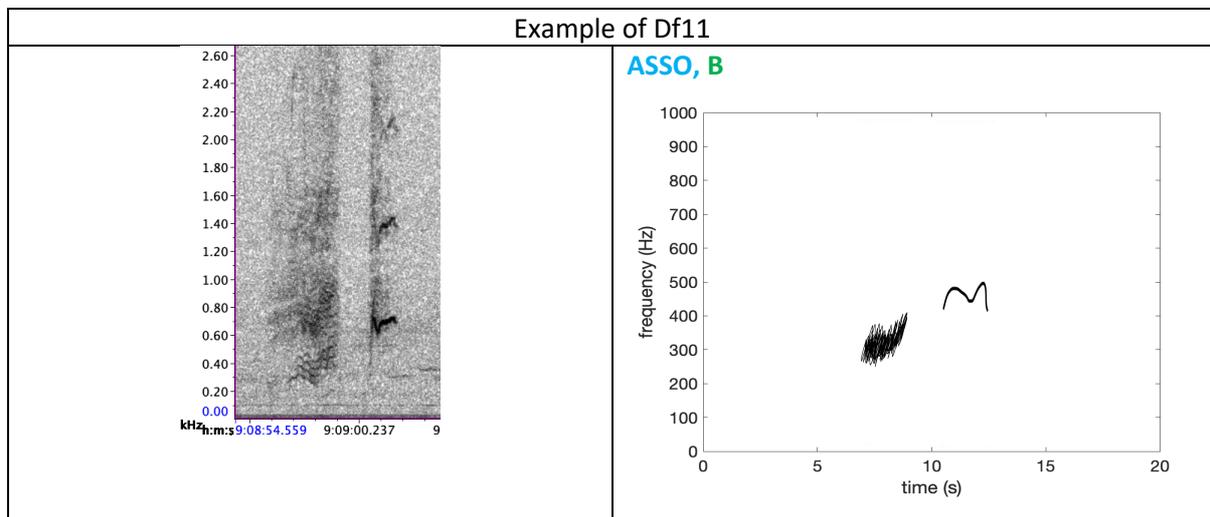
Type Dg

Combination of units CT12, CT10, CT4b

Example of Dg111

ASSO, E
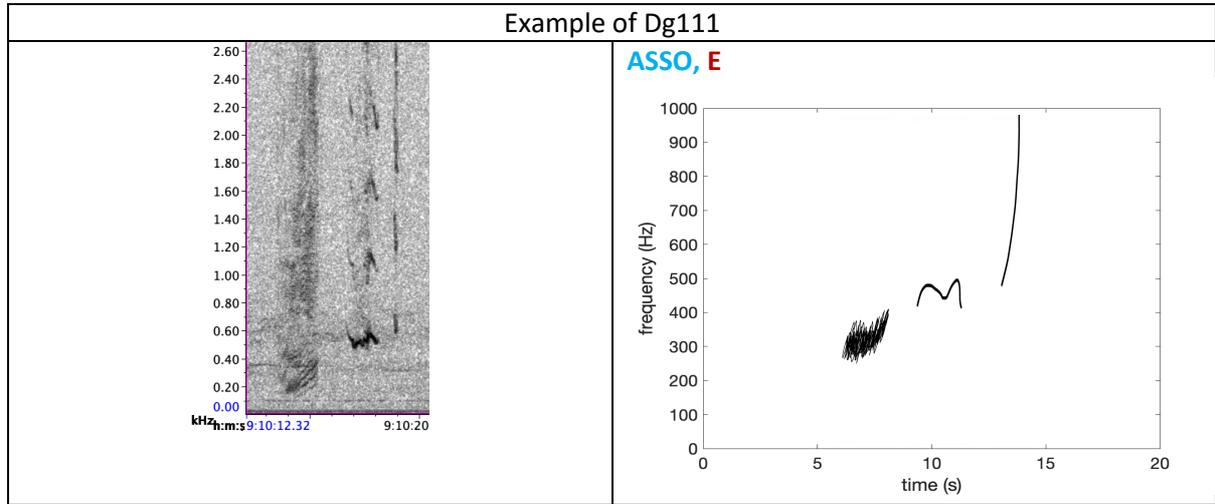
Type Dh

Combination of units CT12, CT10, CT4b, CT4a

Example of Dh1111

ASSO
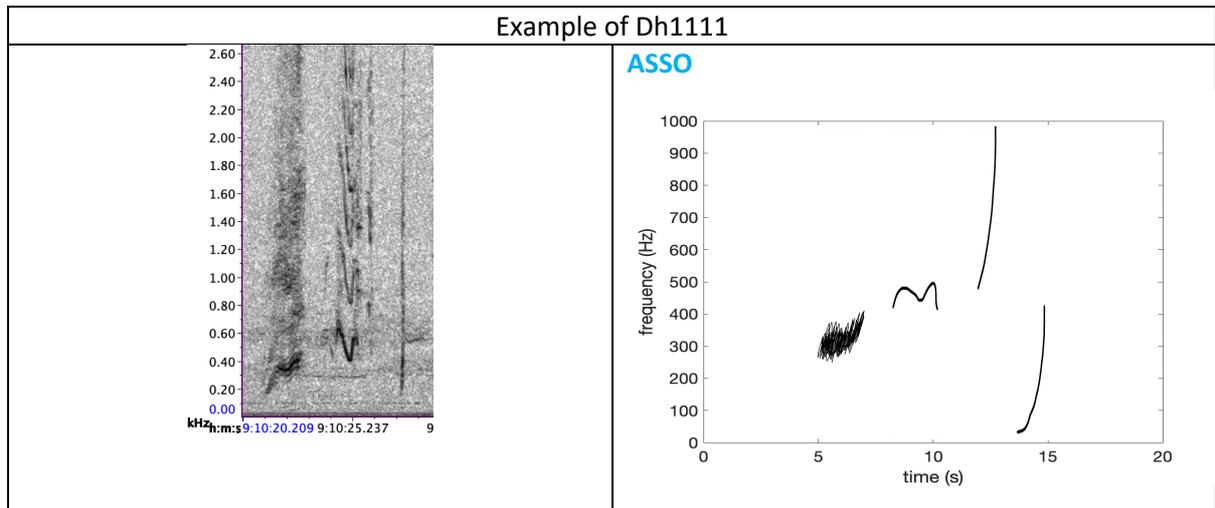
Type Di

Combination of units CT12, CT5b/a, CT8

Example of Di1115
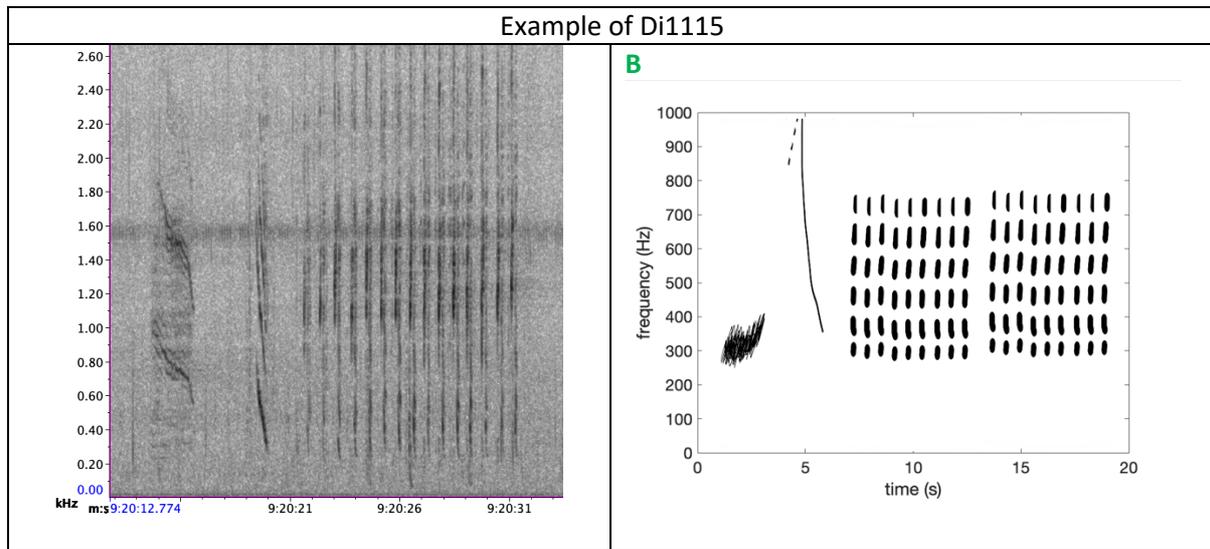
Type Dj

Combination of units CT12, CT19, CT4a

Example of Dj111111111112
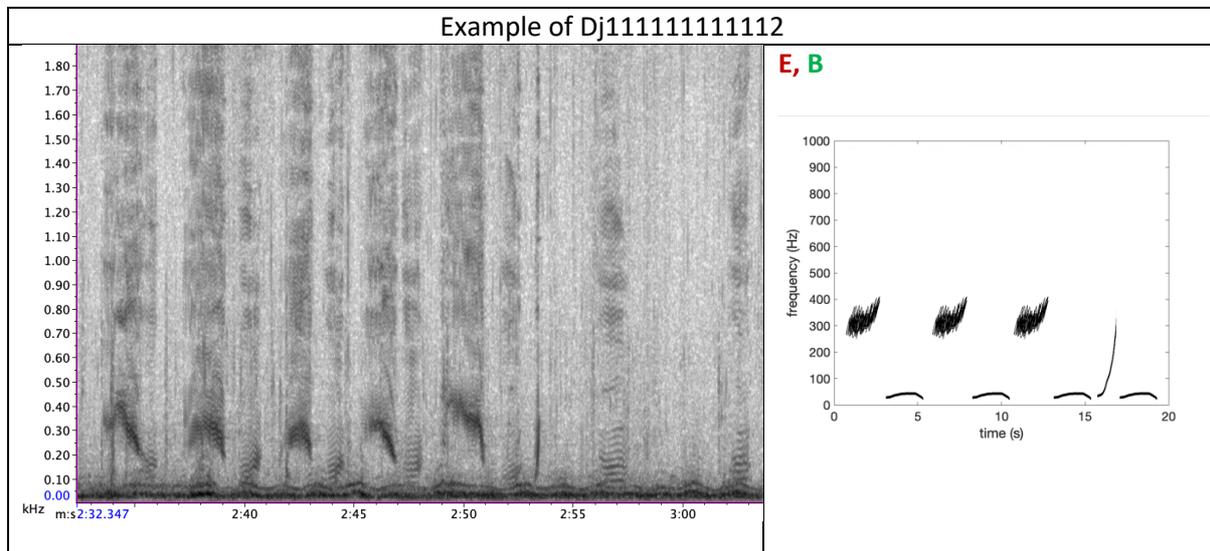
Type Dk

Combination of units CT12, CT8

Example of Dk314
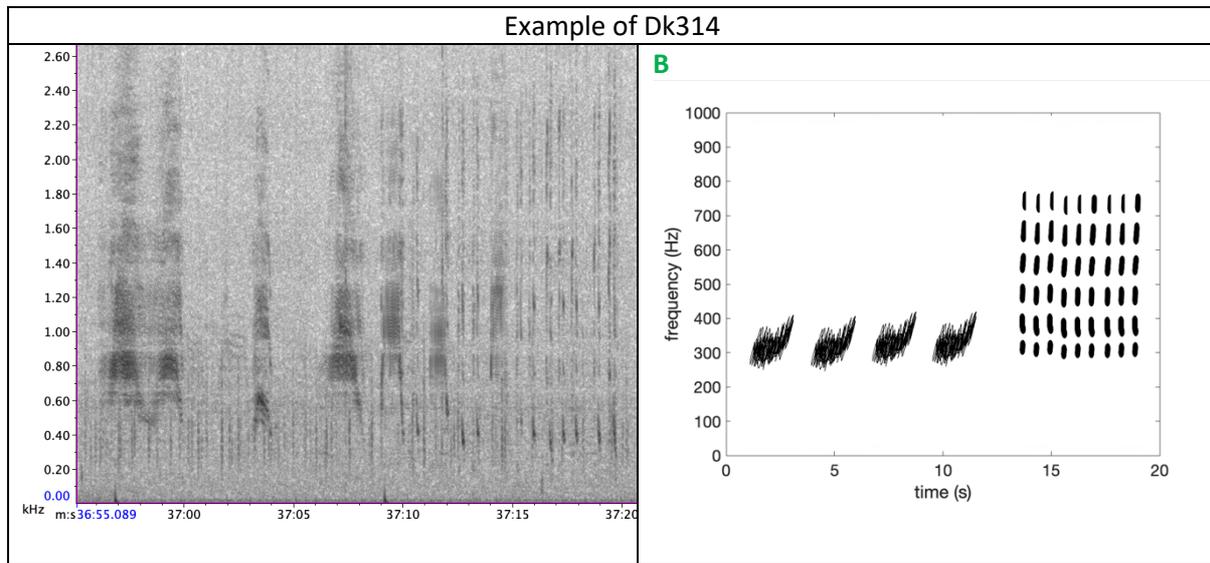
Type Dl

Combination of units CT12, CT7, CT18

Example of Dl12111
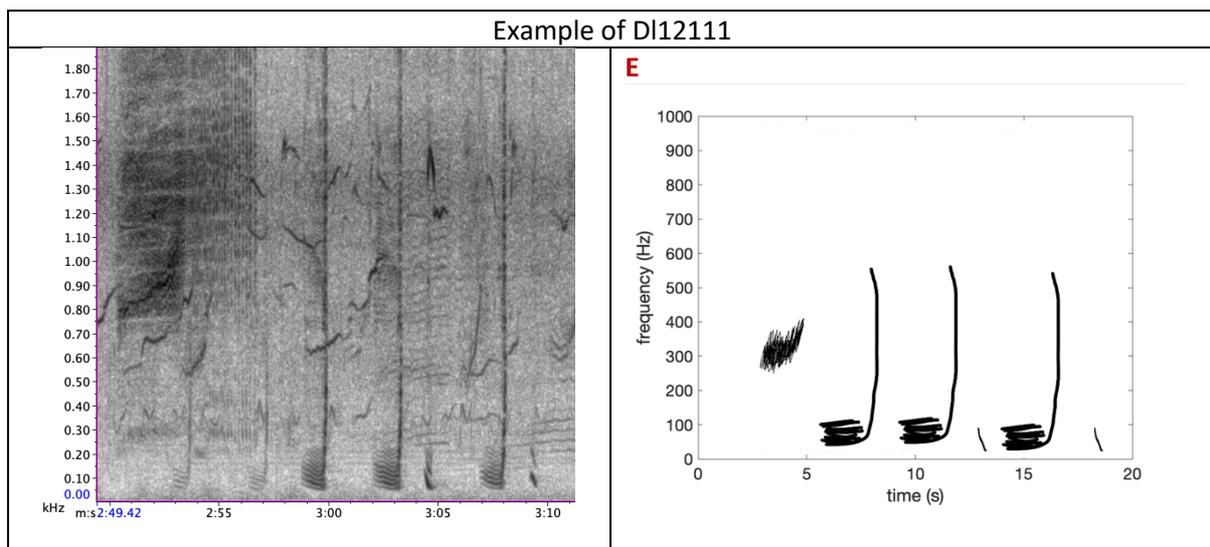
Type Dm
Combination of units CT12, CT13c

Example of Dm12
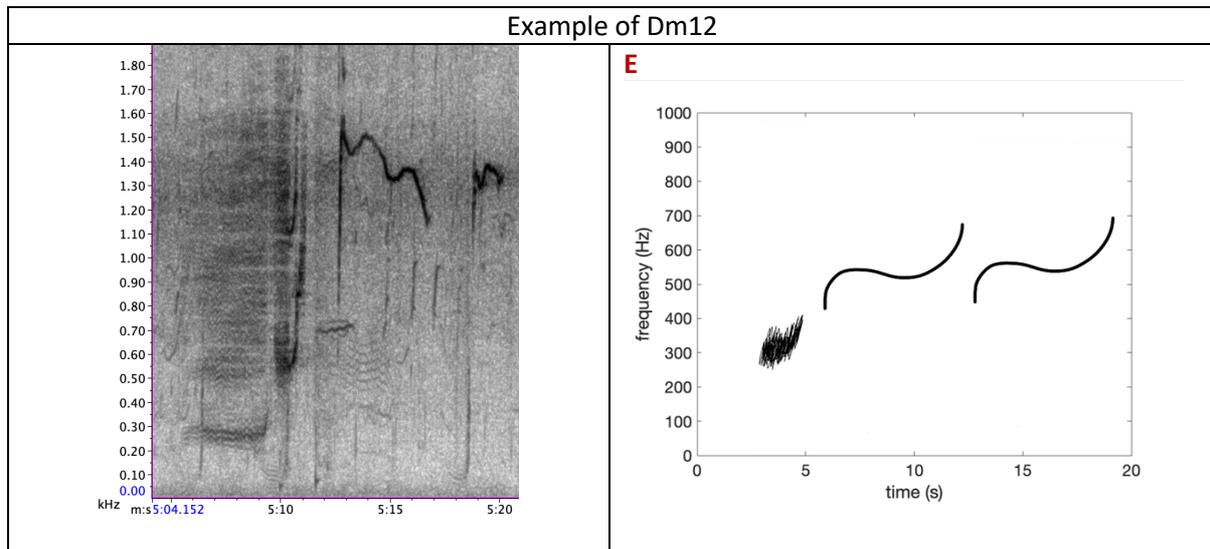
Type Dn
Combination of units CT12, CT8, CT10

Example of Dn141
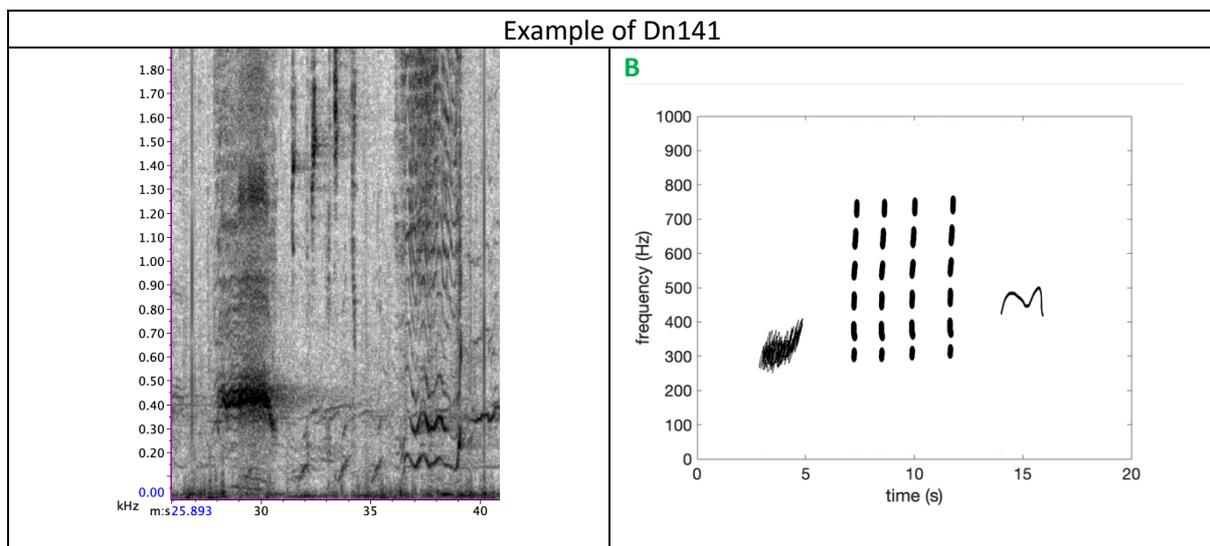
Type Do

Combination of units CT12, CT5a, CT4a

Example of Do121
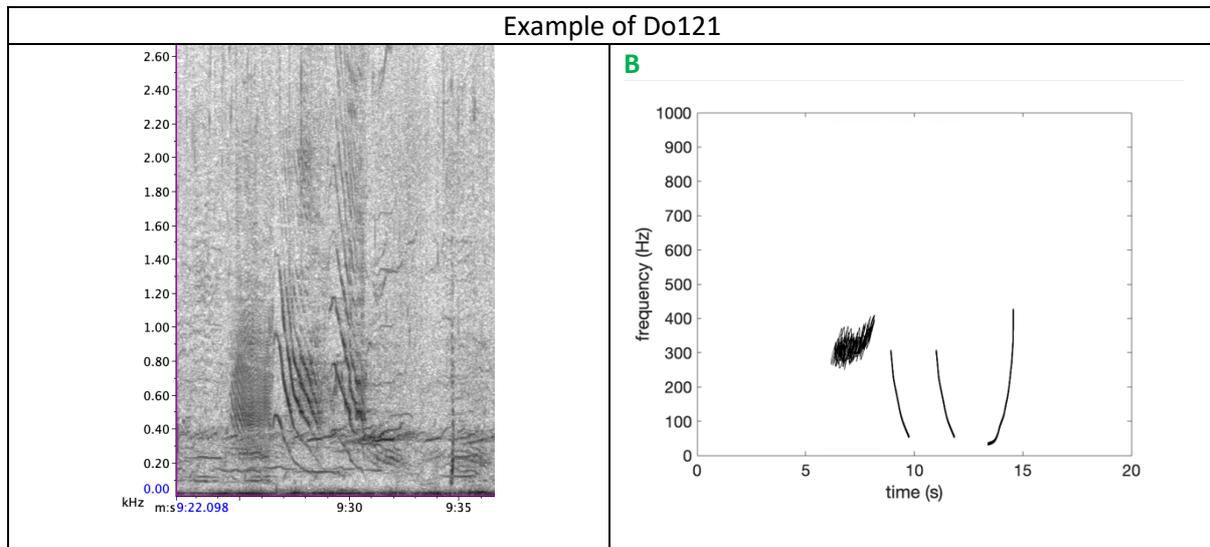
Type Ea

Combination of units CT4a, CT8

Example of Ea13
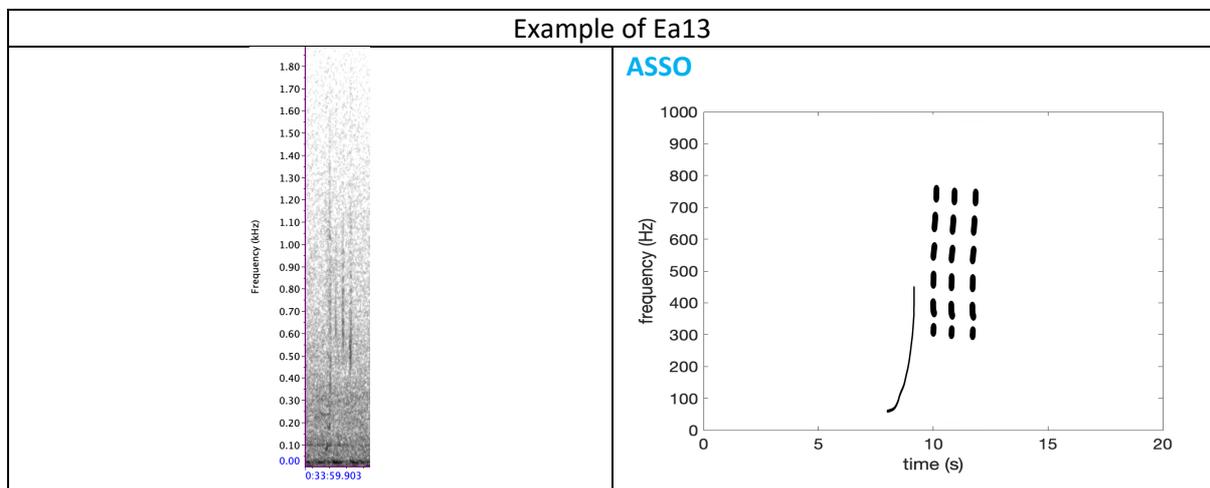
Type Eb

Combination of units CT4a, CT5b

Example of Eb28

ASSO
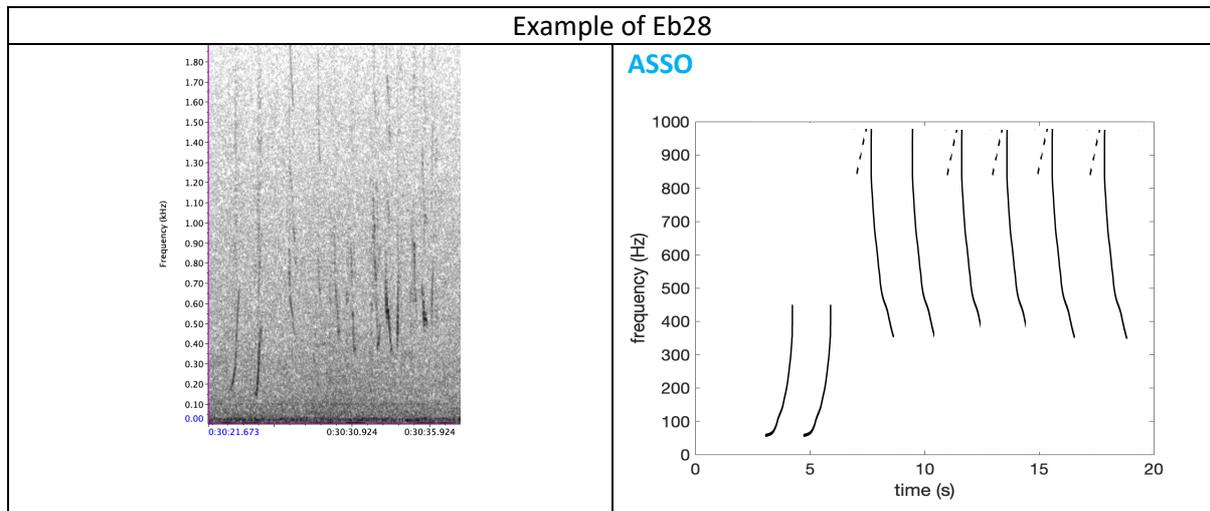
Type Ec

Combination of units CT4b, CT5b

Example of Ec24

ASSO, B, E
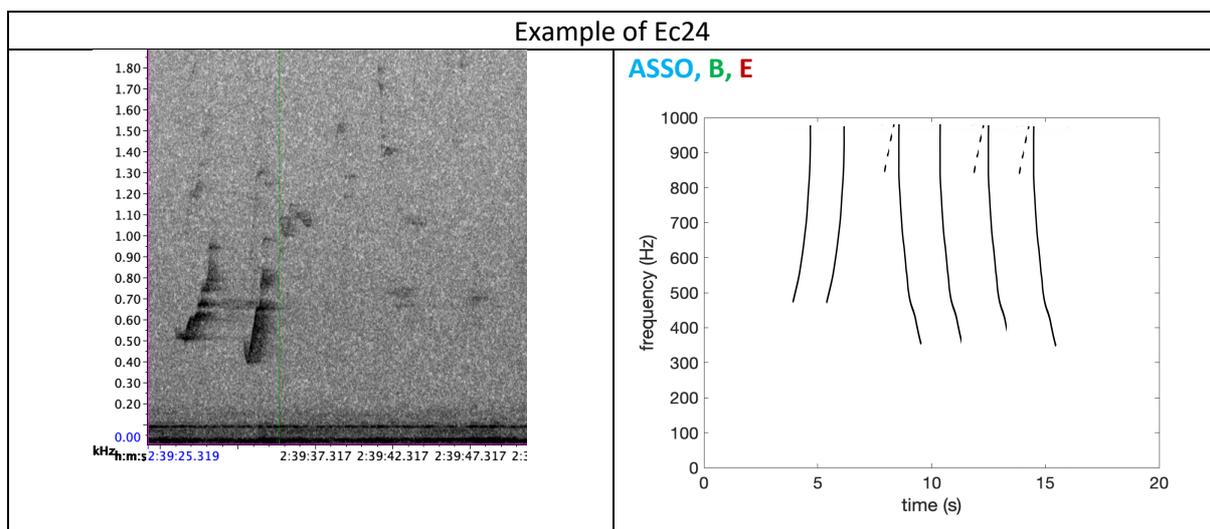
Type Ed

Combination of units CT4b, CT1

Example of Ed31

ASSO, E, B
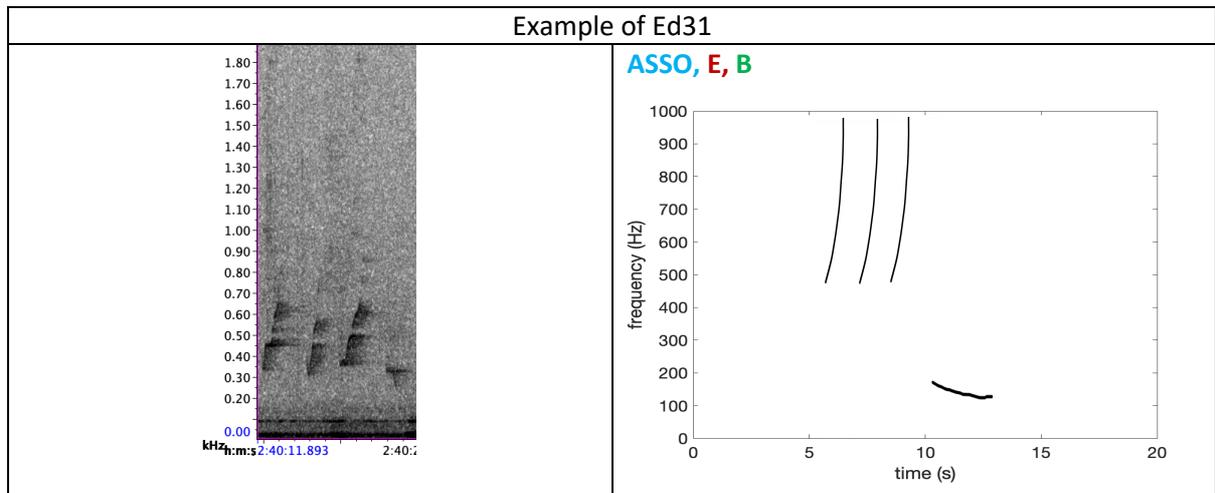
Type Ee

Combination of units CT4a, CT4b

Example of Ee11

ASSO, B
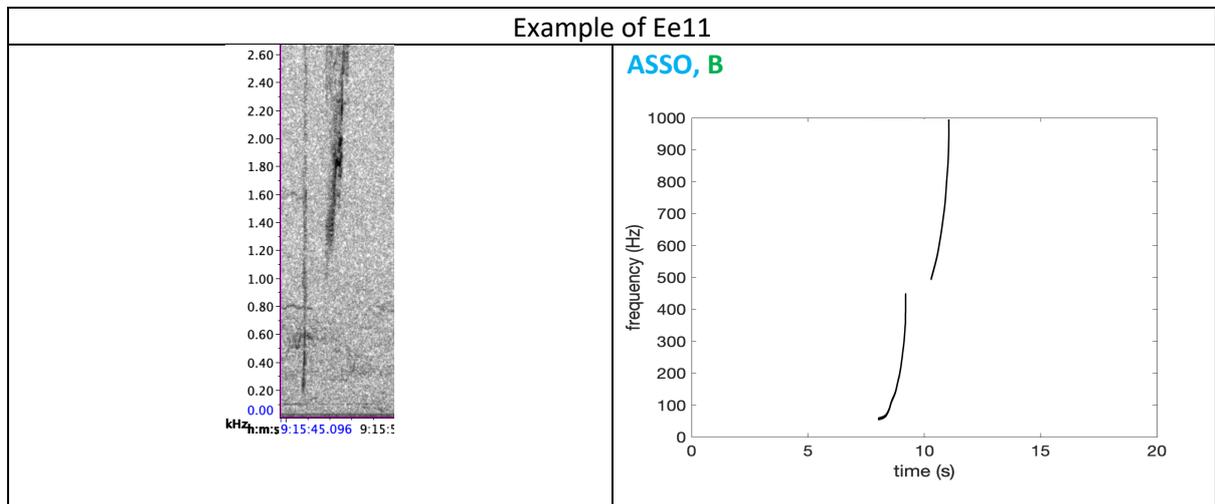
Type Ef

Combination of units CT4a, CT6

Example of Ef11

ASSO, B
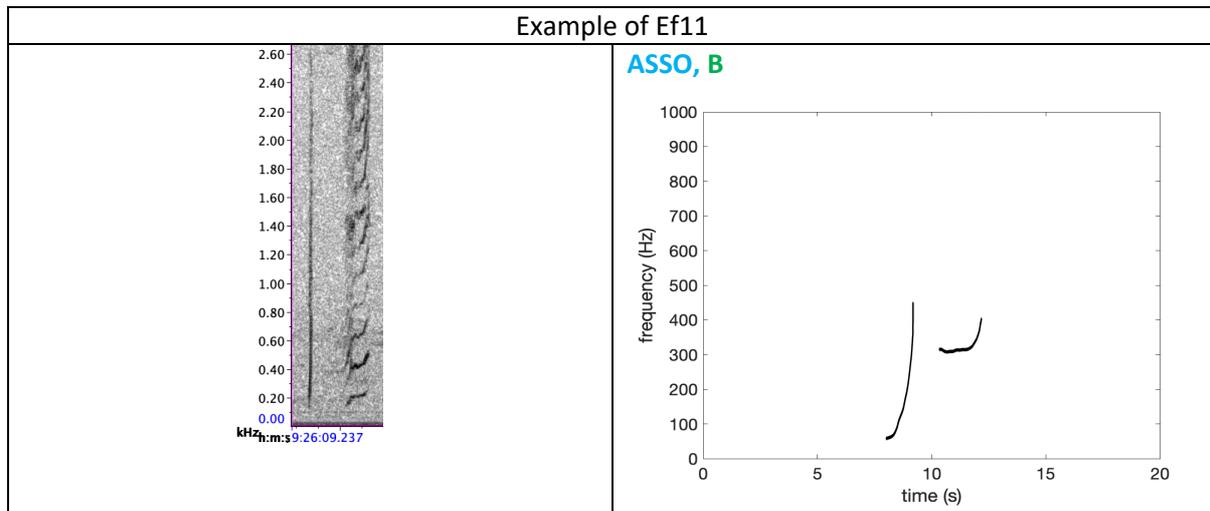
Type Eg

Combination of units CT4a, CT6, CT4b

Example of Eg111

ASSO
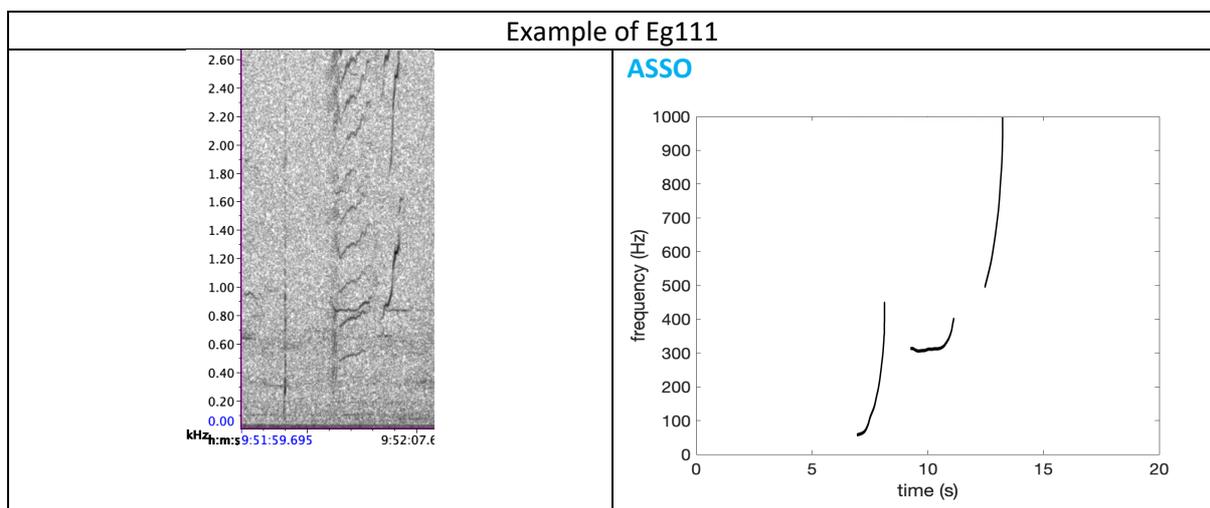
Type Eh

Combination of units CT4b, CT10

Example of Eh24
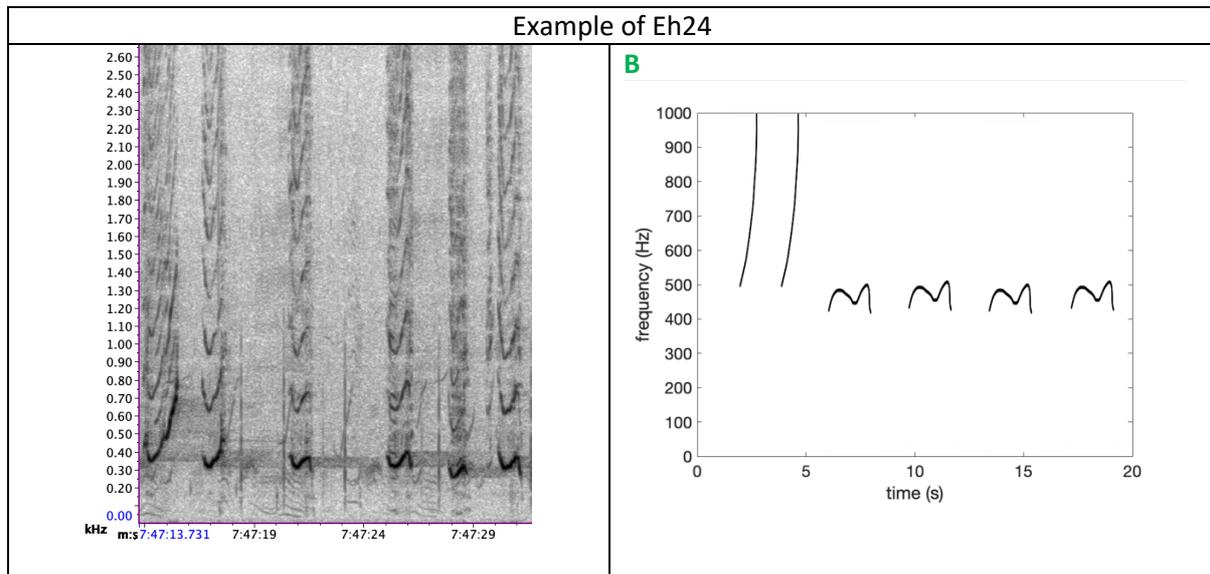
Type Fa

Combination of units CT18, CT5b

Example of Fa16
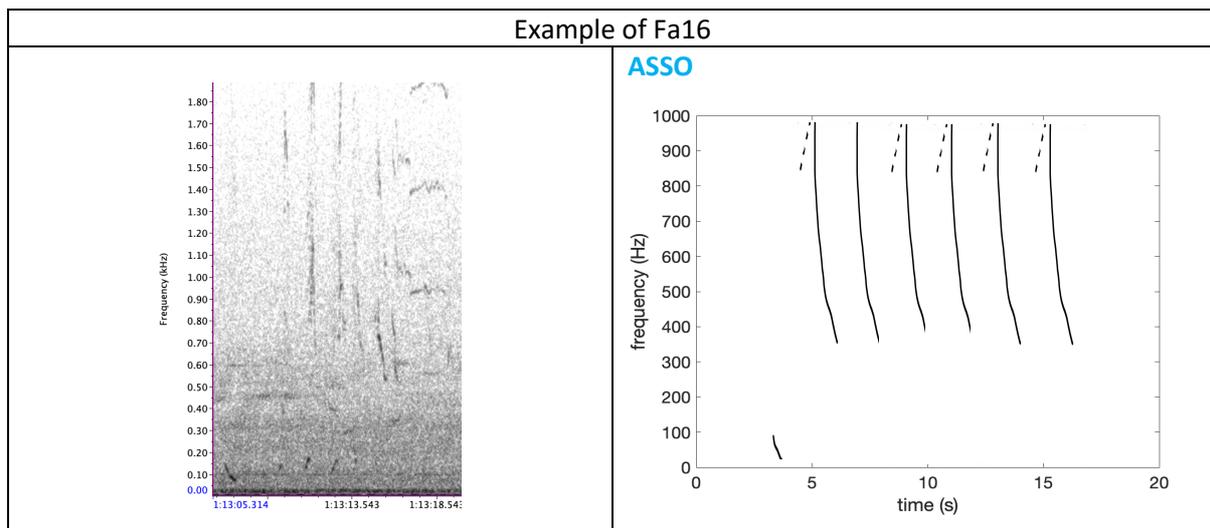
Type Fb

Combination of units CT18, CT1

Example of Fb11
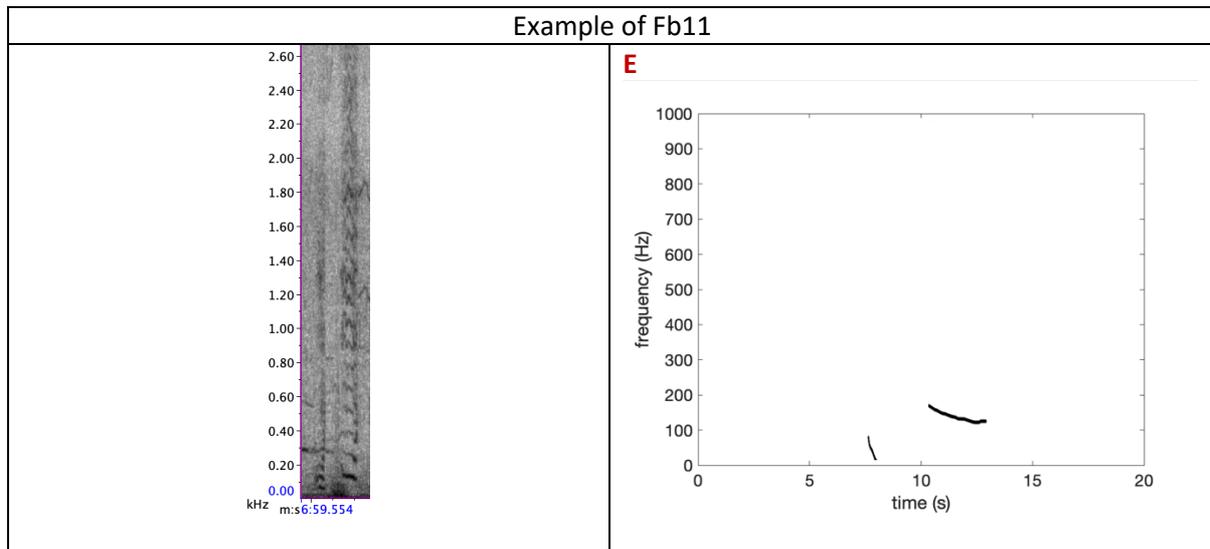
Type Fc

Combination of units CT18, CT13a

Example of Fc11
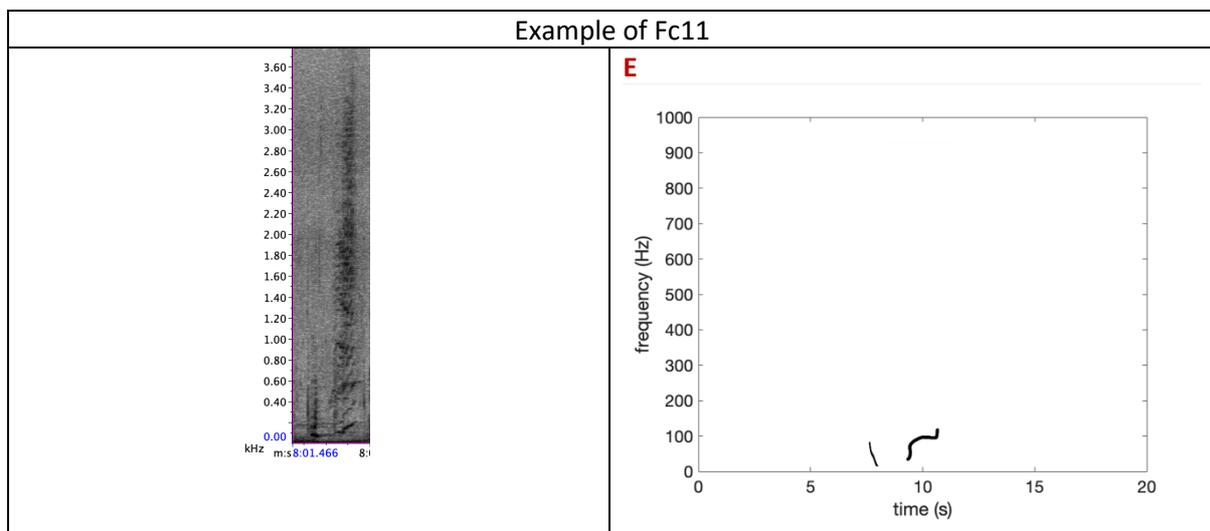
Type Ga

Combination of units CT5a, CT19

Example of Ga11
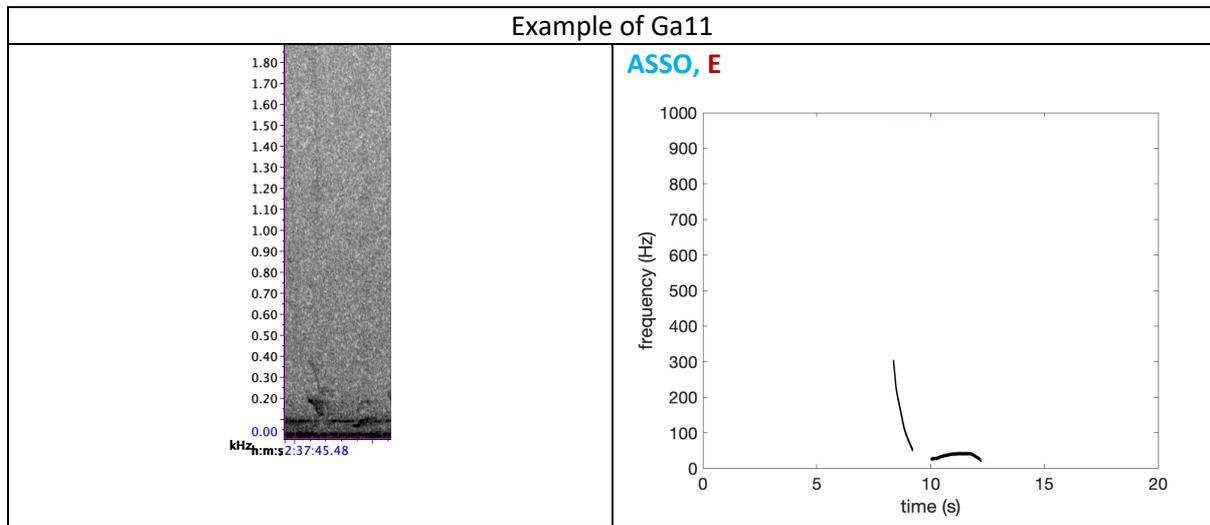
Type Gb

Combination of units CT5a, CT1

Example of Gb11
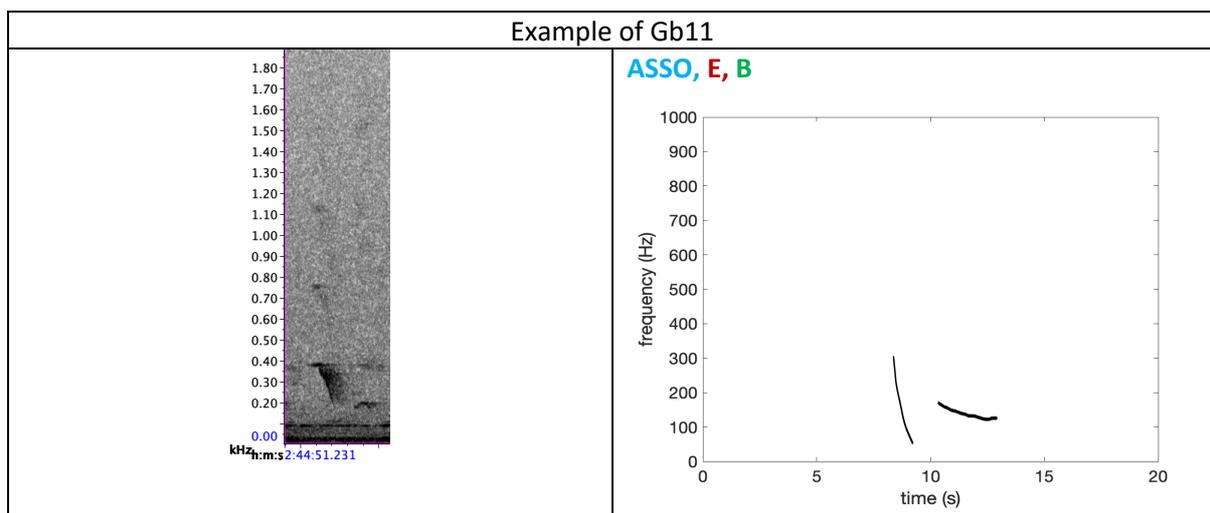
Type Gc

Combination of units CT5a, CT4a

Example of Gc11

ASSO, B
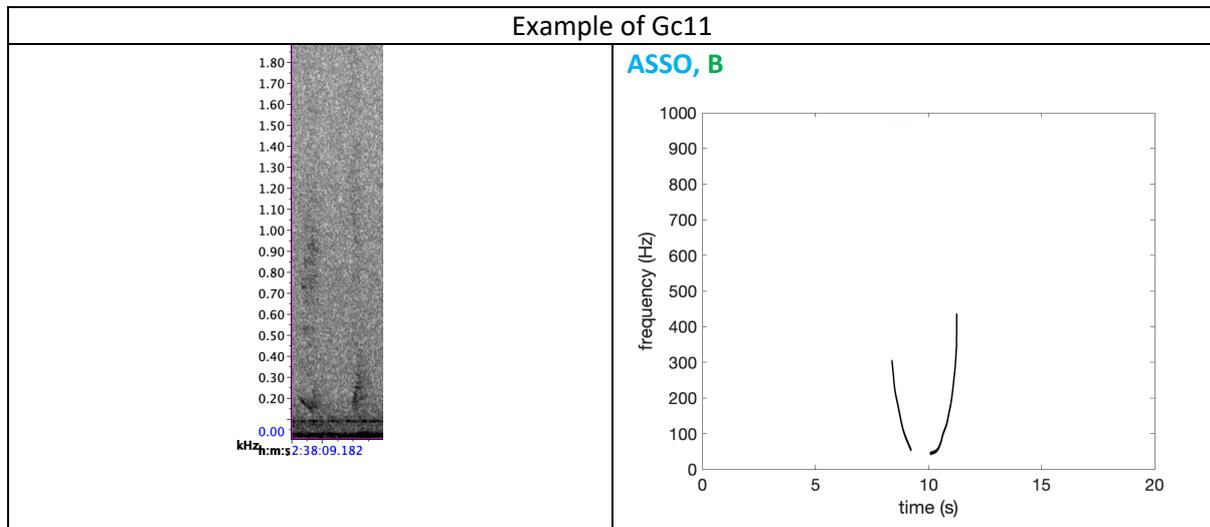
Type Gd

Combination of units CT5b, CT5a

Example of Gd12

ASSO, A
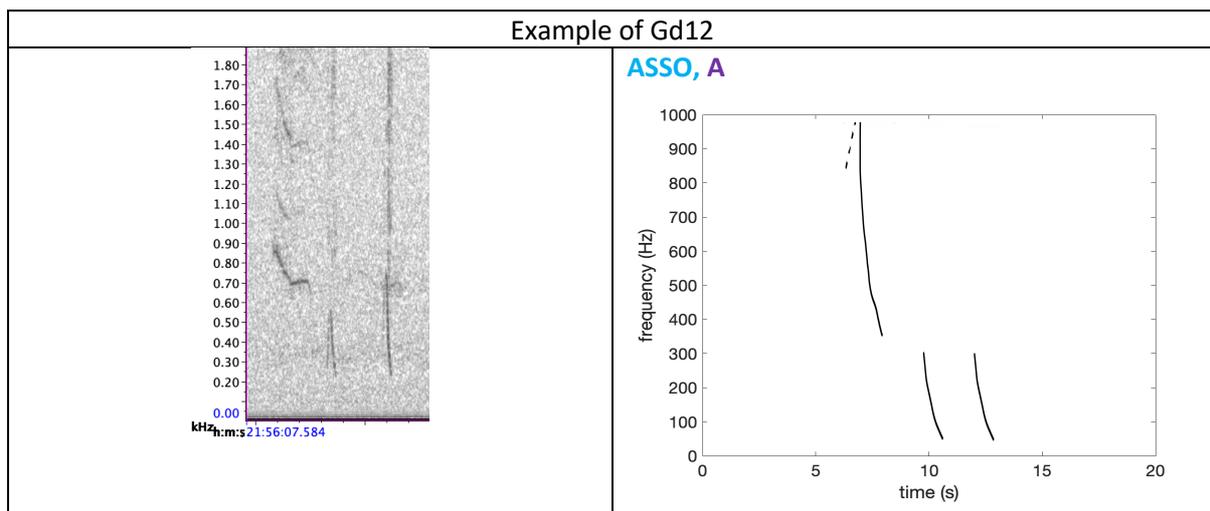
Type Ge

Combination of units CT5b, CT8

Example of Ge111
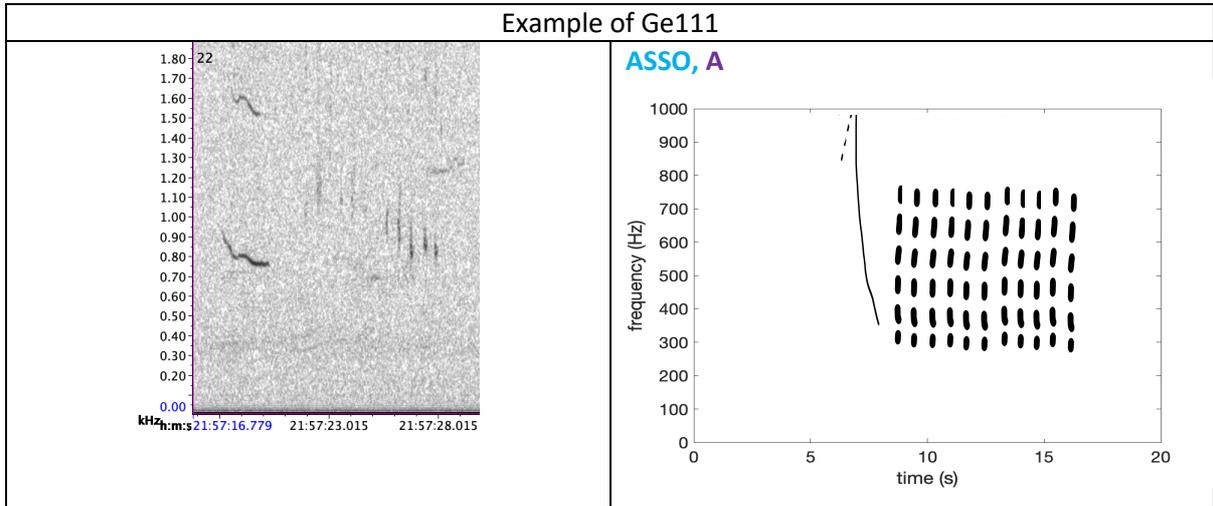
Type Gf

Combination of units CT5b, CT5a, CT8

Example of Gf1113
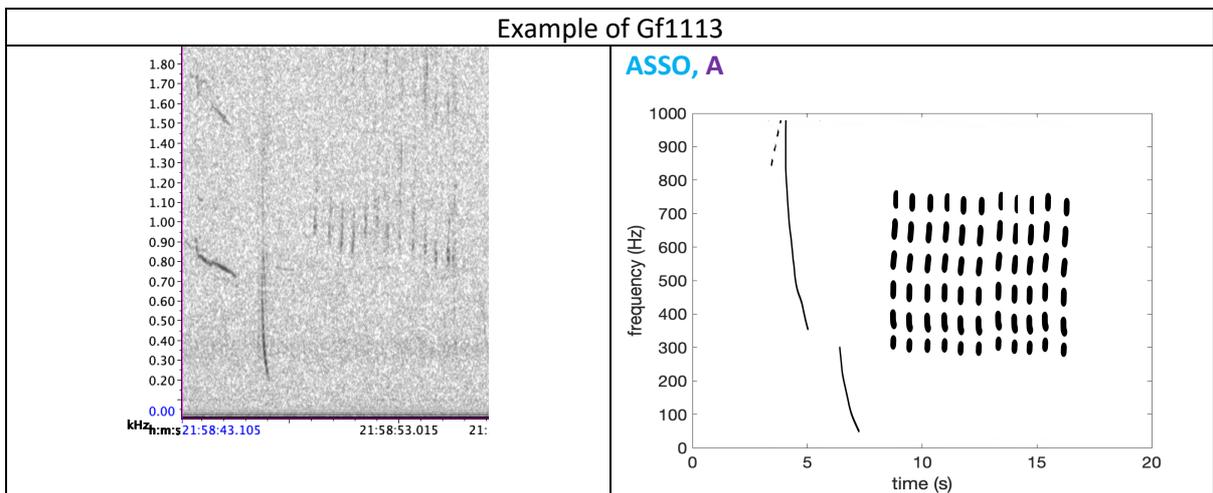
Type Gg
Combination of units CT5b/a

Example of Gg4

ASSO, A
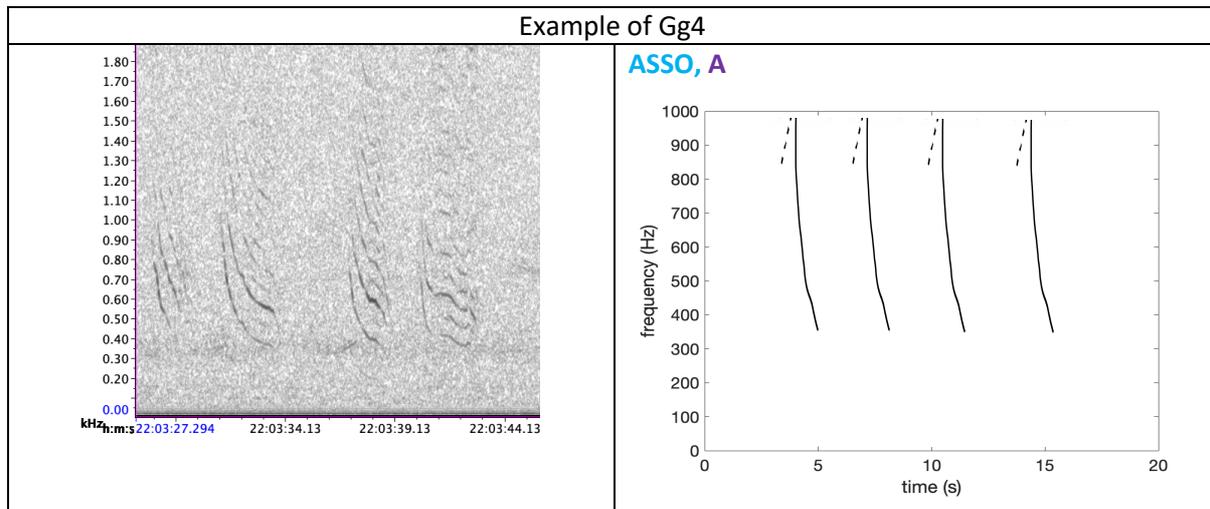
Type Gh
Combination of units CT5b, CT4a

Example of Gh27

ASSO, A
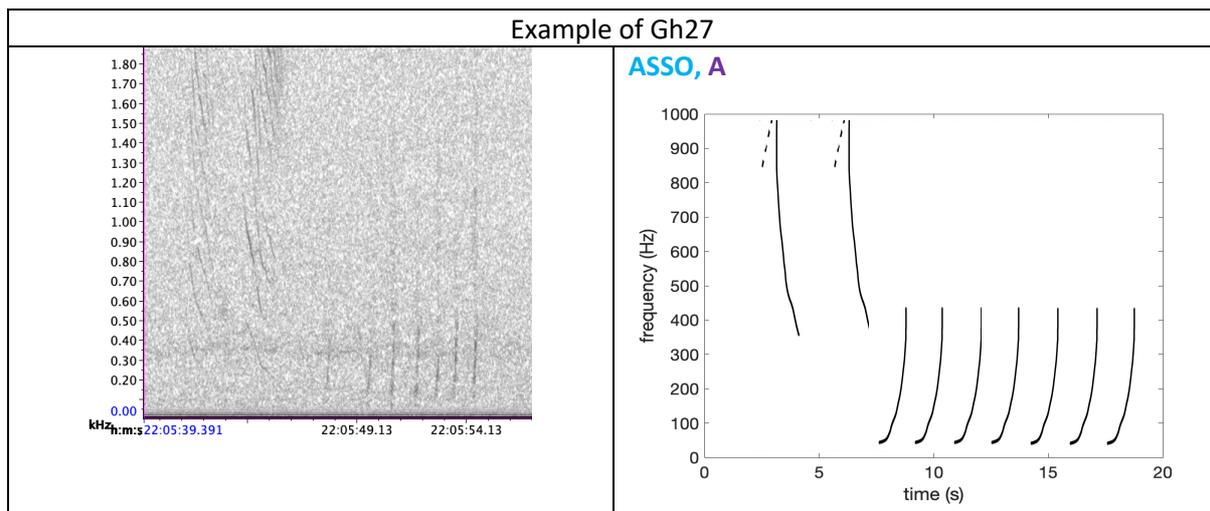
Type Gi

Combination of units CT5b, CT12

Example of Gi12
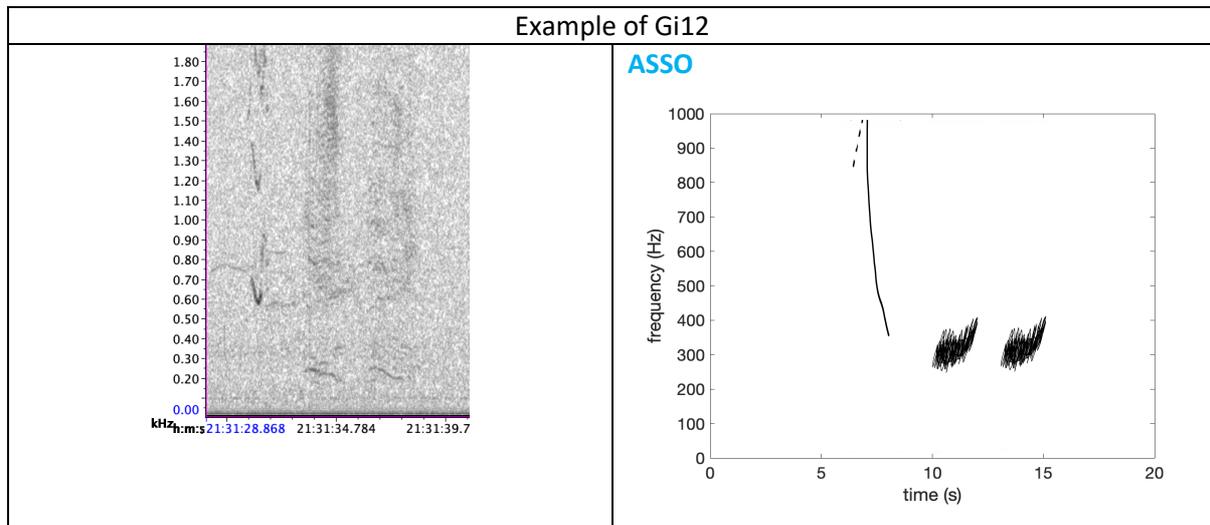
Type Gj

Combination of units CT5a, CT16, CT18

Example of Gj111
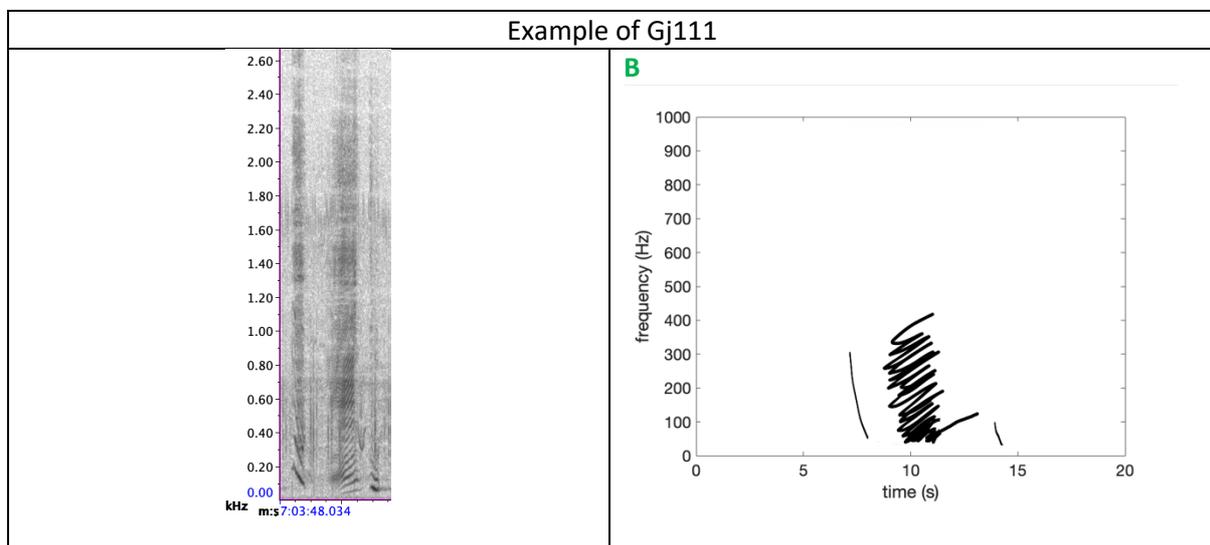
Type Gk

Combination of units CT5b, CT4b

Example of Gk12
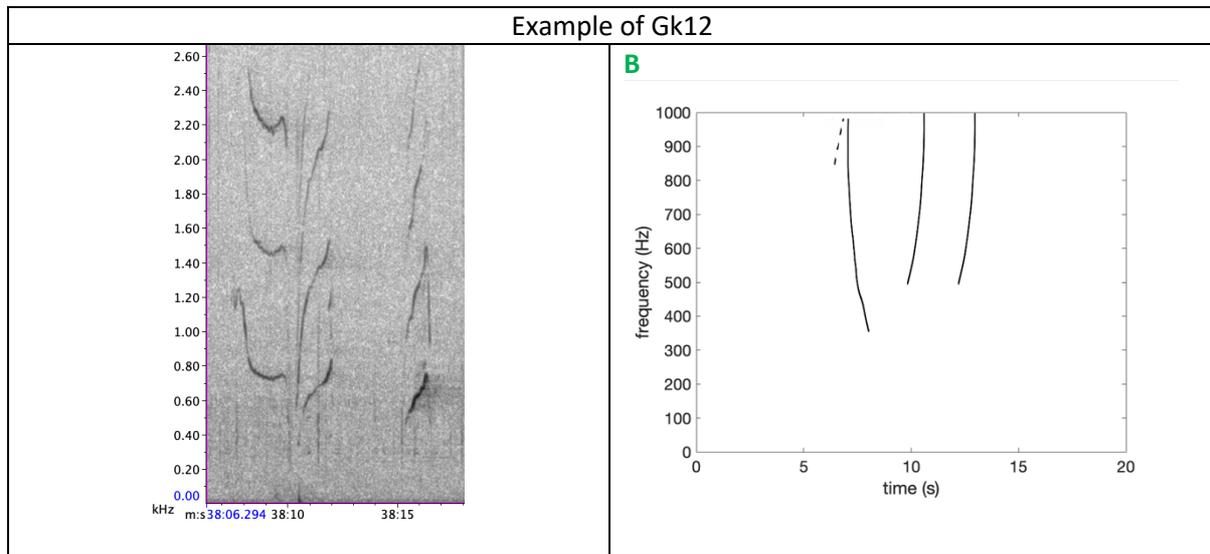
Type Gl

Combination of units CT5a, CT10

Example of Gl41
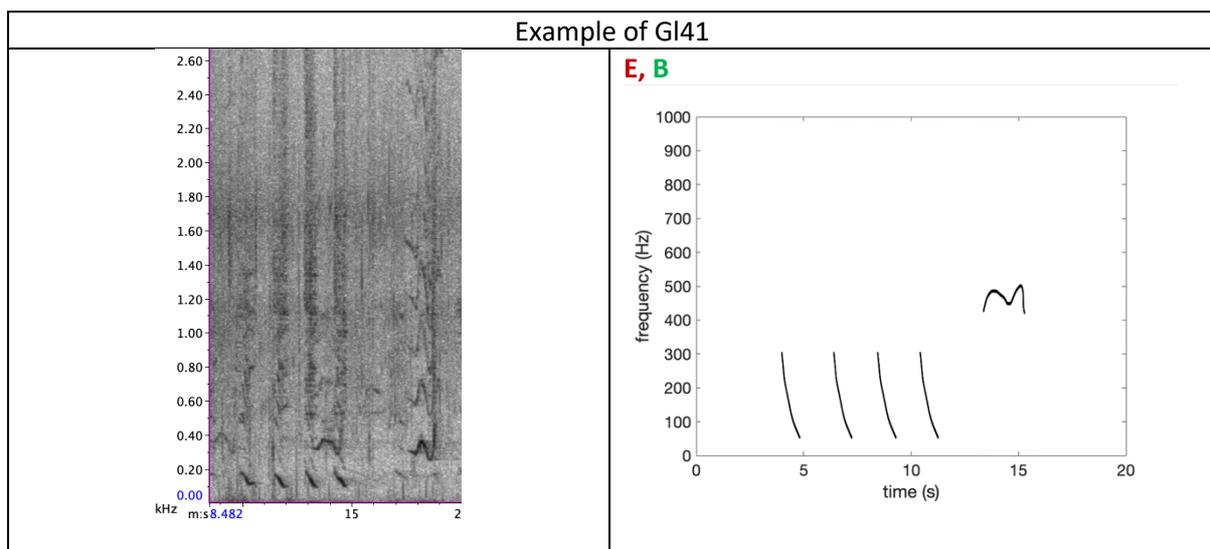
Type Gm

Combination of units CT5a, CT1, CT15

Example of Gm111
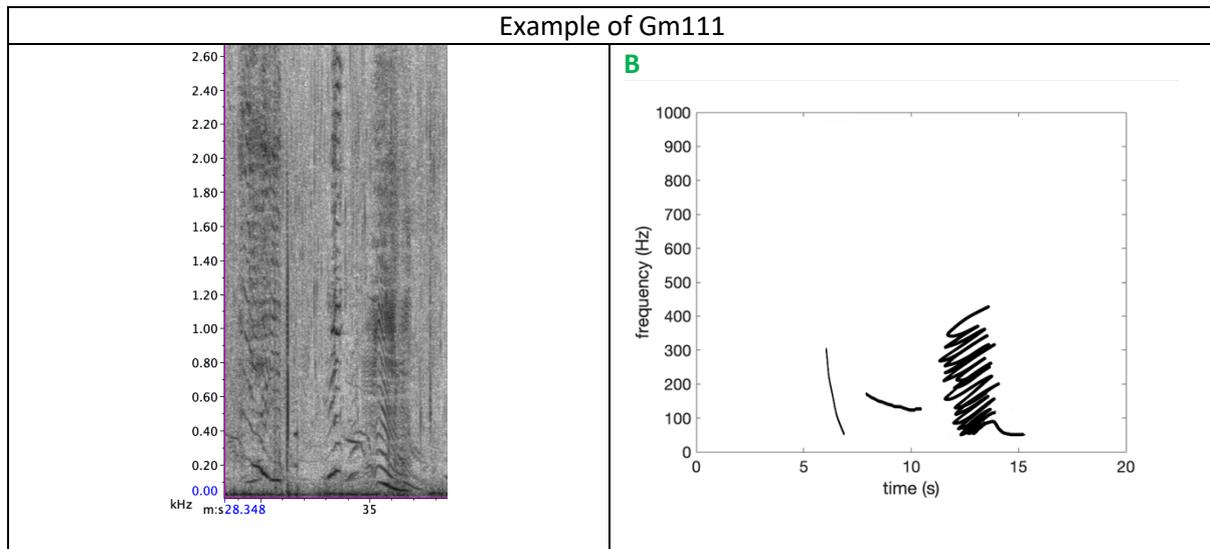
Type Ha

Combination of units CT19, CT4a

Example of Ha11
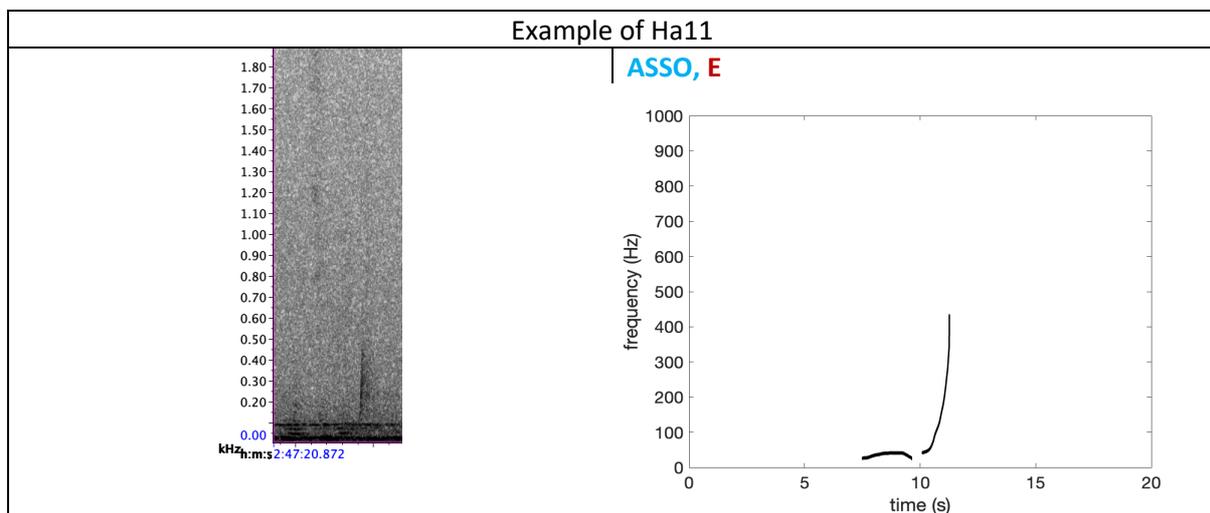
Type Ia

Combination of units CT10

Example of Ia5	
	ASSO, E, B
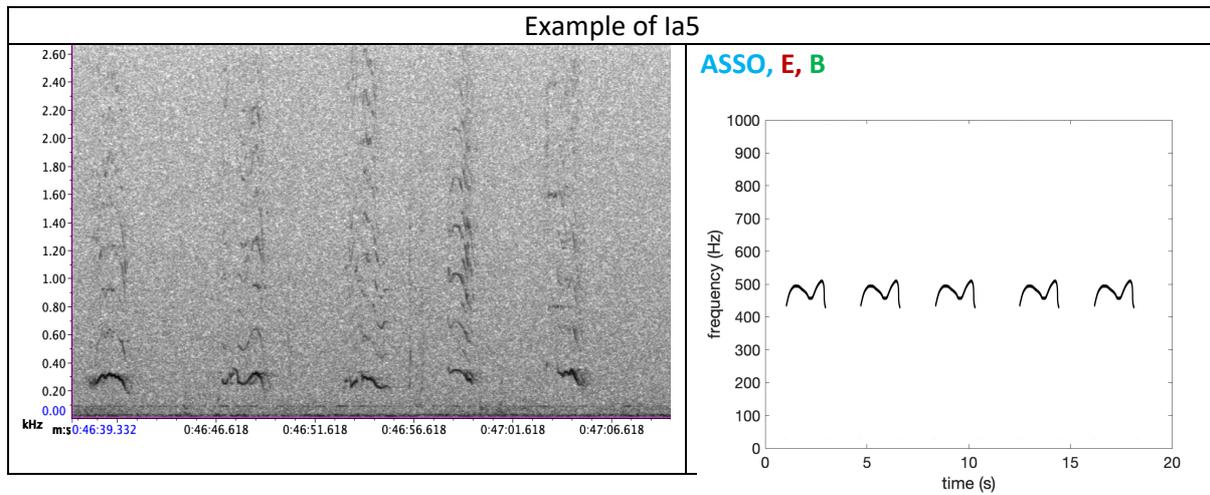
Type Ib

Combination of units CT10, CT8

Example of Ib12	
	ASSO, A
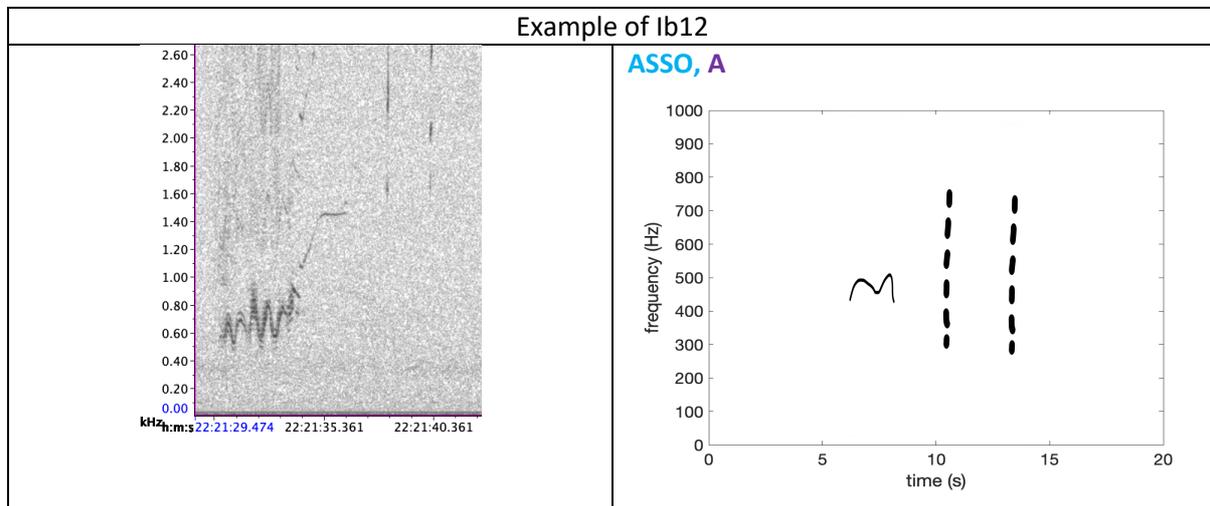
Type Ic
Combination of units CT10, CT13c

Example of Ic25
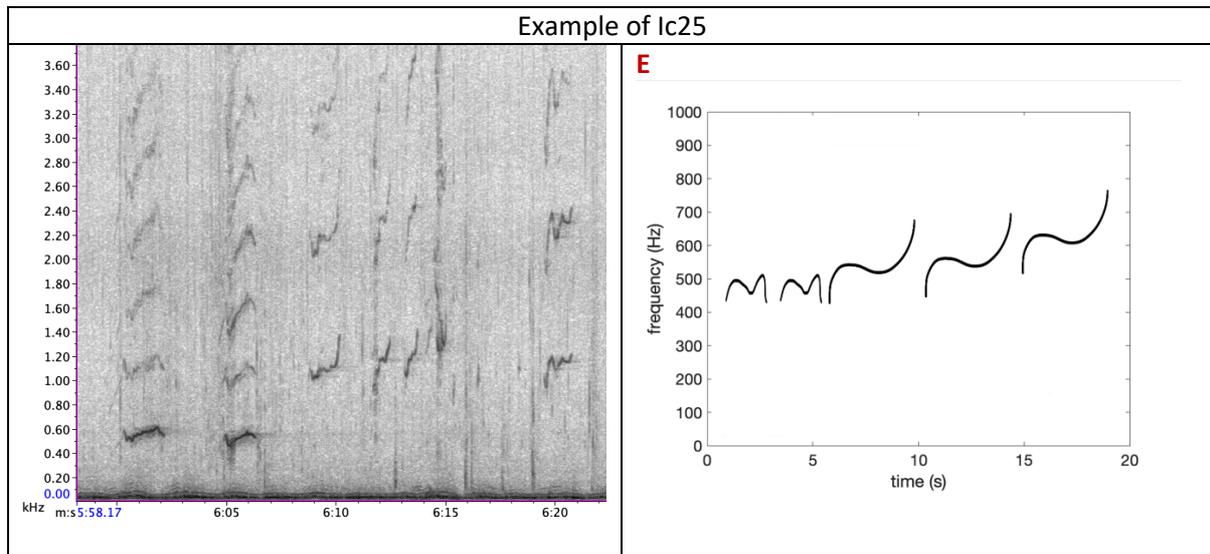
Type Id
Combination of units CT10, CT5b

Example of Id11
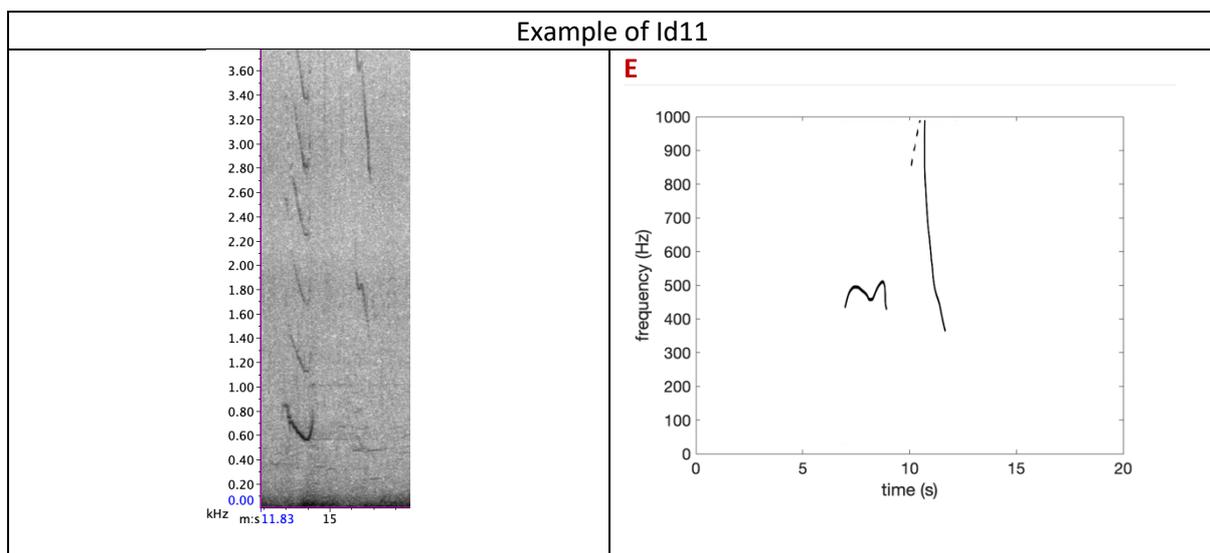
Type Ie

Combination of units CT10, CT1

Example of Ie12
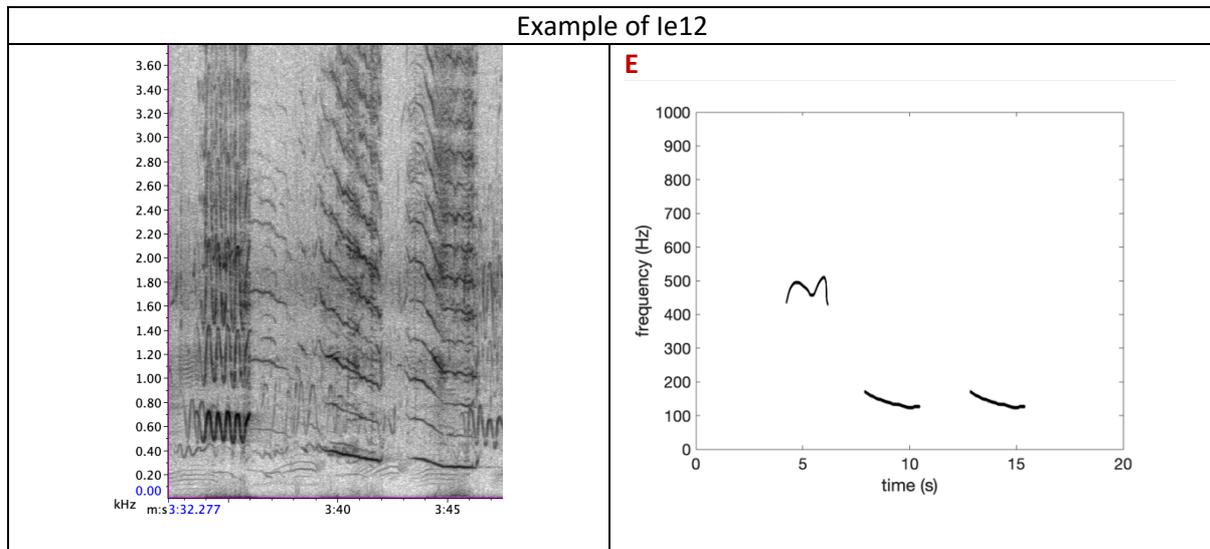
Type If

Combination of units CT10, CT8, CT1

Example of If161
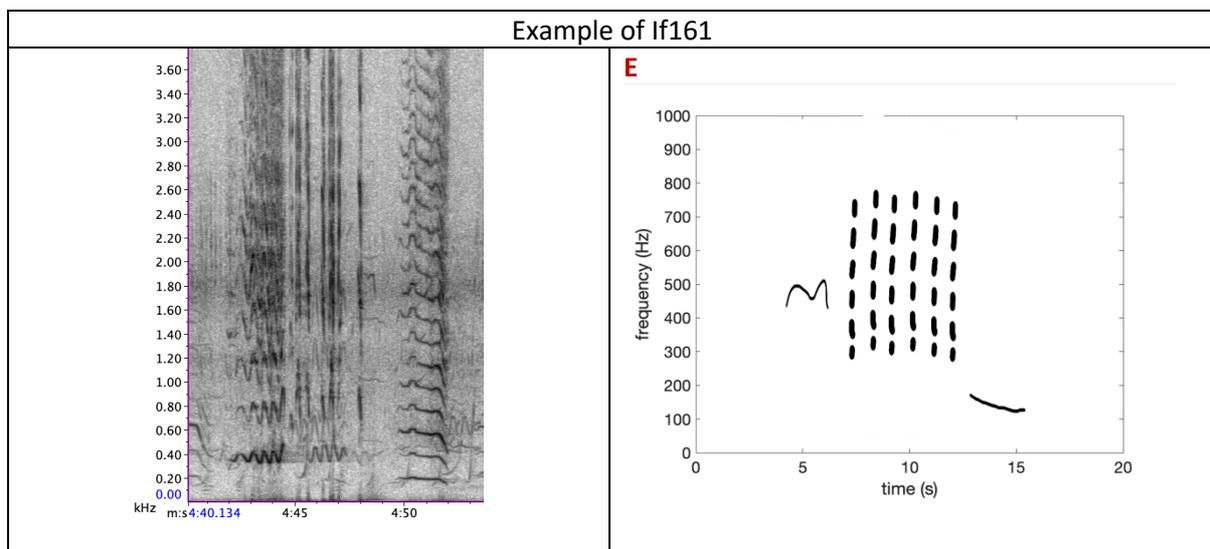
Type Ig
Combination of units CT10, CT19

Example of Ig13
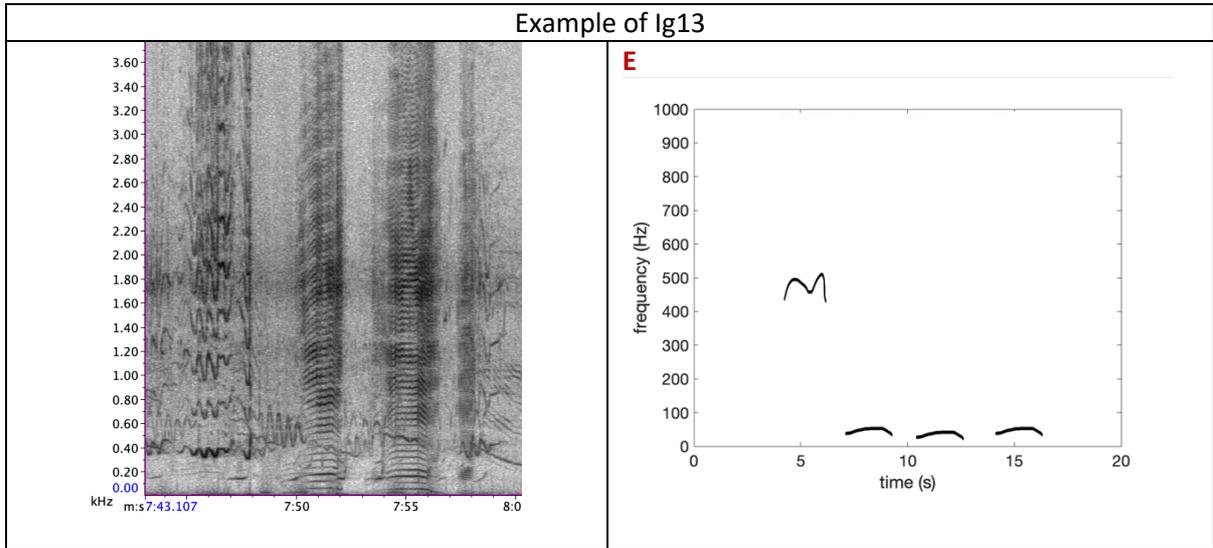
Type Ih
Combination of units CT10, CT1, CT13a

Example of Ih132

Type Ii

Combination of units CT10, CT13b, CT7

Example of Ii11312
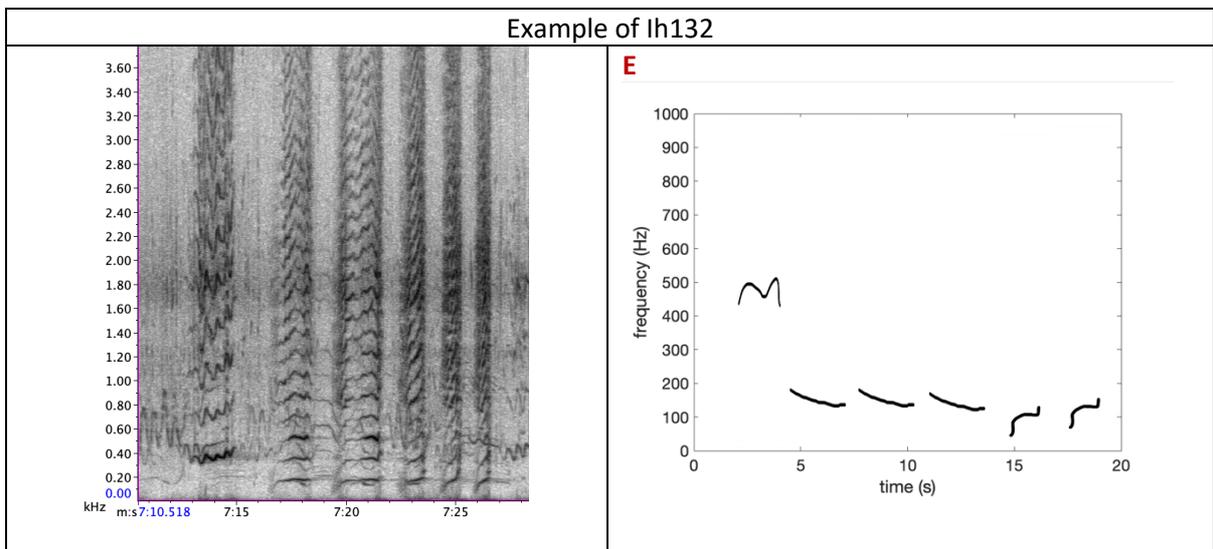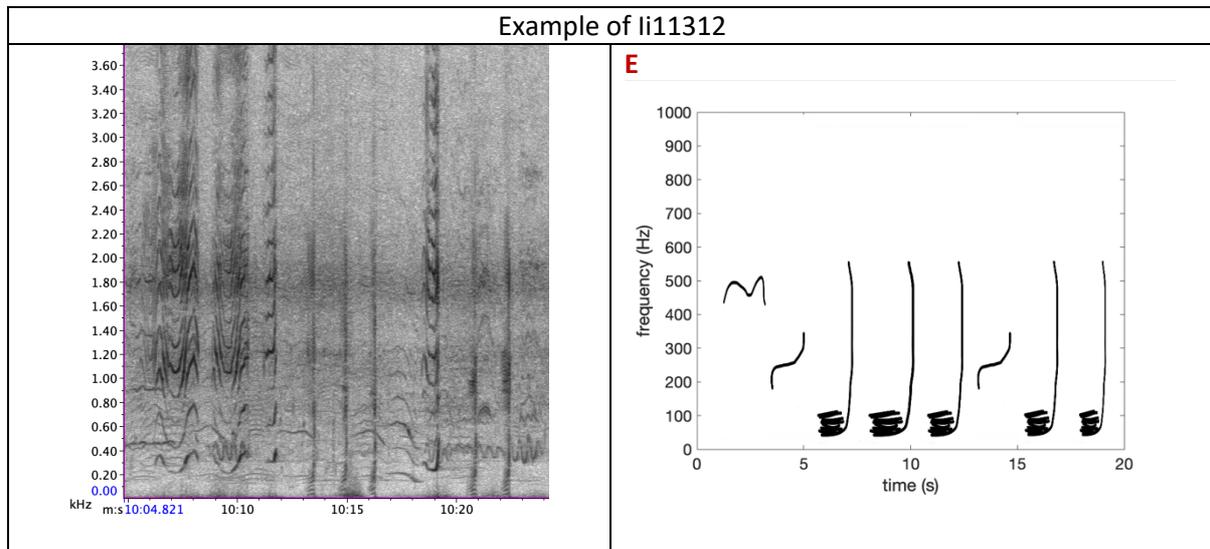
Type Ij

Combination of units CT10, CT4a

Example of Ij16
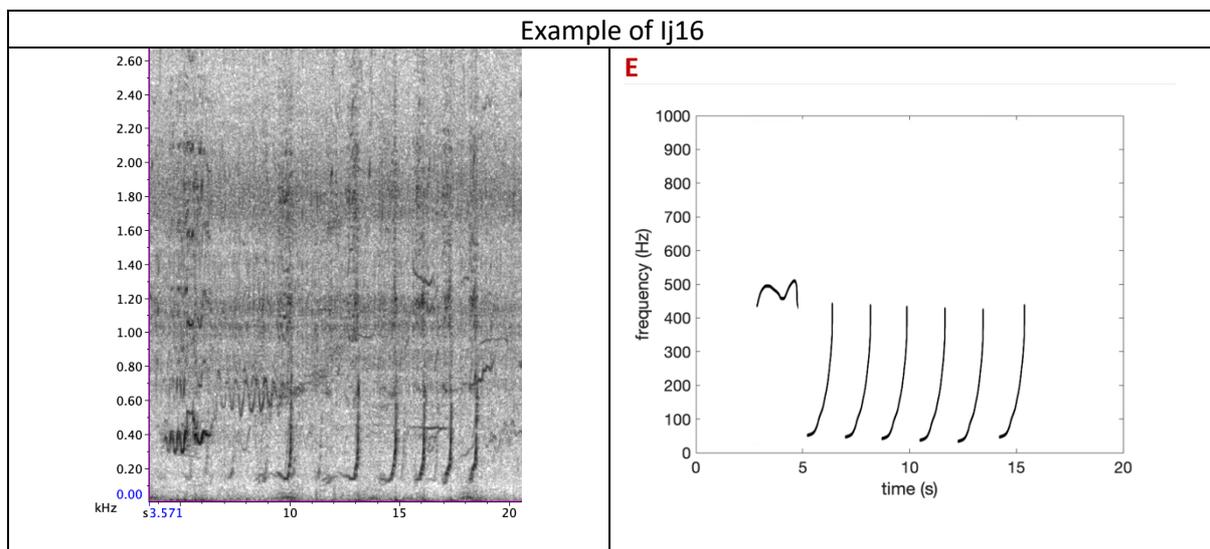
Type Ik

Combination of units CT10, CT19, CT4a

Example of Ik11111
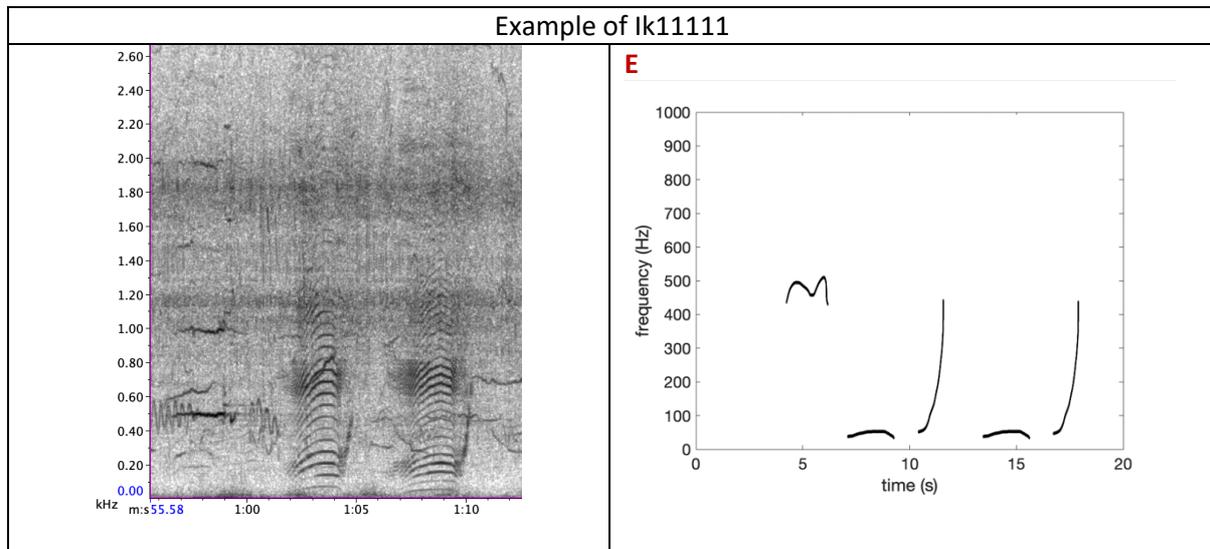
Type Il

Combination of units CT10, CT4b

Example of Il13
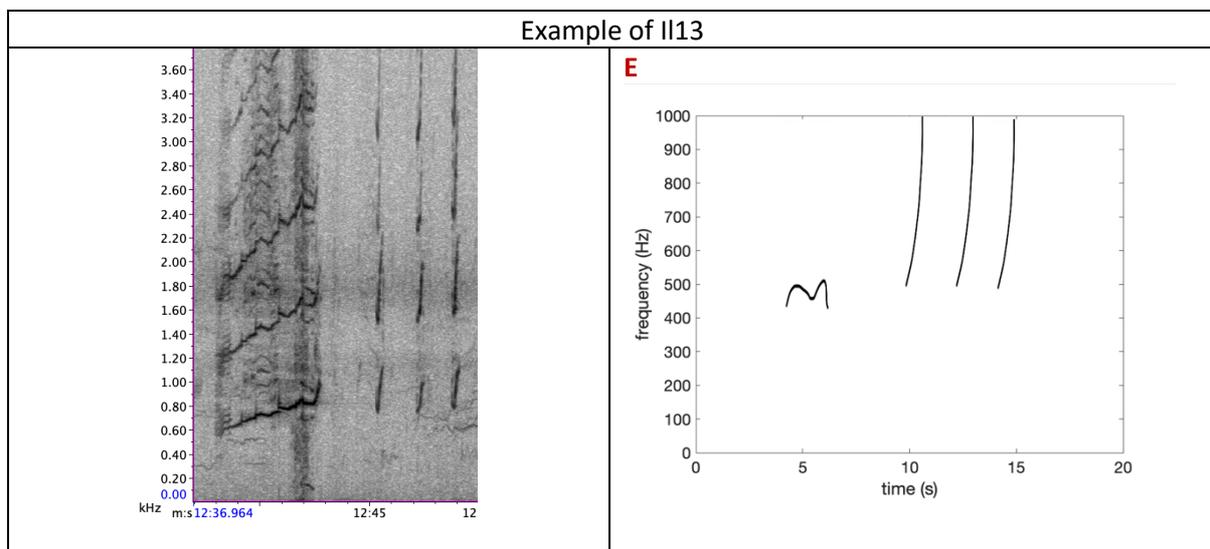
Type Ja

Combination of units CT7, CT4a

Example of Ja11	
	B, E
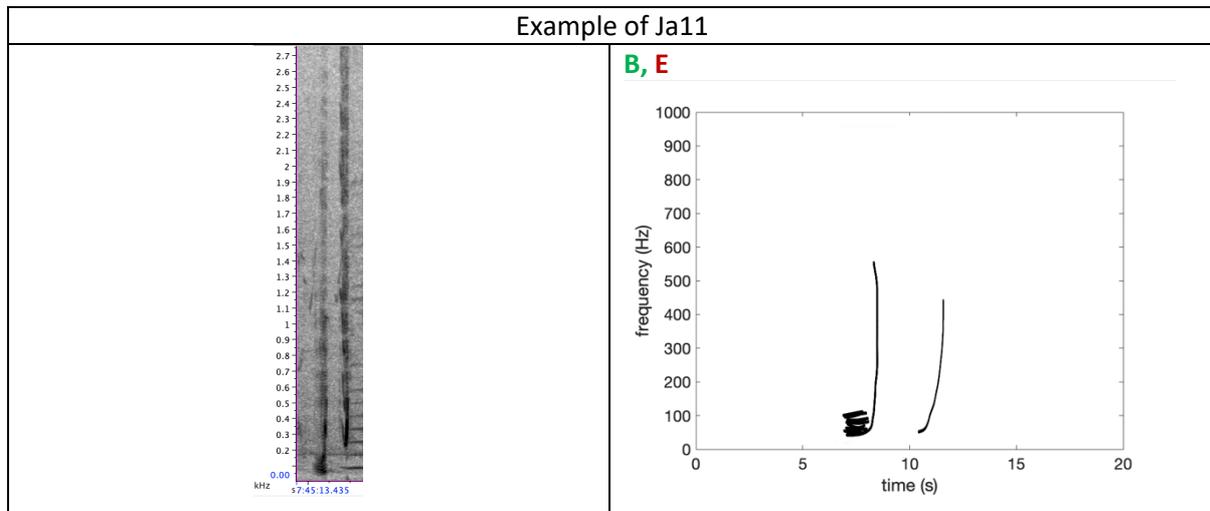
Type Jb

Combination of units CT7, CT12

Example of Jb11	
	B, E

226
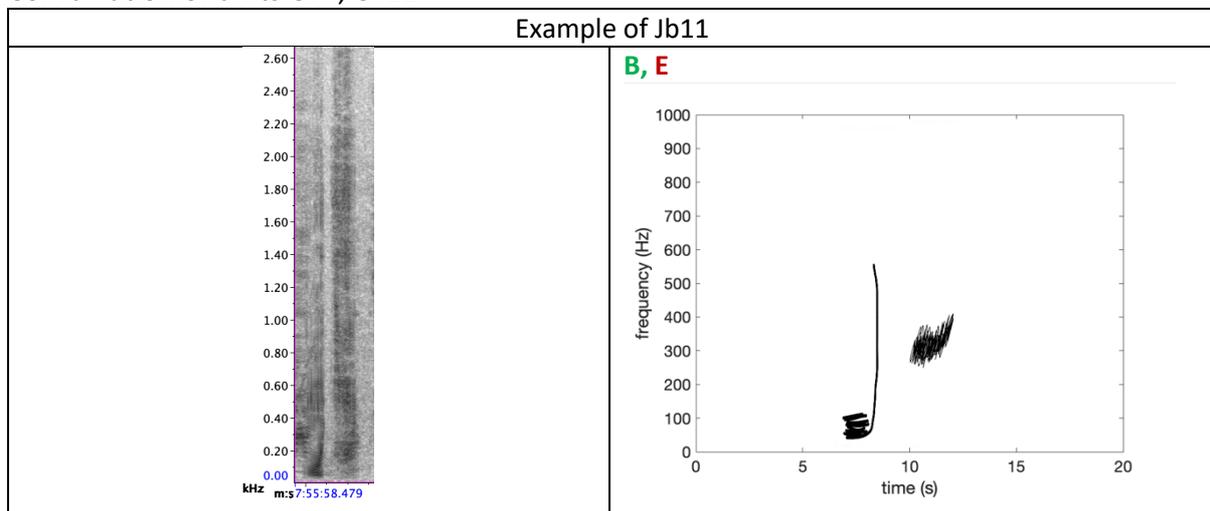
Type Ka

Combination of units CT16, CT18

Example of Ka11
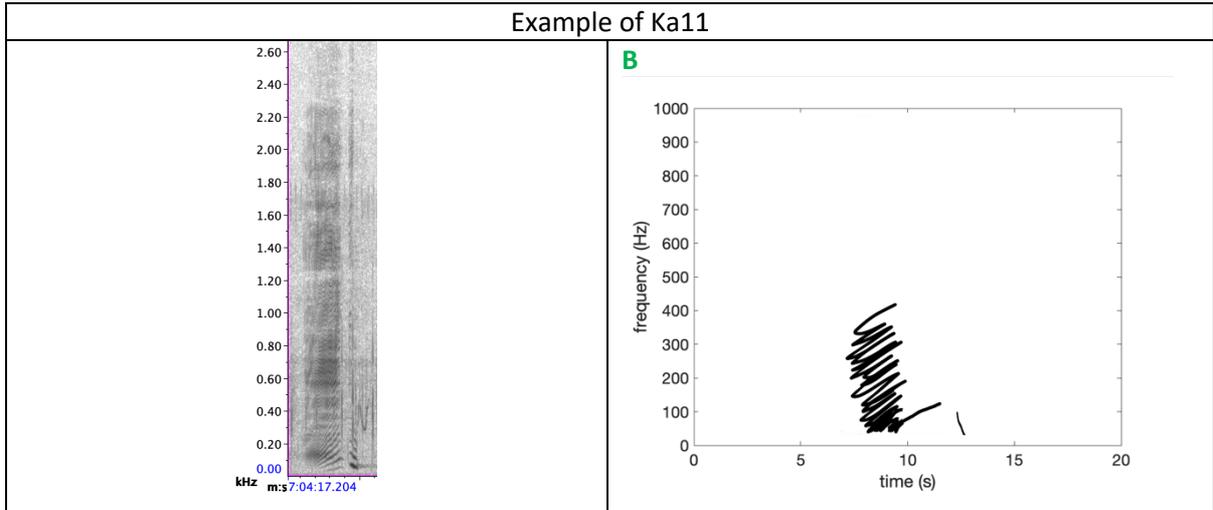
Type Kb

Combination of units CT16, CT12

Example of Kb11
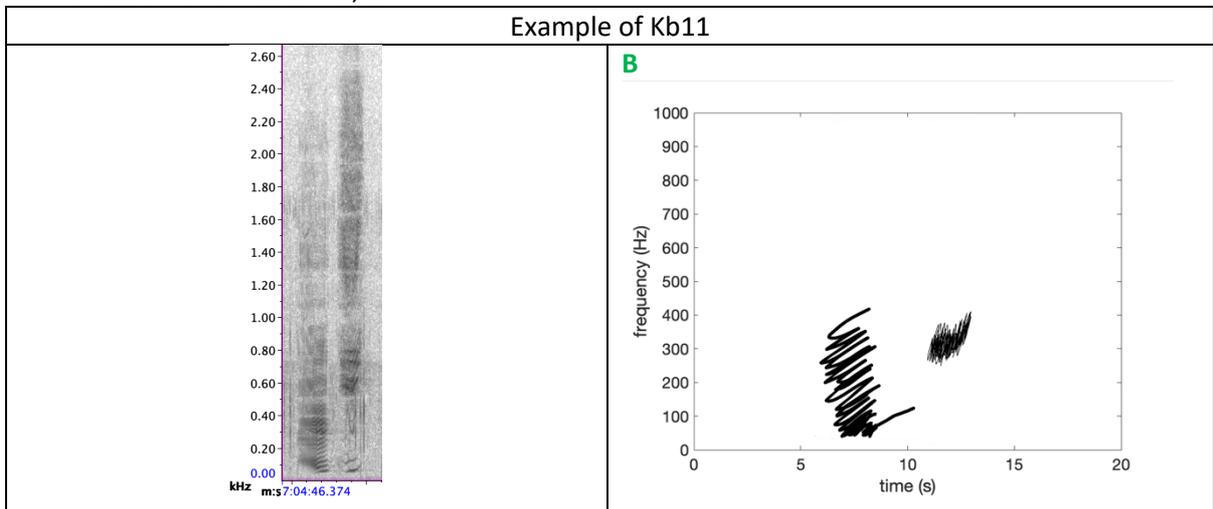
Type Kc

Combination of units CT16, CT10

Example of Kc11
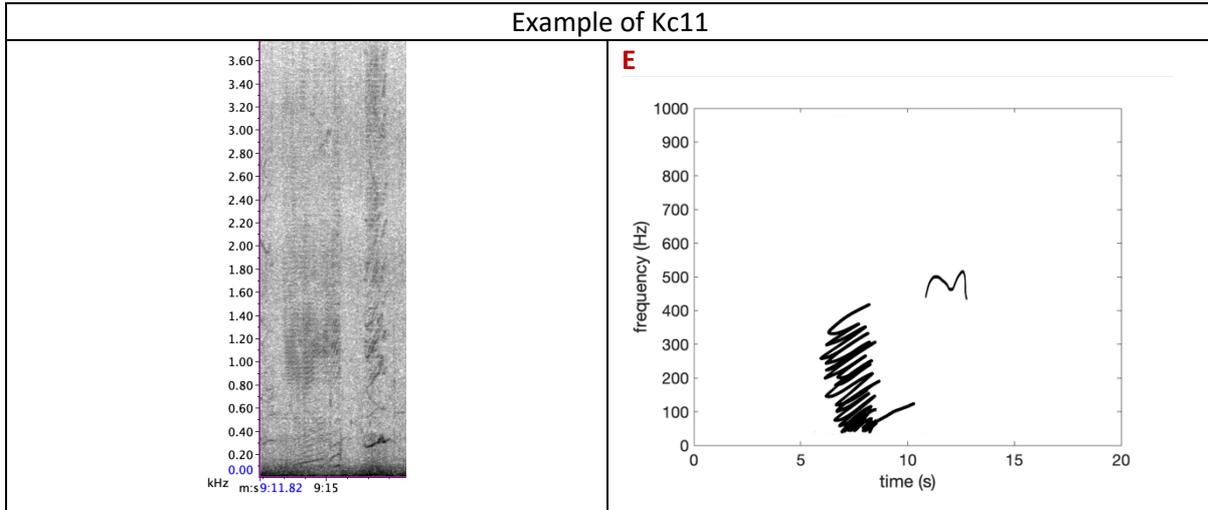
Type Kd

Combination of units CT16, CT13b

Example of Kd11
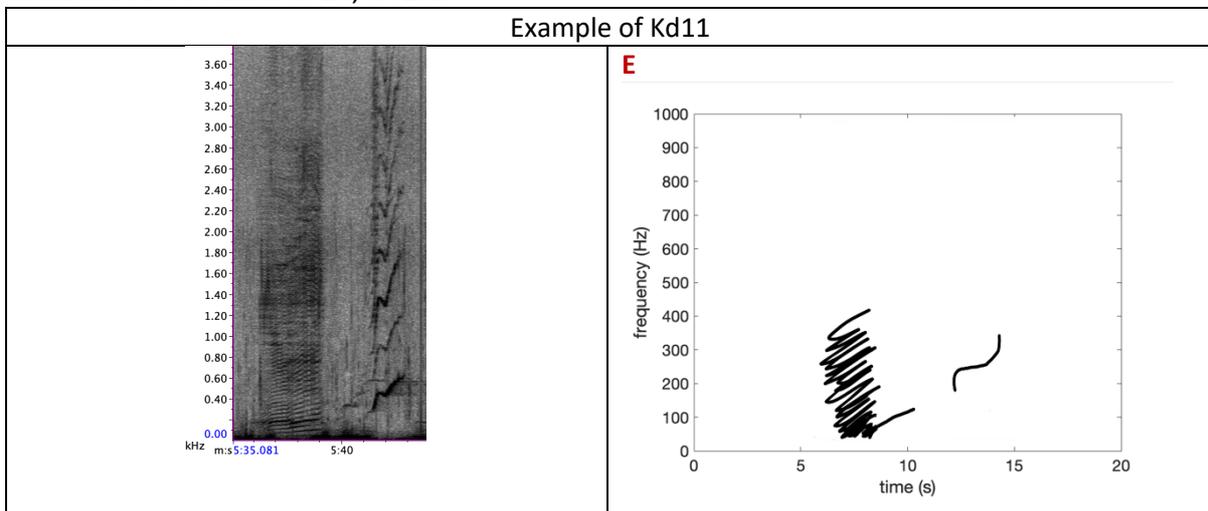
Type La

Combination of units CT13a, CT13b

Example of La41
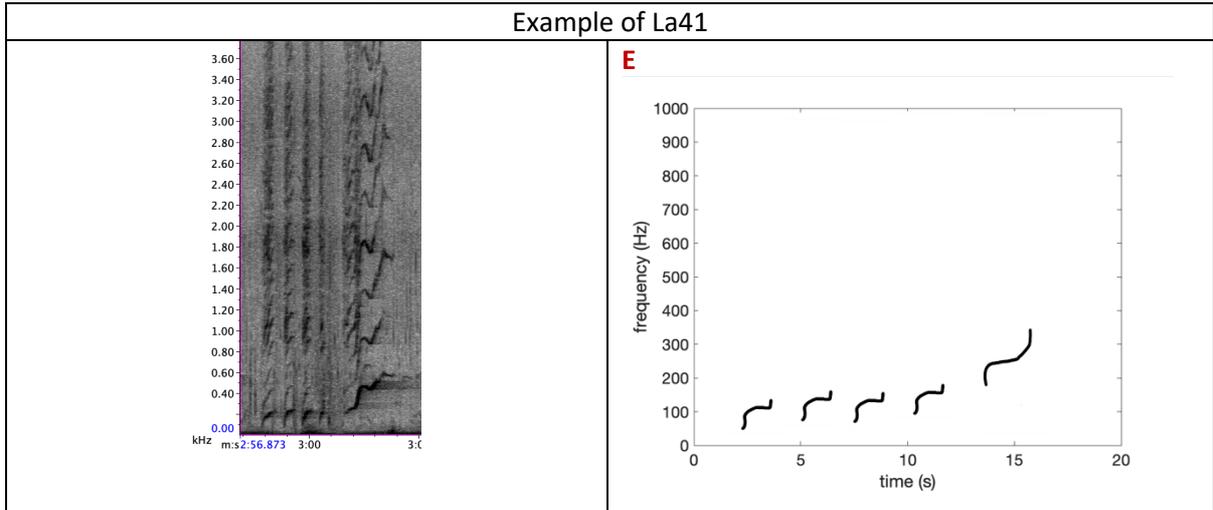
Type Lb

Combination of units CT13b, CT10

Example of Lb11
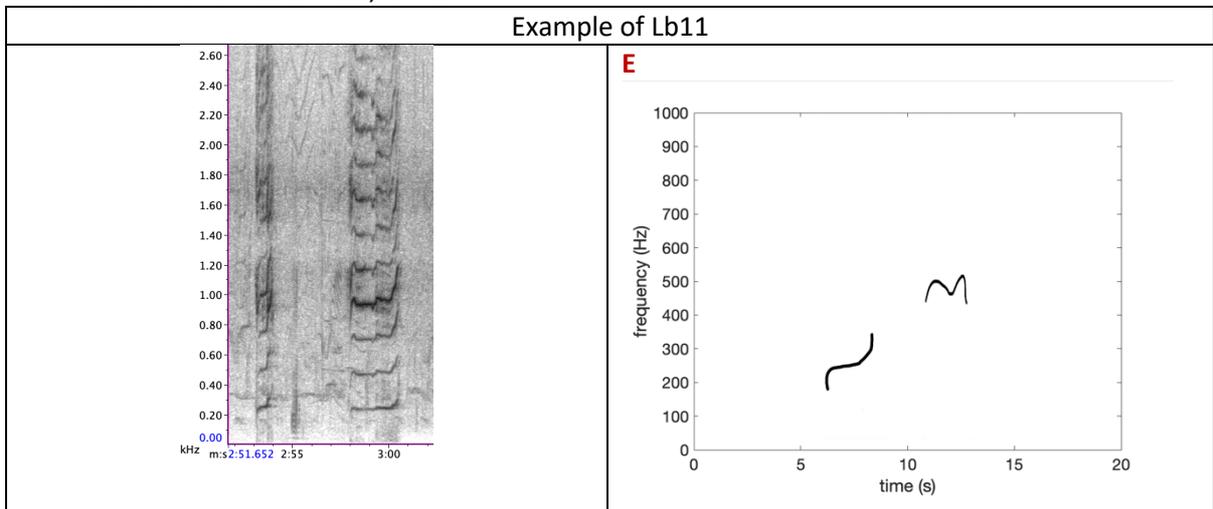
Type Lc

Combination of units CT13a, CT19, CT4b

Example of Lc1112
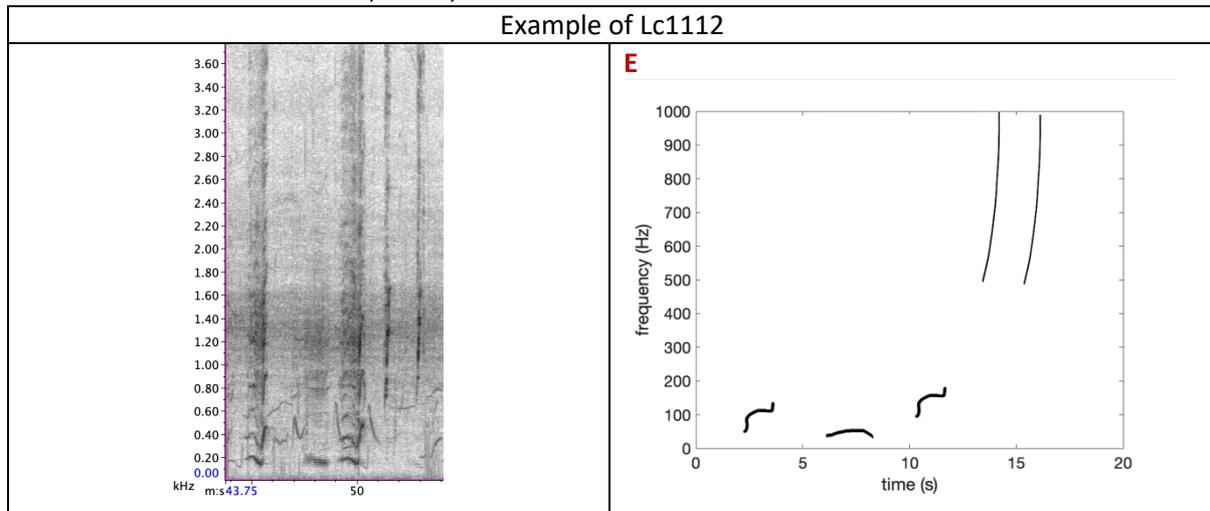
Type Ld

Combination of units CT13a, CT7, CT18

Example of Ld111111
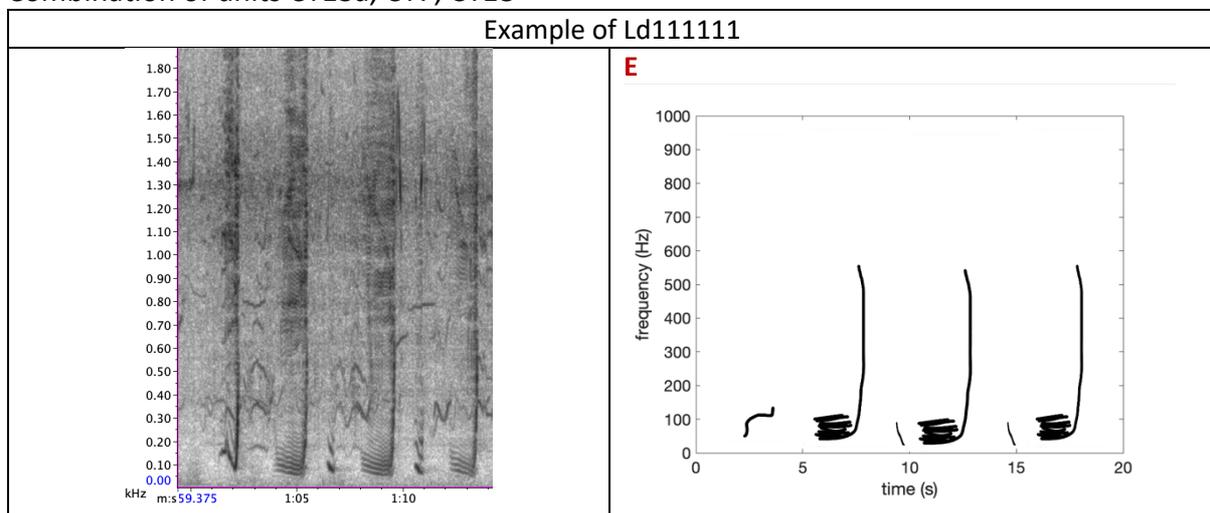
Type Ma

Combination of units CT17, CT4a

Example of Ma11
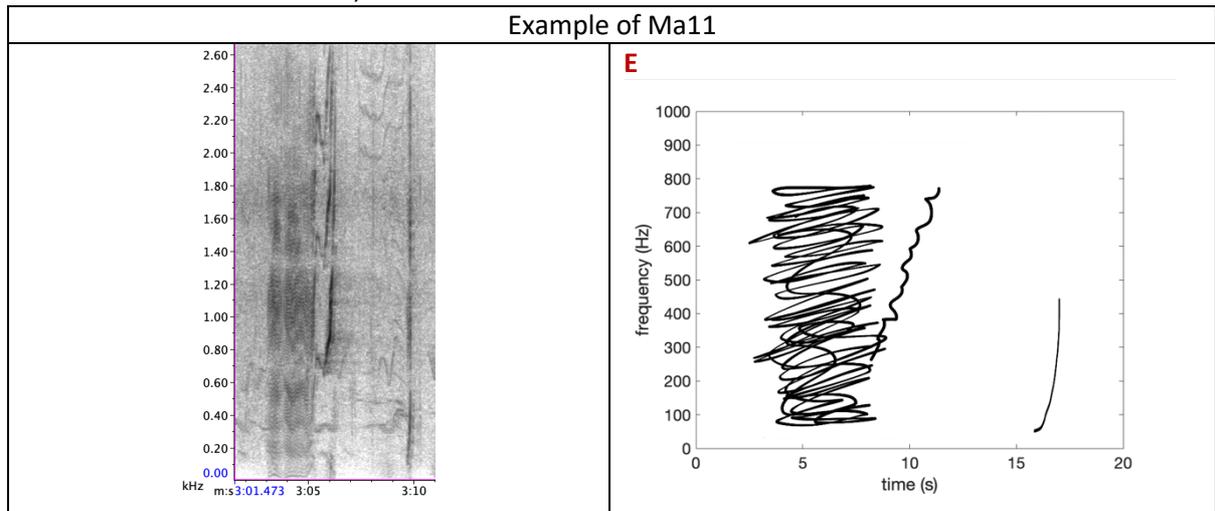
Type Mb

Combination of units CT17, CT10, CT4a

Example of Mb111
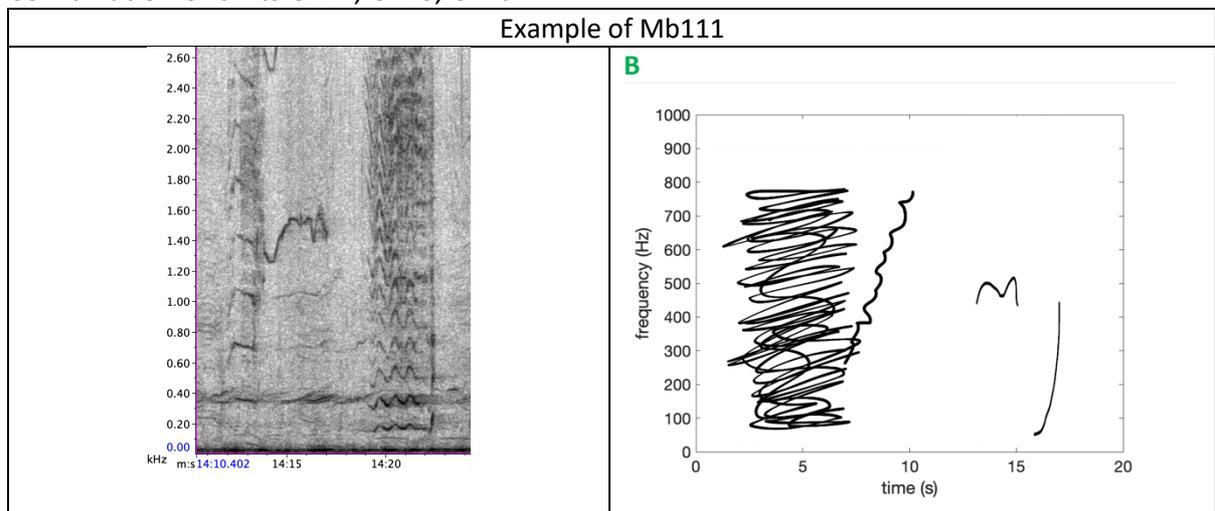
Type Na
Combination of units CT15, CT10

Example of Na11

E