Acoustic signals of Southern Ocean baleen whales

Assessing methods to reliably identify species- and population-specific vocalisations in passive acoustic monitoring data

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Abstract

As acoustic signals play a central role in cetacean ecology, passive acoustic monitoring (PAM) enables the investigation of acoustic presence and related behaviour of cetaceans based on known species-specific signals. Analysis of acoustic signals, whether clicks, pulses, tonal signals or song can yield insights into foraging behaviour, mating, group composition and coordination, as well as population and individual identity. Despite its potential, the effective application of PAM in ecological research depends critically on reliable signal identification, which becomes particularly challenging when signal characteristics overlap substantially. In the Southern Ocean, where multiple baleen whale species co-occur and produce acoustically similar signals, these challenges remain largely unresolved, yet are critical given the limited applicability of alternative monitoring methods. In this PhD thesis, I evaluate the potential and limitations of PAM for studying baleen whales in the Southern Ocean, given persistent challenges in signal interpretation. This includes assessing the reliability of species-level classification of non-song calls, with a focus on southern right (*Eubalaena australis*) and humpback whale (*Megaptera novaeangliae*) upcalls and frequency-modulated calls of blue (*Balaenoptera musculus*) and fin whales (*B. physalus*), as well as examining Southern Hemisphere fin whale song characteristics, particularly high-frequency (HF) components, and their suitability for population identification.

In Chapter 1, vocalisations comparable to southern right whale upcalls detected off Elephant Island were structurally analysed to confirm species identity. Call characteristics were compared with confirmed southern right and humpback whale vocalisations. The detected upcalls were attributed to southern right whales, with time-frequency slope and bandwidth of the vocalisation identified as the key parameters distinguishing the two species.

Chapter 2 combines long-term PAM datasets with animal-borne tag recordings to evaluate whether blue and fin whale frequency-modulated calls can be reliably distinguished at the species level. While the call parameter *Duration 90%* provides partial separation, a more robust approach was achieved by combining deep-learning-based feature extraction with non-linear dimensionality reduction, allowing calls from long-term datasets to be projected into an embedding space derived from the tag data.

In Chapter 3, region-specific HF components of Southern Hemisphere fin whale song are evaluated as acoustic cues to distinguish and monitor fin whale acoustic populations in the Atlantic Sector of the Southern Ocean (ASSO). Passive acoustic data from ten recording positions are used to assess the spatio-temporal distribution of the 86- and 99-Hz HF components present in this region. Results show that while the 99-Hz component was detected at seven recording positions throughout the ASSO, the 86-Hz component was restricted to the western part of the study area, centred around the Western Antarctic Peninsula.

Chapter 4 further investigates the use of HF components of Southern Hemisphere fin whale song as reliable acoustic markers for monitoring fin whale acoustic populations, given the indication of frequency declines. Analysis of multi-year passive acoustic datasets from two recording sites in the ASSO, Elephant Island and the Greenwich Meridian, shows that despite gradual interannual and intra-annual variability, these song features remain distinct and recognizable across regions and years, providing a robust cue to identify acoustic populations.

Overall, the findings and frameworks I developed in this thesis support more reliable passive acoustic monitoring by improving interspecific call discrimination and enabling robust identification of fin whale acoustic populations, thereby strengthening confidence in acoustic assessments of species presence and population structure in the Southern Ocean. At the same time, methodological limitations in regard to call classification are critically evaluated, including constraints arising from transmission loss effects and deep-learning-based feature extraction, along with potential approaches to overcome these limitations. The thesis further considers how additional baleen whale FM calls could be incorporated into the developed frameworks, as well as future challenges in call classification and possible drivers of similarity among non-song calls across baleen whale species. In regard to song characteristics for population identification in Southern Hemisphere fin whales, two additional features, inter-note intervals and song variants, were examined. Both correspond to the results from the HF components, and all three characteristics were evaluated in terms of their applicability, reliability, and potential for monitoring, including how they could contribute to a circumpolar perspective on fin whale populations. Finally, this thesis emphasises that while standardised analytical frameworks are essential for reliable and comparable PAM, human expertise remains indispensable for detecting changes in signal structure, validating results, and ensuring biological relevance.

Zusammenfassung

Da akustische Signale eine zentrale Rolle in der Ökologie von Walen und Delfinen spielen, ermöglicht das passive akustische Monitoring (PAM) die Untersuchung der akustischen Präsenz und des damit verbundenen Verhaltens von Walen auf der Grundlage bekannter artspezifischer Signale. Die Analyse akustischer Signale, darunter Klicks, Pulse, tonale Signale und Gesang, liefert Einblicke in Fress- und Paarungsverhalten, Gruppenstruktur und -koordination sowie in Populations- und Individualidentität. Trotz seines großen Potenzials hängt der erfolgreiche Einsatz von PAM in der ökologischen Forschung entscheidend von einer zuverlässigen Signalidentifikation ab, die insbesondere dann herausfordernd ist, wenn sich Signalmerkmale verschiedener Arten stark ähneln. Im Südlichen Ozean, in dem mehrere Bartenwalarten koexistieren und akustisch ähnliche Signale produzieren, sind diese Herausforderungen bislang weitgehend ungelöst, obwohl alternative Monitoringmethoden nur eingeschränkt anwendbar sind. In meiner Dissertation prüfe ich das Potenzial und die Limitationen des PAM für die Untersuchung von Bartenwalen im Südlichen Ozean unter den bestehenden Schwierigkeiten der Signalinterpretation. Dies umfasst die Untersuchung der Zuverlässigkeit einer artspezifischen Klassifikation von sozialen Rufen, mit Schwerpunkt auf ‘Upcalls’ von Südkapern (*Eubalaena australis*) und Buckelwalen (*Megaptera novaeangliae*) sowie frequenzmodulierten Rufen von Blau- (*Balaenoptera musculus*) und Finnwalen (*B. physalus*). Darüber hinaus werden die Gesangsmerkmale von Finnwalen der Südhalbkugel, insbesondere die hoch-frequenten (HF) Komponenten, und deren Eignung zur Identifikation akustischer Populationen analysiert.

In Kapitel 1 wurden vor Elephant Island aufgezeichnete Signale, die Südkaper ‘Upcalls’ ähneln, strukturell analysiert, um ihre Artzugehörigkeit zu bestätigen. Die Signale wurden mit bestätigten ‘Upcalls’ von Südkapern und Buckelwalen verglichen. Die detektierten ‘Upcalls’ wurden erfolgreich Südkapern zugeordnet, wobei die Steigung und die Bandbreite der Rufe als die entscheidenden Unterscheidungsmerkmale identifiziert wurden.

Kapitel 2 kombiniert langfristige PAM-Datensätze mit Aufzeichnungen aus an Tieren angebrachten Tags, um zu untersuchen, ob frequenzmodulierte Rufe von Blau- und Finnwalen zuverlässig auf Artebene unterschieden werden können. Während der Parameter ‘*Duration 90%*’ eine partielle Zuordnung ermöglicht, wurde ein robusterer Ansatz durch die Kombination Deep Learning-basierter Merkmalsextraktion mit nichtlinearer Dimensionsreduktion erreicht. Dadurch können Rufe aus

Langzeitdatensätzen in ein Embedding projiziert werden, der aus den Tag-Daten abgeleitet wurde.

In Kapitel 3 werden regionsspezifische HF-Komponenten des Gesangs von Finnwalen der Südhalbkugel als akustische Marker zur Unterscheidung und Überwachung akustischer Populationen im atlantischen Sektor des Südlichen Ozeans (ASSO) untersucht. Passive akustische Daten von zehn Aufnahmepositionen wurden verwendet, um die räumliche und zeitliche Verteilung der 86- und 99-Hz Gesangskomponenten in dieser Region zu analysieren. Die Ergebnisse zeigen, dass die 99-Hz-Komponente an sieben Aufnahmepositionen im gesamten ASSO detektiert wurde, während die 86-Hz-Komponente auf den westlichen Teil des Untersuchungsgebietes beschränkt war, mit einem Schwerpunkt um die Antarktische Halbinsel.

Kapitel 4 untersucht weiter die Nutzung der HF-Komponenten des Finnwalgesangs als verlässliche akustische Marker für die Überwachung akustischer Populationen vor dem Hintergrund beobachteter Frequenzabnahmen. Die Analyse mehrjähriger passiver akustischer Datensätze von zwei Aufnahmepositionen im ASSO, Elephant Island und dem Greenwich-Meridian, zeigt, dass diese Gesangsmerkmale trotz gradueller intra- und interannueller Variabilität über Regionen und Jahre hinweg klar unterscheidbar und wiedererkennbar bleiben und somit verlässlich akustische Populationen identifizieren können.

Insgesamt tragen die in dieser Dissertation entwickelten Ansätze dazu bei, durch verbesserte interspezifische Signalunterscheidung und eine robuste Identifikation akustischer Finnwalpopulationen PAM Analysen zu stärken und damit die Aussagekraft akustischer Erhebungen zur Artenpräsenz und Populationsstruktur im Südlichen Ozean zu erhöhen. Gleichzeitig werden methodische Limitationen der Signalklassifizierung kritisch bewertet, insbesondere durch Übertragungsverluste und der Deep Learning-basierten Merkmalsextraktion, sowie mögliche Ansätze zu deren Überwindung diskutiert. Darüber hinaus wird erörtert, wie weitere frequenzmodulierte Rufe von Bartenwalen in die entwickelten Analyseansätze integriert werden können und welche zukünftigen Herausforderungen in der Signalklassifizierung bestehen, einschließlich möglicher Ursachen für die Ähnlichkeit von sozialen Rufen verschiedener Bartenwalarten. Des Weiteren wurden Hinsichtlich der Nutzung von Gesangsmerkmalen zur Populationsidentifikation bei Finnwalen der Südhalbkugel zwei weitere Merkmale untersucht: die Abstände zwischen den Signalen (inter-note intervals) sowie Gesangsvarianten. Beide stimmen mit den Ergebnissen der HF-Komponenten überein und wurden gemeinsam hinsichtlich ihrer Anwendbarkeit, Zuverlässigkeit und ihres

Potenzials für das Monitoring bewertet, einschließlich ihres Beitrags zu einer zirkumpolaren Perspektive auf Finnwalpopulationen. Abschließend zeigt d**iese** Dissertation, dass standardisierte analytische Methoden eine wesentliche Voraussetzung für ein zuverlässiges und vergleichbares PAM sind, die durch menschliche Expertise ergänzt werden müssen, um Veränderungen in der Signalstruktur zu erkennen, Ergebnisse zu validieren und die biologische Relevanz sicherzustellen.

Content

Introduction

The overarching aim of this thesis is to evaluate the potential and limitations of PAM for studying baleen whale vocalisations in the Southern Ocean, given persistent challenges in signal interpretation. In particular, I address difficulties in species-level signal classification, focusing on upcalls of southern right and humpback whales as well as frequency-modulated (FM) calls of fin and blue whales, and examine fin whale song characteristics and their variability to assess their relevance for population identification. The introduction firstly provides a concise overview of the methodology passive acoustic monitoring and the range of information that can be extracted from cetacean vocalisations, before summarising commonly used approaches to identify these acoustic signals. Secondly, the focus is directed towards a more detailed exposition of baleen whale acoustic repertoires and their evolutionary drivers, concluding with an overview of the current knowledge gaps in Southern Ocean baleen whale acoustics, which are addressed in this thesis.

Promises and challenges of passive acoustic monitoring

The limits of traditional observational cetacean research

To study cetaceans (whales and dolphins), scientists have turned the ocean into a living laboratory: systematic transects and animal counts to estimate abundance and density (e.g., Bradford et al., 2017; Gladilina et al., 2017; Laake and Punt, 2023); photography for photo-identification to recognise individuals via natural markings and to assess migratory pathways, social relationships, or scarring and skin condition, allowing the documentation of vessel strikes or fishing-gear entanglements, the identification of predatory encounters, or the assessment of skin diseases (e.g., Bertulli et al., 2012; Bigg, 1982; Bigg et al., 1978; Bradford et al., 2009; Corsi et al., 2022; Franklin et al., 2020; Karczmarski et al., 2005; Whitehead et al., 1986); drone imagery to evaluate body condition or group composition (Christiansen et al., 2023; Hartman et al., 2020); and biological sampling of respiratory, faecal, or biopsy material to analyse health, diet, physiology, or genetics (Carroll et al., 2020; Hunt et al., 2013, 2018). This wide field of approaches allows researchers to collect essential data on cetaceans, from large-scale assessments of species distribution and abundance to individual-specific studies (e.g., Bigg, 1982; Frouin-Mouy et al., 2022; Hammond et al., 2013, 2021; Hunt et al., 2013), ultimately helping to determine their conservation status (e.g., Barratclough et al., 2019; Clapham et al., 2008; Cusano et al., 2019; Mellinger et al., 2007; Rendell et al., 2012).

When collecting these data substantial challenges arise, as many species not only inhabit coastal but also remote offshore habitats, and all species are predominantly submerged below the surface (Evans and Hammond, 2004; Hammond et al., 2021). Traditionally, researchers rely on a range of visual methods to find cetaceans in their natural environment and then obtain data samples, possible via land-based observations, vessel or aerial surveys (Hammond et al., 2021; Hunt et al., 2013; Rodofili et al., 2022). However, these approaches are associated with considerable logistical, financial, and human resources. The need for trained observers, dedicated research platforms, and suitable weather, as well as sea conditions make such surveys resource-intensive and often difficult to sustain. Consequently, most monitoring efforts are limited and biased in their temporal and spatial coverage, often underrepresenting remote areas (Braulik et al., 2018; Hammond et al., 2021; Kaschner et al., 2012). Even where survey implementation is feasible, detection probability and data quality remain constrained. Animals at the surface may be missed or misclassified by the observer due to limitations in experience, adverse environmental conditions, such as weather, daylight, sea state, sea ice or cloud coverage, or simply by chance (Hammond et al., 2021). In addition, the presence of vessels, aircraft or uncrewed aerial systems can cause disturbance and alter animal behaviour, potentially further restricting detection or sampling success (Pomeroy et al., 2015).

Improving remote-sensing visual technologies, such as very-high-resolution satellite imagery are providing logistically efficient observations across large and remote areas, offering a promising complement to traditional observation methods (Bamford et al., 2020; Cubaynes et al., 2019; Fretwell et al., 2014; Stewart et al., 2024). However, their effectiveness remains constrained by environmental conditions (such as cloud coverage and sea state), sensor resolution, and costs (Höschle et al., 2021; Turner et al., 2015), limiting their application in many instances.

Passive acoustic monitoring: an alternative approach

Recognizing the limitations of visual surveys, studies have increasingly turned to acoustic approaches that build on the soniferous nature of cetaceans. In the marine environment, where visibility is greatly restricted, the physical properties of water have shaped the sensory ecology of these species. Because sound travels approximately 4.5 times faster in water than in air, it serves as an efficient medium for acoustic perception and communication (Erbe and Thomas, 2022). Consequently, cetaceans highly rely on hearing and sound production for environmental sensing, navigation, communication and mating (e.g., Clark, 1990; Tyack, 2008; Watkins and Schevill, 1972). Given the importance of acoustic communication and echolocation (the use of self-generated sounds and returning echoes to sense the environment) in cetacean ecology, passive acoustic monitoring (PAM) offers an effective method to monitor underwater vocalisations of cetaceans (Clark, 1990; Van Parijs et al., 2009). Over the last decade, continuously improving technologies increased the possibility of passive acoustic data collection to study large spatial and temporal scales, e.g., from a few hours to several years and from local to basin scales (e.g., Darras et al., 2025; Havlik et al., 2022; Sousa-Lima, 2013; Van Parijs et al., 2009; Wall et al., 2025). Thus, to date, PAM is one of the most efficient tools to collect continuous, long-term, and seasonally unbiased data, especially in remote and logistically challenging areas, allowing for the investigation of acoustic presence and related behaviour of cetaceans based on known species-specific signals (e.g., Baumann-Pickering et al., 2015; Burnham, 2019; Mellinger et al., 2007; Schall et al., 2020; Širović et al., 2006).

Insights from cetacean acoustics

Comprising two suborders - toothed whales (*Odontoceti*) and baleen whales (*Mysticeti*) (Würsig, 1989) - cetaceans produce a diverse repertoire of acoustic signals spanning frequencies from approximately 10 Hz to 250 kHz (Kuroda et al., 2020; McDonald et al., 2001), and ranging from pulsed sounds to tonal vocalisations, which in sum cover a wide spectrum of functions.

Echolocation clicks, produced by toothed whales only, are directional, pulsed and broadband signals serving mainly sensory and foraging tasks, enabling the detection and discrimination of prey and the perception of the surrounding environment (Au, 2000; Verfuß et al., 2005). If these broadband clicks are produced in series with extremely short (~20 ms; Fais et al., 2016) inter-click intervals (ICIs), they are referred to as burst pulses. These are often perceived as ‘creaks’ or ‘buzzes’ because individual clicks can no longer be resolved by the human ear (Rankin et al., 2017). Burst pulses have been attributed to both foraging behaviour and social communication. For example, sperm-whale (*Physeter macrocephalus*) creaks have been identified as a type of foraging-adapted signal. In this context, extremely short ICIs (~20 ms) are produced to provide high-resolution updates during the final stages of prey capture (Fais et al., 2016; Miller et al., 2004). Burst pulses may also actively influence prey behaviour, as observed in fish-eating killer whales (*Orcinus orca*), where high-intensity, low-frequency burst pulses are believed to function as herding calls to manipulate prey movement (Simon et al., 2006).

Clicks and burst pulses have been observed to also occur in social contexts across odontocete species. In sperm whales so called ‘slow-clicks’, characterised by long ICIs (~2-24 s), are believed to enable long-range communication between males (Oliveira et al., 2013). In contrast, burst-pulse trains are frequently observed during close-range interactions among conspecifics and are, in this context, interpreted as signals facilitating social or affiliative behaviour. For instance, Heaviside's (*Cephalorhynchus heavisidii*) and striped dolphins (*Stenella coeruleoalba*) generate dense burst-pulse sequences during group coordination and social exchanges (Martin et al., 2019; Papale et al., 2020).

The effective detection range of these odontocete clicks and pulses in PAM is dependent on the signal type and directionality, source level, and environmental conditions (Frasier et al., 2016). Sperm whale usual clicks, which are highly directional, may be detected at distances of approximately 16 km under optimal conditions, whereas creaks have much shorter detection ranges (~6 km) due to lower output and high repetition rates. In contrast, the slow clicks of sperm whales may be detectable up to 60 km (Madsen et al., 2002). In other toothed whale species, the detection ranges are more limited; e.g., the clicks of foraging common dolphins (*Delphinus delphis*) have estimated detection ranges of approximately 1.5–5 km (Frasier et al., 2016).

Besides click-based signals, tonal vocalisations form a second major category of cetacean sounds and are produced in species of both suborders. In toothed whales, the range of tonal signals typically extends from approximately 5 to 20 kHz, although upper limits of up to 40–48 kHz have been observed in certain species. Under favourable conditions, these tonal calls can propagate over several kilometres. Dolphin whistles, for example, can be still detected at distances of up to 25 km (Janik, 2000; Jensen et al., 2012; Quintana-Rizzo et al., 2006). Tonal sounds, often described as whistles, squawks, screams and barks (Herzing 1996), are predominantly produced in social and communicative contexts. For example, in northern resident killer whales, whistles play a key role in close-range communication within groups (Thomsen et al., 2002). White-beaked dolphins (*Lagenorhynchus albirostris*) produce whistles primarily during social activity, with little to no whistling observed during foraging or travelling (Rasmussen and Miller, 2002). Social calls may also support contact in species that forage cooperatively, e.g., short-finned pilot whales (*Globicephala macrorhynchus*) produce whistles during coordinated foraging activities (Jensen et al., 2011). Furthermore, variation in tonal call structure has been demonstrated to convey information regarding group membership or individual identity. Killer whale populations, for instance, demonstrate pod-specific call repertoires that comprise discrete call types not shared among pods, with subtle variations in the production rates and structures among shared call types (Ford, 1984; Miller and Bain, 2000). In numerous delphinid species, tonal calls serve as individual identifiers, with several species producing individually distinctive ‘signature whistles’ (Janik and Sayigh, 2013; Tyack, 1997).

In contrast, baleen whales exhibit diverse vocal repertoires within a frequency range of 0 to 6 kHz, which is favourable for long-range communication with conspecifics. For instance, blue (*Balaenoptera musculus*) and fin whales (*Balaenoptera physalus*) produce high-intensity low-frequency calls, with fin whale calls estimated to travel up to 56 km, while blue whale calls have been detected at ranges up to 200 km (McDonald et al., 2006; Širović et al., 2007; Watkins et al., 1987). However, other baleen whale species produce calls with more limited propagation. Sei whale low-frequency calls, for example, are unlikely to be detected beyond a distance of ~20 km (Calderan et al., 2014). Tonal signals often reflect social interactions and group coordination, where signal diversity is supposed to reflect the complexity of social behaviour (Clark, 1990; Dombroski et al., 2016; Dunlop et al., 2008; Parks and Tyack, 2005). For instance, the right whale (*Eubalaena spp.*) ‘upcall’ has been shown to support contact between groups and is essential for mother-calf communication, especially when visual contact is lost (Dombroski et al., 2016). Social sounds can also be produced in foraging contexts, potentially serving both communicative and prey-influencing functions. Blue whale D- and fin whale 40Hz-calls, for example, are frequently produced during feeding and are thought to facilitate communication among nearby individuals engaged in the same foraging activity (Oleson et al., 2007c; Romagosa et al., 2021). While these are generally associated with foraging behaviour, other species’ calls have well-documented roles in coordinating cooperative foraging. During group lunge feeding in humpback whales (*Megaptera novaeangliae*), an ascending vocalisation was shown to precede the synchronized vertical lunge, indicating its role in initiating cooperative behaviour (D’Vincent et al., 1985). Moreover, paired burst sounds in humpback whales occur exclusively during bottom feeding, particularly under low-light conditions and when conspecifics are nearby, suggesting that these signals either facilitate coordination among foraging individuals, influence prey behaviour, or potentially serve both functions (Parks et al., 2014). While many tonal signals are produced in social and foraging contexts, some baleen whales also produce song, defined as repetitive acoustic patterns (Janik, 2009); in the case of Humpback whales, song can be detected over distances of roughly 18–45 km (Shabangu and Kowarski, 2022). Song production is confined to males and functions as a reproductive advertisement, mediating both female attraction and male-male interactions (Clark, 1990; Croll et al., 2002; Dunlop et al., 2007; Herman, 2017; Oleson et al., 2007a; Payne and McVay, 1971; Vu et al., 2012). Species-specific songs exhibit geographical differences, and can be used to identify acoustic populations and their distributions (e.g., Barlow et al., 2023; Garland et al., 2015; Leroy et al., 2018b; McDonald et al., 2006; Romagosa et al., 2024; Schall et al., 2021b; Torterotot et al., 2020). These population-specific differences also offer valuable insights into population connectivity and the mechanisms of cultural transmission (e.g., Aulich et al., 2019; Balcazar et al., 2015; Castellote et al., 2012; Garland et al., 2015; Garland and McGregor, 2020; Leroy et al., 2021). Beyond reproductive functions, song may also serve as a form of active acoustic sensing. In humpback whales, for instance, singing males are hypothesized to use the echoes of their long, structured songs to detect non-vocalising females on the breeding grounds, functioning as a long-range sonar (Frazer and Mercado, 2000).

Altogether, the analysis of acoustic signals, whether clicks, pulses, tonal signals or song, allows for differentiation on multiple ecological and behavioural scales. At the species and population level, signal parameters can enable the detection of species-specific signals, which can reveal spatial and temporal patterns of occurrence, seasonal or diel trends, and the distribution of acoustic populations (e.g., Aulich et al., 2023; Risch et al., 2013; Schall et al., 2020; Širović et al., 2004; Thomisch et al., 2016). Such analyses also allow for subsequent analysis of impacts of environmental variabilities on the species' distributions (Davis et al., 2020; Schall et al., 2021a; Seyboth et al., 2023). Moreover, differences in signal characteristics can reflect cultural processes and socially learned patterns across cetaceans (e.g., Castellote et al., 2012; Garland et al., 2015; Garland and McGregor, 2020; Leroy et al., 2021; Oliveira et al., 2016). At the individual level, acoustic chracteristics may even reflect sex, age class, individual identity or social role (e.g., Janik and Sayigh, 2013; Parks and Tyack, 2005).

Analysing PAM signals: reliability and limitations

The effective application of PAM in ecological research is dependent on reliable signal identification. One ongoing challenge lies in establishing the link between detected sounds and their biological sources. While unidentified or unattributed sounds can still be analysed for their acoustic characteristics and spatio-temporal patterns (Calonge et al., 2024; Crance et al., 2017; Di Iorio et al., 2018), determining their ecological relevance requires clear evidence of the sound-producing species. Such evidence can be obtained through concurrent visual observations and acoustic recordings, or through the use of animal-borne acoustic tags. However, the reliable attribution of previously unknown sounds to specific species often requires extensive effort and may take several years (e.g., Bolgan et al., 2019; Gedamke et al., 2001; Risch et al., 2014; Watkins, 1981). Although the exact function of most recognized acoustic signals remains unknown, several acoustic signals are linked to certain behaviours (Antunes et al., 2011; Cazau et al., 2016; Dunlop et al., 2008; Gedamke et al., 2001). Nevertheless, even when both the signal source and behavioural context are known, the accuracy of PAM-based observations still relies on the ability to correctly detect and classify the acoustic signal (Mellinger et al., 2007; Van Parijs et al., 2009).

The detection and classification of acoustic signals commonly relies on differences in acoustic parameters and contour in spectrograms (Mellinger et al., 2011). A typical manual approach is to analyse spectrograms using sound analysis software such as Raven Pro (Charif et al., 2010), where so called selection boxes are drawn around detected signals, according to their temporal and spectral limits. Within these boxes, a variety of acoustic parameters, such as the duration, bandwidth, minimum and maximum frequencies, are automatically computed, allowing quantitative comparison and classification among detected signals (see Figure 1 for a visualisation of acoustic parameters).

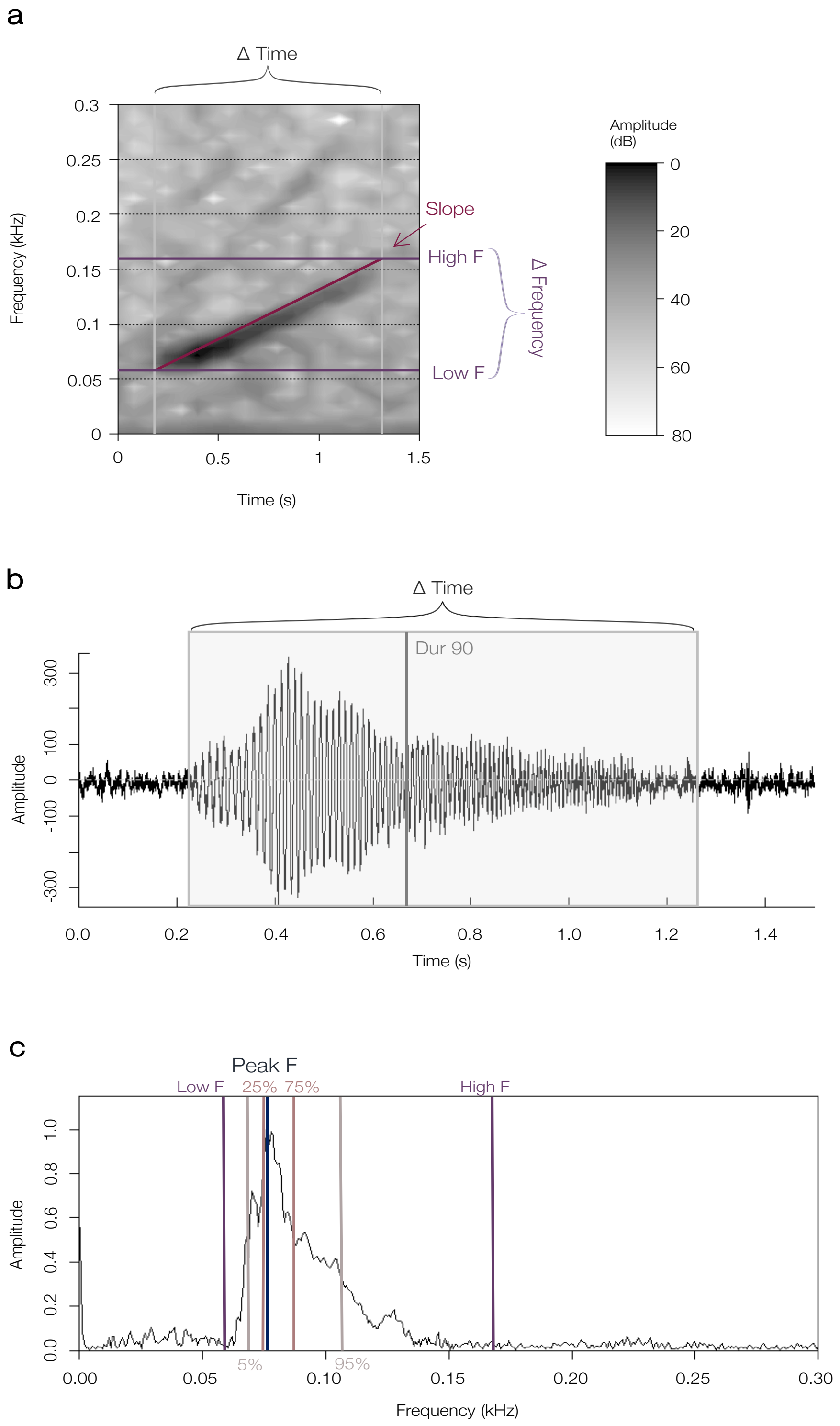

Figure 1. Visualization of exemplary measurements in Raven Pro 1.6. (a) Spectrogram of a southern right whale upcall (recorded on 25 August 2013 off Bahía San Antonio, Argentina) showing the low and high frequency limits (Low F and High F), bandwidth (Δ Frequency) and call duration (Δ Time). (b) Waveform of the same upcall displaying the selected duration (Δ Time) and the duration 90% (Dur 90) measurements. (c) Corresponding frequency spectrum showing low and high frequency limits (Low F and High F), the energy distribution across frequency intervals of 5%, 25% (1st quartile), 75% (3rd quartile), and 95%, and the peak frequency (Peak F), representing the frequency with the highest amplitude. Smoothed spectrogram calculated in a Hanning window with FFT/DFT of 740, and 80% overlap.

However, reliable classification becomes particularly challenging when call characteristics overlap substantially. Distinguishing between calls that share similar contours, frequency limits and bandwidth, or duration can be difficult. Acoustic signals may, for instance, exhibit comparable durations and frequency limits yet differ clearly in their frequency contour. Figure 2 illustrates this using bottlenose dolphin (*Tursiops truncatus*) signature whistles, which show broadly similar durations and lower frequency limits, yet their contours differ clearly: whistle *a* features a down-upsweep pattern, whereas whistle *b* begins with an upsweep followed by repeated down-up modulations.

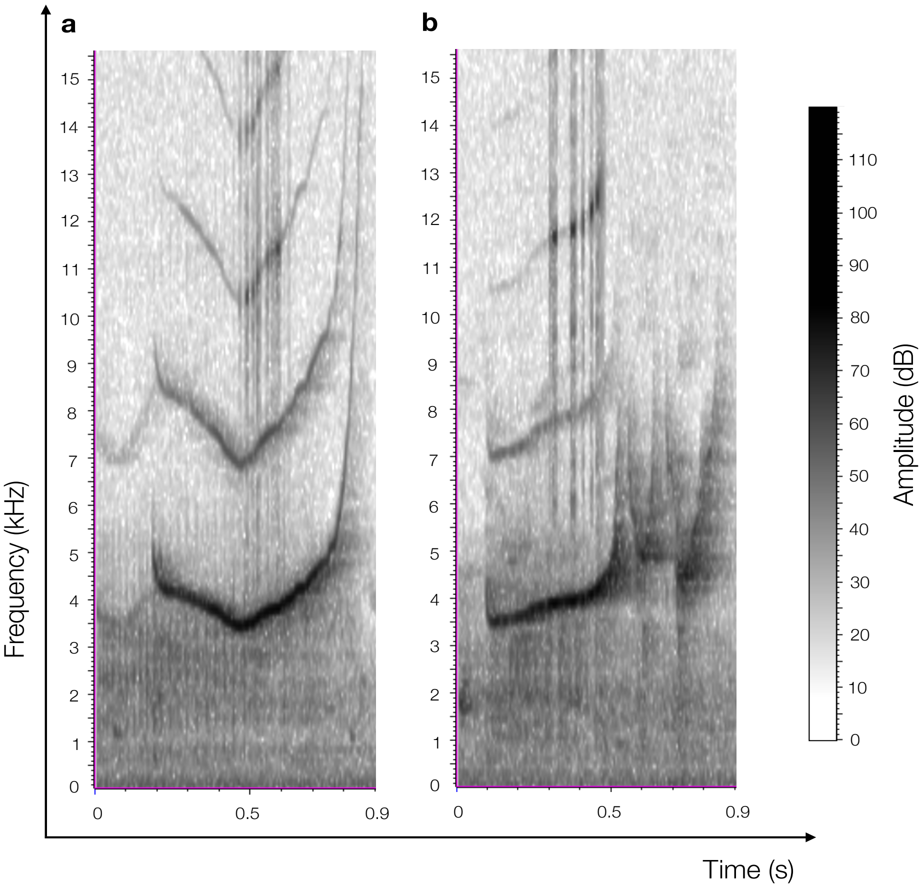

Figure 2. Spectrograms of two bottlenose dolphin signature whistles recorded at the Duisburg Zoo in 2014. Panels a and b each display a different whistle, illustrating their characteristic frequency contours. Smoothed spectrograms calculated in a Hanning window with FFT/DFT of 512, and 80% overlap.

Likewise, the taxonomic classification of toothed whale echolocation clicks remains an ongoing challenge in PAM. Species such as Risso's (*Grampus griseus*) and Pacific white-sided dolphins (*Lagenorhynchus obliquidens*) generate echolocation clicks with similar spectral structures, i.e., comparable distributions of acoustic energy across similar frequency bands (Rankin et al., 2017). In extreme cases, similarity may be so pronounced that calls become nearly indistinguishable. Vocal mimicry, the copying of vocalisations, may provide the clearest example of this challenge. While well documented in birds such as lyrebirds (*Menura spp.*), or European starlings (*Sturnus vulgaris*), which can reproduce heterospecific calls with striking accuracy (Hindmarsh, 1984; Kelley et al., 2008; Townsend, 1924; Zann and Dunstan, 2008). Mimicry also occurs in delphinids: bottlenose dolphins, for example, may copy the signature whistles of conspecifics, likely to directly address specific individuals (Tyack, 1986). Although mimetic copies may show subtle mismatches in frequencies or duration (Zann and Dunstan, 2008), species can reproduce heterospecific calls with such high mimetic accuracy, that they become nearly indistinguishable from the original signal. In such cases, acoustic cues alone are insufficient for reliable caller identification (Hindmarsh, 1984; Townsend, 1924; Tyack, 1986; Zann and Dunstan, 2008).

In addition to acoustic parameters, contextual information, such as the species distribution can assist in signal classification by constraining the range of possible species. However, this approach becomes less effective in regions where species occurrence is greatly overlapping (e.g., Al-Badrawi et al., 2022; Austin, 2021; IWC SORP, 2016, 2019), a challenge that might intensify as climate change drives shifts in species' distributions (Simmonds and Eliott, 2009). Signal classification may also be supported either by the presence of well-known, species-specific call types occurring in close temporal proximity, or by characteristic calling rates that provide additional contextual cues for attributing acoustically similar signals to the correct species (Español-Jiménez et al., 2019; Kowarski et al., 2022). However, environmental and increasing anthropogenic noise may complicate this approach, as many cetacean species adjust their vocal behaviour, such as call rate, in response to changing acoustic conditions (e.g., Dunlop, 2016; Holt et al., 2011; Melcón et al., 2012; Parks et al., 2009). Thus, distinguishing cetacean vocalisations with overlapping acoustic parameters remains a critical challenge, highlighting the need for reliable and standardized classification methods.

Signal diversity: Acoustic communication in baleen whales

Acoustic repertoires: non-song calls vs. song

In the vast and acoustically dynamic marine environment, communication ranges of individuals, groups and sympatric species often overlap. This overlap may impact how signals evolve, particularly when vocalisations play a crucial role in reproduction. The evolution of acoustic signals in baleen whales are likely driven by an interplay of anatomical, environmental, and social factors (Clark, 1990; Clark and Gagnon, 2022; Croll et al., 2002; Elemans et al., 2024; Forrest, 1994; Payne and Webb, 1971).

Adaptation to the marine environment has driven changes in baleen whale vocal anatomy, including modifications of the larynx, which impose physiological limits on frequency range and the water depth of sound production (Elemans et al., 2024). Larger body size further favours the production of lower-frequency sounds that propagate over longer distances underwater, with interspecific differences in body size closely linked to the species-specific frequency ranges and signal structures (May-Collado et al., 2007). Yet, the acoustic environment itself also exerts a strong selective pressure on vocal behaviour.

The physical and biological properties of the ocean – including bathymetry, temperature, salinity, and biological communities – determine how sound propagates (Erbe et al., 2022; Forrest, 1994; Urick, 1984). Consequently, species-specific frequency ranges have evolved to maximise transmission efficiency within their species-specific habitats. Pelagic baleen whale species in particular predominantly produce low-frequency calls (often <100 Hz) that are capable of long-distance transmission, facilitating communication among widely dispersed individuals (e.g., Edds-Walton, 1997; Payne and Webb, 1971; Širović et al., 2009; Watkins, 1981). Another factor influencing the vocal evolution of frequency ranges may be predation risk. By producing low-frequency calls below the detection threshold of potential predators such as killer whales (<100 Hz), some baleen whale species may reduce the risk of being acoustically detected by these predators (Branch, 2025; Parks et al., 2019).

In addition to ecological pressures, social learning and cultural transmission play a crucial role in shaping baleen whale acoustic behaviour. Vocal traditions can spread and evolve within populations, allowing acoustic signals to change independently of genetic differentiation (Garland and Carroll, 2022).

Context-dependent, unpatterned sounds, referred to as ‘social sounds’, may be primarily shaped by ecological pressures (Español-Jiménez et al., 2019; Kowarski et al., 2022). By contrast, structured sounds, known as ‘song’, and confined to males, may be mainly driven by sexual selection (Au et al., 2006; Buchan et al., 2019; Crance et al., 2019; Croll et al., 2002; Herman, 2017; McDonald et al., 2006; Oleson et al., 2007a). Male song functions as a reproductive advertisement, mediating both female attraction and male-male interactions (Clark, 1990; Croll et al., 2002; Dunlop et al., 2007; Herman, 2017; Oleson et al., 2007a; Payne and McVay, 1971; Vu et al., 2012). Sexual selection can operate through both intra-sexual competition, where song signals a challenge to other males within hearing range, and inter-sexual selection, where females use song to assess mate quality (Janik, 2009). However, not all species produce song. Right (*Eubalaena spp.*) and gray whales (*Eschrichtius robustus*), for example, do not appear to sing, although the reasons for this remain unclear. One hypothesis suggests that differences in mating strategies may be a factor. Some species, like right whales, may rely more on sperm competition as their primary reproductive tactic than on acoustic display (Eichenberger et al., 2023).

Produced by both males and females, social sounds are used across a wide range of behavioural contexts (e.g., Calderan et al., 2021; Cerchio and Dahlheim, 2001; Oleson et al., 2007a; Širović et al., 2013). Numerous baleen whale species exhibit distinct call types associated with specific behaviours, with both call rates and acoustic characteristics varying according to individual or group activity (Clark, 1982; Dunlop et al., 2008). For example, unpatterned fin whale 20-Hz pulses function as contact calls and facilitate long-range communication, allowing individuals to maintain contact with conspecifics over large distances (Edds, 1988; McDonald et al., 1995; Širović et al., 2013). Similarly, Antarctic minke whales produce downsweeps primarily as contact calls when conspecifics are out of sight, whereas growls and rumbles are associated with group feeding (Casey et al., 2022). In humpback whales, low-frequency 'grumbles' are thought to mediate social roles within male groups and coordinate interactions. Call rates can also vary with social context; for instance, 'wops', a humpback whale contact call, occurs at lower rates in mother-calf pairs compared to larger groups (Dunlop et al., 2008). Differences in acoustic parameters may further reflect age, as seen in North Atlantic right whale upcalls, where adults tend to produce longer calls than juveniles (Parks et al., 2011).

In contrast to social sounds, song consists of repetitive acoustic patterns and can last up to multiple hours (Janik, 2009; Watkins et al., 1987). Functioning as reproductive display, song production generally follows an annual cycle (Janik, 2009; Tyack, 2022). Most baleen whales undertake seasonal migrations between summer feeding and winter breeding grounds (Horton et al., 2022; Szesciorka et al., 2020), although the extent of migration, the degree of spatial separation between feeding and breeding areas, and the timing of migration can vary across species, populations, and individuals, potentially including sex- and age-dependent differences (e.g., Brown et al., 1995; Geijer et al., 2016; Horton et al., 2022; Mikhalev, 1997; Van Opzeeland et al., 2013). At the onset of the breeding season, both song complexity and calling rate typically increase, reaching a peak during the mating period and subsequently declining towards the end of the season (Oleson et al., 2014; Tervo et al., 2009). Yet song production is not confined to breeding grounds. It has also been documented along migratory routes and on feeding grounds (e.g., Cato, 1991; Clapham, 1996; Noad et al., 2000; Schall et al., 2020; Vu et al., 2012). Clapham (1996) hypothesized that feeding-ground song by humpback whales could act as a low-cost advertisement to oestrous females that did not conceive the previous breeding season, or help reinforce pair bonds in preparation for the upcoming breeding season.

Across species, baleen whale song spans a broad range of structural complexity. While some species produce highly stereotyped song composed of simple, repetitive patterns of a single vocalisation type, as observed in fin whales (Aulich et al., 2019; Gedamke, 2009; Širović et al., 2009), other species, such as blue and pygmy blue whales, produce more complex song that can include combinations of a few vocalisation types forming song phrases (Leroy et al., 2021; McDonald et al., 2001, 2006; Rankin et al., 2005). In contrast, humpback and bowhead whales produce highly complex and hierarchical songs organized into units (vocalisation types), sub-phrases, phrases, and themes (Cholewiak et al., 2013; Delarue et al., 2009; Mercado, 2021; Stafford et al., 2018; Winn et al., 1981). Similar to songbirds, in which females often prefer local dialects and males with foreign dialects may struggle to establish territories, baleen whale songs also exhibit within-species variation that could serve reproductive isolation and, thus, population differentiation (McDonald et al., 2023; Romagosa et al., 2024; Schall et al., 2021b; Slabbekoorn et al., 2002). At least in fin, blue, pygmy blue (*B. musculus brevicauda*), and humpback whales, clear geographic variation among songs recorded at different breeding grounds has been documented (Garland et al., 2015; Gedamke, 2009; Leroy et al., 2021; McDonald et al., 2023). Differences in song structure can occur across several dimensions, forming a continuum of variability and complexity rather than distinct, categorical types.

In species producing simpler song types, such as fin and blue whales, variation often involves changes in the frequencies of specific song components or in the intervals between repetitive calls or song sequences, referred to as inter-note or inter-song intervals (e.g., Aulich et al., 2019; Gedamke, 2009; Jolliffe et al., 2023; Širović et al., 2009). In the more complex songs of humpback and bowhead whales, variation can occur at multiple structural levels. Such changes may include morphing of units and phrases along multiple acoustic dimensions, including e.g., shifts in duration, contour shape, and frequency, or variation in the number of repeated units within a phrase (Cholewiak et al., 2013; Delarue et al., 2009; Stafford et al., 2008; Winn et al., 1981). Independent of the complexity of variations, these differences can be used to identify distinct acoustic populations and their distributions if the type and level of variation is clearly defined (e.g., Barlow et al., 2023; Garland et al., 2015; Leroy et al., 2018; McDonald et al., 2006; Schall et al., 2021; Torterotot et al., 2020). Geographically distinct songs also show both inter- and intra-annual variability across different temporal scales. In species with structurally simpler song types, these variations are often reflected in gradual shifts in signal parameters, including decreases in song frequency and changes in inter-note or inter-song intervals over time (e.g., Jolliffe et al., 2023; Leroy et al., 2018a; Malige et al., 2020; Miller et al., 2014; Oleson et al., 2014; Rice et al., 2022; Romagosa et al., 2024). Humpback whales, with their complex hierarchical songs, exhibit a more dynamic evolution, showing progressive modifications within and between seasons, and occasionally complete replacement of the song, referred to as song revolution (e.g., Allen et al., 2018; Garland et al., 2015; Garland and McGregor, 2020; Noad et al., 2000). While the geographic and temporal differences allow identification of acoustic populations and highlight the interplay between cultural transmission and sexual selection in shaping baleen whale song, the inter- and intra-annual variability may complicate the distinction among populations, making it essential to incorporate such temporal variability into the classification of song types in order to reliably identify population-specific acoustic characteristics.

Given the diversity, variability, and complexity of baleen whale acoustic repertoires, the development of reliable, consistent, and well-defined criteria and analytical methods to differentiate among call types and identify stable acoustic cues is essential (Usman et al., 2020). Such standardised approaches enable robust and comparable analyses across studies and datasets, allowing reliable inference of reproductive behaviour, population structure, or cultural processes from song, as well as group composition, individual characteristics, social interactions, or coordinated foraging from non-song vocalisations. Integrating information from both song- and non-song-signal types within standardised PAM frameworks supports reliable mapping of distribution patterns, habitat use, and effective management and conservation, ultimately providing a comprehensive understanding of baleen whale ecology and population dynamics.

Knowledge gaps in Southern Ocean baleen whale acoustics

Building on the considerations outlined above regarding the interpretation of baleen whale acoustic repertoires, this section focuses on knowledge gaps in Southern Ocean baleen whale acoustics. Available long-term PAM data from a large-scale monitoring system in the Atlantic Sector of the Southern Ocean (Rettig et al., 2013), combined with well-recognised knowledge gaps in baleen whale acoustics, provide a valuable opportunity to assess reliable criteria and methods for signal classification and stability. Accordingly, this thesis addresses challenges in interspecific acoustic signal classification based on four Antarctic baleen whale species - southern right, humpback, Antarctic blue (*B.*

musculus intermedia), and fin whales (Boyd, 2009) - and in using fin whale song characteristics for population monitoring in the Southern Ocean. All four species addressed in this thesis were heavily exploited by historical and industrial whaling. While knowledge of their current abundance, distribution, and behavioural ecology has increased, recovery trends and population connectivity may still be uncertain (e.g., Clapham et al., 2008; Jackson et al., 2020; Savoca et al., 2024; Seyboth et al., 2023). The reliable classification of species-specific acoustic signals and identification of population-specific song characteristics would help to inform these ecological knowledge gaps, by facilitating acoustic monitoring and supporting conservation efforts.

Southern right and humpback whale upcalls

Southern right whales (*Eubalaena australis*) produce a wide range of non-song signals below 1 kHz, including the tonal upcall, which rises in frequency from approximately 50 to 200 Hz over 0.5–1.5 s (Clark, 1982). However, previous studies indicate variation in the frequency limits and bandwidth between and within right whale species (McCordic et al., 2016; Parks et al., 2007, 2009). A similar vocalisation referred to as 'whoop call' or upsweep, is produced by humpback whales as both a non-song signal and as part of song (hereafter also referred to as upcall; Dunlop et al., 2008). The humpback whale upcall rises from approximately 50–740 Hz over a mean duration of around 0.2 s exhibiting overlapping characteristics with southern right whale upcalls, which can be further influenced by transmission loss, shortening or distorting parts of the call and making the signals appear more similar, reportedly complicating reliable species attribution (see Figure 3 for a comparison of upcall types; Forrest, 1994; Gillespie, 2004). Both upcall types function primarily as contact calls, occurring across a range of social contexts, with call rates providing insights into social interactions and group composition, including mother-calf interactions (Dombroski et al., 2016; Dunlop et al., 2008). Accurate species classification of upcalls is therefore critical for interpreting spatio-temporal distribution patterns, recovery trends, and social structure.

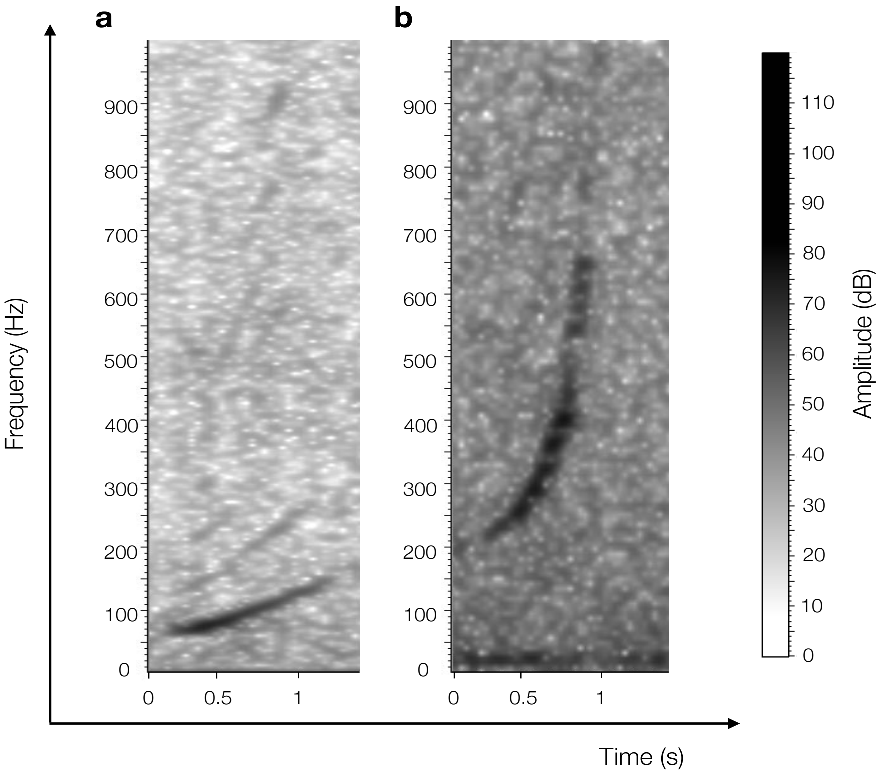

Figure 3. Spectrograms of the two upcall types, illustrating their characteristic frequency contours and ranges. (a) Southern right whale upcall detected in the Bahía San Antonio in 2015 (Zitterbart & Cammareri, SAMBAY), and (b) humpback whale upcall detected at the Greenwich Meridian in 2011 (Schall et al., 2020; Thomisch et al., 2025). Smoothed spectrograms calculated in a Hanning window with FFT/DFT of 512, and 80% overlap.

Fin and blue whale frequency-modulated non-song calls

Another class of non-song vocalisations that is reported as difficult to distinguish in marine passive acoustic recordings comprises the frequency-modulated (FM) calls of baleen whales. Across species, these calls are thought to serve communicative functions, including the coordination of group foraging (Edds-Walton, 1997; Español-Jiménez et al., 2019; Oleson et al., 2007b; Romagosa et al., 2021). Blue, fin, sei and minke whales all produce FM calls that overlap strongly in frequency (~35–150 Hz) and duration (~200 ms to 5 s; Dominello and Širović, 2016; Miller et al., 2021; Ou et al., 2015; Pivari et al., 2024), making reliable species attribution particularly challenging. To date, differentiation among FM calls has largely relied on differences in call duration (Dominello and Širović, 2016; Miller et al., 2021), call contour shape (Ou et al., 2015) or the co-occurrence of other species-specific vocalisations within a defined time window around the FM call (Kowarski et al., 2022). However, these approaches have not been demonstrated to be robust and may limit the possibilities, both spatially and temporally, for attributing calls. To address these limitations, this thesis aims to develop a more robust method for FM call classification, to improve species-level discrimination. Among the mentioned baleen whale species, distinguishing blue and fin whale FM calls, also referred to as D- (McDonald et al., 2001) and 40Hz-calls (Širović et al., 2013; Vega et al., 2023), respectively (see Figure 4 for comparison of calls), is particularly problematic given the extensive global overlap in their distributions (IWC SORP, 2016, 2019). Given that habitat use, population structure, and recovery trajectories of both blue and fin whales in the Southern Ocean remain poorly understood, reliable classification of FM calls, particularly in combination with blue and fin whale song, which exhibit only partly overlapping seasonality (e.g., Huang et al., 2016; Nguyen Hong Duc et al., 2025; Širović et al., 2013) could substantially improve understanding of species occurrence and foraging behaviour in this region. These ecological knowledge gaps, combined with the availability of extensive annotated PAM datasets (Miller et al., 2021), motivated the selection of blue and fin whales as focal species for addressing FM call classification in this thesis.

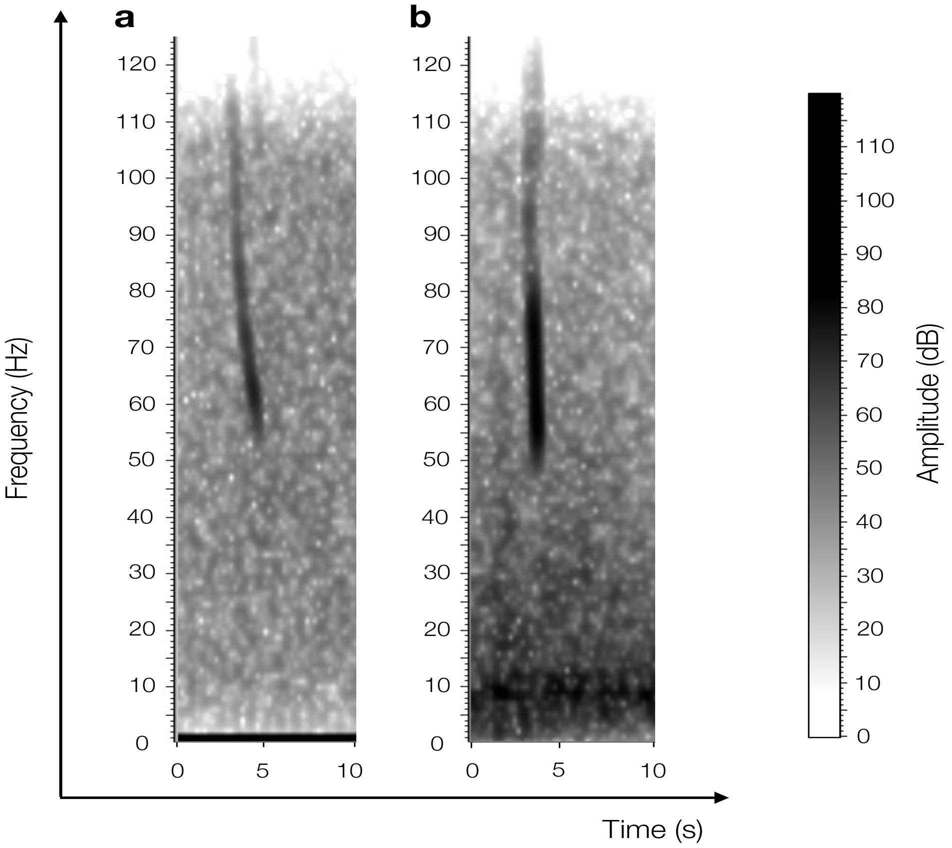

Figure 4. Spectrograms of (a) blue and (b) fin whale FM calls, illustrating their characteristic and highly overlapping frequency contours and ranges. Recorded on animal-borne acoustic tags off California in 2012 (Lewis et al., 2018) and Chile in 2024 (Buchan, unpublished), respectively. Smoothed spectrograms calculated in a Hanning window with FFT/DFT of 256, and 80% overlap.

Fin whale song – population specific cues

Beyond the challenges of classifying non-song signals, identifying stable and population-specific cues in fin whale song is crucial to monitor acoustic populations in this species. As observed in other baleen whale song, fin whale song undergoes both inter- and intra-annual changes (e.g., Leroy et al., 2018a; Rice et al., 2022; Romagosa et al., 2024; Wood and Širović, 2022), underscoring the importance of evaluating which acoustic parameters remain stable enough to serve as reliable population indicators. In the absence of genetic or morphological data, these acoustic parameters can provide insights into population structure and distribution, supporting targeted and effective conservation management strategies (e.g., Balcazar et al., 2015; Bérubé et al., 1998; Clapham et al., 2008; Henry et al., 2015). Globally, fin whale song consists primarily of the well-known, stereotyped 20-Hz pulse. A short (~1 s), high-intensity sound (160–186 dB re 1 µPa at 1 m) centred around 20 Hz and typically sweeping from approximately 28 Hz down to 15 Hz (see Figure 5; Širović et al., 2013; Thompson, n.d.; Watkins, 1981). Differentiation of song types in fin whales is predominantly based on song characteristics such as the inter-note interval (INI), which refers to the time between the start of consecutive notes or pulses within a song sequence (see Figure 5, for illustration of fin whale song characteristics; Castellote et al., 2012; Romagosa et al., 2024; Watkins et al., 1987; Wood and Širović, 2022). The INI is the most distinctive and region-specific song parameter, particularly across the Northern Hemisphere, and has been used globally to identify acoustic populations, partly corresponding to genetic differentiation (Bérubé et al., 1998; Castellote et al., 2012; Delarue et al., 2009; Hatch and Clark, 2004; Romagosa et al., 2024). However, INIs exhibit both inter- and intraannual variation, and can change substantially over time (e.g., Romagosa et al., 2024; Wood and Širović, 2022).

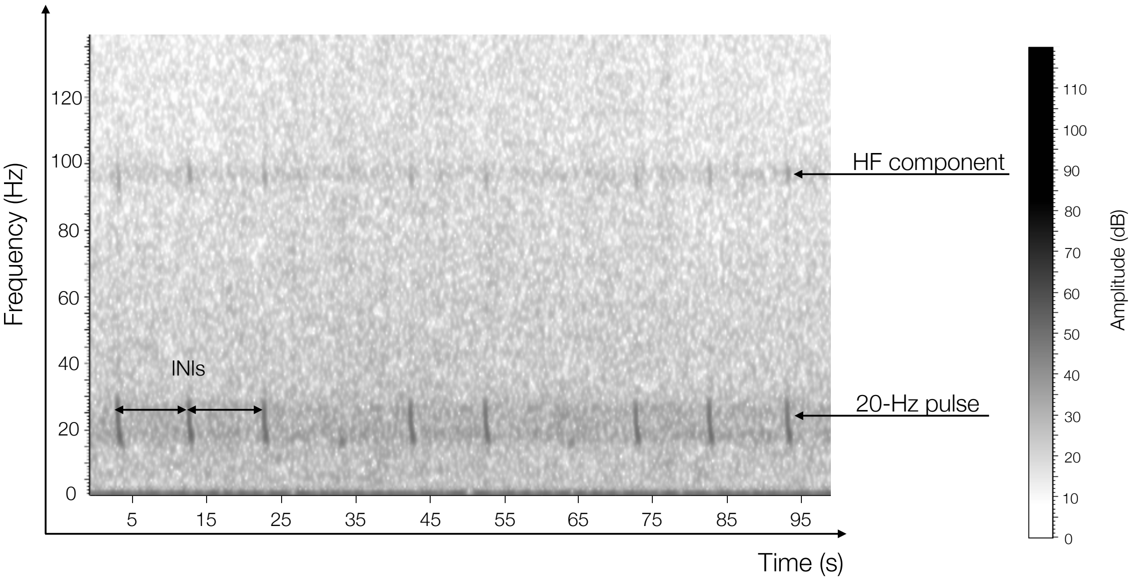

Figure 5. Visualization of Southern Hemisphere fin whale song recorded along the Greenwich Meridian on 7 March 2013. Spectrogram displaying 20-Hz pulses with associated high-frequency (HF) component, showing a peak frequency around 99 Hz, and illustrating the inter-note interval. Grey background bands represent choruses generated by spectrally and temporally overlapping 20-Hz pulses and their corresponding HF components. Smoothed spectrograms were calculated using a Hanning window with a 5000-point FFT/DFT and 80% overlap.

In some cases, the presence of a high-frequency (HF) component, which accompanies the 20-Hz pulse (but which is not harmonically related to its fundamental), has likewise been suggested as a valuable characteristic for identifying acoustic populations in the Southern Ocean (Gedamke, 2009; Simon et al., 2010; Wood and Širović, 2022). In the Northern Hemisphere, a single HF component has been reported around 125–130 Hz, showing little evidence of regional differentiation (Garcia et al., 2019; Romagosa et al., 2024). In contrast, five region-specific HF components have been described in the Southern Ocean, ranging between 60 and 100 Hz, with two varieties recorded in the Atlantic Sector of the Southern Ocean at ~86 and 99 Hz (e.g., Åsvestad et al., 2024; Burkhardt et al., 2021; Constaratas et al., 2021; Gedamke, 2009; Leroy et al., 2018b; Shabangu et al., 2020; Širović et al., 2004). In addition to the geographical differences the HF component appears to be relatively consistent over time (Castellote et al., 2012; Constaratas et al., 2021; Gedamke, 2009; Širović et al., 2009). However, like INIs in fin whale song, HF components also undergo inter- and intraannual changes, with decreases in frequency reported across and within seasons (Leroy et al., 2018a). This variability highlights the importance of identifying which acoustic parameters remain sufficiently stable to serve as reliable population indicators, providing insights into the spatio-temporal distribution and population structure of fin whales in the Southern Ocean, and, thus, supporting targeted conservation strategies.

Objectives

The overarching aim of this thesis is to evaluate the potential and limitations of PAM for studying baleen whales in the Southern Ocean, given persistent challenges in signal interpretation and population identification. While PAM offers extensive temporal and spatial coverage, its effective application depends on the ability to reliably interpret acoustic signals and attribute them to species or populations. This thesis addresses these challenges by investigating both non-song calls and structured song, with a particular focus on identifying reliable acoustic cues and assessing methods for interpreting baleen whale acoustic signals.

To achieve this aim, the thesis is structured around two overarching objectives, which are addressed through four individual chapters. Each chapter targets specific research questions, outlined below.

Objective 1: Interpreting non-song calls and assessing species specificity

The first objective is to assess acoustic behaviour, with a focus on non-song calls across multiple baleen whale species. This includes evaluating the reliability of species attribution using PAM, particularly where similar signal properties and calling contexts complicate identification. This objective is addressed in:

Chapter 1 – Verifying the acoustic presence of Southern Right Whales (*Eubalaena australis*) off Elephant Island

Chapter 1 addresses the question of which call characteristics drive the differences between southern right and humpback whale upcalls, to improve species attribution in regions of overlapping occurrence.

Chapter 2 – Searching for Separation between frequency-modulated calls of blue and fin whales

Chapter 2 investigates how frequency-modulated (FM) calls of blue and fin whales can be reliably differentiated, testing approaches of separation using traditional call characteristics and features extracted through pre-trained deep-learning models.

Remaining open questions of Chapters 1 and 2, particularly regarding the emerging challenges for reliable call classification under changing acoustic conditions, will be addressed in the synthesis of this thesis.

Objective 2: Characterising and evaluating song-based cues for fin whale population identity

The second objective is to examine different characteristics of fin whale song, including frequency bands of choruses and individual pulses, to analyse the spatio-temporal patterns of acoustic population presence, providing baseline information relevant to management in the Southern Ocean. This objective is addressed in:

Chapter 3 – Geographical distribution of two acoustic fin whale populations across the Weddell Sea

This chapter examines the spatial distinctiveness of high-frequency components in fin whale song across the Atlantic Sector of the Southern Ocean and evaluates their potential relevance for inferring population specificity.

Chapter 4 – Shifts in Acoustic Signature of Southern Hemisphere Fin Whales: Declining Peak Frequency of High-Frequency Components

Chapter 4 addresses whether high-frequency components represent stable and robust acoustic cues for identifying Southern Hemisphere fin whale populations over time.

Remaining open questions of Chapters 3 and 4, specifically on the use of INIs and different song variants in Southern Ocean fin whales, will be addressed in the synthesis of this thesis.

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Exploring and verifying the acoustic presence of southern right whales (*Eubalaena australis*) off Elephant Island, Antarctica

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JASA ARTICLE

Exploring and verifying the acoustic presence of southern right whales (*Eubalaena australis*) off Elephant Island, Antarctica

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ABSTRACT:
Passive acoustic monitoring (PAM) can be used to monitor acoustic presence and behaviour of cetaceans, providing continuous, long-term, and seasonally unbiased data. The efficiency of PAM methods, however, depends on the ability to detect and correctly interpret acoustic signals. The upcall is the most prevalent vocalization of the southern right whale (*Eubalaena australis*) and is commonly used as a basis for PAM studies on this species. However, previous studies report difficulties to distinguish between southern right whale upcalls and similar humpback whale (*Megaptera novaeangliae*) vocalizations with certainty. Recently, vocalizations comparable to southern right whale upcalls were detected off Elephant Island, Antarctica. In this study, these vocalizations were structurally analyzed, and call characteristics were compared to (a) confirmed southern right whale vocalizations recorded off Argentina and (b) confirmed humpback whale vocalizations recorded in the Atlantic Sector of the Southern Ocean. Based on call features, detected upcalls off Elephant Island could be successfully attributed to southern right whales. Measurements describing slope and bandwidth were identified as the main differences in call characteristics between species. With the newly gained knowledge from this study, additional data can be analyzed providing further insight into temporal occurrence and migratory behaviour of southern right whales in Antarctic waters. https://doi.org/10.1121/10.0019633

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I. INTRODUCTION

Since acoustic signals play a major role in cetacean ecology (Clark, 1990), passive acoustic monitoring (PAM) methods can be used to monitor underwater vocalizations of cetaceans and even help to investigate related behaviors (Clark, 1982; Van Parijs *et al.*, 2009). Over the last decades, continuously improving technologies increased the possibility of passive acoustic data collection over large spatial and temporal scales (Van Parijs *et al.*, 2009), providing continuous, long-term, and seasonally unbiased data of sound-producing marine fauna in different types of marine environments (Mellinger *et al.*, 2007). These features make PAM invaluable for studies on marine mammals in logistically challenging areas (Ahonen *et al.*, 2019; Calderan *et al.*, 2021; Frouin-Mouy *et al.*, 2019). Within recordings, vocalizations are identified based on variations in signal duration, frequency range and bandwidth, and their general visio-aural appearance in spectrographic images, thereby allowing the differentiation of species, and in some cases even of populations or individuals (Janik and Sayigh, 2013; Mellinger *et al.*, 2007). The efficiency of PAM methods depends on the ability to detect and correctly attribute acoustic signals to certain species, relying on baseline information on the species-specific signature features and acoustic behavior (Mellinger *et al.*, 2007; Van Parijs *et al.*, 2009). Such knowledge, in most cases, is obtained from concurrent acoustic and visual observations of the species. The bio-duck sound, for example, was an unidentified sound for several decades in the Southern Ocean before it was successfully attributed to the Antarctic minke whale through the deployment of dTAGs (*Balaenoptera bonaerensis*; Risch *et al.*, 2014).

In some cases, similarities in vocalization parameters of sympatric species are problematic for PAM studies, as this may cause difficulties in correctly identifying species based on their vocalizations with certainty (Gillespie, 2004). For instance, the effective acoustic detection and discrimination of blue whale (*Balaenoptera musculus*) D-calls, fin whale (*Balaenoptera physalus*) 40 Hz-calls, and sei whale (*Balaenoptera borealis*) downsweeps in PAM recordings was reported as being not a trivial task, since all three vocalizations represent a downsweep over a similar frequency range (Huang *et al.*, 2016; Ou *et al.*, 2015). Recently, Ross-Marsh *et al.* (2022) proposed that humpback whales (*Megaptera novaeangliae;* hereafter referred to as HW) also produce high-intensity vocalizations similar to the so-called gunshots, which so far only have been attributed to right whales (*Eubalaena spp.*; Parks and Tyack, 2005), possibly causing problems in correct species identification for PAM studies. Additionally, Gillespie (2004) indicates difficulties to distinguish between right whale upcalls, the most

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commonly detected right whale call (e.g., Clark, 1982; Parks and Tyack, 2005; Urazghildiiev *et al.*, 2009; Calderan *et al.*, 2021), and similar vocalizations of HWs, since the acoustic characteristics of these signals overlap (Gillespie, 2004; Wild and Gabriele, 2014). In the context of understanding long-term species-specific distribution patterns and ecological niches, it is relevant to develop robust methods to acoustically distinguish species, without the need for simultaneous visual observation.

The waters off Elephant Island (hereafter EI, 61 °S 55 °W), which is part of the South Shetland Islands and located at the tip of the Antarctic Peninsula (Orsi *et al.*, 1995), are considered to represent an important foraging ground for baleen whales (Santora *et al.*, 2010; Santora and Veit, 2013; Burkhardt *et al.*, 2021). The presence of southern right whales (*Eubalaena australis*; hereafter referred to as SRW) has not been acoustically verified at EI to date, but opportunistic sighting and tagging data indicate at least sporadic presence (Vermeulen *et al.*, 2021; Zerbini *et al.*, 2018). Previous analyses by Schall *et al.* (2020) detected unknown vocalizations similar to SRW upcalls (Calderan *et al.*, 2021; Clark, 1982; Urazghildiiev *et al.*, 2009; Webster *et al.*, 2016) in passive acoustic data from EI from 2013. Therefore, the aim of this study was to investigate available acoustic datasets for the potential acoustic presence of SRWs off EI, by comparing upcalls of SRWs and HWs and developing a reliable decision structure to distinguish these species acoustically.

II. MATERIAL AND METHODS

A. Study area and sampling

Passive acoustic data from EI (hereinafter referred to as unidentified upcalls) were obtained using a SonoVault autonomous recorder (Develogic GmbH, Hamburg, Germany, Reson TC4037-3 hydrophone, -193 dB re1 V μPa^{-1} hydrophone sensitivity, 48 dB amplification gain, 24-bit resolution), which continuously recorded at a sampling frequency of 5333 Hz (Fig. 1 and Table I) from 15 January 2013 to 09 November 2013. The recorder was attached to a mooring at 212 m depth. As baseline data for SRW upcalls (hereinafter referred to as confirmed SRW upcalls), passive acoustic recordings with visual confirmation of SRWs gathering in Bahía San Antonio (BSA), Argentina, were analyzed (Fig. 1). Acoustic data were recorded using an array of six SoundTrap 202 STD recorders (Ocean Instruments, New Zealand, -205 dBV re 1 μPa sensitivity, max level before clipping of 186 dB re 1 μPa gain, 16-bit successive approximation resolution) at a 4000 Hz sampling frequency, for 14 days from 24 August to 6 September 2015. HW song including similar vocalizations to SRW upcalls were recorded in the Southern Ocean along the Greenwich Meridian (GM1, GM2, and GM3, summarized as GM) in 2011 and were also obtained with SonoVaults using the identical recording setting as EI (see Table I for deployment information).

B. Data processing

1. Data selection

Information on the presence of unidentified upcalls was available for EI through previous work within the Ocean Acoustics Group of the Alfred-Wegener-Institute. In previous analyses of passive acoustic data from EI from 2013 the "low frequency detection and classification system," (LFDCS; Baumgartner and Mussoline, 2011) and a custom-made acoustic-context filter to detect HW vocalizations were used. The detector found vocalizations allegedly produced by HWs, but which could not be visually confirmed as such in the spectrogram by a human analyst (Schall *et al.*, 2020). With this method, only even hours of the full dataset of EI recordings were previously analyzed, therefore only even hours containing detections of unidentified upcalls, and the adjacent odd hours were considered in this study. For the multi-channel BSA data, only one of the six channels was used for analysis in this study to avoid logging the same vocalization multiple times. Of the 14 recorded days, only

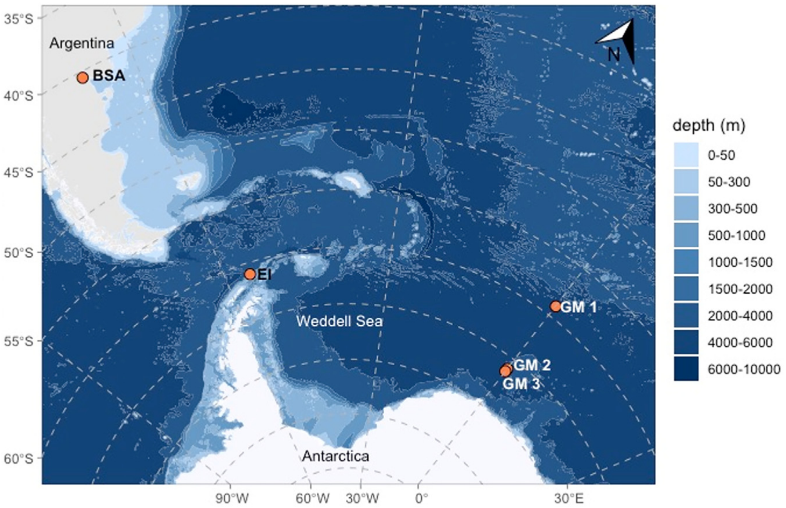

FIG. 1. (Color online) Bathymetric map of the southern Atlantic and the Southern Ocean including the geographical locations of the five acoustic recorders used in this study. Bathymetry data from Amante and Eakins (2009).

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TABLE I. Deployment information on passive acoustic recordings.

Recording ID	Latitude	Longitude	Sampling frequency (Hz)	Recorder depth (m)	Duration of recordings
EI - AWI251-01_SV1008	61 0.88 °S	55 58.53 °W	5333	212	2013-01-15 – 2013-11-09
BSA - Argentina	40 48.46 °S	65 58.20 °W	4000	10–25	2015-08-24 – 2015-09-06
GM1 - AWI227-11_SV0002	59 3.02 °S	000 6.63 °E	5333	1007	2010-12-11 –2011-08-22
GM2 - AWI230-07_SV1001	66 1.9 °S	000 3.25 °E	5333	934	2010-12-16 – 2012-09-17
GM3 - AWI231-09_SV1002	66 30.71 °S	000 1.51 °W	5333	1083	2010-12-17 – 2011-08-14

ten days (i.e., from 25 August to 05 September) were considered to avoid effects of noise pollution caused by deployment and retrieval of equipment. The passive acoustic data of GM recorders in the Atlantic sector of the Southern Ocean (ASSO) had also been pre-processed for song structure analysis of HW songs in a previous study by Schall *et al.* (2021). Seven days of song recordings with confirmed HW song units from the ASSO, were chosen for this study. The recordings are assumed to be of different HW individuals (see Schall *et al.*, 2021b for details on singer differentiation) and song units include vocalizations which can be described as upcalls.

2. Manual data processing

The upcall is produced by all age classes and both sexes, on both breeding and foraging grounds (Calderan *et al.*, 2021; Clark, 1982; Dombroski *et al.*, 2016) and can therefore be used as a reliable indicator of SRW (acoustic) presence. The SRW upcall represents a social, low-frequency signal rising in frequency from a mean low of 50 Hz, to a mean high frequency of 200 Hz as described by Clark (1982) and was identified in the recordings as such.

Compared to SRWs, HWs are known to produce social sounds and songs (D'Vincent *et al.*, 1985; Payne and McVay, 1971; Silber, 1986). One specific HW vocalization, in the literature described as "wop," "whup," or "upsweep" (hereafter also referred to as upcall; Dunlop *et al.*, 2007; Wild and Gabriele, 2014) also represents a tonal signal rising in frequency with mean low and high frequency limits of 52 and 743 Hz, respectively. As the HW upcall is used in a broad range of contexts (Wild and Gabriele, 2014), it is often produced as social sound (Dunlop *et al.*, 2007), but is also found in HW song (Payne and McVay, 1971). In order to ensure that only HW upcalls (hereinafter referred to as confirmed HW upcalls) were considered for the comparative analyses, only upcalls from HW songs were analyzed (see Schall *et al.*, 2020).

All passive acoustic recordings were analyzed using the sound analysis software Raven Pro 1.6 (The Cornell Lab of Ornithology, Center for Conservation Bioacoustics, Ithaca, NY), with which spectrograms were calculated and visually scanned for upcalls. The upcalls for acoustic measurements were chosen based on the visibility within the spectrogram. We did not filter out vocalizations according to their signal-to-noise ratio (SNR) because topographic features and therefore acoustic propagation were different at each sampling site (Forrest, 1994; McKenna *et al.*, 2021). Instead, we focused on finding the largest number of upcalls in the recordings in order to produce a robust acoustical characterization of the different upcall groups. All analyses were performed using smoothed spectrograms in a Hanning window, with 50% overlap. To allow for a precise comparison of acoustic measurements from spectrograms between the different sampling rates of the recorders, window sizes for spectrogram calculation were adjusted for each recording position (see Table SII in the supplementary material[1]). A series of acoustic parameters were automatically extracted using available measurements in Raven Pro 1.6, to allow for numeric comparisons among vocalizations and with other studies (Table II).

C. Statistical analysis

Selection tables containing quantitative acoustic measurements were exported from Raven Pro 1.6 and imported into RStudio Version 2021.09.02 (RStudio Team, 2020) for statistical analysis. To attempt to statistically verify the influence of the factor "group" (the different upcall classes detected off EI, BSA, and GM, respectively) on the variability of acoustic measurements, several non-parametric statistical approaches within the R package "vegan" were implemented (Oksanen *et al.*, 2020). An analysis of similarities (ANOSIM) based on the rank order of dissimilarities using the function "anosim" and a permutational analysis of variance (PERMANOVA) using the function "adonis" were performed to examine if the groups are different from each other (we performed both tests, since the sensitivities towards particular assumptions are different). Both tests were performed with 10 000 permutations, using the Bray-Curtis and the Euclidean distance as distance measures. Further, a pairwise comparison using the packages "vegan" and "pairwiseAdonis" (function "pairwise.comparison") was conducted to determine which groups' vocalizations were different based on their acoustic characterization (Martinez Arbizu, 2020). Additionally, to avoid biased results through an un-balanced design, all three tests were also performed with ten random subsets of 350 samples each from the EI dataset, using the original dataset-sizes from BSA and GM (i.e., $n_{BSA} = 348$, $n_{GM} = 354$). Furthermore, a Similarity Percentage (SIMPER) analysis within the package "vegan" was applied (function "simper") using the Bray-Curtis distance measure to determine the contribution of each acoustic measurement to the dissimilarities between groups. To visualize groupings of samples based on the quantitative acoustic measurements, a non-

TABLE II. Quantitative measurements to describe detected upcalls of southern right and humpback whales in Argentina and the Atlantic sector of the Southern Ocean. Parameters were calculated according to the temporal and spectral limits of the respective vocalizations by drawing selection boxes around detected vocalizations. Details on measurements according to the Raven Pro 1.4 User's Manual (Charif *et al.*, 2010).

Measurement	Description
Low frequency	Lower frequency limit of the selection box in Hz.
High frequency	Upper frequency limit of the selection box in Hz.
Delta frequency	The difference between the upper and lower frequency limits of the selection box in Hz.
Center frequency	The frequency that divides the selection into two frequency intervals of equal energy in Hz.
Frequency 25%	The frequency that divides the selection into two frequency intervals containing 25% and 75% of the energy in Hz.
Frequency 75%	The frequency that divides the selection into two frequency intervals containing 75% and 25% of the energy in Hz.
Frequency 5%	The frequency that divides the selection into two frequency intervals containing 5% and 95% of the energy in Hz.
Frequency 95%	The frequency that divides the selection into two frequency intervals containing 95% and 5% of the energy in Hz.
Delta Time	The difference between begin time and end time of the selection in s.
Duration 90%	The difference between the point in time that divides the selection into two time intervals containing 5% and 95% of the energy (Time 5%) and the point in time that divides the selection into two time intervals containing 95% and 5% of the energy in the selection in s.
Slope	The slope of the selection, calculated as delta frequency divided by delta time in Hz/s.

metric multidimensional scaling (NMDS) was used to reduce the multiple dimensions of conducted measurements to two dimensions within the R package "vegan."

D. Automatic classification of vocalizations

To evaluate the discrimination potential of conducted measurements we used a random forest classification model in RStudio (Breiman, 2001), a supervised machine learning algorithm. The Boruta algorithm (Kursa and Rudnicki, 2010) was additionally applied to identify relevant measurements as predictor variables for the classification model. We used the Boruta function in the R Boruta package (Kursa and Rudnicki, 2010). To develop the random forest model, we used the randomForest function from the randomForest package (Liaw and Wiener, 2002). The training data set consisted of the measurements from vocalizations detected off BSA and GM, while the validation data set consisted of the ones from EI. We grew 500 trees with a node size of 1 and tested three predictor variables at each split.

III. RESULTS

In the total amount of 496.5 analyzed hours of acoustic recordings 1827 upcalls were logged and measured. From a total of 102 h of EI data, 1125 unidentified upcalls were logged. Upcall vocalizations off EI were detected from January to May and in August. While 1120 upcalls were detected in austral summer with a peak in April, only five upcalls were detected during the austral winter month of August (see Fig. S3 in the supplementary material[1]). For comparison, 348 and 354 confirmed upcalls from SRWs and HWs were logged in the 226.5 h of BSA and 168 h of GM data, respectively.

A. Manual data processing

The frequency of unidentified upcalls recorded off EI rose from a mean minimum of 113 Hz to a mean maximum of 181 Hz. Vocalization frequency in some cases did range from a minimum low frequency of ∼44 Hz to a maximum high-frequency value of ∼401 Hz. EI upcalls had a mean bandwidth of ∼67 Hz and an average duration of 0.56 s. The detected vocalizations were characterized by a mean slope of ∼137 Hz/s. Confirmed SRW vocalizations detected in the BSA had a mean low frequency of ∼75 Hz and a mean high frequency of ∼162 Hz. The slope of the vocalization averaged to 104 Hz/s with a mean bandwidth of ∼86 Hz and a mean duration of 0.89 s. Frequencies of the HW vocalizations detected at GM ranged on average from 116 to 568 Hz, while the mean duration was 0.51 s. The mean bandwidth was 452.27 Hz resulting in a mean slope of ∼1024 Hz/s (Fig. 2 and Table III).

When scaling the various acoustic measurements with the NMDS method, two dimensions were chosen to collapse information. The measurements are arbitrarily represented in the dimensions to optimally display the dissimilarities in the ranked data. A low stress value ($<0.1 =$ good) indicates the distances are well represented in only two dimensions. Accordingly, the stress value of 0.037 indicates an excellent fit of ordination (Clarke, 1993). All analyzed vocalizations are clearly split into two groups, namely, the EI and BSA vocalizations as a single group and the GM vocalizations as a separate group (Fig. 3).

For brevity, only the results of the ANOSIM and PERMANOVA that were based on the Bray-Curtis distance measures on the whole data set will be reported here, since statistics using the Euclidean distance measures, as well as multiple random subsamples resulted in similar outputs and lead to the same conclusions as the statistical results presented here. The ANOSIM applied to the complete data set (R-value $= 0.8174$ and p-value $= 9.999 \times 10^{-05}$) suggested greater dissimilarities between than within groups, with a high significance level. The F-value of the performed PERMANOVAs (F-value $= 3148.1$, p-value $= 9.999 \times 10^{-05}$ and $R^2 = 0.77537$) demonstrates a significant group separation, while the determination coefficient value indicates a good fit for the variation explained by groups. Since the assumption of homogeneity was violated when conducting

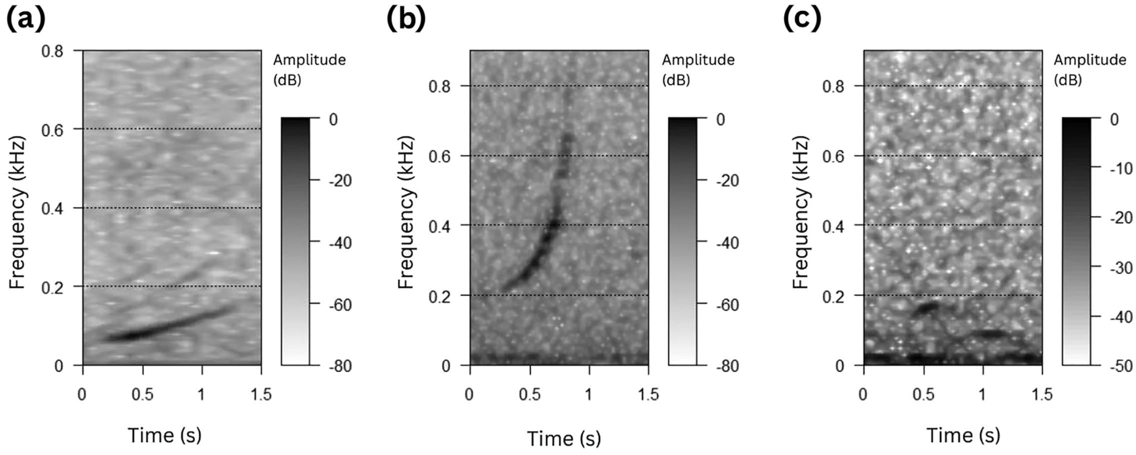

FIG. 2. Spectrograms of analyzed upcalls. (a) Southern right whale upcall detected off BSA, (b) humpback whale upcall detected at the GM, and (c) unidentified upcall detected off EI. Spectrograms calculated with fast Fourier transform (FFT) 740 (a,b), and FFT 850 (c), a Hanning window and 50% overlap.

TABLE III. Summary statistics of measured upcall vocalization characteristics: minimum (min), mean, maximum (max) values, and standard deviation (sd), shortened to a single decimal digit. Explanations on how the different measurements were conducted can be found in Table II.

Group	Measurement	Mean	SD	Min	Max
EI	Low freq (Hz)	113.9	24.3	44.0	353.4
	High freq (Hz)	181.9	21.3	103.6	401.2
	Delta freq (Hz)	68.0	19.3	23.6	154.8
	Duration (s)	0.6	0.3	0.18	2.4
	Center freq (Hz)	146.4	25.1	72.9	375.0
	Freq 25 (Hz)	134.3	25.9	62.5	369.8
	Freq 75 (Hz)	159.0	23.1	83.3	380.2
	Freq 5 (Hz)	121.2	25.2	46.9	364.6
	Freq 95 (Hz)	172.2	21.6	93.7	390.6
	Dur 90 (s)	0.4	0.2	0.1	20.2
	Slope (Hz/s)	137.3	51.3	34.6	418.6
BSA	Low freq (Hz)	75.7	38.3	42.4	321.5
	High freq (Hz)	162.3	46.7	99.0	442.9
	Delta freq (Hz)	86.6	24.3	36.0	177.8
	Duration (s)	0.9	0.3	0.3	1.7
	Center freq (Hz)	103.8	42.0	66.4	371.1
	Freq 25 (Hz)	93.0	40.2	62.5	339.8
	Freq 75 (Hz)	117.0	43.6	70.3	382.8
	Freq 5 (Hz)	83.6	39.0	50.8	332.0
	Freq 95 (Hz)	137.5	44.7	82.0	410.2
	Dur 90 (s)	0.6	0.2	0.1	1.3
	Slope (Hz/s)	104.4	41.7	33.9	370.3
GM	Low freq (Hz)	116.6	55.5	30.2	464.9
	High freq (Hz)	568.8	147.4	238.4	1006.6
	Delta freq (Hz)	452.3	139.7	109.7	910.5
	Duration (s)	0.5	0.2	0.1	0.9
	Center freq (Hz)	252.2	76.5	72.9	593.7
	Freq 25 (Hz)	198.7	65.9	52.1	531.2
	Freq 75 (Hz)	317.1	87.0	104.2	677.0
	Freq 5 (Hz)	146.3	59.4	31.3	510.4
	Freq 95 (Hz)	434.4	112.8	187.5	812.5
	Dur 90 (s)	0.3	0.1	0.3	0.7
	Slope (Hz/s)	1024.5	508.4	336.5	3090.6

the previously listed tests, the reported statistical results have to be interpreted with caution. Therefore, we also describe in the following the visual comparison of vocalization characteristics in the form of boxplots and a random forest analysis, which does not rely on the assumption of heterogeneity.

To better reveal the drivers of similarities and dissimilarities between the groups, the median and range values of the calculated measurements were compared (Fig. 4). In conjunction with the boxplots, we examined the median, since it is unaffected by extreme outliers in the data. Low-frequency measurements of upcalls from EI had similar overall ranges compared to BSA but with a higher median and interquartile range at EI. In comparison to EI, the low-frequency limits of vocalizations recorded at GM had a greater overall range. High-frequency limits of EI

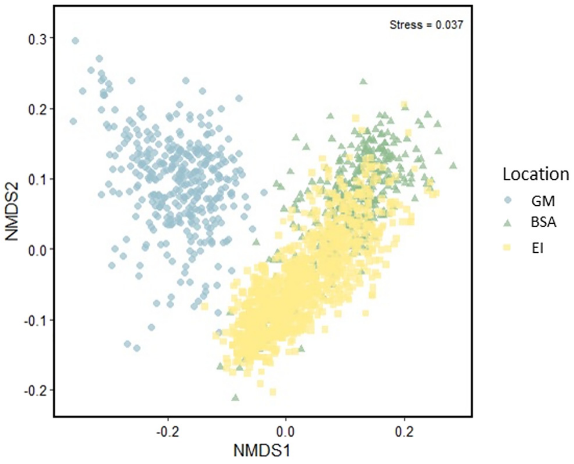

FIG. 3. (Color online) NMDS plot representing the two-dimensional grouping of analyzed vocalizations. Stress value = 0.037. (GM, confirmed humpback whale upcalls; BSA, confirmed southern right whale upcalls; EI, unconfirmed upcalls).

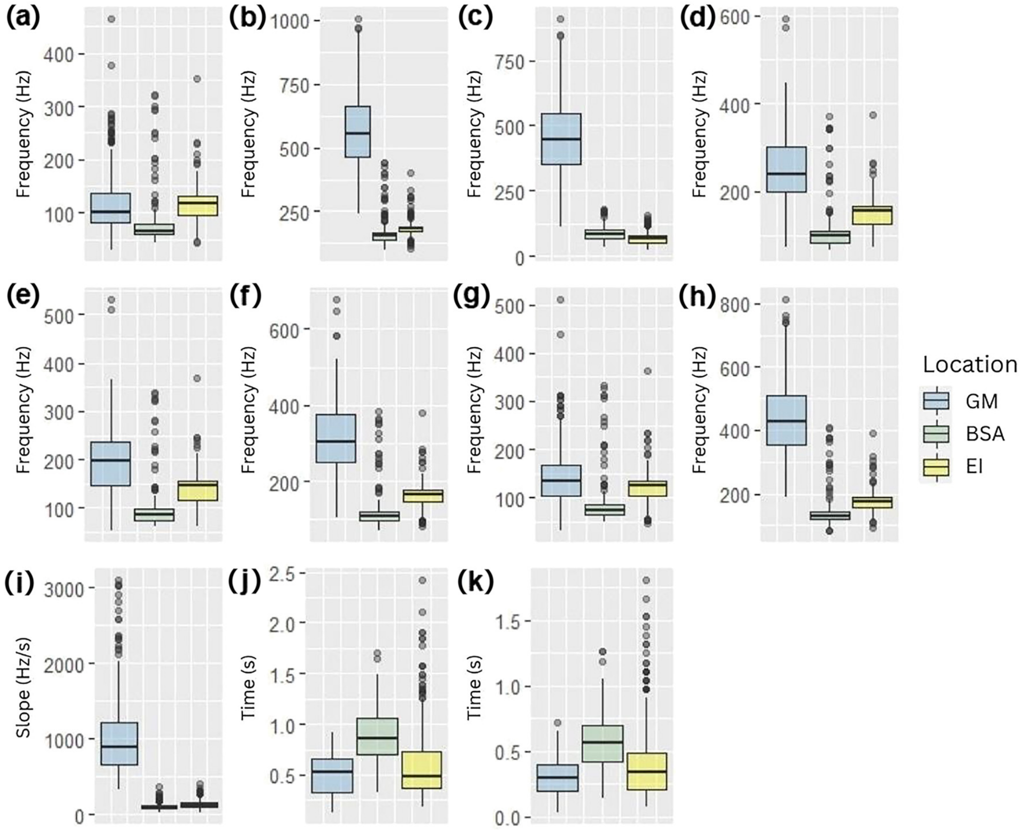

FIG. 4. (Color online) Boxplots representing quantitative acoustic measurements for the three groups GM, confirmed humpback whale upcalls; BSA, confirmed southern right whale upcalls; and EI, unconfirmed upcalls. (a) low frequency, (b) high frequency, (c) delta frequency, (d) center frequency, (e) frequency 25%, (f) frequency 75%, (g) frequency 5%, (h) frequency 95%, (i) slope, (j) duration, and (k) duration 90%.

vocalizations resulted in a relatively small interquartile range, also similar to BSA vocalizations, where slightly lower high frequencies were recorded. GM upcalls were characterized by a far greater overall and interquartile range of high-frequency limits than EI and BSA upcalls. The bandwidths of EI vocalizations resulted in a relatively small interquartile range similar to BSA measurements but had slightly lower values compared to vocalizations from BSA. However, bandwidths of GM vocalizations were spanning a larger overall and interquartile range. The remaining robust frequency measurements (center frequency, frequency 25%, frequency 75%, frequency 5%, frequency 95%) all indicated a very similar pattern. Robust frequency measurements of upcalls detected at EI had a comparable range to BSA vocalizations, while GM upcalls were characterized by a much greater range, including a greater and higher interquartile range, as well as a higher median. However, EI vocalizations had a higher and greater interquartile range than BSA vocalizations. The slope of analyzed vocalizations showed very similar and small ranges for EI and BSA upcalls, all located below 500 Hz/s, while the overall range of GM vocalizations was considerably different. Analyzed upcalls spanned from around 400 Hz/s up to over 3000 Hz/s, with a median of around 900 Hz/s. These median and range differences in frequency measurements are reflected in the performed pairwise comparison, which also indicated greater, but similar differences between GM vocalizations and detected vocalizations at EI and BSA, respectively (GM – EI SumOfSqs = 38.776119 and *p*-value = 0.001, GM – BSA SumOfSqs = 38.5435545 and *p*-value = 0.001). Temporal measurements of the vocalization (duration and duration 90%) showed similar patterns with respect to the parameter ranges of groups. The overall range for EI upcalls was comparable to BSA upcalls, but the median and height of the interquartile range was more similar to GM upcalls. These variations are reflected in the pairwise comparison between EI and BSA applied to the whole dataset (SumOfSqs = 6.143 and *p*-value = 0.001), which indicated small dissimilarities between EI and BSA upcalls. Consistent with these results are the outcomes of the performed SIMPER analyses, which indicated that the measurements slope, delta frequency and high frequency mainly drove differences between GM and EI, and GM and BSA. According to this analysis, the minor differences between EI and BSA were driven by slope, frequency 75%, and center frequency.

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B. Automatic classification of vocalizations

The random forest model using manual measurements successfully discriminated between SRW and HW upcalls and classified the vocalizations detected off EI as SRW upcalls. The average model out-of-bag (OOB) estimate of error rate was 0%, with HW and SRW vocalizations having a miss rate of 0%, resulting in a 100% accurate classification. While the conducted Boruta algorithm considered all performed manual measurements relevant for classification, the most important measurements to discriminate between species vocalization using the model were slope and delta frequency.

IV. DISCUSSION

A. Southern right whale vocalizations

Previously unidentified vocalizations recorded at EI, Antarctica in 2013 were characterized and successfully attributed to SRWs. The measured mean start frequency of the EI vocalizations was 113 Hz monotonically increasing to a mean end frequency of 181 Hz, with a mean slope of 137 Hz/s. These upcall characteristics are broadly similar to the measured characteristics of SRW vocalizations at BSA. Apart from a similar mean duration (EI, 0.56 s and GM, 0.52 s), EI vocalizations were notably different from HW vocalizations recorded at GM, with a mean slope of 1024 Hz/s and a mean bandwidth of 452 Hz as the main contributors to differences between groups, allowing to successfully differentiate SRW upcalls from HW vocalizations (Tables III and IV). We cannot exclude the possibility that the acoustic measurements are biased by the analyst's manual logging of individual vocalizations, but this method is widely used in the literature to investigate call parameters (e.g., Dombroski *et al.*, 2016; Webster *et al.*, 2016; Calderan *et al.*, 2021). Further, we extracted robust measurements (center frequency, frequency 25% and frequency 75%, frequency 5% and 95%, duration 90%) that do not entirely rely on time and frequency end points but on the energy distribution within the selection. Thus, small changes in borders of the selection should have little influence on the resulting robust measures (Charif *et al.*, 2010).

Based on the manual measurements the random forest model was able to accurately (100%) discriminate between SRW and HW upcalls, and successfully attributed the unidentified EI upcalls to SRWs. Similar to other studies (Hannay *et al.*, 2013; Rankin *et al.*, 2017) our model is showing a high achieved accuracy. In general, the random forest approach ingesting the measurement's bandwidth and slope has a high potential to support and facilitate automated detections of right whale upcalls in PAM data.

The measured means of vocalization parameters of SRWs at EI and BSA are within the time and frequency ranges of right whale vocalizations first described by Clark (1982). The EI vocalizations' bandwidths are broadly similar to approximated bandwidths of SRW vocalizations detected off South Georgia (Calderan *et al.*, 2021), off the Auckland Islands (Webster *et al.*, 2016), and on breeding grounds off Brazil (Dombroski *et al.*, 2016). The measured mean of the upper frequency limit of EI upcalls is similar to upcalls recorded by Širović *et al.* (2006) off South Georgia (Table IV). The mean duration of analyzed EI upcalls is relatively short, compared to previously mentioned studies. Only Dombroski *et al.* (2016) describe SRW upcalls off Brazil with similar durations (0.6 s).

In addition to the evident similarities of the EI upcalls with other SRW upcalls, we found a remarkable increase in 21 Hz on average for the low frequency limit of EI upcalls compared to SRW upcalls from other regions (Calderan *et al.*, 2021; Širović *et al.*, 2006; Webster *et al.*, 2016). Comparable low-frequency limits have only been measured in North Atlantic right whale upcalls detected in the northwest Atlantic (Parks *et al.*, 2007), an area characterized by high levels of anthropogenic noise e.g., from shipping and fishing (Parks *et al.*, 2009; Parks *et al.*, 2011). Changes in background noise conditions are known to not only be possible drivers for changes in vocalization amplitudes, also known as the Lombard-effect (Helble *et al.*, 2020; Scheifele *et al.*, 2005), but also for changes in frequency limits of vocalizations, as well as their duration (Parks *et al.*, 2011; Parks *et al.*, 2016). Parks *et al.* (2016) found that the low-frequency limit of SRW vocalizations shifted to higher frequencies compared to baseline conditions, when dominant background noise at lower frequencies than SRW

TABLE IV. Selected acoustic characteristics of vocalizations of two right whale species and humpback whales from different studies. (Values in parentheses are standard deviations, not available for Webster *et al.*, 2016).

	Right whale								Humpback whale	
	This study - EI	This study - BSA	Calderan *et al.* (2021)	Webster *et al.* (2016)	Širović *et al.* (2006)	Dombroski *et al.* (2016)	Parks *et al.* (2007)		This study - GM	Wild and Gabriele (2014)
Species	E. australis	E. australis	E. australis	E. australis	E. australis	E. australis	E. australis	E. glacialis	M. novaeangliae	M. novaeangliae
Area	Elephant Island	Bahía San Antonio	South Georgia	Auckland Islands	South Georgia and Scotia Sea	Brazil	Argentina	Bay of Fundy	Greenwich Meridian, ASSO	Southeastern Alaska
Mean duration	0.56 (0.27)	0.89 (0.26)	0.8 (0.27)	0.9	0.7 (0.1)	0.6 (0.2)	0.82 (0.23)	0.87 (0.27)	0.51 (0.2)	0.2 (0.1)
Mean low frequency	113.97 (24.26)	76.67 (38.28)	86 (10)	87	92 (11)	58 (22)	78 (15)	101 (22)	116.57 (55.48)	52 (13)

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vocalizations was present. This phenomenon has also been studied in other species (e.g., *Parus major*; Slabbekoorn and den Boer-Visser, 2006) and in *Stenella coeruleoalba* (Papale *et al.*, 2015). Background noise conditions are not only influenced by anthropogenic noise but also by biological sound sources (e.g., fish chorus). To avoid acoustic competition among species sharing the same acoustic environment, many animal species are thought to adapt to specific acoustic niches (i.e., timespans and frequency bands with comparatively little overlap with other species). This niche can be extended through frequency modulation, for example, when an (acoustic) invasion of another species occurs (Both and Grant, 2012; Mossbridge and Thomas, 1999). Off EI, fin whales are known to produce a variety of low-frequency, but high-intensity vocalizations within frequency limits of 15–89 Hz (Burkhardt *et al.*, 2021; Širović *et al.*, 2004). Fin whales aggregate in great numbers off EI from mid-February to August, during the same time period as SRWs are acoustically present in our data. Since this is resulting in high amplitude levels within the frequency bands used by the local fin whales (Burkhardt *et al.*, 2021), they may compete for acoustic space with SRWs off EI, possibly leading to shifts in SRW vocalization parameters. An acoustic energy analysis in the typical fin whale frequency bands of 13–28 and 84–89 Hz for the analyzed recording snippets from this study shows different energy levels in background noise at the three different locations. The results suggest that fin whales are a significant source of background noise at EI in comparison to the other two locations, which may be the cause for a shift of the low frequency limit of SRW upcalls. The shift in frequencies might be a short-term adjustment of the Argentinian SRW population, since a study by Zerbini *et al.* (2018) shows SRWs migrating from Argentinian breeding grounds to feeding grounds off South Georgia and even further south. However, this short-term adjustment could not only be triggered by acoustic presence of fin whales but also through a functional change of the vocalization on the feeding ground in comparison to on breeding grounds or the competition for an acoustic niche with other sound sources, including anthropogenic noise (while no other potentially interfering sounds could be identified in the data). The clarification of this phenomenon requests further research.

B. Potential applications using PAM

The upcall is the most prevalent and best-studied vocalization within the SRW's vocal repertoire, thought to be used as a contact call between individuals (Clark, 1982). Since upcalls are produced by both sexes, all age classes, and during a range of behavioural contexts (Parks *et al.*, 2011), it represents an adequate signal for the comprehensive assessment of acoustic presence of this species, therefore most commonly used for passive acoustic detection (Urazghildiiev *et al.*, 2009). The automated detection of upcalls can also serve as an indicator for the potential presence of other SRW vocalizations which can subsequently be identified and analyzed in more detail and provide additional information on group composition, breeding, feeding, or social behaviour (McDonald and Moore, 2002). In addition to behavioural insights, detections of right whale upcalls can provide information on single whale identity and age class, which are mainly dependent on spectral entropy and duration (McCordic *et al.*, 2016). In addition, acoustic cue counting using upcalls has proven successful in estimating right whale density in the northern Pacific (Marques *et al.*, 2011). In the northwest Atlantic, PAM is used for the real-time detection of North Atlantic right whale (*Eubalaena glacialis*) upcalls (Spaulding *et al.*, 2009; Van Parijs *et al.*, 2009) not only for information on their distribution but also for collision mitigation, as ship strikes are a major mortality cause for the highly endangered North Atlantic right whale (Campbell-Malone *et al.*, 2008). For all these applications of PAM, the ability to correctly detect vocalizations and distinguish between co-occurring species is essential. This study shows that especially frequency related measurements such as slope, delta frequency and high frequency can be applied to distinguish between SRW and HW upcalls in future acoustic studies.

In addition to a direct automated classification to discriminate between SRW and HW upcalls, another approach is to include the acoustic context (e.g., Kowarski *et al.*, 2023), which we applied for the confirmed HW upcalls in the GM data by only logging upcalls within HW song. However, HWs produce upcalls not only in the song context but also as social sounds (Dunlop *et al.*, 2007). Therefore, only relying on HW song patterns would not be a sufficient approach for the discrimination of upcalls. Moreover, in the case of the EI data, no other SRW vocalizations could be identified which could have been used for an acoustic context decision. This missing of other SRW vocalizations at EI could be due to shallow topography at the recording location leading to a complex acoustic propagation scenario (Burkhardt *et al.*, 2021; Forrest, 1994; Kularia *et al.*, 2016; McKenna *et al.*, 2021). Kowarski *et al.* (2023) considered upcalls to be produced by right whales, only, if there was not a HW vocalization confirmed or suspected within 2 h of the detection, or if it occurred with a right whale gunshot. However, since gunshots are thought to be produced by males only the acoustic presence of right whales would be sex-biased. Moreover, the approach by Kowarski *et al.* (2023) might miss right whales present at the same time as HWs. Therefore, we believe that an automated detection and classification approach for SRWs based on the acoustic features of upcalls is more likely to produce unbiased and comprehensive results for long-term and large-scale studies.

C. EI—A potential foraging ground

The combined investigation of environmental factors, anthropogenic impacts, and soundscapes including the specific identification of SRWs' and other species' vocalizations is of high interest to understand the future of Southern Ocean ecosystems. In order to protect and conserve species or populations as effectively as possible, the identification of areas of importance for the species or population is crucial. While current SRW breeding grounds are well-studied, contemporary data on feeding ground locations south of 40 °S are sparse. The identification of feeding grounds could lead not only to an improved understanding of SRWs spatiotemporal distribution but also to a better knowledge of environmental variables that may be linked to reproductive success. Thus, the identification of possible feeding grounds is a key part of the International Whaling Commission–Southern Ocean Research Programme (IWC-SORP) research theme 6 (Vermeulen *et al.*, 2021). Based on the analyzed vocalizations SRW presence off EI was detected in austral summer (January and February), austral autumn (March to May), and in austral winter (August; see Fig. S3 in the supplementary material[1]), with a peak of 775 detected upcalls on a total of 11 days in April. At EI, the SRWs' temporal acoustic presence is accompanied by phytoplankton blooms from January to March, and the waters are characterized by high krill densities, including Antarctic krill (*Euphausia superba*), a main food source of SRWs and other baleen whales (Siegel, 2005). Therefore, EI could not only be a key feeding ground for fin whales (Burkhardt *et al.*, 2021) and HWs (Schall *et al.*, 2020), but presumably also for SRWs.

V. OUTLOOK

Our study shows the feasibility of successfully and accurately distinguishing between SRW and HW upcalls, providing the vocalization parameters determining the main differences in call characteristics between species for future PAM studies, and facilitating the correct detection of SRW acoustic presence and behavior. The present analysis only provides the first insights into the spatiotemporal distribution of SRWs in the ASSO, and confirmed sightings are located not only around the Antarctic Peninsula but also in other sub-Antarctic and Antarctic areas (Vermeulen *et al.*, 2021), indicating that there is potential for future PAM studies. For example, all available acoustic data of the EI recorders since 2012, spanning nine years of recordings (Rettig *et al.*, 2013), should be analyzed for the presence of SRW upcalls using the newly gained knowledge on how to classify these vocalizations. Additional PAM effort should preferably overlap with sighting data presented in Vermeulen *et al.* (2021), and extend eastwards in a transect around 60 °S from EI. Since contemporary data on possible SRW feeding grounds south of 40 °S is scarce, more comprehensive analyses of acoustic recordings would help to understand SRWs spatiotemporal distribution and migration patterns. Joint analyses of environmental conditions and SRWs' distribution data could help to identify drivers of distribution patterns and habitat choice (Payne *et al.*, 2017). These analyses together with ecological knowledge of trophic relationships and a quantitative understanding of spatial and temporal lags between physical drivers and ecological response can be used to calculate forecasts on monthly, annual, or even decadal scales (Barlow and Torres, 2021). Such spatiotemporal predictions are vital for effective management implementations (Barlow and Torres, 2021; Williams *et al.*, 2006), such as marine protected areas, especially in a region like the Antarctic Peninsula facing one of the fastest regional warming rates on Earth (Rogers *et al.*, 2020; Vaughan *et al.*, 2003) and rising anthropogenic pressure (Morley *et al.*, 2020).

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[1] See supplementary material at https://doi.org/10.1121/10.0019633 for additional tables and figures.

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2

Searching for separation between frequency-modulated calls of blue and fin whales.

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Abstract

Reliable differentiation of similar acoustic signals remains a major challenge for passive acoustic monitoring (PAM) of sympatric marine mammal species. Blue (*Balaenoptera musculus*) and fin whales (*Balaenoptera physalus*) produce frequency-modulated (FM) downsweeping calls with overlapping frequency ranges and durations, making species attribution difficult. This study combines long-term PAM datasets with animal-borne tag recordings to evaluate whether these FM calls can be reliably distinguished by species. In long-term PAM datasets, where FM calls were labelled using contextual information, measured call parameters and deep learning features from pre-trained models failed to reveal species-specific separation. Tag recordings with confirmed species identity also showed substantial similarities, but the parameter Duration 90% offered partial separation: with most fin whale FM calls < 0.6 s, and most blue whale FM calls > 0.7 s. Which applied conservatively to unconfirmed high-quality calls (Signal to Noise Ratio > 14 dB), could provide a limited rule-based solution. A more robust approach was achieved by combining deep learning feature extraction with a non-linear dimension reduction that can project selected calls from long-term data onto an embedding space built on the tag data. Together, these approaches provide a practical framework for more reliable call attribution, enhancing long-term PAM-based monitoring of blue and fin whales.

Introduction

Acoustic signals produced by marine mammals can contain important information related to species identity, acoustic population structure, individual identity and behavioral context. Variations in signal properties, such as duration, bandwidth, and frequency range, as well as their overall spectro-temporal patterns in spectrograms, often allow insights into the previously mentioned biological aspects [1–5].

While passive acoustic monitoring (PAM) technologies are continuously improving, allowing data collection over large spatial- and temporal scales [4], a potential challenge remains - the reliable differentiation of acoustic signals among species. A similarity in signal parameters and visio-acoustic appearance of calls among sympatric species causes difficulties in accurate species identification [6]. For example, a high-intensity vocalization termed “gunshot call” was originally attributed exclusively to right whales (*Eubalaena spp.*) [7], but has since been proposed to be produced by humpback whales (*Megaptera novaeangliae*) as well [8]. Humpback and right whales also produce another similar vocalization type, the upcall, a common contact call in both species, which has likewise been reported as difficult to distinguish with certainty [6]. Although the acoustic features of upcalls show considerable overlap between the two species, recent analyses suggest that they can be reliably distinguished based on specific acoustic metrics [9]. Another example reported as difficult to distinguish in marine passive acoustic recordings involves the frequency-modulated downsweep vocalizations of baleen whales, particularly blue (*Balaenoptera musculus*), fin (*Balaenoptera physalus*), and sei whales (*Balaenoptera borealis*) [10]. All three species produce downsweeps, also referred to as frequency-modulated (FM) calls, which are non-song vocalizations likely serving a communicative function, such as coordinating group foraging [11–14]. FM calls of blue, fin and sei whales exhibit similar frequency ranges (~35–150 Hz) and durations (~200 ms to 5 s) [10,15], making species attribution particularly challenging [10,16,17]. Among these species, distinguishing blue and fin whale FM calls is especially problematic given the extensive overlapping their distribution [18,19].

Although fin and blue whale FM calls, also referred to as 40Hz- [12,20] and D-calls [21], respectively, can be difficult to distinguish, the ability to reliably differentiate between them could significantly improve information obtained by PAM efforts. Both species were severely depleted by commercial whaling [22], and their habitat use, population structures and recovery rates remain poorly understood. Thus, combining the detection of FM calls, as well as blue and fin whale song, which both show only partly overlapping seasonality [e.g., 12,16–18] would provide a more robust understanding of their occurrence.

Several approaches have been proposed to improve discrimination between similar acoustic signals produced by different whale species. In the case of right and humpback whale upcalls a combination of call parameters, such as slope and bandwidth, has been proven effective [9]. When call parameters overlap substantially, contextual data can be taken into account to confirm the species identity, such as the known geographic distribution. However, this is often not feasible, when species' ranges overlap. Thus, including co-occurring well-known species-specific vocalizations, or call patterns (e.g., sei whale FM calls are supposed to occur in pairs or triplets) may support the decision process for species attribution [14].

To date, species differentiation between fin and blue whale FM calls, has primarily relied on differences in call duration [15], or the presence of other species-specific vocalizations co-occurring within a defined time window around the FM call [24]. However, these approaches have never been proven to be reliable and can limit the possibilities, both spatially and temporally, for attributing calls particularly in the absence of any visual confirmation of species presence. Therefore, there is a need to develop a robust method for correctly classifying FM calls in long-term PAM datasets.

In this study, we aim to explore acoustic differences between blue and fin whale FM calls, with the intention of identifying potential approaches for distinguishing between the FM calls of these two species. As part of this process, we specifically investigate: Can blue and fin whale FM calls be reliably distinguished, and if so, are such distinctions driven by acoustic parameters, such as call duration? How is call discrimination affected by transmission loss, and is reliable classification limited to high-quality calls with high signal-to-noise ratios (SNR)?

Results

Datasets and labelling

To explore possible differences in call parameters among blue and fin whale FM calls, we analyzed a large passive acoustic dataset from multiple mooring sites across the Southern Ocean as well as a smaller ground-truth dataset from tagging studies off California and Chile. The mooring dataset provides broad temporal and spatial coverage but requires contextual information from other species-specific calls to assign FM calls to fin or blue whales. In contrast, the tag dataset contains only a limited number of calls but provides direct confirmation of species, enabling exploration of differences between known blue whale D-calls and fin whale 40Hz-calls. Together, these complementary datasets allowed us to assess call parameter variation while testing whether the tag dataset can serve as a reference for attributing call types in long-term mooring data.

From the mooring recordings two datasets were compiled: the AllSNR- dataset consisting of 18,209 FM calls, and a subset of those labeled HighSNR- dataset, created to improve data quality by reducing the influence of low SNR calls. Excluding all calls with an SNR approximation below 12dB (Raven Pro 1.6 parameter SNR NIST Quick (dB) >12; The Cornell Lab of Ornithology, Center for Conservation Bioacoustics in Ithaca, NY), this subset comprised 8,537 FM calls. The 12dB threshold was chosen operationally as a compromise between data quality and sample size, ensuring reliable measurements while retaining a sufficient number of FM calls, as higher thresholds would have excluded too many calls. Complementarily, the ground-truth dataset from the tagging studies, labeled Tag- dataset contained 66 confirmed 40Hz fin whale calls and 165 confirmed blue whale D-calls.

To assume species identity in the mooring datasets (AllSNR- and HighSNR-) a contextual rule-based labelling approach for encountered FM calls was established. This method relied on the presence or absence of well-known species-specific call types within ±30 minutes of a FM call. For fin whales, we used the stereotyped 20Hz-pulse, a short-duration high-energy call produced globally as either single vocalization, or as structured song, the latter exclusively produced by males [25–29]. To attribute FM calls to Antarctic blue whales, we used the stereotypical, easily identifiable, high-energy Z-call, which is likewise often produced in repetitive song patterns [3,29]. To increase the reliability of the labelling, only 20Hz-pulses and Z-calls with an SNR NIST Quick (dB) >15 were considered, thereby excluding faint calls of most likely distant animals. Using this approach, FM calls were assumed a 40Hz-call if only fin whale 20Hz-calls were present in the set time window, a D-call if only blue whale Z-calls were present, and a frequency-modulated call (FM; unclassified) if both species or neither species' calls were present. Call duration as a classification rule was not considered for our approach to avoid introducing a bias from call parameters at the labelling stage. This resulted in the assumptions of 1,130 40Hz fin whale calls, 4,162 blue whale D-calls, and 12,917 unclassified FM calls in the AllSNR-, and 634 40Hz-calls, 1,719 D-calls, and 6,184 unclassified FM calls in the HighSNR- datasets.

Exploratory data analyses and clustering

For all datasets, 12 quantitative acoustic features were extracted from all analyzed FM calls using RavenPro 1.6, hereinafter referred to as Raven features. The distributions of these 12 quantitative acoustic features extracted from Raven were examined using boxplots for the AllSNR- and HighSNR-datasets (Figure 1 for the AllSNR-RavenFeatures and Figure S1 for the HighSNR-RavenFeatures in the supplementary material). Enabling comparison of medians and ranges across call types for each feature, the boxplots revealed largely overlapping distributions with similar ranges and no clear differences between call types, a pattern that is also visible in the HighSNR-RavenFeatures dataset.

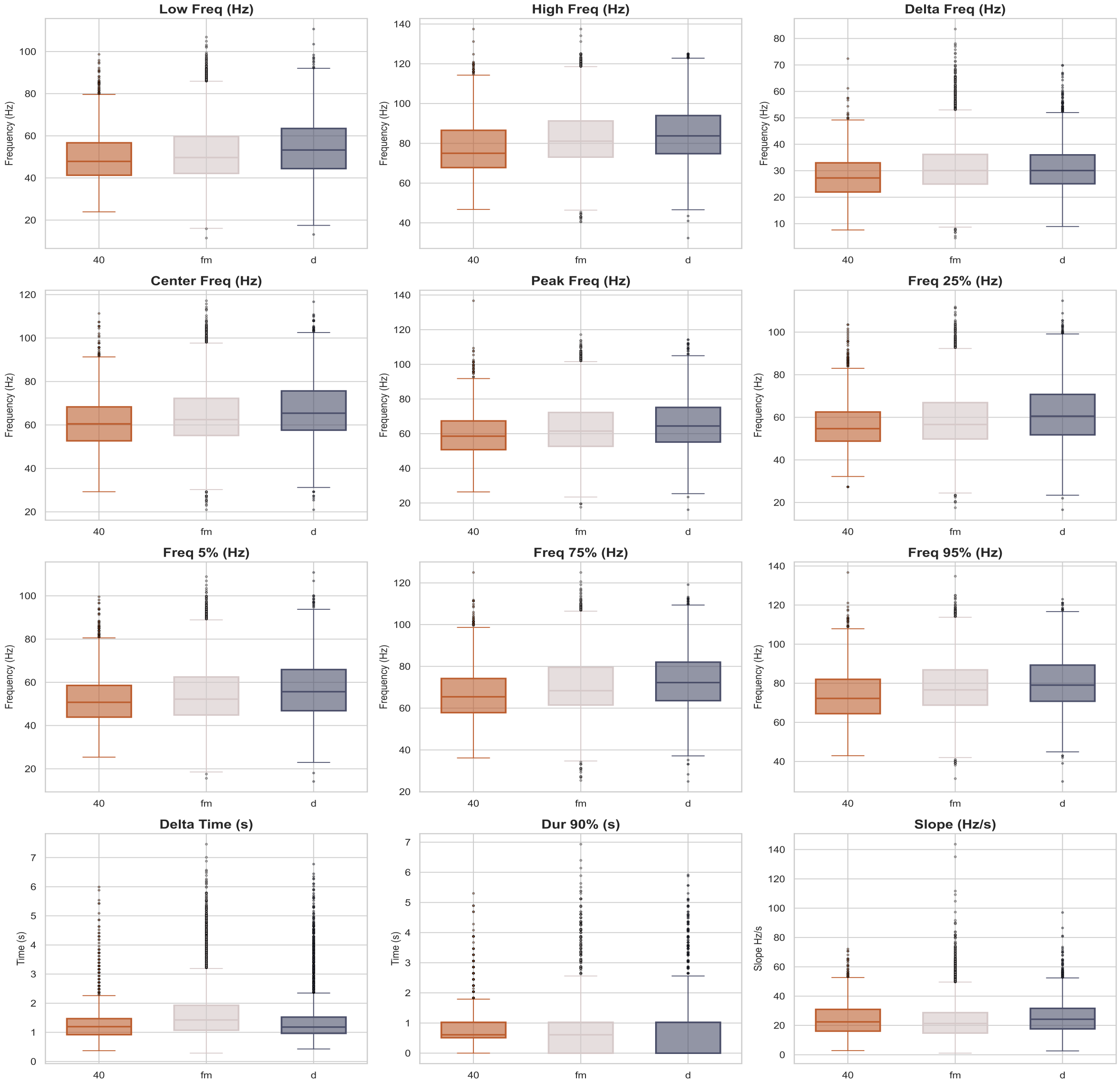

Figure 1. Boxplots representing the 12 quantitative acoustic measurements from the AllSNR-RavenFeatures dataset for the three groups of labelled FM calls: 40Hz-calls of fin whales (40 - orange), D-calls of blue whales (d - blue), and frequency-modulated (FM) calls with uncertain attribution (fm – light gray).

Given the absence of clear differences in one or more of the measured Raven features, a Principal Component Analysis (PCA) on the AllSNR- and HighSNR-RavenFeatures was implemented to investigate a potential linear multivariate structure. The PCA results of both datasets (Figure 2) also failed to show differences between the assumed call types - all analyzed vocalizations are clearly forming one single cluster.

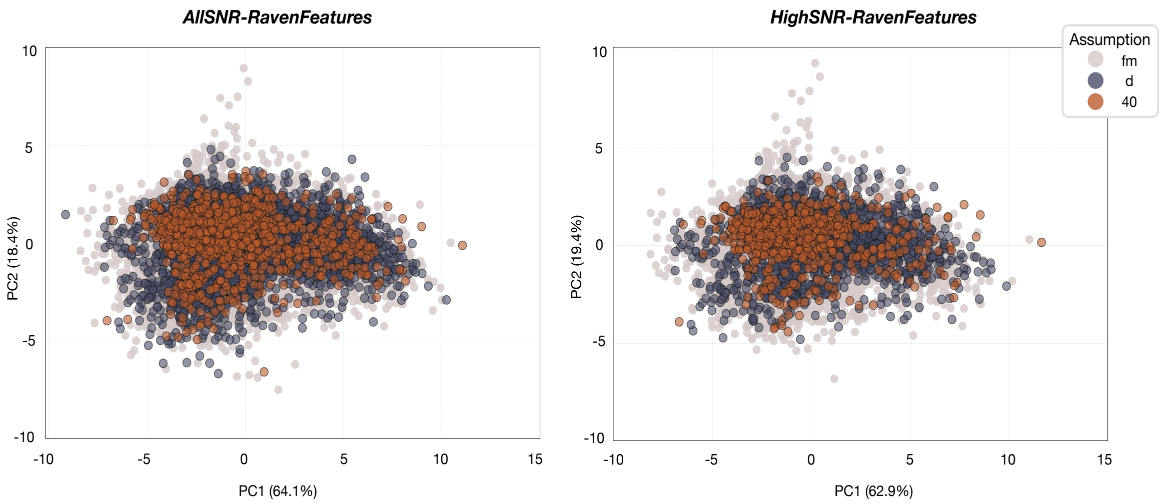

Figure 2. Principal Component Analysis (PCA) on the AllSNR- and HighSNR-RavenFeatures, showing the two-dimensional distribution of the three groups of labelled FM calls: 40Hz-calls of fin whales (40 - orange), D-calls of blue whales (d - blue), and frequency-modulated (FM) calls with uncertain attribution (fm – light gray).

In addition to the linear analyses, a non-linear dimensionality reduction was conducted using a Uniform Manifold Approximation and Projection (UMAP), to explore potential non-linear relationships in the data. Figure 3 presents both unsupervised and semi-supervised UMAP projections for the AllSNR- and HighSNR-RavenFeatures datasets, with both approaches tested to evaluate whether incorporating partial class information yields improved separation. Across all four projections, two broad clusters are visible. Within these clusters, local groupings of data points sharing the same label can be observed. None of the clusters or substructures, however, are composed solely of a single call type; instead, the call types are intermixed throughout the projection. Overall, the patterns observed in the AllSNR- and HighSNR-RavenFeatures datasets are similar, with no notable improvements in clustering structure or separation between call types.

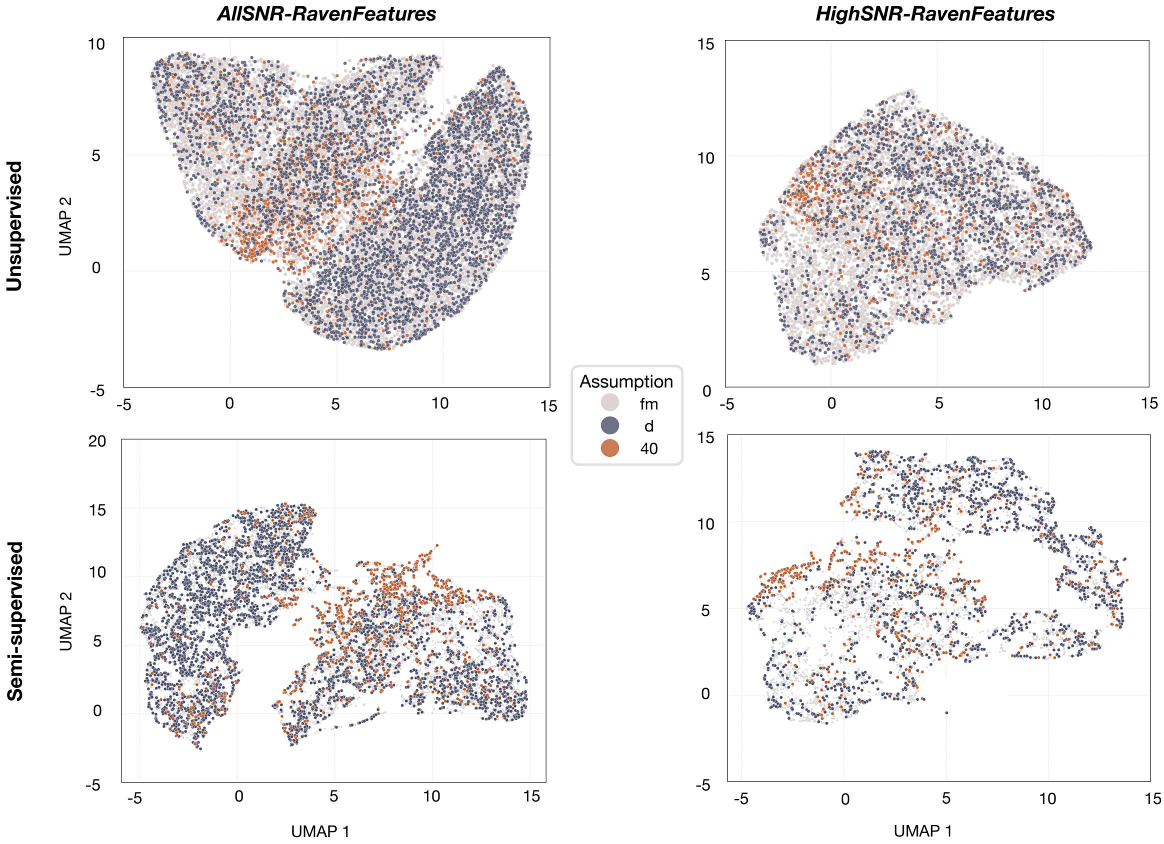

Figure 3. Dimension reduction using UMAP on both the AllSNR- and HighSNR-RavenFeatures datasets. Panels show UMAP projections generated using unsupervised and semi-supervised approaches. 40Hz-calls of fin whales (40 - orange), D-calls of blue whales (d - blue), and frequency-modulated (FM) calls with uncertain attribution (fm – light gray).

To explore differences between call types beyond the limited measured Raven features, deep learning feature extraction was applied to the AllSNR- and HighSNR- datasets using four pre-trained models, Biolingual [30], GoogleWhale [31], Surfperch [32], and Perch [33]. This process produced separate datasets of deep learning-derived features for each model, referred to as AllSNR-DLFeatures-[model name] and HighSNR-DLFeatures-[model name], respectively. UMAP projections computed from the deep learning features from all models, under both unsupervised and semi-supervised settings, produced relatively consistent results. The projections from the model Biolingual are shown in Figure 4. The remaining model projections are provided in the supplementary material (Figures S2 and S3), as they did not yield better separation.

In both the unsupervised and semi-supervised projections based on the Biolingual deep learning features, the UMAP visualizations reveal no distinct clusters with a single label. The projections, however, still show varying levels of mixing of the assumed call types in substructures, always revealing one area that primarily contains 40Hz-labelled calls, and a relatively large area of multiple presumed D-calls projected in closer proximity.

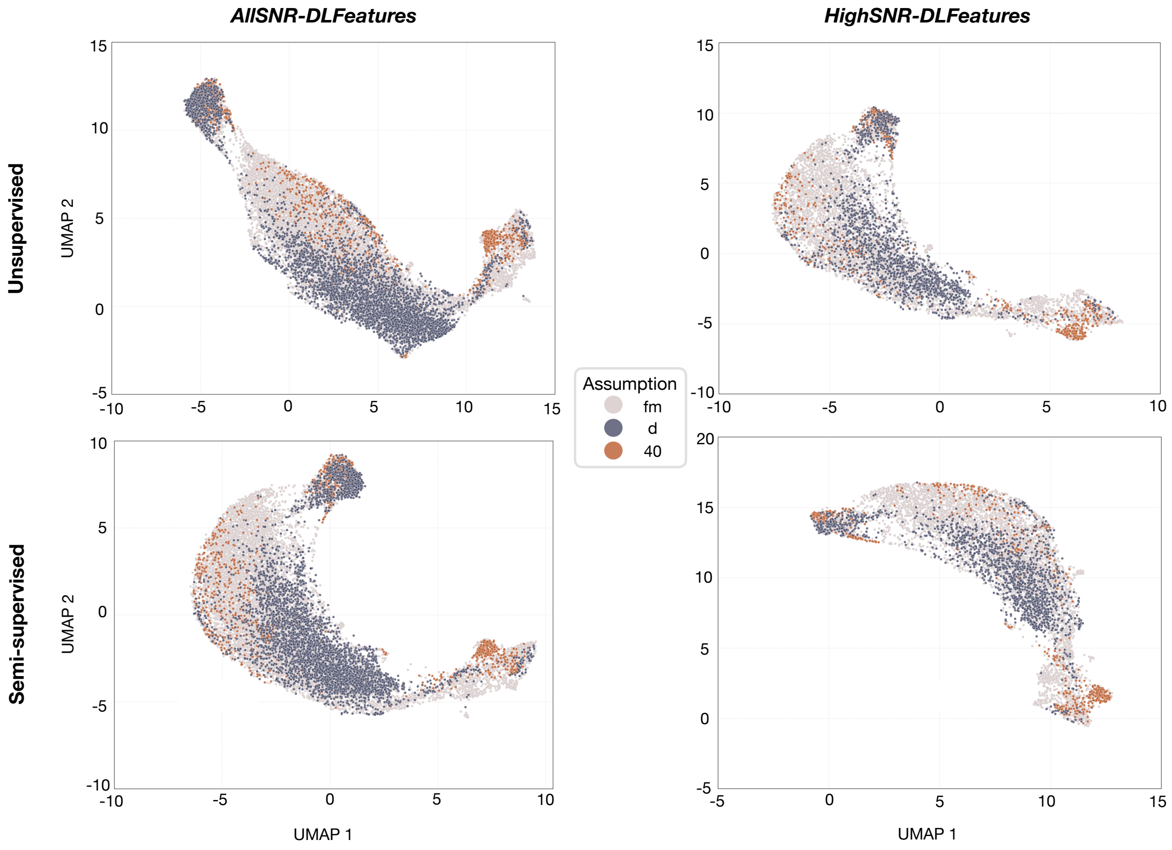

Figure 4. Dimension reduction using UMAP on the AllSNR- and HighSNR-DLFeatures datasets using the model Biolingual. Panels show UMAP projections generated using unsupervised and semi-supervised approaches. 40Hz-calls of fin whales (40 - orange), D-calls of blue whales (d - blue), and frequency-modulated (FM) calls with uncertain attribution (fm – light gray).

As a final step, Hierarchical Density-Based Spatial Clustering of Applications with Noise (HDBSCAN) was applied to the AllSNR-, and HighSNR- datasets to identify potential clusters, using the Raven features and the deep learning features, respectively. Table 1 summarizes the results for the AllSNR-, and HighSNR-RavenFeatures, as well as for the Biolingual AllSNR- and HighSNR-DLFeatures (HDBSCAN results on the three remaining deep learning feature datasets can be found in Table S1 in the supplementary material). Across datasets, HDBSCAN predominantly identified two clusters (occasionally three), with no cluster showing a clear dominance of a single assumed call type. In the AllSNR-, and HighSNR-RavenFeatures, HDBSCAN identified, in addition to a large proportion of unassigned points, two clusters where most FM calls were labeled as D-calls. Both clusters (1 and 2) show similar label distributions. While Cluster 1 contains 8.3% and 8.7% 40Hz-labeled calls in the AllSNR-, and HighSNR-RavenFeatures datasets respectively, both Cluster 2 include only a single 40Hz-labeled call, revealing D-call dominated clusters. In contrast, the HDBSCAN output on the Biolingual AllSNR- and HighSNR-DLFeatures reveals two clusters for the AllSNR- and three clusters for the HighSNR-DLFeatures. In both datasets, Cluster 1 consists of a higher percentage of D-call labeled calls, along with a majority (~90%) of calls with unclassified labels. Clusters 2 contain fewer calls than Clusters 1, but with a higher number of attributed calls, only ~44% unclassified calls, and 17-19% labeled as 40Hz-calls. Only Cluster 3 in the HighSNR-DLFeatures contains a higher proportion of 40Hz-labeled calls (9.9%) than that of D-call (3.7%), though the majority of calls in this cluster (86.4%) remain unclassified.

Table 1. Absolute and relative number of FM calls per cluster based on the three groups of assumed call types - 40Hz-calls of fin whales (40), D-calls of blue whales (d), and FM calls with uncertain attribution (fm) - across the various datasets (AllSNR-RavenFeatures, HighSNR-RavenFeatures, Biolingual AllSNR-DLFeatures, and HighSNR-DLFeatures), as determined by the HDBSCAN algorithm. Each entry shows the count of FM calls belonging to a given assumed call type within a cluster, followed by the corresponding percentage (in parentheses) relative to the total number of FM calls in the respective cluster. Data points considered as noise by the algorithm are listed as unassigned in the cluster column. Clustering was performed independently on each dataset using HDBSCAN with different min_cluster_size values chosen to optimize cluster detection: AllSNR-RavenFeatures (min_cluster_size = 25), HighSNR-RavenFeatures (min_cluster_size = 30), and Biolingual (AllSNR- and HighSNR-DLFeatures; min_cluster_size = 50).

Dataset	**Cluster**	**No. of '40' (%)**	**No. of 'd' (%)**	**No. of 'fm' (%)**	**No. total**
AllSNR -RavenFeatures	unassigned	996 (6)	3847 (23.2)	11758 (70.8)	16601
	1	133 (8.7)	294 (19.3)	1097 (72)	1524
	2	1 (1.1)	21 (25)	62 (73.8)	84
HighSNR -RavenFeatures	unassigned	289 (6.6)	935 (21.4)	3137 (71.9)	4361
	1	344 (8.3)	774 (18.7)	3017 (73)	4135
	2	1 (2.4)	10 (24.4)	30 (73.2)	41
BiolingualAllSNR -DLFeatures	unassigned	900 (6.2)	3458 (23.7)	10230 (70.1)	14588
	1	30 (1.3)	228 (9.6)	2118 (89.1)	2376
	2	187 (17.9)	404 (38.8)	451 (43.3)	1042
BiolingualHighSNR -DLFeatures	unassigned	539 (7.5)	1474 (20.5)	5166 (72)	7179
	1	14 (1.8)	61 (7.8)	705 (90.4)	780
	2	60 (19.2)	115 (36.4)	138 (44.1)	313
	3	8 (9.9)	3 (3.7)	70 (86.4)	81

Tag Data Call Classification and its projection on long-term PAM data

In addition to the mooring datasets, the ground-truth Tag-RavenFeatures dataset was used to explore differences between confirmed D- and 40Hz-calls, and to test whether it could serve as a reference for attributing call types in passive acoustic monitoring data.

For the Tag-RavenFeatures dataset, the distribution of acoustic features extracted in Raven was also first examined using boxplots (Figure 5). Similar to the mooring datasets, most measurements show largely overlapping distributions between D- and 40Hz-calls. Duration 90% is the parameter showing the highest degree of separation, with the exception of a single overlap at 0.612 s, where one call from each species coincides with its 90%-energy call duration. A PCA was also performed to investigate potential linear multivariate structure, but the results (Figure A5) failed to reveal clear differences between the call types.

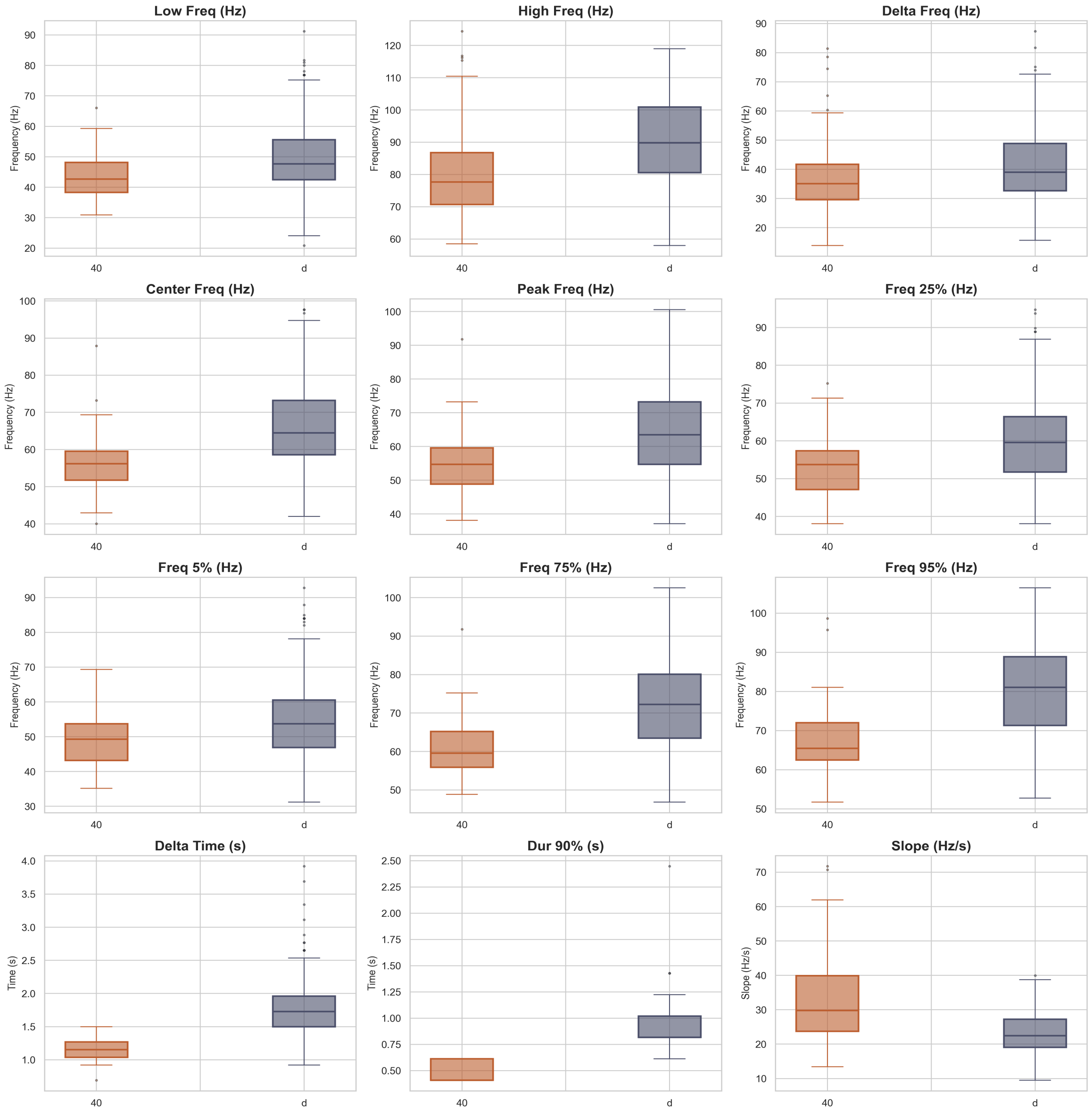

Figure 5. Boxplots representing the 12 quantitative acoustic measurements from the Tag-RavenFeatures dataset for the two confirmed call types: 40Hz-calls of fin whales (40 - orange), and D-calls of blue whales (d - blue).

UMAP projections of Tag-RavenFeatures were generated under unsupervised, and supervised conditions (Figure 6). Across both projections (only Tag-RavenFeatures and Tag-RavenFeatures plus HighSNR.2-RavenFeatures) under unsupervised conditions, a single broad cluster is visible, although two strong local groupings of points sharing the same label can be observed, but call types remain partially intermixed. Consequently, the overlaid HighSNR.2-RavenFeatures cannot always be clearly attributed to a single species' call type. In the supervised projections the Tag-RavenFeatures form two distinct clusters corresponding to D- and 40Hz-calls. Here, a large part of the HighSNR.2-RavenFeatures overlay aligns with the respective clusters, while other points form a continuous connection between these two clusters.

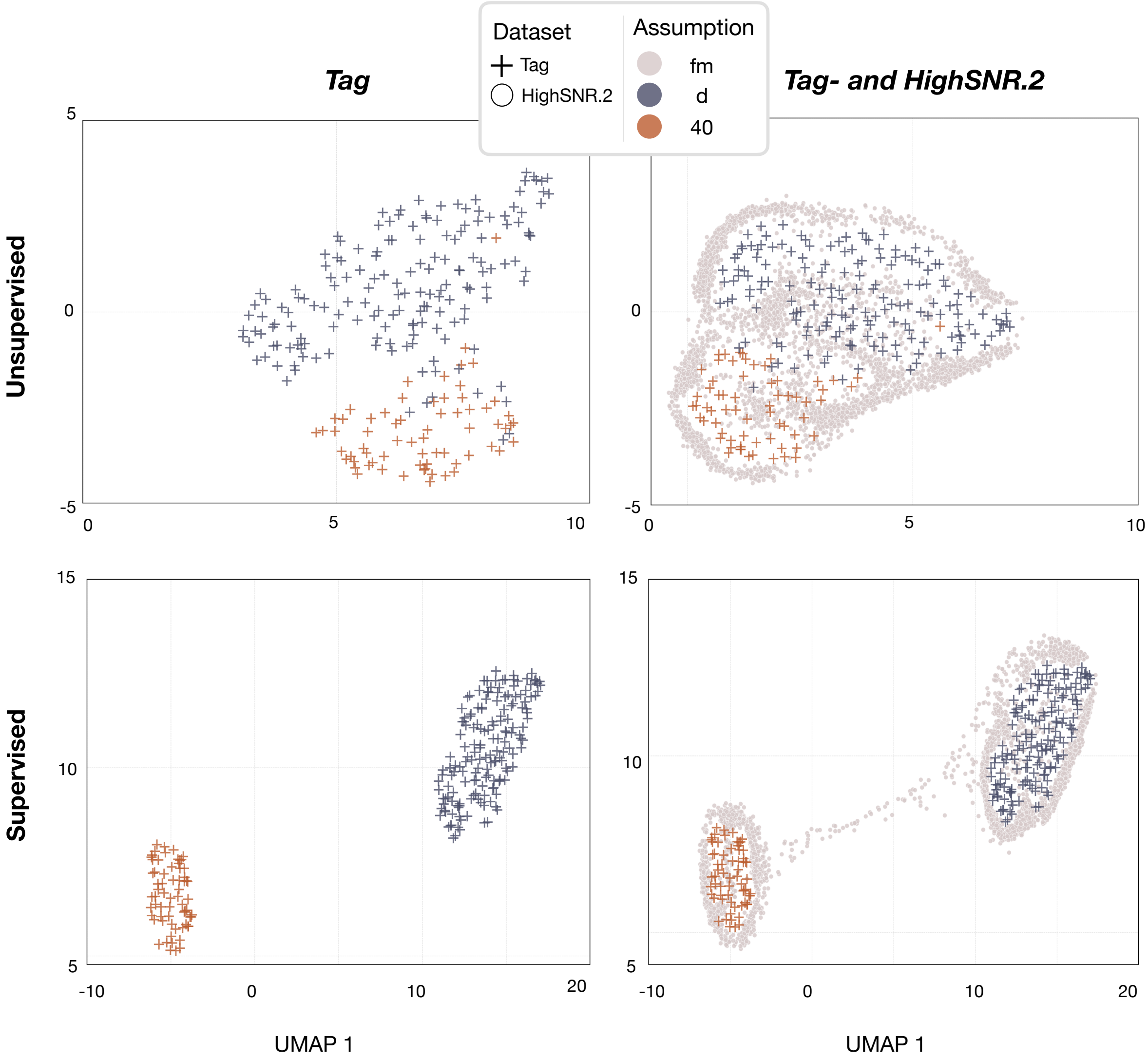

Figure 6. Dimension reduction using UMAP on Tag-RavenFeatures. Panels show UMAP projections generated using unsupervised, and supervised approaches. The HighSNR.2-RavenFeatures, (AllSNR-RavenFeatures filtered for SNR NIST Quick (dB) > 14), are projected onto the Tag-RavenFeatures UMAP space and their source is assumed unknown (fm – light gray). 40Hz-calls of fin whales (40 - orange), and D-calls of blue whales (d - blue) from the tag data are shown accordingly.

To test whether improved separation could be achieved, deep learning features were also extracted from the Tag- and HighSNR.2- datasets using the four models: Biolingual[30], GoogleWhale[31], Surfperch[32], and Perch[33]. For each model, a separate dataset of deep learning-derived features was created, hereinafter referred to as Tag-DLFeatures-[model name] and HighSNR.2-DLFeatures[model name]. UMAP projections based on deep learning features (again with the HighSNR.2-DLFeatures projected into the Tag-DLFeatures UMAP space), under unsupervised, and supervised settings, produced results broadly consistent with the Raven features dataset. GoogleWhale deep learning features are shown in Figure 7, with the remaining models output provided in the supplementary material (Figures S6 and S7). In the unsupervised projections, minor overlaps between call types can be still observed. In contrast, the supervised projections of the GoogleWhale deep learning features produced two completely distinct clusters, with the HighSNR.2-DLFeatures data projected entirely and unambiguously into the two clusters.

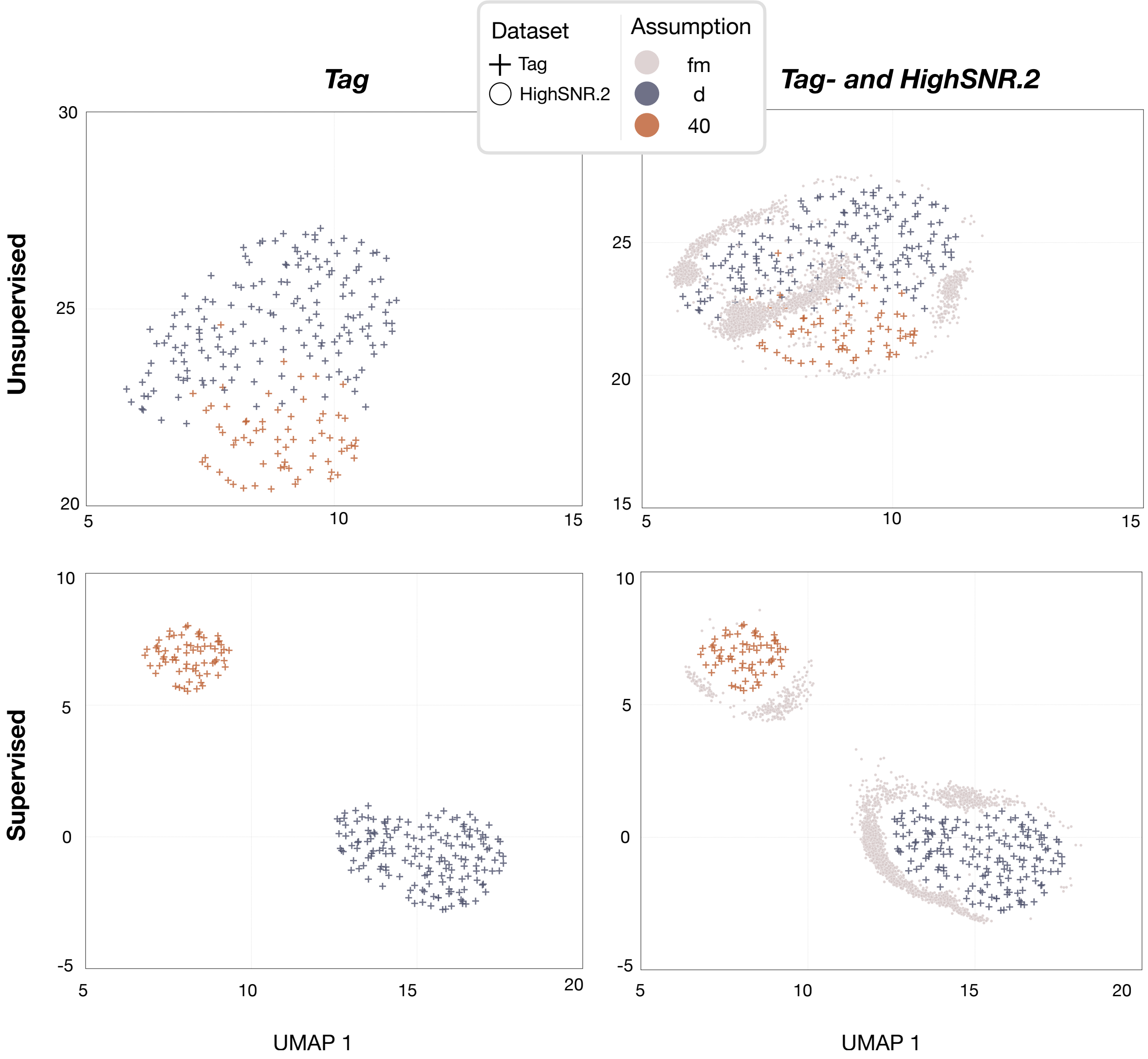

Figure 7. Dimension reduction using UMAP on the deep learning feature extraction of the Tag-DLFeatures using the GoogleWhale model. Panels show UMAP projections generated using unsupervised, and supervised approaches. The HighSNR.2-DLFeatures, are projected onto the Tag-DLFeatures UMAP space and their source is assumed unknown (fm – light gray). 40 Hz calls of fin whales (40 - orange), and D-calls of blue whales (d - blue) from the tag data are shown accordingly.

For consistency with the analyses performed on the AllSNR- and HighSNR- datasets, HDBSCAN was applied to both the Tag-RavenFeatures and Tag-DLFeatures. In the parameter-based dataset, alongside a proportion of unassigned calls, HDBSCAN identified one cluster composed entirely of D-calls (5 calls, 100%) and another cluster dominated by D-calls (131, 81.4%), but also containing a smaller number of 40Hz-calls (30, 18.6%; Table 2). For the GoogleWhale deep learning features, HDBSCAN detected two smaller clusters in addition to mostly unassigned calls. One cluster consisted of nearly equal numbers of D- (3, 42.9%) and 40Hz-calls (4, 57.1%), while the other cluster represented entirely D-calls (35, 100%). HDBSCAN results for the deep learning features retrieved from the other models are provided in the supplementary material (Table S2).

Table 2. Number and proportion of data points per cluster based on the two call types - 40Hz-calls of fin whales (40), and D-calls of blue whales (d) of the Tag-RavenFeatures, and the corresponding Tag-DLFeatures-GoogleWhale as determined by the HDBSCAN algorithm. Each entry shows the count of data points belonging to a given call type within a cluster, followed by the corresponding percentage (in parentheses) relative to the total number of data points in the respective cluster. Data points considered as noise by the algorithm are listed as unassigned in the cluster column. Clustering was performed using min_cluster_size = 5.

Dataset	Cluster	No. of '40' (%)	No. of 'd' (%)	No. total
Tag-RavenFeatures	unassigned	36 (55.4)	29 (44.6)	65
	1	30 (18.6)	131 (81.4)	161
	2	0 (0)	5 (100)	5
Tag-DLFeatures GoogleWhale	unassigned	62 (32.8)	127 (67.2)	189
	1	0 (0)	35 (100)	35
	2	4 (57.1)	3 (42.9)	7

Discussion

We investigated acoustic differences between blue and fin whale FM calls, D- and 40Hz-calls, using long-term PAM and tag recordings with the goal of identifying acoustic differentiation rules for distinguishing between the two species. FM calls could not be reliably separated using long-term PAM data alone, whereas tag recordings with confirmed species identity revealed approaches that allow partial distinction. The described approach supports limited but potentially meaningful attribution of FM calls to species in datasets where species identity is otherwise unknown (i.e., moored, long-term PAM datasets).

Important limitations must be considered when interpreting our results. In the mooring datasets (AllSNR and HighSNR), the species' assumption for the FM calls detected represents a potential source of error in this study. Because species identity could not be confirmed by other means (e.g., concurrent sightings), call labels were assumed based on contextual information, which may have resulted in misclassification and contributed to intermixing in the results presented. An additional limitation arises from analyst bias during manual detection and boxing of calls in Raven [34]. Call parameters are derived from the selection box drawn around the call. This process is sensitive to spectrogram settings such as time-frequency resolution and the color scale chosen [35], with the potential to introduce systematic differences across datasets. The application of deep learning features is robust to this type of measurement-error, however, a soundscape bias (i.e., related to the geographic location) can in turn affect this method of differentiation. For the tag data, it is important to note that the blue and fin whales studied represent different populations from those occurring in Antarctic waters. Although 40Hz- and D-calls have been described across many populations globally [e.g., 12,13,33–35], little population-specific differences may influence the results. Ideally, tag and long-term mooring PAM data would be collected from the same populations; however, to our knowledge, no acoustic tag data are currently available for Antarctic blue or fin whales. Thus, the results presented in this study should be interpreted with caution.

In addition to contextual information, as applied in our labelling approach, the differentiation of FM calls in long-term PAM datasets to date primarily relies on differences in acoustic parameters. Call duration (Delta Time), has been proposed as the key parameter for distinguishing between blue and fin whale FM calls in previous studies [15,24]. In our mooring datasets, however, this parameter showed substantial overlap between assumed species. In general, all 12 parameters examined in the linear explorations of the AllSNR- and HighSNR-RavenFeatures display similar overlaps. Although such parameters have previously proven useful for distinguishing other species signals [9], our results do not indicate that these solely can be used for species attribution in the case of Antarctic blue and fin whales.

Further, despite applying contextual labeling, SNR-based filtering, deep learning feature extraction, and multiple clustering approaches to the mooring datasets, no clear separation nor underlying structures between blue and fin whale FM calls could be observed. Instead, the revealed substructures appeared to be influenced primarily by recording location (supplementary material Figure S4). The deep learning features from the pre-trained models are computed for the full audio snippet (i.e., duration of the corresponding FM call annotation, and the full frequency range of 0-125 Hz). While deep learning feature extraction is a valuable method for soundscape analysis [38], the observed location bias in our data is most likely an artefact of the local soundscapes being considered important by the deep learning features. Despite this influence, call types within the location-driven substructures still overlap. One potential approach would be to explore whether deep learning features reveal clearer clustering when models are applied within individual recording locations, thereby accounting for local soundscape effects. However, such an approach would still be constrained by the lack of ground-truth caller identity in long-term PAM data. Taken together, these findings suggest that neither call parameters (RavenFeatures) nor deep learning features (DLFeatures) can reliably separate blue and fin whale FM calls in long-term mooring PAM datasets using the current contextual labelling approach.

To overcome this limitation, we examined tag recordings where species identity is confirmed. Call parameter statistics of the Tag-RavenFeatures (Figure 5) showed that most parameters overlapped substantially between species, similar to the mooring data results. Again, call duration (Delta Time) did not reliably distinguish 40Hz- from D-calls, as most 40Hz-calls (98.5%) fell within the D-call range. Calls longer than ~1.5 s were D-calls only, suggesting that this threshold could serve as a simple D-call classification criterion. However, the most promising parameter was Duration 90% (Dur90%), a robust measurement of call duration defined as the interval between the 5% and 95% cumulative energy points [35]. In the tag dataset, fin whale FM calls reached a maximum Dur90% of 0.612 s, whereas blue whale FM calls had a minimum of 0.612 s, indicating minimal overlap yet suggesting a potential boundary. Although considering that transmission loss is expected to still affect this parameter [39], it is less sensitive to analyst bias than other measures. To ensure confident parameter-based classification in long-term PAM datasets, analysis could be restricted to high-quality calls with SNR NIST Quick (dB) > 14 dB (the minimum SNR NIST Quick (dB) value in the tag dataset). FM calls could then be assigned to fin whales if Dur90% < 0.6 s, and to blue whales if Dur90% > 0.7 s. However, the projection of HighSNR.2-RavenFeatures FM calls into the Tag-RavenFeatures UMAP embedding supports this approach only partially (supplementary material Figure S8), likely because the UMAP representation integrates all measured call parameters. Thus, while these proposed thresholds may provide a parameter-based separation for FM calls in long-term PAM datasets, they inevitably exclude intermediate calls and lower-quality signals, and should be applied with caution.

Beyond call parameter exploration, UMAP projections of Tag-RavenFeatures and -DLFeatures (GoogleWhale model) revealed generally more distinct structures for fin and blue whale calls. However, some overlap remained at the cluster boundaries in the unsupervised approaches. Indicating that even at the source, without the influence of transmission loss, complete separation of FM calls into species categories remains challenging. This result is also indicated by the HDBSCAN clustering on both the Tag-RavenFeatures and -DLFeatures (GoogleWhale model). For both datasets only a small blue whale cluster could be identified, with no distinct fin whale cluster, while most calls were left unassigned.

Full separation of confirmed call types in the Tag-datasets could only be achieved under supervised approaches, where data points were forced into clusters based on labels. In this setting, overlaying the Tag-datasets with high-SNR (with NIST Quick method > 14 dB) mooring dataset calls (HighSNR.2) showed clearer separation of calls. For the HighSNR.2-RavenFeatures, a great part of calls aligned with the respective tag clusters, but other points formed a continuous connection between them. In contrast, in the HighSNR.2-DLFeatures, all mooring dataset calls are projected entirely and unambiguously into the two tag-based clusters. Although it cannot be proven that all long-term mooring dataset calls were attributed correctly, this method appears to be the most promising approach for FM call classification at present, as it uses tag recordings with confirmed species identity as training data for long-term PAM FM call attribution.

While most HighSNR.2 FM calls were initially assigned the assumed label 'FM' due to the absence of other species-specific calls or the simultaneous presence of both call types in the context window, projection into the tag UMAP embeddings and comparison with the ground-truth tag clusters shows that even the few calls assigned as 40Hz- or D-calls often did not correspond to the confirmed species identities. Only a small fraction of contextually assumed call labels matched the confirmed Tag call types, with the highest correspondence observed for assumed D-calls being assigned in the DLFeatures UMAP to D-calls at 17.4% (supplementary material Table S3). This demonstrates the limited reliability of context-based labelling for fin and blue whale FM calls and supports the need for non-context-based approaches to assign labels reliably.

In summary, the results of this study point out two potential approaches for distinguishing high-quality blue and fin whale FM calls (SNR NIST Quick (dB) > 14 dB), that are not context-based and therefore not spatially or temporally restricted. The parameter-based rule uses Duration 90% (Dur90%) and assigns FM calls to fin whales if Dur90% < 0.6 s, and to blue whales if Dur90% > 0.7 s. This may be useful for manual inspection of spectrograms; however, manual classification requires expertise and is prone to observer bias [34], limiting its reliability. The more robust approach is to use deep learning features, which have proven effective for call classification [38,40]. Projecting the deep learning features of high-SNR FM calls from long-term mooring PAM onto UMAP spaces trained on confirmed tag data yielded the most consistent separation, and we recommend this approach as the most reliable method currently available for FM call attribution. However, although this approach appears to assign all calls clearly, the deep learning features from the pre-trained models are computed for the full audio snippet and audio context corresponding to each FM call annotation. Therefore, the extracted deep-learning features may be influenced not only by the call itself, but also by the surrounding soundscape (i.e., abiotic, biotic and anthropogenic background noise) present in the audio snippet. Consequently, the deep-learning features may partially reflect recording-site-specific characteristics, rather than species-specific call characteristics, possibly introducing some uncertainty in species' attribution. The assessment of which elements of each audio snippet are predominantly captured by the feature extraction would require explainable-AI methods, which were outside the scope of this study.

Beyond the methodological limitations associated with deep-learning feature extraction, there are also practical constraints on the applicability of the two non-contextual differentiation approaches. Both are restricted to high-quality calls (SNR NIST Quick (dB) > 14), which substantially limits the proportion of FM calls for which species attribution is currently feasible. Lowering the SNR NIST Quick (dB) threshold may eventually be possible if long-term PAM recordings become available that can be paired with simultaneous sightings confirming the exclusive presence of a single species. However, this remains challenging given the broad distributional overlap of blue and fin whales [18,19].

Together, the classification approaches presented here provide a practical framework for reliably classifying blue and fin whale FM calls in long-term PAM datasets. Applying these methods can expand knowledge of species occurrence in the Southern Ocean during non-song periods, inform on acoustic presence and feeding behavior [13,41], and support effective monitoring and management efforts. While restricted to high SNR NIST Quick (dB) calls, this study demonstrates that integrating tag data into PAM analyses is a promising avenue for improving species attribution and monitoring efforts.

Methods

Data acquisition and labelling

Passive acoustic monitoring data

Manually annotated FM calls of fin and blue whales were collected from multiple data sources collected from long-term mooring-mounted hydrophones in the Southern Ocean (see Figure 4 and Table 2 for details). One primary source was recordings from the Alfred Wegener Institute (AWI), collected at two sites in the Weddell Sea: AWI251 off Elephant Island and AWI227 on the Greenwich Meridian. An additional source was an open-access annotated library of underwater acoustic recordings, developed for testing and training automated detection algorithms for Antarctic blue and fin whale sounds [15]. This dataset includes recordings from seven sites across the Southern Ocean, spanning five years (2005, 2013–2015, 2017), with site coverage varying by year.

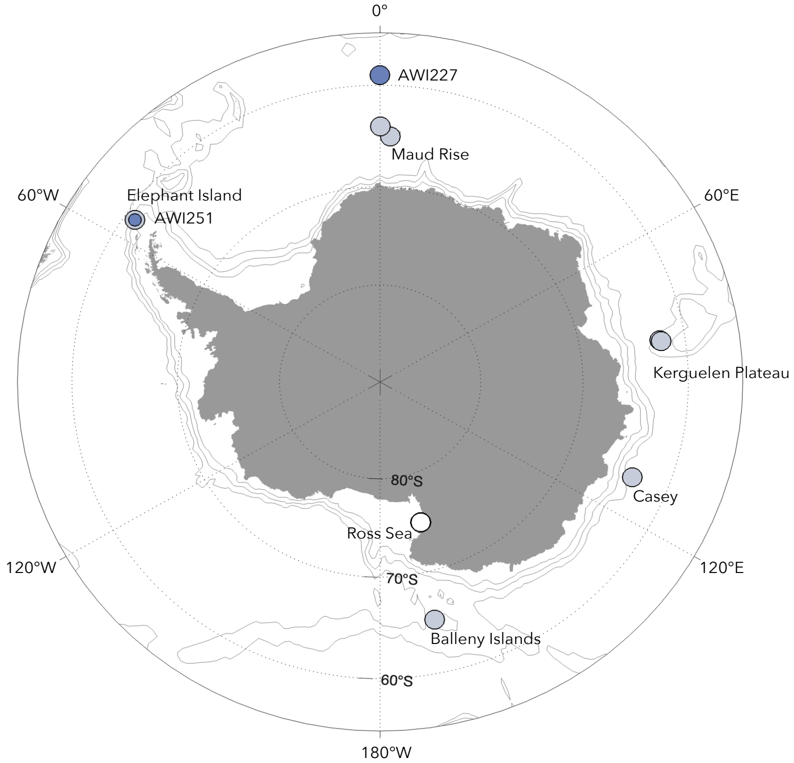

Figure 8. Map of the Southern Ocean showing the locations of passive acoustic recorders contributing to the datasets used in this study. AWI recorder sites (AWI251 and AWI227) are indicated in blue. Six additional sites from the open-access dataset where FM calls were detected are shown in light gray, while the Ross Sea mooring, where no FM call data were detected, is shown in white. Note that the Elephant Island recording site from the open-access dataset and AWI251 are overlapping in the map due to their nearly identical coordinates. The map was generated using M_Map [42] in MATLAB (Version 2022b; The MathWorks Inc., 2022).

Table 2. Summary of annotated passive acoustic mooring datasets used in this study. This table includes both manually annotated datasets (AWI) and datasets obtained from the open-access library of underwater acoustic recordings [15]. Available call types include fin whale 20-Hz calls (20), blue whale A-, B-, and Z-calls (abz), as well as frequency-modulated (fm) calls from either species.

Data source	**Dataset ID**	**Latitude**	**Longitude**	**Analysed Period**	**Total hours annotated (h)**	**Available call types**	**Total no. fm calls**	**Data access**
AWI	AWI227	59 2.82° S	000 5.78° E	2012-12-11 - 2013-07-11	140	fm, abz, 20	1507	https://doi.org/10.1594/PANGAEA.966612
	AWI251	61 0.13° S	55 97.78° W	2013-01-18 - 2013-12-31	86.6	fm	528	https://doi.org/10.1594/PANGAEA.966766
Open-access data[Miller et al. 2021; 23]	Open access dataset from 7 Southern Ocean sites over 5 years (2005, 2013–2015, 2017); sites not consistently represented across years.				1661	fm, abz, 20	16174	doi:10.26179/5e6056035c01b

For conformity between the open access and AWI data, AWI recordings were decimated to a sampling rate of 250 Hz and visually scanned for blue and fin whale calls using the sound analysis software Raven Pro 1.6 (The Cornell Lab of Ornithology, Center for Conservation Bioacoustics, Ithaca, NY). Analysis was performed using smoothed spectrograms in a Hanning window, with window and DFT size of 256 and 80% overlap. For the AWI227 dataset, annotations included FM calls, clearly identifiable fin whale 20-Hz pulses, and blue whale A-, B-, and Z-calls. In contrast, the AWI251 dataset was manually analyzed for FM calls only. For each annotation, 12 quantitative parameters describing call characteristics were extracted from Raven Pro (see Table 3) for both AWI and open-access datasets. These two datasets were then combined into a single ALL-RavenFeatures dataset for further analysis. To improve data quality and ensure that only the most representative calls were included, a HighSNR-RavenFeatures subset was created by excluding all frequency-modulated (FM) calls with a signal-to-noise ratio (SNR) proxy below 12 dB (SNR

NIST Quick (dB) > 12). This threshold was chosen to minimize the influence of low-SNR detections and emphasize well-defined, high-quality acoustic signals.

Table 3. Raven features to describe detected FM calls of fin and blue whales in the various datasets. Parameters were calculated according to the temporal and spectral limits of the respective vocalizations by drawing selection boxes around detected vocalizations. Details on measurements according to the Raven Pro 1.4 User's Manual [35,43].

Measurement	**Description**
Low frequency	Lower frequency limit of the selection box in Hz.
High frequency	Upper frequency limit of the selection box in Hz.
Delta frequency	The difference between the upper and lower frequency limits of the selection box in Hz.
Center frequency	The frequency that divides the selection into two frequency intervals of equal energy in Hz.
Peak frequency	The frequency at which the maximum amplitude occurs within the selection in Hz.
Frequency 25%	The frequency that divides the selection into two frequency intervals containing 25% and 75% of the energy in Hz.
Frequency 75%	The frequency that divides the selection into two frequency intervals containing 75% and 25% of the energy in Hz.
Frequency 5%	The frequency that divides the selection into two frequency intervals containing 5% and 95% of the energy in Hz.
Frequency 95%	The frequency that divides the selection into two frequency intervals containing 95% and 5% of the energy in Hz.
Delta Time	The difference between begin time and end time of the selection in s.
Duration 90%	The difference between the point in time that divides the selection into two time intervals containing 5% and 95% of the energy (Time 5%) and the point in

	time that divides the selection into two time intervals containing 95% and 5% of the energy in the selection in s.
Slope	The slope of the selection, calculated as delta frequency divided by delta time in Hz/s.
SNR NIST Quick	Signal-to-noise ratio (SNR) estimated as the difference between root mean square (RMS) power values that divide the selection into 15% (noise level) and 85% (signal level) of windows in dB, using overlapping 20 ms windows. This feature provides an approximate measure of the selection's signal strength relative to ambient noise.

A rule-based labelling approach was chosen to assign each FM call to a presumed species or label it as unclassified. The open-access dataset included pre-labelled FM calls, which were based on call duration (>1s for blue whale D-calls, <1s for fin whale 40Hz-calls). This approach was considered unsuitable for this study, as it would introduce a parameter-based bias in the classification attempt, and because this classification rule has never been proven to be reliable beforehand. Instead, FM call labels for the combined datasets were assigned based on the presence or absence of well-known species-specific calls - fin whale 20-Hz calls, as well as blue whale A, B, Z-calls - within a ±30min window around each FM call. For higher certainty we only used high quality species-specific calls with SNR NIST Quick (dB) >15. A FM call was assumed to be a 40Hz fin whale call if only fin whale calls were present, a D-call if only blue whale calls were detected, and a frequency-modulated (FM) call of unclassified if calls from both, or neither, species occurred within the time window.

Blue and fin whale acoustic tag data

An acoustic tag dataset (Tag-dataset) was included, consisting of FM calls recorded during acoustic tag deployments on blue and fin whales, providing species-verified labels. This dataset comprises 165 blue whale D-calls recorded during three deployments off the Coast of California, as well as 66 fin whale 40Hz-calls documented in 12 deployments off Chile (see Table 4 for details). All tag recordings were decimated to 250Hz and manually analyzed in Raven Pro 1.6 using the same spectrogram settings and measurements as used when analyzing the AllSNR- dataset. Since the calls were attributed to individually tagged animals, species identity was known, and all labels in this dataset are treated as ground truth, with no unassigned FM calls.

Table 4. Summary of the tag datasets used as ground-truth in this study. This table includes the manually annotated tag datasets on blue and fin whale FM calls, D- (d) and 40Hz- (40) calls respectively, from deployments off California and Chile.

Data source	Species tagged	Latitude	Longitude	No of deployments	Total hours analysed (h)	Call type	Total no. calls	Data availability
Isla Chañaral, Chile	fin whale	29 3.53° S	71 57.94° E	12	~333.4	40	66	Buchan, Unpublished
California, USA	blue whale	33 47.96° N 33 42.85° N	118 31.09° E 118 23.87° E	3	~44.6	d	165	Lewis 2018 [44]

Deep learning feature extraction

In addition to the acoustic features extracted using Raven (Raven features), deep learning features were computed for the audio snippet corresponding to each annotation from the AllSNR-, HighSNR- and Tag-datasets, referred to as AllSNR-, HighSNR- and Tag-DLFeatures. These deep learning features are high-dimensional vectors of acoustic properties, extracted from the last layer of the respective pre-trained model. The features were computed using bacpipe, an open-access software tool implemented in Python[45]. The models chosen for evaluation from all the available options were the ones which were at least partly trained on underwater acoustic PAM data. These included Biolingual [30], GoogleWhale [31], Surfperch [32], and Perch [33].

Biolingual [30] directly produced a 1D vector as it is a transformer model which allows for different window sizes as input. In contrast, the other models operate with a fixed window size, producing multi-dimensional embeddings per snippet. These multi-dimensional embeddings had to be pooled along the time axis to obtain a 1D vector per audio snippet. We applied median pooling, which was chosen after testing several alternatives (mean, max, min). The choice of pooling strategy has been shown to influence the quality and shape of the resulting clusters[40]. In our case, median pooling produced more compact and better-separated clusters than the alternatives. Due to some audio snippets being too short for deep learning feature extraction (due to the fixed window size setting for most models), the AllSNR-DLFeatures dataset contains 203 fewer data points than the AllSNR-RavenFeature dataset (18006 and 18209 data points, respectively).

Exploratory data analyses and clustering

To assess differences in temporal-spectral parameters among call types, boxplots were used to visualize the distribution of the 12 individual Raven features in the AllSNR- and HighSNR-RavenFeatures. To investigate possible groupings of call types based on the acoustic measurements, a Principal Component Analysis (PCA) was applied. PCA is a linear dimensionality reduction technique to project data onto a lower dimensional space. It was conducted using the scikit-learn package [46] in Python.

To further explore potential non-linear differences, a Uniform Manifold Approximation and Projection (UMAP) [47] was applied to both the Raven and deep learning features to reduce dimensionality and visualize call similarity in a 2D space. UMAP requires the specification of two key hyperparameters: the number of neighbors, which balances local and global structure, and the minimum distance, which controls how closely points are distributed in the reduced space. Because the optimal settings are data-dependent, different ranges were tested for Raven and deep learning features.

After a range of hyperparameters were tested by combining each value of n_neighbors = {2, 5, 10, 20, 50, 100} with each value of min_dist = {0.1, 0.3, 0.5}, a configuration with 5 neighbors and a minimum distance of 0.1 for the Raven features, and 50 neighbors and a minimum distance of 0.3 was chosen for the deep learning features. These settings allowed for a more exploratory view of the projection, revealing structures within broader clusters in the different datasets. UMAP was performed on the AllSNR-, HighSNR- and Tag- datasets, and ran in unsupervised and semi-supervised modes, respectively. For the Tag- datasets a supervised approach was applied additionally. In the unsupervised setting, the algorithm identifies structure based solely on the input features, without any label information. In contrast, semi-supervised projections partially incorporate label information, while supervised projections fully incorporate label information to guide the structure of the projection.

To quantify the existence of possible clusters in the datasets, a Hierarchical Density-Based Spatial Clustering of Applications with Noise (HDBSCAN)[48] was applied to both the Raven feature datasets (AllSNR-, HighSNR- and Tag-RavenFeatures) and to the according -DLFeatures datasets, using the hdbscan library[48]. This algorithm identifies regions of varying density to form stable clusters, while allowing to consider dissimilar or sparse samples as noise. The minimum cluster size was explored individually for each dataset (n_components = {5, 10, 20, 50, 100, 200}), aiming at reducing the amount of noise while yielding stable and interpretable clustering results.

Using Tag data as a reference for call classification in long-term PAM data

To evaluate whether ground-truth tag data could serve as a reference for classifying FM calls in the AllSNR-datasets, data subsets matching the SNR range of the corresponding Tag-datasets had to be created to ensure comparability. Both the AllSNR-RavenFeatures and AllSNR-DLFeatures were therefore filtered for a SNR NIST Quick (dB) of at least 14 dB, creating the HighSNR.2-RavenFeatures and HighSNR.2-DLFeatures, respectively. All FM calls in the AllSNR-datasets were treated as FM calls and projected into the respective tag UMAP space (Tag-RavenFeatures and Tag-DLFeatures), meaning that their features were transformed into the same 2-dimensional embedding (dimensionality-reduced) retrieved from the respective Tag-datasets. The alignment between the assumed context-dependent labels of the AllSNR FM calls and the ground-truth tag call types was then examined by comparing each AllSNR call to its closest tag neighbour within the projection. For each FM call, the five nearest ground-truth tag call types were identified, and the most common tag call type among these neighbors was assigned to the FM call as the corresponding label. FM calls whose nearest ground-truth tag call exceeded a Euclidean distance of 2 were treated as unassigned. This allowed calculation of the number and percentage of HighSNR.2 calls from each assumed call type that corresponded to each ground-truth Tag call type.

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Geographical distribution of two acoustic fin whale (*Balaenoptera physalus*) populations across the Weddell Sea

3

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Research

Geographical distribution of two acoustic fin whale (*Balaenoptera physalus*) populations across the Weddell Sea

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Understanding and identifying population-specific acoustic features is crucial to passive acoustic monitoring-based remote sensing of population distributions. Fin whales are known to produce 20-Hz pulses, often accompanied by a simultaneous higher frequency (HF) component. The centre frequency of this component has been found to differ regionally, presumably representing a population-specific acoustic characteristic. Within the Southern Ocean, five distinct HF components have been identified so far, two of which are present in the Atlantic Sector of the Southern Ocean (ASSO) with peak frequencies around 86 and 99 Hz. This study investigates the extent to which these HF components indicate distinct acoustic fin whale populations and their spatial distribution across the ASSO. By automatically analysing passive acoustic data from 2013, across 10 recording positions, our data show that while the 99-Hz component was detected at seven recording positions throughout the ASSO, the 86-Hz HF component is only present in its western area, centred around the Western Antarctic Peninsula. Additional 2019 data from the Western Antarctic Peninsula confirmed the consistent presence of the 86-Hz component, suggesting that these components are robust indicators of distinct acoustic populations. Knowledge on population-specific key habitats is key to strategic and effective conservation efforts.

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1. Introduction

Acoustic signals play a crucial role in the ecology of many animal species, serving functions ranging from echolocation for orientation to vocalizations for communication such as mating display (e.g. [1–4]). Like human language, animal communication often exhibits within-species vocal variations or 'dialects', offering valuable insights into the species' ecology.

In the absence of genetic and morphological data, acoustic signals can in some cases indicate acoustic populations and support management decisions since understanding a species' population structure and their spatial distribution is essential for developing targeted and effective conservation management strategies [5–9]. This is particularly relevant in logistically challenging environments where traditional monitoring methods are impractical. Here passive acoustic monitoring (PAM) methods are invaluable for long-term studies on the distribution of soniferous marine mammals, their main habitats and related behaviour [10–12].

For instance, regional differences in humpback whale (*Megaptera novaeangliae*) song were shown to reflect population identity and structure, as well as cultural exchange among populations (e.g. [13,14]). Similarly, the stereotyped song of several other cetacean species such as blue whales (*Balaenoptera musculus*), pygmy blue whales (*Balaenoptera musculus brevicauda*) and fin whales (*Balaenoptera physalus*) can be used to identify acoustic populations and their distribution [15–21].

This study focuses on identifying a reliable and easily recognizable acoustic cue to differentiate acoustic populations of Southern Hemisphere fin whales (SHFW) to contribute to knowledge vital to the implementation of targeted and successful conservation strategies. After decades of severe exploitation during the commercial whaling era, effective management measures are key to restore the SHFW stocks. However, the rarity of observations which is due to the difficult logistics of studying the species has led to data deficiency on the species' habitat use, ecology, population structures and recovery rates (IWC-SORP, https://www.marinemammals.gov.au/sorp/southern-hemisphere-fin-whales/). Consequently, by lack of further data, the SHFW are currently managed as one circumpolar stock (IWC-SORP, https://www.marinemammals.gov.au/sorp/southern-hemisphere-fin-whales/).

Globally, fin whales are known to produce stereotyped 20-Hz pulses, characterized as short (approx. 1 s), loud impulse sounds (160–186 dB re 1 μPa at 1 m) centred around 20 Hz, with a frequency range typically sweeping from approximately 28 Hz down to approximately 15 Hz. These pulses occur both as single vocalizations and as song, produced exclusively by males. In contrast to the complex and hierarchical structure of humpback whale songs, fin whale song is less complex, consisting of repetitive and structured pulse sequences [22–24]. Mainly, fin whale acoustic populations are differentiated based on song characteristics such as the inter-note intervals (INIs; e.g. [20,25]) or the occurrence of '20-Hz pulse doublet calls' [26], but also the high-frequency (HF) component accompanying the 20-Hz pulse has been suggested to be a valuable characteristic helping to identify acoustic populations [20,27,28]. In the Northern Hemisphere, one HF component was observed ranging between 125 and 130 Hz, not necessarily occurring simultaneous to the 20-Hz pulse or seeming to be reflective of geographical differences [12,20]. In contrast, in the Southern Ocean (SO) five presumably region-specific HF component varieties have been identified so far. These components range between 60 and 100 Hz and seem to consistently occur simultaneously with the 20-Hz pulses [10,11,18,26,27,29–32]. Two HF component varieties have been found present in the Atlantic Sector of the Southern Ocean (ASSO) with peak frequencies around 86 and 99 Hz [11,31,33]. The 99-Hz HF component was also detected throughout the Indo-Pacific Ocean towards the western coast of Australia, whereas different doublet HF components with peak frequencies at 82 and 94 Hz were found off the Australian east coast. Two further geographically separate doublet HF components were found in waters north and south of New Zealand with peak frequencies at 77 and 88 Hz and 67 and 73 Hz, respectively [26,27,34,35]. These different peak frequencies and the geographical distinction imply that the HF component varieties may represent different acoustic populations of SHFW [27,31,34]. Simon *et al*. [28] suggested that, in the SO, unlike in the Northern Hemisphere, the HF component possibly is a more reliable indicator than INI information to assess population identity, particularly in areas where songs and single vocalizations of multiple simultaneously vocalizing individuals spectrally and temporally overlap.

Given these findings, this study aims to further explore the regional specificity of the HF component and the potential to identify SHFW acoustic populations within the ASSO. We will improve the knowledge on SHFW (i) by investigating the acoustic presence and distribution of the HF components and the respective acoustic fin whale populations in the Weddell Sea by automatically analysing

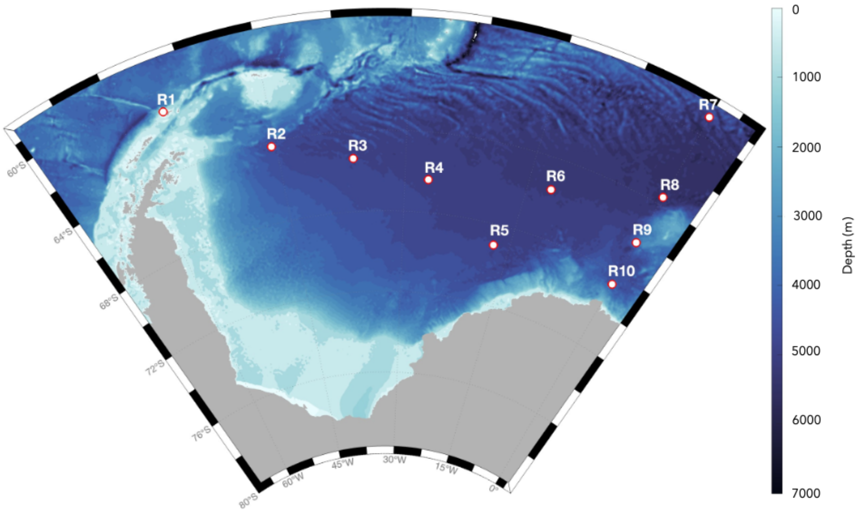

Figure 1. Bathymetric map of the Atlantic Sector of the Southern Ocean indicating the geographical locations of the 10 acoustic recorders (R1–R10) used in this study. Map was generated with M-MAP [36] in MATLAB [37].

passive acoustic data from 2013; (ii) by comparing HF components from 2013 and 2019 data to assess their spectral stability; and (iii) by providing an overview on the distribution of additionally described HF components in the SO.

2. Material and methods

2.1. Passive acoustic data

Fin whale acoustic presence was investigated using passive acoustic data from 10 recording positions throughout the ASSO (figure 1). Data selection involved visual examination of long-term spectrograms not only to assess data quality but also to ensure the best possible spatial coverage, using all available Alfred Wegener Institute recorders within the ASSO, accessible through the Open Portal to Underwater Soundscapes (https://opus.aq/).

Acoustic data were obtained using SonoVault autonomous recorders (Develogic GmbH, Hamburg, Germany, Reson TC4037-3 hydrophone, with a linear frequency range of 1 Hz–50 kHz), which continuously recorded at a sampling frequency of 5333 Hz in 2013 (see table 1 for detailed deployment information). Preparation and standardization of passive acoustic data were implemented according to the standard operating procedures of the Ocean Acoustics Group at the Alfred Wegener Institute in Bremerhaven, Germany [48].

2.2. Automatic detection of fin whale vocalizations

All available passive acoustic datasets were processed using the automated detector developed by Schall & Parcerisas [49]. This detector operates on a threshold-based approach, requiring signal-specific metrics to exceed predefined thresholds to identify fin whale vocal activity. It is designed to identify fin whale 20-Hz pulses, as well as low-frequency and high-frequency choruses generated by spectrally and temporally overlapping 20-Hz pulses and their respective HF components (see figure 2). For chorus detection, the detector calculates three metrics: signal-to-noise ratio (SNR), power spectral density slope (PSD Slope) and power spectral density area (PSD Area). These metrics are compared against predefined thresholds to identify the presence of low- and high-frequency choruses. For 20-Hz pulse detection, the detector evaluates the features kurtosis, temporal and spectral SNR, and signal bandwidth. It employs a decision tree approach that applies multiple thresholds to filter potential detections. The selection of optimal threshold values was performed by maximizing true positive detections while minimizing false positives in two different test datasets. For the chorus test dataset, true positives referred to the correct identification of chorus presence within 5 min audio files. Whereas for the pulse test dataset, true positives referred to the correct identification of time-stamped individual

Table 1. Deployment information on passive acoustic recordings included in this study. Depth refers to recorder deployment depth. All recorders were operating with a sampling frequency of 5333 Hz, resulting in a bandwidth of 2666.5 Hz.

recorder	deployment ID	latitude	longitude	depth (m)	recording period	data citation
R1	AWI251–01_SV1008	61 0.88° S	55 58.53° W	212	15 Jan 2013–9 Nov 2013	https://doi.org/10.1594/PANGAEA.97313891 [38]
R2	AWI217–05_SV1020	64 22.94° S	045 52.12° W	960	23 Feb 2013–19 Jun 2013	https://doi.org/10.1594/PANGAEA.973149 [39]
R3	AWI208–07_SV1030	65 37.23° S	036 25.32° W	956	2 Jan 2013–20 Oct 2013	[40] https://doi.org/10.1594/PANGAEA.968560
R4	AWI209–07_SV1028	66 36.45° S	027 7.26° W	1085	31 Dec 2012–22 Oct 2013	[41] https://doi.org/10.1594/PANGAEA.973151
R5	AWI245–03_SV1012	69 3.480° S	017 23.32° W	1065	28 Dec 2012–11 Nov 2013	[42] https://doi.org/10.1594/PANGAEA.973236
R6	AWI248–01_SV1013	65 58.09° S	012 15.12° W	1081	18 Jan 2013–14 Nov 2013	[43] https://doi.org/10.1594/PANGAEA.973408
R7	AWI227–12_SV1025	59 2.82° S	000 5.78° E	1020	11 Dec 2012–13 Jul 2013	[44] https://doi.org/10.1594/PANGAEA.966612
R8	AWI229–10_SV1010	63 59.85° S	000 1.84° E	998	14 Dec 2012–2 Aug 2013	[45] https://doi.pangaea.de/10.1594/PANGAEA.973171
R9	AWI230–08_SV1009	66 2.01° S	000 3.12° E	949	7 Jan 2013–27 Sep 2013	[46] https://doi.pangaea.de/10.1594/PANGAEA.973185
R10	AWI232–11_SV1011	68 59.94° S	000 4.38° E	958	17 Dec 2012–13 Nov 2013	[47] https://doi.org/10.1594/PANGAEA.973160

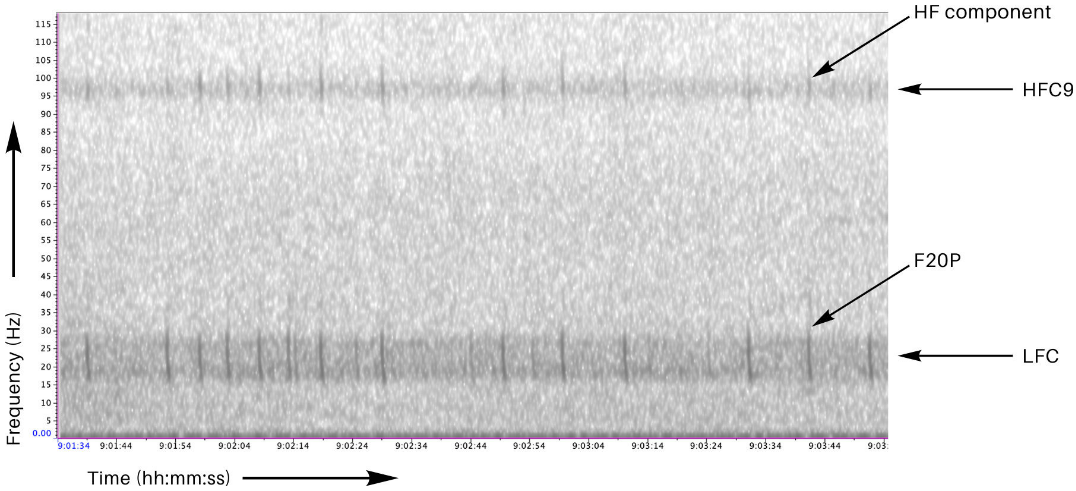

Figure 2. Fin whale call spectrograms of recordings from 28 March 2013 at the Greenwich Meridian (R7). Spectrogram is showing 20-Hz pulses (F20P), the resulting low-frequency chorus (LFC), as well as the simultaneous higher frequency (HF) component centred at approximately 99 Hz, resulting in the 99-Hz chorus (HFC9). Spectrogram parameters: Hanning window with a window size of 5000, discrete Fourier transform size of 8192 and an 80% overlap.

Table 2. Threshold values for the respective signal detection methods and corresponding true positive rates when allowing for the stated false positive rates as estimated by Schall & Parcerisas [49]. Note that the detection metrics for the choruses are independent algorithms that yield three independent indications of chorus presence, while the detection metrics for the 20-Hz pulses combine to a single detection algorithm yielding a single indication of 20-Hz pulse presence. A multi-step decision was conducted, allowing for fainter 20-Hz pulse detection within a chorus (i.e. lower temporal SNR.2 than temporal SNR), if a certain bandwidth was exceeded and the 20-Hz pulse represents a clear pulse (i.e. a higher kurtosis than the signal's kurtosis 1.2). SNR, signal-to-noise ratio; PSD, power spectral density; TPR, true positive rates; FPR, false positive rates.

signal type	detection method	threshold value	TPR	FPR
low-frequency chorus	SNR	4	0.89	0.03
86-Hz chorus	PSD Area	0.3	0.93	0.03
99-Hz chorus	PSD Area	0.35	0.76	0.03
20-Hz pulse	signal kurtosis	3.25	0.8	≤0.01
20-Hz pulse	kurtosis product	40		
20-Hz pulse	spectral SNR	9		
20-Hz pulse	temporal SNR	−2		
20-Hz pulse	temporal SNR.2	−7		
20-Hz pulse	signal bandwidth	75		
20-Hz pulse	signal kurtosis 1.2	4		

20-Hz pulses. Manual annotations served as the reference for identifying true positives and false positives.

For low-frequency chorus detection in the frequency band 17–25 Hz and high-frequency chorus detection in the frequency bands 84–87 Hz (86-Hz chorus) and 96–100 Hz (99-Hz chorus), we employed the detection metrics and the corresponding threshold values that lead to the optimal balance between true (TPR) and false positive rates (FPR), as determined by the test dataset used by Schall & Parcerisas [49]. These detection metrics and thresholds, along with the corresponding values of TPR and FPR (estimated in the test dataset from Schall & Parcerisas [49]), can be found in table 2. The chosen detection method for the low-frequency chorus was the SNR metric. For each audio file, the SNR is calculated by estimating the spectral energy within the 17–25 Hz band and comparing it to the noise level in adjacent frequency bands. The median noise level is used to exclude high-energy transient sounds. For the high-frequency choruses, the PSD Area metric was chosen as the optimal detection method. These methods were found to be most effective for detecting the respective choruses in the analyses by Schall & Parcerisas [49]. To minimize the detection of environmental noise within the high-frequency chorus frequency bands, detections of the high-frequency choruses were only counted when the low-frequency chorus was detected concurrently, since the HF component is thought to only occur in relation with the 20-Hz pulses in the SO [12,26].

For the detection of 20-Hz pulses, we also selected thresholds that yielded the optimal balance between TPR and FPR (table 2), as outlined in Schall & Parcerisas [49]. This selection was applied across various detection metrics, including the signal's kurtosis, kurtosis product, temporal SNR, spectral SNR and bandwidth.

For consistency and to ensure comparability, the thresholds for both chorus and pulse detection were applied uniformly across all recording positions analysed in this study.

2.2.1. Manual post-processing of detector results

To assess the presence of low- and high-frequency choruses and pulse detections at each recording position, we conducted a series of checks on the data for each recording location.

Specifically, we randomly selected 10 days for each recording position to manually assess the presence of both low- and high-frequency choruses. From those 10 days, four days were further used to check the 20-Hz pulse detections. Moreover, we revised outlier days, which appeared as temporal exceptions in the timelines exceeding the 1% FPR threshold for 20-Hz pulse detection or the 3% FPR threshold for chorus detection, respectively. This revision of outliers encompassed both detection types across all recording positions and only addressed cases that were not initially covered in the random checks.

Due to an unexpected high number of pulse detections at recording position R5, we extended the evaluation efforts specifically for this recording position, by examining 7 random days per month. All recordings were evaluated in RavenPro 1.6 (The Cornell Lab of Ornithology, Center for Conservation Bioacoustics in Ithaca, NY) using smoothed spectrograms in a Hanning window with a window size of 5000, discrete Fourier transform size of 8192 and 80% overlap.

2.3. Analysis of high-frequency components

Since 20-Hz pulses were detected at R1 and R7 only, the analysed recording files of these two locations were filtered for the highest 20-Hz pulse SNR values in combination with 86-Hz chorus or 99-Hz chorus presence, respectively. The ten 10 min files with the highest SNR values and high-frequency chorus presence per recorder position R1 and R7 were used to analyse the detailed frequency content of the HF components detected in this study. In addition to the R1 data from 2013, data from 2019 at R1 were also processed in the same manner to facilitate a comparison between those years to explore the consistency of the peak frequencies over time. Recording snippets from Juan Fernandez [25], the Western Antarctic Peninsula (WAP) [30] and the South Orkney Islands [10] were provided by the respective study authors upon request and were analysed in the same manner as the data of this study. This allowed for a direct comparison of different HF components also from sites outside the study area (see electronic supplementary material, figure S3, for the respective recording positions). To enable direct and optimal comparison, all audio files were decimated to 250 Hz, and analyses were performed in Raven Pro 1.6 (The Cornell Lab of Ornithology, Center for Conservation Bioacoustics, Ithaca, NY) in a Hanning window, with a fast Fourier transform of 256 and 80% overlap. For all encountered HF components, the peak frequency, representing the frequency at which the peak amplitude occurs within the selection box (so-called robust measurement [50]), was measured by drawing selection boxes around the rough HF component's frequency limits in order to minimize the analysts' bias. Additionally, a Kruskal–Wallis test was conducted in RStudio (v. 2023.06.1+524 [51]) to assess differences in HF components across sites, followed by a Dunn's *post hoc* test for pairwise comparisons.

2.4. Sound propagation modelling

To estimate the range over which vocalizing fin whales were detected in this study, sound propagation modelling was employed. The site-specific sound propagation of 20-Hz pulses at recording positions R1 and R7 was inversely modelled in three dimensions using the software dBSea (dBSea Ltd, v.2.2.5, developed by Marshall Day Acoustics and Irwin Carr Consulting, UK). For this purpose, the vocalizing virtual whale was assumed to be situated at the respective recorder positions and depths (see table

Table 3. Information on the recorders, the virtual senders and settings used for sound propagation modelling using the dBSea software (dBSea Ltd, v.2.2.5, developed by Marshall Day Acoustics and Irwin Carr Consulting, UK) for recording positions R1 and R7.

	R1 (Elephant Island)	R7 (Greenwich Meridian)
gains and sensitivity levels of recorder	set gain 48 dB, sensitivity level of 192.6 dB at 251 Hz	set gain 24 dB, sensitivity level of 192.6 dB at 251 Hz
location	61 0.88° S, 55 58.53° W	59 2.82° S, 000 5.78° E
water depth at location	320 m	4600 m
receiver depth	215 m	1020 m
water temperature (summer)	0.8°C	−0.3°C
sender depth	15 m	15 m
sediment type	sand [52]	mud [52]
number of grid points in *x*-directions (resulting step size)	2000 (354.4 m)	610 (353.1 m)
number of grid points in *y*-directions (resulting step size)	2000 (343.4 m)	635 (346.8 m)
number of grid points in *z*-directions (resulting step size)	500 (10.7 m)	525 (10.7 m)
source solution radial slices (resulting slice step angle of source)	100 (3.6°)	100 (3.6°)
source solution range points (resulting range steps of source)	500 (354.2 m)	620 (354.7 m)

3 for details), while the received levels (RLs) were calculated for 10.7 m, the depth of the model grid points best representing the assumed fin whale calling depth of 15 m [53]. The virtual sender was assumed to signal omnidirectional, with a source level (SL) of 180 dB re 1 μPa (based on a conservative approach using SLs of previous reported fin whale 20-Hz pulses; [54–57]).

While Burkhardt *et al*. [11] used silt as a sediment type based on Diekmann & Kuhn [58] for their sound propagation modelling at Elephant Island, the same location as R1 in our study, the sediment types for R1 and R7 were chosen according to the latest information from Jerosch *et al*. [52]. The sediment types were implemented in the model by using the software's default settings after Jensen *et al*. [59] for the respective sediment properties (see table 3 for details on the recorder and chosen software settings). Water temperature was determined calculating the water column mean temperature of the location closest to the recording positions, using the austral summer statistical means from 2005 to 2017 with a 1° resolution from the World Ocean Atlas [60].

The models for R1 and R7 were solved for normal modes and, due to different spatial extents of the bathymetry data, respective grid sizes were chosen to ensure comparable resulting step sizes into all three dimensions (i.e. resolution in x, y and z direction; see table 3 for the calculated grid points and the respective resulting step sizes). Further, a source solution of 100 radial slices was chosen for both models (R1 and R7), while the range points were adjusted according to the respective grid sizes. For the slice step angles, range points and resulting steps see table 3.

For comparison of the modelled RL at the recording positions, the received sound pressure levels ($\mathrm{SPL_{rms}}$ (dB re: 1 μPa)) of the detected 20-Hz pulses in this study were determined in MATLAB (v. 2022b [37]), by extracting single audio snippets based on the 20-Hz pulse detections and filtering for frequencies between 15 and 26 Hz.

3. Results

A total of 65 640 h of recordings collected from 10 positions over a period starting December 2012 until November 2013, spanning 2735 days, were analysed to assess the acoustic presence of fin whales. Out of these recorded days, 150 randomly selected days (15 per recording position) were post-processed by human analysts to verify automated detections, with 7 additional random days per month specifically examined for R5 due to the unexpectedly high number of pulse detections at that location. Subsequent

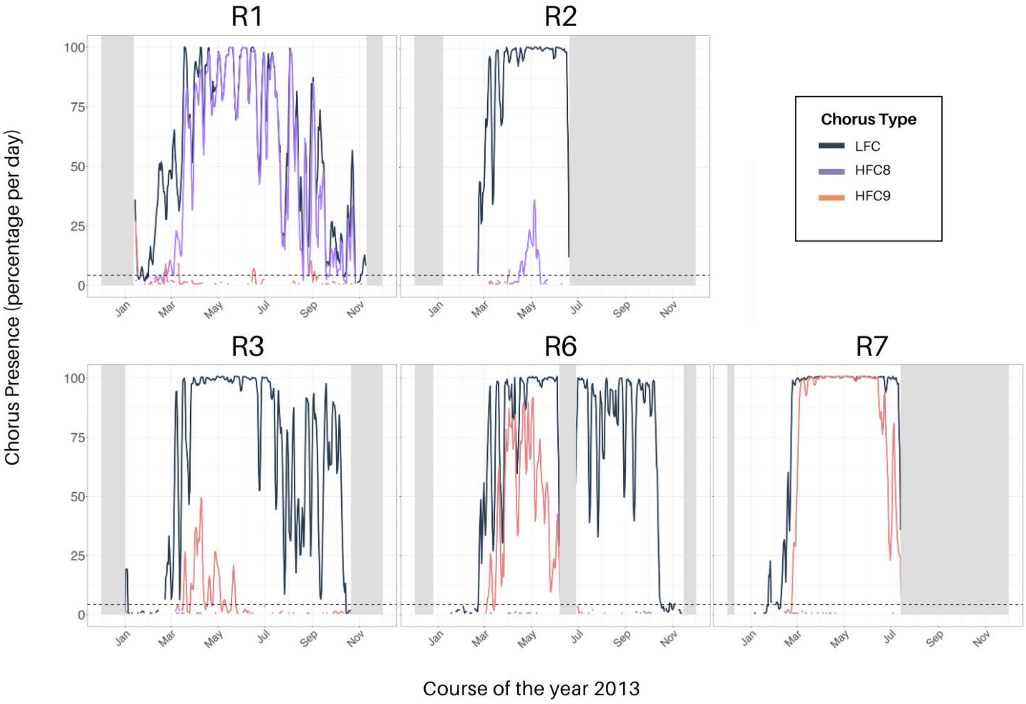

Figure 3. Line plots representing the percentage of files containing low- and high-frequency chorus per day over the course of the year 2013. Recordings consisted of 144 10 min files per day. Low-frequency chorus (LFC) is displayed in dark grey, 86-Hz chorus (HFC8) in purple and 99-Hz chorus (HFC9) in orange. The lines were computed with a three-day running mean to smooth out spikes for a better overview. Dashed horizontal lines indicate the false positive rate of 3%, representing 4.3 recording files per day, as calculated by Schall & Parcerisas [49]. The grey bars indicate time periods where no data were available. The low- and high-frequency chorus presence patterns of R3, R6 and R7 are representative of patterns observed also at R4, and R8–R10; thus, the respective plots will not be discussed further but are available in electronic supplementary material, figure S1.

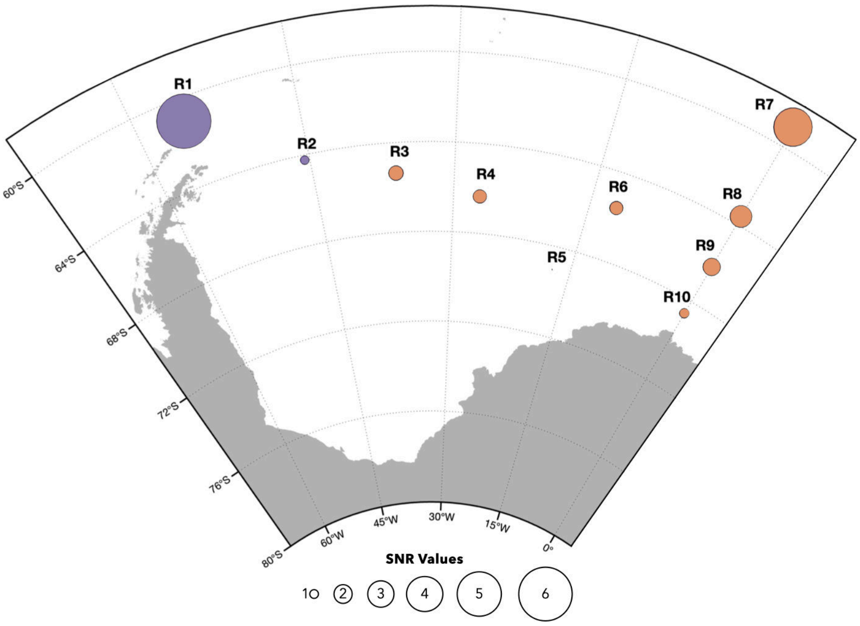

Figure 4. Map indicating the relative differences of the signal-to-noise ratios (SNRs) in dB of the two detected high-frequency choruses at the geographical locations of the ten acoustic recorders used in this study (86-Hz chorus is displayed in purple and 99-Hz chorus in orange). The displayed SNRs were computed as the average of SNR values determined by the automated chorus detector over the respective recording periods. Values were multiplied by 12 to create suitable sized markers (1–6). SNR values of chorus detections below the false positive rate of 3% were neglected. Map was generated with M-MAP in MATLAB [37].

manual examinations on these days revealed that the detections were caused by noise, as no fin whale vocalizations were found in the R5 recordings. Consequently, this recording location is not considered hereafter.

3.1. Chorus detection

The low-frequency chorus was detected at all recording positions. Daily chorus presence showed an overall seasonal pattern of low-frequency chorus presence from end of February throughout mid-October, corresponding to periods when recordings were available (see figure 3). Low-frequency chorus was present at R1 throughout November, with a drop in September. At R7, low-frequency chorus was often measured continuously in the period from the end of February to the end of June, while at monitoring sites R1–R4, R6 and R8–R10 this was the case from mid-March to the end of June (see figure 3 and electronic supplementary material, figure S2).

In contrast to the low-frequency chorus presence, the overall presence pattern of the high-frequency chorus was shorter, revealing a delayed onset around the beginning of March. At R2, a less prominent high-frequency chorus presence started with an even greater delay between low- and high-frequency chorus onset at the end of April. At R1 and R7, following the delayed onset, the high-frequency chorus was recorded continuously throughout most days, often revealing identical patterns to the low-frequency chorus (see figure 3).

While both previously reported high-frequency choruses at 86 and 99 Hz were present in our data, there appears to be a geographical boundary in their occurrence within the ASSO (see figures 3 and 4). Strikingly, the 86-Hz chorus was only detected in considerable amounts at R1 and R2, while 99-Hz chorus was only detected in considerable amounts at locations R3, R6 and R7. In individual files, 86-Hz chorus was also detected at R3, R6 and R7, as well as 99-Hz chorus at R1 and R2. However, these daily percentages either fall below the FPR of 3% or presence could not be confirmed during manual cross-checking the files and therefore not considered any further.

In addition to the already described differences in chorus presence, we also observed differences in the annual average SNR values. Highest annual SNR values were measured at the northernmost recording locations R1 and R7 with values of 6.08 and 4.31 dB, respectively, and continuously decreasing values towards the southern locations. This can be seen best in the recording transect along the Greenwich Meridian (R7–R10), where the lowest calculated average was 1.06 dB at R10. Additionally, a decrease in SNR values is not only observed along the longitudinal gradient, but with a latitudinal influence from locations R1 and R7 toward the central region of the Weddell Sea.

3.2. Detection of 20-Hz pulses

Fin whale 20-Hz pulses were detected and confirmed at R1 and R7 only, revealing a disparity in local call activity between the recording positions (see figure 5). At R1, 20-Hz pulses were detected from the beginning of March throughout the beginning of August, with an additional smaller peak at the end of September and beginning of October. The temporal maximum occurs at the beginning of June with 16 028 detected calls on 6 June 2013, before the call activity decreases and peaks again in July. Compared to R1, the call activity at R7 was detected during a shorter period of the year, and 20-Hz pulse detections were overall less abundant. Calls were occasionally detected on days in February, May and June, whereas the majority of calls were detected in March and the first half of April with a peak on the 29 March 2013 with a total of 5215 20-Hz calls detected.

3.3. High-frequency components

Peak frequencies of the detected HF component revealed clear differences between the 99- and the 86-Hz chorus but also indicate a broader range of peak frequencies for the HF component considered as 86-Hz chorus across the different locations in the ASSO, South Pacific and South Atlantic (figure 6). While the means of the western locations (Juan Fernandez, WAP, South Orkney Islands and R1) were situated between approximately 85 and 90 Hz, the HF component at R7 was characterized by a clearly higher peak frequency with a mean at 96.82 (±0.86) Hz.

Among the western locations, the means of peak frequencies of Juan Fernandez at 85.79 (±0.37) Hz, the South Orkney Islands at 86.58 (±1.26) Hz and R1 (2013) at 86.48 (±1.25) Hz, as well as R1 (2019) at

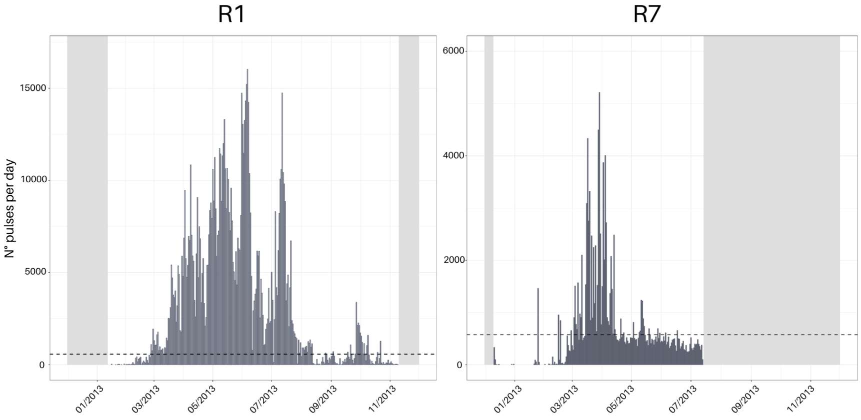

Figure 5. Barplots representing the number of detected fin whale 20-Hz pulses per day over the recording periods for recording positions R1 and R7. Dashed lines indicate the false positive rate of 1%, representing 575 pulses per day, as estimated by Schall & Parcerisas [49]. Note the difference in the scaling of the *y*-axis. No 20-Hz pulses were detected at the remaining recording positions. (Light) grey bars indicate periods where no data were available.

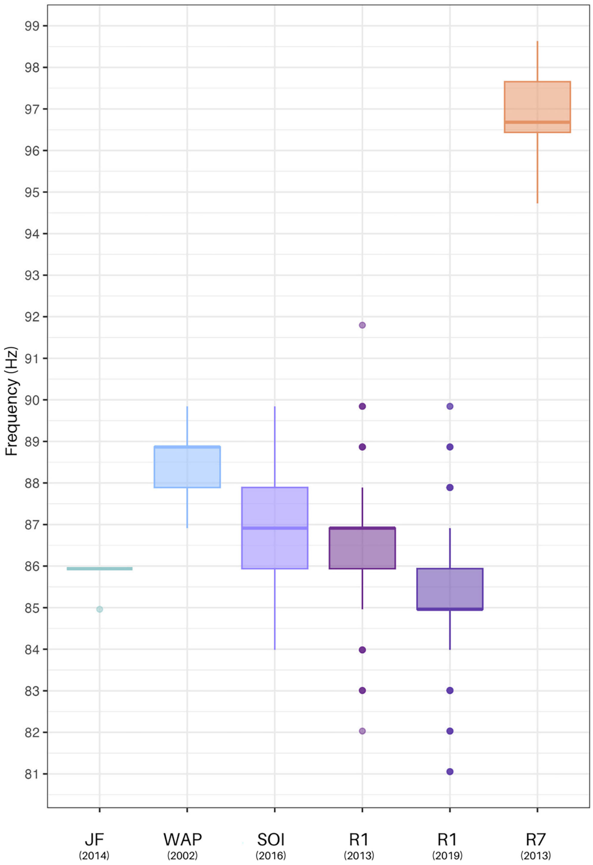

Figure 6. Boxplots comparing the peak frequencies of high-frequency components from this study (R1 (2013) $n = 225$, R1 (2019) $n = 220$, and R7 $n = 212$), as well as recording snippets from Juan Fernandez (JF), Chile recorded in 2014 ($n = 7$ [25]), Western Antarctic Peninsula (WAP) in 2002 ($n = 21$ [30]) and South Orkney Islands (SOI) in 2016 ($n = 126$ [10]).

85.26 (±1.5) Hz showed high similarities, while off the WAP a higher mean value at 88.45 (±0.85) Hz was measured.

The boxplots in figure 6 showing the detailed distribution of measured frequencies reveal highest overall variabilities with maximum values of approximately 92 Hz and minimum values of approximately 81 Hz at R1 (2013 and 2019)—a range encompassing all analysed peak frequencies from Juan Fernandez, WAP and the South Orkney Islands. However, peak frequencies at R1 (2013 and 2019)

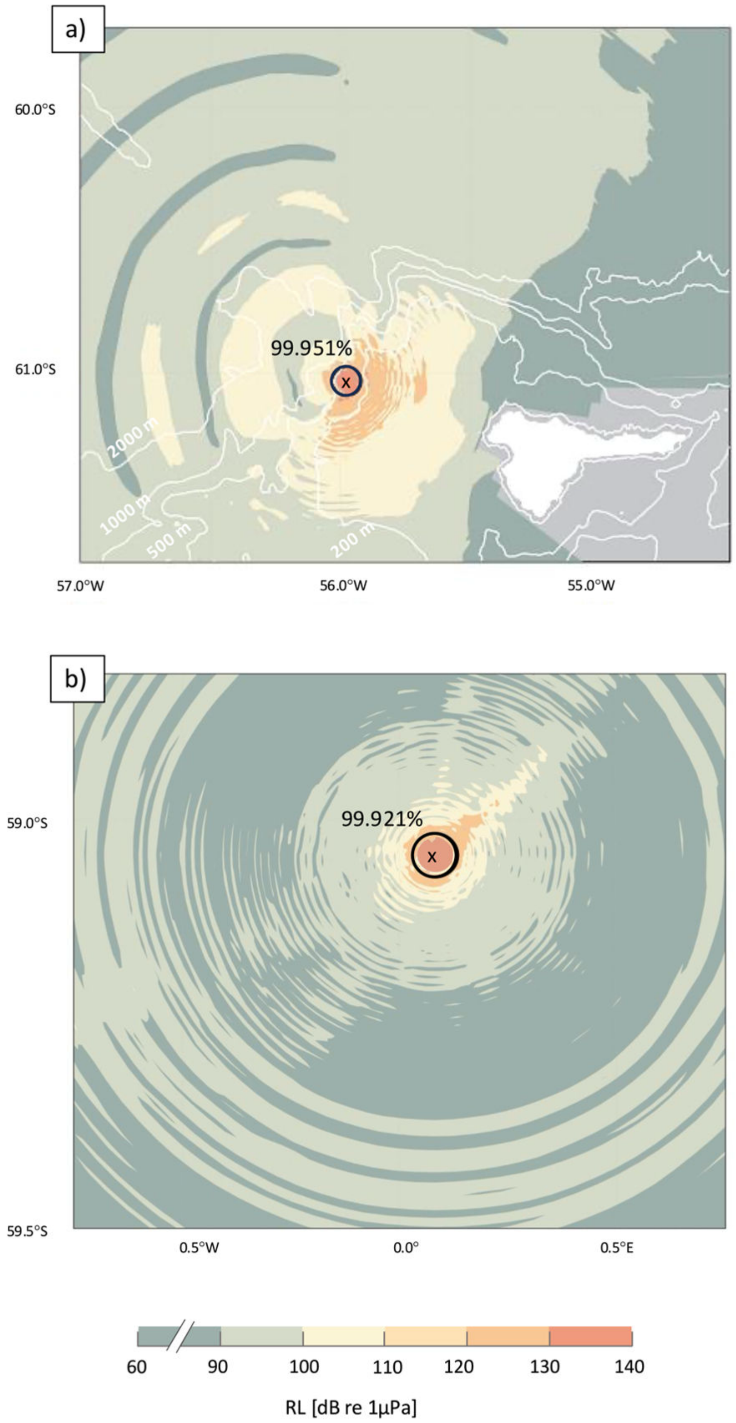

Figure 7. Modelled received sound pressure levels calculated for locations (*a*) R1 off Elephant Island and (*b*) R7 on the Greenwich Meridian. Received levels represent the sound pressure levels at a depth of 10.7 m as received from a virtual source placed at the recorder's position at (*a*) 215 m depth and (*b*) at 1020 m depth in accordance with the respective recorder depths and assuming a source of SL = 180 dB between 18 and 22 Hz. This set-up serves as a model proxy for the real, reverse situation, i.e. a source situated at 10.7 m and the recorder deployed at 215 or 1020 m depth, respectively. The black circle indicates a 3 km radius around the recording positions R1 and R7. Map created in MATLAB [37,61,62].

result in smaller interquartile ranges than off the South Orkney Islands, whereas the medians of R1 2013 and the South Orkney Islands show more overlap than the medians from R1 2013 in comparison to 2019, representing the lowest measured median (see electronic supplementary material, table S2, for details). Moreover, the Kruskal–Wallis test revealed significant differences across sites (χ^2 = 571.61, p <

2.2×10^{-16}). The pairwise comparisons provide more detailed insights into the differences between sites. As shown in the boxplots, R7 stands out as the most distinct site, displaying significant differences with all other locations. R1 from 2019 and the WAP also show differences from other western sites, although less pronounced (see electronic supplementary material, table S3 for detailed results).

3.4. Sound propagation modelling

While at R1 the sound propagation modelling with dBSea shows a highly anisotropic detection range, due to local bathymetric features, it reveals a relatively isotropic RL distribution at R7 when assuming a source at 10 m depth with a SL at 180 dB re 1μPa (virtual fin whale; see figure 7 for colour coded modelled RL distribution at the respective recording positions).

Based on the model output and the calculated SPL_{rms}, the average RL was calculated for a maximum distance of 3 km (indicated by the black circles in figure 7, resulting in RL values of 115.75 and 115.86 dB re 1 μPa for R1 and R7, respectively). Thus, the SPL_{rms} calculation of the detected 20-Hz pulses in this study revealed that presumably 912 674 calls (with RL > 115.75 dB re 1 μPa), making up 99.951% of all detected calls at R1, originate from within a 3 km radius around the recording position. In comparison, 127 016 calls (with RL > 115.86 dB re 1 μPa) of all detected pulses, accordingly 99.9%, presumably originate from within a 3 km radius at R7.

4. Discussion

The detection methods used to automatically detect fin whale acoustic presence relied on various metrics including but not exclusively simple SNR measurements. While commonly and effectively used [30,31,63], the calculation of SNR has limitations in environments where background noise overlaps with the target frequency range, potentially leading to false positives or missed detections. However, it is important to highlight that this detector was specifically designed to minimize false positives and avoid overestimating fin whale presence. As Schall & Parcerisas [49] note, the goal was to reduce false positives and prevent the misclassification of similar sounds, ensuring that fin whale presence is not overrepresented. This approach may result in an underestimation of fin whale presence in noisy environments, but it effectively prevents the overestimation of acoustic presence. Therefore, we are confident that detected fin whale acoustic presences are not caused by noise to a greater extent (>1% accepted FPR), allowing us to reliably interpret these results in an ecological context in the following paragraphs.

4.1. High-frequency components as population identifier

We found a clear geographical distribution of HF components in the Weddell Sea, with main presence of 99-Hz chorus along the Greenwich Meridian and 86-Hz chorus detected at the westernmost locations off the WAP. However, our study spans only 1 year of data (2013; with additional analysis at R1 from 2019), which may limit our ability to detect annual variability in the geographic distribution of these HF components.

Acoustic variation across different geographical regions does not necessarily indicate genetic divergence. SHFWs are thought to represent a single circumpolar genetic population and show low genetic differentiation across regions [64,65]. At the same time, as this study shows, SHFWs differ regionally in their acoustic characteristics.

Acoustic divergence in calling behaviour in the absence of significant genetic differences between calling populations has been found in species such as North Pacific sperm whales [66] and bird species like *Campylopterus curvipennis* and *Sylvia atricapilla* [67,68]. Hatch & Clark [17] also observed acoustic differences in NHFW calls and suggested that these may represent intraspecific variation that is too recent to be detectable in the genome [17]. This advocates that acoustic traits can be shaped by the social environment and learning rather than by genetic differences [66]. Cultural transmission, the transfer of shared behaviour or information through social learning, however, has the potential to affect the gene distribution. Culture includes vocalizations as well as habitat use, migration patterns, foraging strategies, prey selection and social behaviour [69,70]. Transmission of culture can occur directly from parents to offspring (vertical) and between unrelated individuals from the previous to later generation (obliquely [71]). One very prominent example is killer whales (*Orcinus orca*), where stable cultural traditions within ecotypes, including distinct vocal repertoires and prey choice, have led to functional gene evolution up to a level of ecological speciation [72–75]. Moreover, in various bird and cetacean species with less advanced ongoing speciation, horizontal cultural transmission (between unrelated individuals or even between neighbouring populations within the same generation) is found [76–79]. Southern Hemisphere humpback whales are managed as distinct breeding stocks characterized by their stock-specific song [14,80]. Despite gene flow and horizontal transmission of specific songs still occurring on shared summer feeding grounds [13,81], genetic differences between these breeding stocks are already detectable [82]. While cultural transmission may eventually be reflected in the genome, it seems cultural divergence, not genetic variation, drives acoustic differences first.

Considering this, bottleneck events may impact not only the genetic diversity of a population but also its cultural traits. In bird species, population size has been shown to correlate with acoustic diversity, which tends to decline following decimation events that isolate subpopulations or reduce population numbers [83–86]. Severe decimation events may also lead to cultural conformism and the loss of traditional knowledge, including the loss of traditional foraging grounds [87]. This has been suggested as a factor limiting the recovery of species like the North Atlantic right whale [88]. Thus, historical and industrial whaling may have affected subpopulations of whales, without necessarily reducing their genetic diversity. For instance, studies on North Atlantic fin whales and Southern Hemisphere humpback whales found no significant impact of whaling on genetic diversity [89,90]. And although the extensive depletion of SHFW populations might not be detectable through genetic data either, it may have severely disrupted social structures and cultural groups, potentially leading to cultural losses that cannot be identified through genetic analysis alone. Therefore, from a conservation perspective, it may not only be important but possibly more effective to focus on identifying and protecting culturally distinct subpopulations before prioritizing genomic differentiation [66].

While SHFW are currently considered a single circumpolar genetic population, they seem to represent several distinct acoustic subpopulations, with divergence too recent or subtle to be detectable in the genome. Given that differences in acoustic characteristics provide a reliable identifier for acoustic subpopulations, differences in acoustic behaviour like song characteristics and HF components can offer a suitable alternative for defining acoustic subpopulations [91]. However, in order to employ differences in acoustic characteristics as a robust method to identify acoustic populations, the acoustic signal needs to contain at least one cue that is stereotyped by this cultural group, ideally remaining stable over multiple years. Baleen whale song characteristics such as INIs in fin whale song are commonly used to differentiate between acoustic populations (e.g. [20,92,93]). The duration of INIs can seasonally change from shorter to longer patterns towards the beginning of the migration to breeding grounds [25,94] and hence might not provide a sufficiently stable characteristic to determine population identity. Furthermore, identification of clear INI patterns can be particularly challenging in regions with high fin whale densities, given the overlap in calling bouts [11]. Unlike INIs, HF components may offer a more reliable and temporally stable cue for population identification, if they remain consistent over multiple years.

Previous work reported that the frequency of the fin whale calls is decreasing over years, which seem to render the HF component less suitable as population identifier. A steady decrease in frequencies over several years was reported in HF components produced by North Atlantic fin whales [20], in 20-Hz pulse song and the 99-Hz HF component of SHFW [35,95], as well as in song of other baleen whales, such as blue and pygmy blue whales [35,96,97]. When comparing reanalysed HF components recorded off the WAP between 2002 and 2019, our results show a similar decline (figure 6). Širović *et al*. [30,31] detected a HF component at 89 Hz (88.45 ± 0.85 Hz) further west off the WAP in 2002 recordings. Burkhardt *et al*. [11] detected a HF component around 86 Hz (85.6 ± 1.5 Hz) off Elephant Island (R1 in this study) in 2013, while Buchan *et al*. [25] recorded a similar HF component at 85.79 ± 0.37 Hz off Chile in 2014. This was suggested to reflect a downward shift in frequency, similar to that observed in other baleen whale populations [11,25,33]. However, our data from R1 in 2013 and 2019 reveal an overall range of HF components that include the 89-Hz HF component from Širović *et al*. [30,31]. Additionally, the reanalysed data from the South Orkney Islands in 2016 [10] show a similar median to the R1 data from 2013, while the interquartile range extends to higher peak frequencies, more similar to values observed off the WAP in 2002. This may indicate a less steady frequency decline in these regions over time or suggest the presence of an acoustic population with a broader HF component range in these waters. Our reanalysis at Juan Fernandez and the WAP was based on a relatively small sample size and requires more in-depth evaluation. Further analysis of PAM data from areas such as the South American east coast and both African coastlines would be valuable before drawing final conclusions.

4.2. Main habitats and migration of SHFW across the ASSO

This study reveals seasonal SHFW occurrence in the ASSO starting in late February (late austral summer) and continuing through austral autumn until October (austral winter), consistent with previous findings [11,29,30,98,99]. Notably the low-frequency chorus was recorded with a high daily percentage at all locations (except R5), while the high-frequency chorus showed a weaker overall pattern with a higher daily presence at R1 and R7. This pattern is corroborated by the calculated relative SNR (figure 4), which shows higher values towards the northeastern and northwestern edges of the ASSO. Moreover, 20-Hz pulse detection was limited to R1 and R7, and the sound propagation modelling additionally further indicates that >99.9% of all detected 20-Hz pulses were produced within a radius of 3 km around the respective locations. The results align with the current understanding of SHFW being a pelagic species that is negatively correlated with sea-ice and the general distribution north of 60° S [30,100–102]. Our findings of 20-Hz pulses at the northernmost locations only confirm reported high habitat suitability for SHFW along and between the southern boundary of the Antarctic Circumpolar Current and the southern Antarctic Circumpolar Current Front [102–106]. Furthermore, exceptionally high densities of Antarctic krill (*Euphausia superba*) can be found in regions east and west of the Weddell Sea, respectively, explaining the acoustic presence predominantly towards our recording positions R1 and R7. These regions are characterized by oceanographic features enhancing productivity thereby increasing prey availability for SHFW [107–109]. In particular, Elephant Island (R1), the location with the highest number of 20-Hz pulse detections, is a confirmed and important feeding area not only for SHFW but also for other baleen whale species [11,103,110,111]. The variability in fin whale 20-Hz pulse detections in this area (figure 5) may reflect fluctuations in krill patch quality that might change over the season. Different whale species may prefer different krill demographics, and fin whales have been associated with large (>45 mm), mature Antarctic krill located offshore [111]. Additionally, foraging efficiency in rorquals, such as blue whales, has been shown to depend on prey density [112,113], which may also vary seasonally. These changes in prey demographics and density could drive movement patterns, with whales moving in and out of the region. Such movements, including groups feeding and departing, were observed and could contribute to the observed variability in 20-Hz pulse detections (E.B. 2024, personal communication).

4.2.1. Detection ranges of calls

The high-frequency chorus showed similar but weaker daily and delayed seasonal patterns compared with the low-frequency chorus. One possible explanation could be that the HF component is intended for communication over shorter distances than the fin whale 20-Hz pulses and is therefore not always detectable when low-frequency chorus is present. Simon *et al*. [28] found that for 20-Hz pulses and HF pairs, the HF component has a lower amplitude. This would imply that at the beginning of February, when only the low-frequency chorus is present in our data, fin whales are still further away from the recorder. However, visual sightings showed SHFW present as early as January until February in waters off Elephant Island [106], when 20-Hz pulses and the respective chorus are not present in our data. Irregular migration and/or year-round presence in high-latitude feeding areas has been reported for various baleen whale species (e.g. [114,115]). Given that no fin whale song, which is thought to be produced by males only [22], was recorded before February when visual sightings already confirmed fin whale presence, it may be females or juveniles that overwinter in these waters, as has been suggested for other baleen whale species as well (e.g. [116,117]).

4.3. Circumantarctic patterns in fin whale high-frequency components

Generally, our overall comparison of HF components spanning a scale from Chile to New Zealand over 17 years reveals five geographical groups, potentially stocks, throughout the SO.

Nearly all HF components mentioned in here and shown in figure 8 (and in electronic supplementary material, table S4) were detected with stable but geographically distinct frequencies over several years. Occasional spatial overlaps in HF component occurrence appear, such as off the west coast of Australia. In 2006 data, Aulich *et al*. [34] and Gedamke [27] detected only the 99-Hz component in their recordings. However, the doublet song and corresponding HF component of 82 and 94 Hz were found in recordings from later years at the same recording site. The fact that the two acoustic populations have their latitudinal migratory route from Antarctic feeding grounds along the western or eastern Australian coasts with little longitudinal exchange may explain this slight spatial overlap in HF

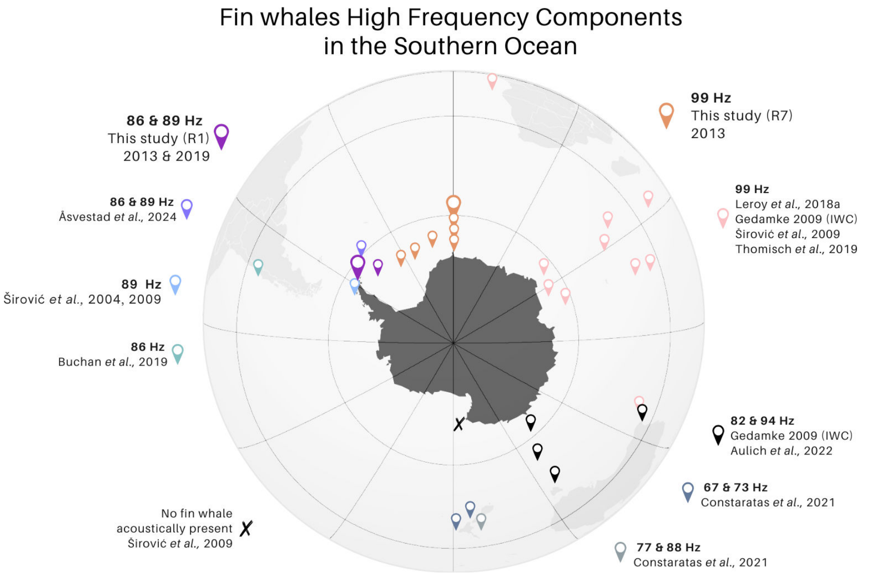

Figure 8. Map illustrating an overview on the different high-frequency (HF) components that were recorded in our and in previous studies in the Southern Ocean [10,25–27,30–32,35]. This map was created on Canva.com as a visual aid in understanding the spatial distribution of fin whale HF components; thus, the accuracy of coordinates of the data points is limited.

component types [34]. Interestingly, when examining circumantarctic HF component patterns, doublet songs and corresponding HF components appear only in waters off Australia and New Zealand. Although this song type has not been found elsewhere yet, data from additional locations, comprising both feeding and breeding areas, could help to determine if this phenomenon is truly specific to this region.

The identification of SHFW acoustic populations using the HF components will not only enhance our knowledge on distribution and migratory patterns but enable and facilitate tailored conservation management approaches for the respective populations. Fin whales are not only expected to face further population declines due to climate change by 2100 [118], but they are also increasingly impacted by growing human activities in the SO, such as tourism and fisheries. In the eastern Weddell Sea, the expanding krill fishery poses a rising threat [119], while in the waters off the WAP, fisheries targeting toothfish and increasing tourism are significant stressors [120,121]. This study adds to a growing body of evidence that these areas are vital for endemic as well as seasonal species, and that specific populations rely exclusively on relatively small regions for critical life stages. Our work supports the need for designing and implementing (seasonal) management measures, such as Marine Protected Areas, tailored to conserve and protect the species in this vulnerable region.

Ethics. Permission to deploy moorings in the Scotia Sea was granted by the German Federal Environmental Agency (UBA) under permits I 3.5-94003/286 and II 2.8-94003-3/347.

Data accessibility. The passive acoustic datasets analysed in this study are available through the PANGEA database (Thomisch *et al*., in preparation). The long-term spectrograms of the analysed recorders can be accessed via the Open Portal to Underwater Soundscapes (OPUS) accessible at CC BY 4.0, AWI 2023 (Thomisch K, Flau M, Heß R, Traumueller A, Boebel O. 2021 OPUS: an open portal to underwater soundscapes to explore and study sound in the global ocean. In *5th Data Science Symposium*; https://www.opus.aq/).

Supplementary material is available online [122].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. S.W.: conceptualization, data curation, formal analysis, investigation, methodology, visualization, writing—original draft, writing—review and editing; K.T.: software, writing—review and editing; E.B.: conceptualization, resources, supervision, writing—review and editing; I.V.O.: conceptualization, resources, supervision, writing—review and editing; E.S.: conceptualization, methodology, project administration, supervision, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

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4

Shifts in acoustic signature of Southern Hemisphere fin whales: Declining peak frequency of high-frequency components

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Shifts in acoustic signature of Southern Hemisphere fin whales: Declining peak frequency of high-frequency components

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Abstract: Population-specific acoustic features are vital for using passive acoustic monitoring to study marine mammal populations in remote regions. Southern Hemisphere fin whale (*Balaenoptera physalus*) songs include region-specific high-frequency components, with the 86- and 99-Hz high-frequency components present in the Atlantic Sector of the Southern Ocean. Using long-term passive acoustic monitoring data, we show that, despite gradual interannual and intra-annual variabilities, these features remain distinct and recognizable across regions and years. Our findings support their use as reliable acoustic markers for monitoring fin whale populations, providing valuable insights into distribution and population structure.

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1. Introduction

Acoustic signals serve important functions in animal communication, for example, conveying information during territorial defense or reproductive displays, while they can also contain information about the signaler's identity (Slabbekoorn, 2004). The natural variation in an acoustic signal's properties is an important factor in information transmission and has been documented over a wide range of taxa, such as birds (e.g., Henry *et al.*, 2015), mammals (e.g., Braune *et al.*, 2008), insects (e.g., Gray and Cade, 2000), and frogs (e.g., Boul *et al.*, 2007), enabling both interspecific and intraspecific discrimination. Ecological selection can drive acoustic divergence through morphological traits (e.g., beak and body size, vocal tract anatomy) or environmental signaling conditions (Henry *et al.*, 2015; Slabbekoorn, 2004; Wilkins *et al.*, 2013). When ecological factors are minimal, divergence or "dialects" within populations is proposed to be primarily driven by sexual selection (Wilkins *et al.*, 2013), producing variation in calling behavior that may be too recent to be detected at the genetic level, but is likely to impact population dynamics and speciation (Hatch and Clark, 2004; Wilkins *et al.*, 2013). For example, Southern Hemisphere humpback whales (*Megaptera novaengliae*) show distinct breeding stock songs correlated with already detectable genetic differences (Garland *et al.*, 2015; Winn *et al.*, 1981).

Passive acoustic monitoring provides a valuable approach for studying population structures of sound-producing marine mammals, particularly in remote areas (e.g., Balcazar *et al.*, 2015; Garland and McGregor, 2020; Mellinger *et al.*, 2007). Understanding these structures is essential for developing targeted and effective conservation management strategies (Clapham *et al.*, 2008). However, reliable distinction of acoustic populations requires at least one stereotyped signal cue that remains stable over multiple years (Delarue *et al.*, 2009).

In the Southern Ocean, fin whale (*Balaenoptera physalus*) song includes five region-specific high-frequency (HF) components (Burkhardt *et al.*, 2021; Constaratas *et al.*, 2021; Gedamke, 2009; Leroy *et al.*, 2018b; Shabangu *et al.*, 2020; Širović *et al.*, 2004, 2009; Wöhle *et al.*, 2025), offering potential as acoustic population identifier. Two varieties occur in the Atlantic Sector of the Southern Ocean (ASSO), with peak frequencies around 86 and 99 Hz (Burkhardt *et al.*, 2021; Širović *et al.*, 2009; Wöhle *et al.*, 2025; Wood and Širović, 2022). If these cues remain stereotyped and consistent within the cultural groups over multiple years, they provide a reliable method for population identification (e.g., Delarue *et al.*, 2009). However, a progressive decrease in baleen whale vocalizations frequencies, including blue (*Balaenoptera musculus*), pygmy blue (*B. m. brevicauda*), and fin whales has been observed worldwide (Gavrilov *et al.*, 2011; Leroy *et al.*, 2018a;

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McDonald *et al.*, 2009; Miller *et al.*, 2014), although the causes, natural or anthropogenic, remain uncertain (Gavrilov *et al.*, 2011; Leroy *et al.*, 2018a; McDonald *et al.*, 2009; Miller *et al.*, 2014).

This study analyzes the detailed frequency content of the two HF components present in the ASSO over multiple years, assessing their long-term spectral stability and potential as acoustic population identifiers.

2. Methods

2.1 Passive acoustic data acquisition

Presence of 20-Hz pulses and corresponding HF components of fin whales was investigated using passive acoustic data from two recording positions, Elephant Island (EI) and the Greenwich Meridian (GM), over several years within the ASSO (Fig. 1; see the supplementary material for recorder information). These sites were selected based on the distribution of the two fin whale acoustic populations (Wöhle *et al.*, 2025) and the availability of recordings from March to July, a period of peak fin whale acoustic presence (Burkhardt *et al.*, 2021; Širović *et al.*, 2004; Širović *et al.*, 2007; Širović *et al.*, 2009).

2.2 Preliminary data assessment

All passive acoustic data were pre-analyzed using the automated detector developed by Schall and Parcerisas, (2022), as applied in Wöhle *et al.* (2025), where the method is described in more detail. The detector identifies fin whale 20-Hz pulses, and low- and high-frequency choruses using the parameter settings and thresholds from Schall and Parcerisas (2022), optimized based on parts of the data corpus used in this study, leading to true positive rates above 76% and false positive rates below 3% (see the supplementary material). HF components were not detected directly, but because they seem to be characteristically produced simultaneously with 20-Hz pulses (e.g., Gedamke, 2009), periods with reliable 20-Hz pulse detections and concurrent HF chorus presence defined time windows for targeted manual inspection of individual HF components (Fig. 2).

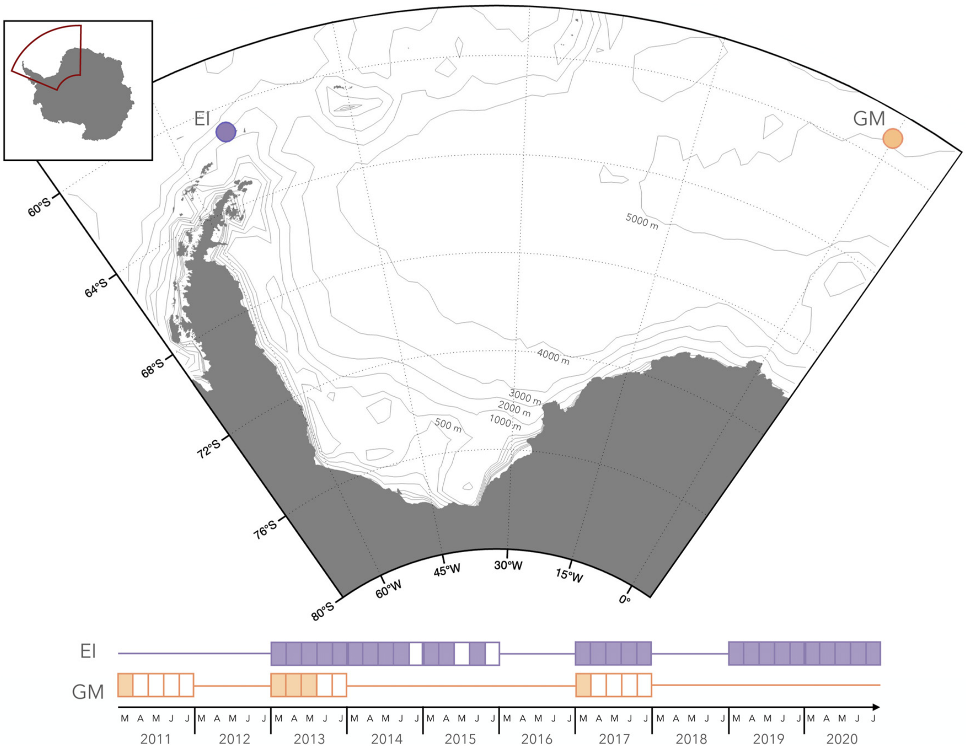

Fig. 1. Map of the ASSO indicating the two acoustic recording sites: EI and the GM. Timeline indicates March–July recording availability for each year and site [March (M), April (A), May (M), June (J), July (J)]; empty squares represent periods when the recorders were deployed but no recordings were available. Map generated in MATLAB using M-MAP (Pawlowicz, 2020; The MathWorks Inc., 2022). Data were prepared following standard procedures of the Ocean Acoustics Group at the Alfred Wegener Institute in Bremerhaven, Germany (Thomisch *et al.*, 2023).

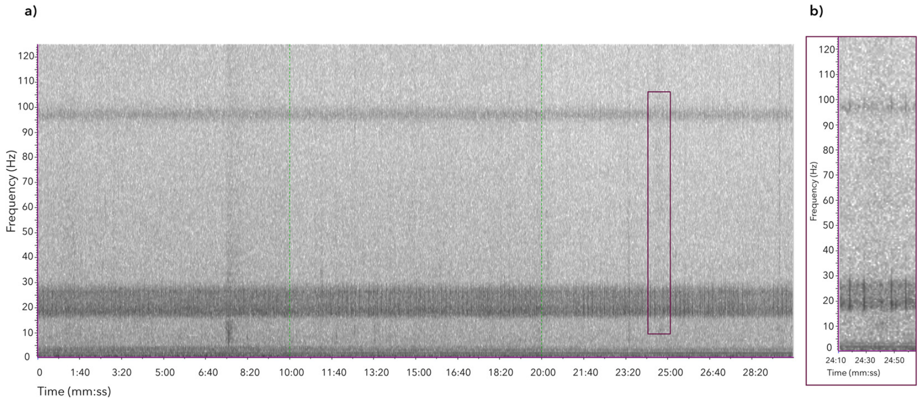

Fig. 2. (a) Thirty-minute spectrogram from the GM on March 28, 2013, showing fin whale low- and high-frequency chorus. Purple box highlights (b), a zoomed-in spectrogram showing individual 20-Hz pulses with corresponding HF components. Smoothed spectrograms calculated in a Hanning window with FFT/DFT of 512, and 50% overlap.

2.3 Data analyses

While all data were pre-analyzed, subsampling for the manual analysis focused solely on the period between March and July, the peak of fin whale acoustic presence. To ensure a comprehensive analysis of 20-Hz pulses and respective HF components from various individual fin whales, recordings were specifically chosen based on the co-occurrence of good-quality 20-Hz pulses (i.e., those with a high signal-to-noise ratio) and the respective HF choruses. Every sixth day was included in the analysis; and for each selected day, one 10-min recording with the highest signal-to-noise ratio was chosen from each of the three time intervals: 00:00–08:00 h, 08:00–16:00 h, and 16:00–00:00 h. While this approach was effective for data from EI, the selection process for GM data was adjusted due to the limited occurrence of HF components. To ensure sufficient data for analysis, all available GM recordings from every third day were analyzed.

2.3.1 Analysis of call parameters

All selected passive acoustic recordings were decimated to a sampling frequency of 250 Hz to assure comparability. Spectrograms for the decimated recordings were calculated and visually scanned using the sound analysis software Raven Pro 1.6 (Cornell Lab of Ornithology, Center for Conservation Bioacoustics, Ithaca, NY). Analysis was performed using smoothed spectrograms in a Hanning window, with FFT 256, DFT 512, and 80% overlap. For all identified 20-Hz pulse signals and their corresponding HF component, the peak frequency, defined as the frequency at which the peak amplitude occurs within the selection (so called robust measurement) (Charif *et al.*, 2010), was measured in order to minimize the analysts' bias.

2.3.2 Statistical analysis

To assess interannual and intra-annual variation in HF components' peak frequencies, values from both locations were plotted chronologically by year and month (Figs. 3 and 4). A linear regression was first fit with "year" as the explanatory variable and peak frequency as the response, assuming Gaussian distribution. Model assumptions were checked via QQ-residuals for normality and homogeneity of variance. Intra-annual variation was then examined using a linear mixed-effects model, with month as a fixed effect and random intercepts for each year-month combination. This approach accounted for both seasonal and yearly variability in peak frequencies. The models were fit using lme4's lmer() function (Bates *et al.*, 2015). All statistical analyses were performed in RStudio (version 2023.06.1 + 524; R Core Team, 2017).

3. Results

A total of 2880 h of recordings spanning 19 years were manually analyzed across the two recording positions, EI and GM. The analysis of high-quality signals encompassed 1783 HF components at EI, as well as 1487 HF components at GM.

3.1 Long-term trends in peak frequencies

Although the extent of analyzed years differs between the two locations, Fig. 3 reveals downward trends in peak frequencies at both locations, with decrease rates of 0.101 and 0.184 Hz/year at GM and EI, respectively (see the supplementary material). At GM, the 99-Hz components' overall range shows similarities across the three analyzed years; however, the median declined from 97.168 Hz in 2011 down to 96.191 Hz in 2017 ($n = 295$ and $n = 59$, respectively; see the supplementary material). Peak frequency variability was highest in 2013, the year with most detected calls ($n = 1134$). Also, for the 86-Hz HF component recorded off EI, a trend in frequency decrease is visible from 2014 to 2020, with the median peak

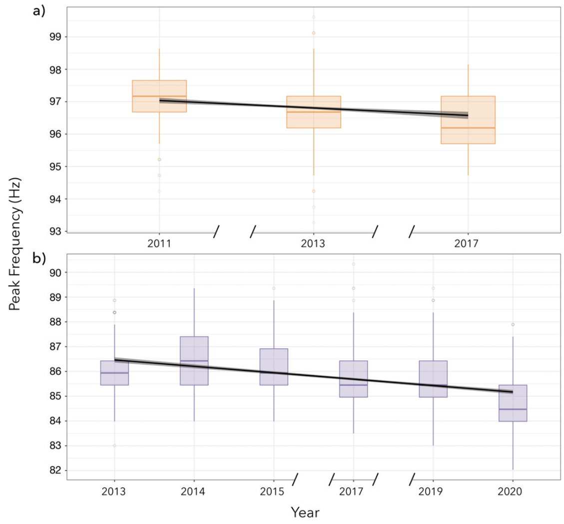

Fig. 3. Boxplots showing annual variation in peak frequencies of HF component at (a) GM (2011–2017) and (b) EI (2013–2020). Black lines indicate fitted linear regressions. Shaded gray areas represent confidence intervals, with decrease rates of 0.101 and 0.184 Hz/year at GM and EI, respectively. Data gaps are indicated by the interrupted *x* axis.

frequency highest at 86.426 Hz in 2014 declining to 84.473 Hz in 2020 ($n = 423$). However, the first year of recording (2013; $n = 257$) shows a smaller range of peak frequencies and a lower median compared to 2014 ($n = 134$).

Despite frequency decrease, the overall and interquartile ranges each year consistently include the previous year's median, producing a gradual decline at both locations. Importantly, although both HF components exhibit slight annual variability, the interquartile ranges of the 86- and 99-Hz components never overlap.

3.2 Intra-annual variation

Extending the subsampling at GM increased the number of calls analyzed yearly, but limited seasonal variability in call availability prevents intra-annual analysis. In contrast, at EI, coverage was better, with only three months missing over six years (Fig. 4), allowing for the exploration of seasonal patterns.

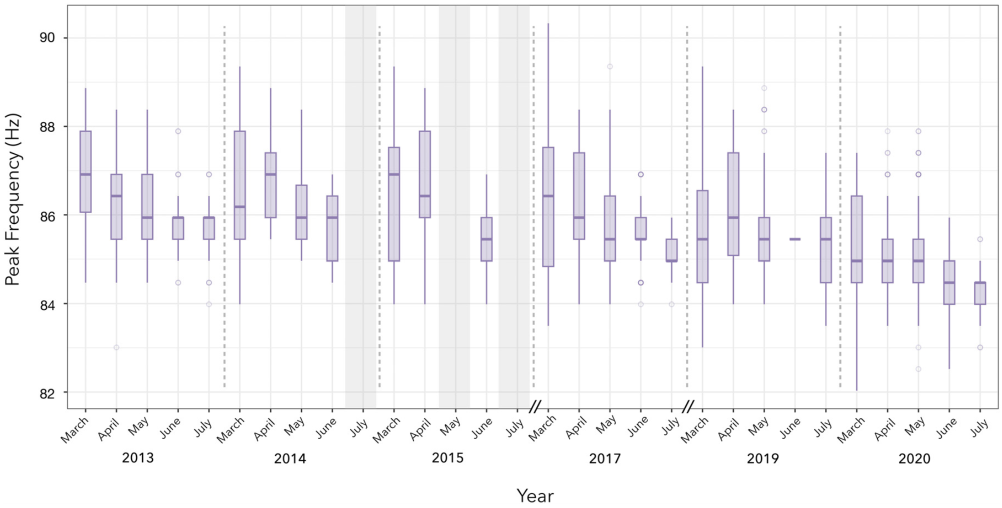

Fig. 4. Boxplots showing intra-annual variation in peak frequencies of fin whale HF components off EI from March to July 2013–2020. Gray shaded bars represent months with no data; interrupted *x* axis indicates data gaps in 2016 and 2018.

Figure 4 shows a recurring seasonal pattern, most pronounced in 2017 and 2020. While March 2014 and 2019 deviate slightly, peak frequency generally decreases from March to July. March shows the greatest frequency range, encompassing nearly all values measured within the respective year as well as those from the previous July. Additionally, March generally exhibits a higher median peak frequency than the preceding July but a lower median compared to March of the previous year. The linear-mixed model confirms this seasonal trend (Month L estimate $= -0.9339$, $t = -3.498$; see supplemental material for more detailed information).

4. Discussion

Decreases in signal frequencies have been observed across multiple baleen whale species. Globally, blue whale song types, including various populations in the Indian, Pacific, Atlantic, and Southern Ocean (Gavrilov *et al.*, 2011; Leroy *et al.*, 2018a; Malige *et al.*, 2020; McDonald *et al.*, 2009; Miller *et al.*, 2014; Rice *et al.*, 2022), as well as fin whale songs in the North Atlantic (Romagosa *et al.*, 2024), have shown long-term downward trends in their fundamental frequencies. This trend is also evident in different acoustic populations of pygmy blue whales in the Indian Ocean and Southwest Pacific (Leroy *et al.*, 2018a). All of these song types are characterized by repetitive, stereotyped calls, with the contour and structure of the vocal units remaining seemingly consistent despite long-term frequency changes.

In accordance with these findings, this study detected a gradual decline in the 86- and 99-Hz HF components' peak frequencies, with annual decreases of 0.184 and 0.101 Hz, respectively. Notably, the decline in the HF components approximately aligns with the rate reported by Leroy *et al.* (2018a), for the 99-Hz HF component, which documented a decrease in 0.21 Hz per year in the Indian Ocean from 2007 to 2015. Although these frequency shifts indicate that the HF component is not entirely stable, the decline occurs at a slow and predictable rate. Importantly, this variability in peak frequencies is minimal, especially when manual analysis of spectrograms is used for the classification of HF component types; both HF components remain visually recognizable in the spectrograms over the season and the consecutive years. Moreover, the interquartile ranges of the 86- and 99-Hz components do not overlap at any point during the analyzed timescale. As a result, the signals remain spectrally recognizable and distinguishable, ensuring that both manual and automated detection methods remain effective. However, to maintain detection accuracy over time, these methods may require periodic adjustment or retraining with updated examples that reflect the gradual frequency shift. Consequently, despite these gradual changes, the HF components can still serve as reliable acoustic markers for population monitoring.

There have been multiple attempts to explain this global phenomenon of frequency decreases, including adjustments to ambient noise levels, changes in sound propagation, and changes in whale anatomy (Gavrilov *et al.*, 2011; Leroy *et al.*, 2018a; McDonald *et al.*, 2009; Miller *et al.*, 2014); however, the frequency decreases are likely driven by a combination of factors. The current most plausible hypothesis points to increasing population densities, leading to reduced interindividual distances, resulting in lower call source levels and a linked decrease in call frequencies, with frequency decline rates potentially reflecting population recovery (Leroy *et al.*, 2018a; McDonald *et al.*, 2009). However, this mechanism does not explain the observed intra-annual patterns. The analyzed 86-Hz component in this study exhibits a recurring intra-annual pattern across years in addition to the long-term trend. Showing an overall decrease in peak frequency from March to July, with highest overall peak frequencies in March, whereas the mean in some years is higher in April. This seasonal variation is consistent with findings by Leroy *et al.* (2018a), Gavrilov *et al.* (2012), and Miller *et al.* (2014) who reported similar intra-annual frequency dynamics in Southern Hemisphere fin, blue, and Madagascan pygmy blue whales. Their results showed increasing peak frequencies early in the year, peaking in March or April, followed by a decline until October, and then a subsequent rise. In all cases, the peak frequency at the start of the following year never surpasses the previous year's maximum, emphasizing the presence of both intra-annual and interannual trends. A possible explanation for the intra-annual variation in call frequencies could be a link to hormonal cycles. Seasonal testosterone variations have been documented in multiple cetacean species, including fin whales (e.g., Kjeld *et al.*, 2004, 2006), and have been proposed to cause changes in singing behavior, such as cue rates and inter-note intervals (e.g., Oleson *et al.*, 2014). Hormonal effects on vocal behavior, such as delayed decreases in vocal frequency following hormonal shifts, are also described in various other species, both mammals and birds (e.g., Cynx *et al.*, 2005). In Southern Hemisphere fin whales, testosterone levels likely peak around March–April, preceding the reported maximum in spermatozoa production (Mackintosh and Wheeler, 1929), coinciding with the period when the highest peak frequencies are observed. Thus, the frequency decrease could also reflect a delayed long-term result of hormonally mediated changes. However, while these physiological processes may account for intra-annual frequency variability, they are unlikely to explain the observed long-term decrease in frequency, which may be driven by other mechanisms.

Social processes, such as cultural transmission, through vocal learning, and cultural conformity, are also shown as drivers for humpback whale song evolution (e.g., Garland *et al.*, 2011). Population-specific songs evolve over time through vocal learning, as individuals adapt to progressive changes introduced by conspecifics to maintain cultural cohesion (e.g., Garland and McGregor, 2020). This was also proposed more recently for blue and fin whale song structures (Gavrilov *et al.*, 2012; Malige *et al.*, 2020; Romagosa *et al.*, 2024), where the long-term declines in peak frequencies may reflect a simpler form of song evolution shaped by vocal learning and reinforced by cultural conformity. Thus, seasonal variation in peak frequencies could similarly arise from socially mediated modifications or perhaps from an interaction between social and physiological influences. For instance, the aforementioned variation in testosterone levels in adult males might drive changes in individual vocal behavior, while cultural conformity ensures that these shifts are adopted at the population level and embedded in the shared vocal repertoire. However, cultural transmission processes do not always proceed gradually and indefinitely. In humpback whales, for example, abrupt changes in song structure and reduction in complexity, so-called cultural revolutions, have been suggested to reflect the limits of vocal learning (Allen *et al.*, 2018). A comparable process might also apply to acoustic features, such as peak frequency. If fin whale frequencies approach physiological boundaries, gradual changes may no longer be viable. In such cases, an abrupt shift or reset in frequency could occur, analogous to the revolutions in humpback whale songs.

While the exact mechanisms remain uncertain, both interannual and intra-annual frequency shifts are likely shaped by an interplay of social and physiological factors. Given that these changes currently follow predictable seasonal patterns, the acoustic cues remain spectrally stable and distinctive enough to serve as reliable population identifiers. Nevertheless, as call characteristics continue to shift over time, automated detection methods will require regular adjustments to ensure long-term accuracy. Given the stable nature of the shift in call characteristics, synthetic call models that automatically evolve over time may support adapting automated detection methods. Additionally, incorporating manual revision of a subset of detections might be crucial to catch significant and unexpected changes, such as a potential revolution in frequencies. This kind of adaptive approach would ensure that shifts in call characteristics, whether gradual or abrupt, do not affect the accuracy of population monitoring.

5. Conclusion

Our study shows that the HF components in Southern Hemisphere fin whale song provide an efficient and reliable cue for acoustic population identification. Although their peak frequencies show inter- and intra-annual variation, they remain spectrally stable and visually recognizable, never overlapping, which ensures consistent distinction across years. These characteristics make them practical markers for long-term passive acoustic monitoring and highlight their importance for conservation management in the region.

Supplementary Material

See the supplementary material for additional tables and figures.

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Author Declarations

Conflict of Interest

We declare we have no competing interests.

Ethics Approval

Any research permission to deploy moorings in the Scotia Sea was granted by the German Federal Environmental Agency (UBA) under permits I 3.5-94003/286, I 3.5-94003-3/255, II 2.2-94/033/183, II 2.8-94003-3/347, and II 2.8-94003/137.

Data Availability

The datasets that support the findings of this study are openly available in PANGAEA, and the corresponding DOIs are available within the article's supplementary material Table SII.

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Synthesis

In this synthesis, I will discuss the potential and limitations of methodological approaches used in baleen whale acoustic signal analyses, based on the outcomes of the four chapters presented in this thesis. The synthesis is structured into two main parts: In the first part, I summarise the methodological advances and limitations in the classification of interspecific acoustic signals that were developed in Chapters 1 and 2, discuss potential reasons why baleen whales produce highly similar call types, and outline emerging challenges for reliable call classification under changing acoustic conditions. In the second part, I will present and discuss my results from Chapters 3 and 4 on differences in fin whale song characteristics, as well as the spatio-temporal patterns of acoustic population presence in the Atlantic Sector of the Southern Ocean. Within the second part, I also present preliminary analyses of two additional fin whale song characteristics, the inter-note intervals and song variants, that extend beyond the individual chapter results. By integrating these analyses with the findings of the preceding chapters, I provide a comparison of alternative song parameters with respect to their suitability for acoustic population identification.

Finally, I will discuss methodological limitations and outline the potential of standardised passive acoustic monitoring approaches for advancing baleen whale acoustic research.

Non-Song signals and acoustic separation of baleen whales

Methodological achievements

Over the last decades, advances in passive acoustic monitoring (PAM) technologies have substantially increased the availability of acoustic data across large spatial and temporal scales (Havlik et al., 2022; Tyack et al., 2023; Wall et al., 2025). At the same time, methodological developments, including automated signal detection and classification, have expanded the analytical potential of PAM datasets (e.g., Baumgartner and Mussoline, 2011; Huang et al., 2016; Knight et al., 2017; Rasmussen and Širović, 2021; Schall and Parcerisas, 2022). However, the effective and reliable application of PAM fundamentally depends on accurate signal identification. Accordingly, my first objective was to assess methods for reliably distinguishing non-song signals of different baleen whale species with highly similar acoustic signatures, focusing on upcalls produced by southern right and humpback whales, and frequency-modulated (FM) calls produced by fin and blue whales.

Parameter-based classification of upcalls: when simple methods are sufficient

The detection and classification of acoustic signals commonly rely on differences in acoustic parameters and signal contour in spectrograms (Mellinger et al., 2011). In Chapter 1, I demonstrated that southern right whale upcalls can be reliably distinguished from humpback whale upcalls using call characteristics derived from manual spectrogram analysis. Among the evaluated call parameters, slope and bandwidth were the primary parameters driving differences between the species' upcalls. Despite partial overlap in individual call characteristics, reliable distinction between species was possible, demonstrating that parameter-based manual analyses can support interspecific classification of upcalls. While manual classification requires expertise and is prone to observer bias (Leroy et al., 2018b), it remains a recognised and widely used approach for analysing baleen whale vocalisations (e.g., Dominello and Širović, 2016; Parks et al., 2007; Pivari et al., 2024). I showed in Chapter 1, that in the case of southern right and humpback whale upcalls the differences observed in key call parameters are large enough that small inconsistencies in manual annotation (e.g., bounding of calls in spectrograms) are unlikely to alter species attribution, making it a reliable method to distinguish calls. The results in Chapter 1 also highlight that for certain non-song signals relatively simple acoustic parameters can provide reliable interspecific classification without the need for more complex analytical frameworks.

From parameter-based classification to deep learning feature extraction

Such a level of separability was not observed for fin and blue whale FM calls in Chapter 2 when I examined simple call parameters, as the ones described in Chapter 1. I used FM calls with confirmed species identity from animal-borne tag recordings, providing high-confidence examples of each species' calls. I applied the same parameter-based approach to these confirmed calls, yet all 12 examined call characteristics showed substantial overlap between species. Only a single parameter, Duration90%, a robust measure of call duration defined as the interval between the 5% and 95% cumulative energy points (Charif et al., 2010), showed a potential discriminatory value. Based on this metric, I can provide a conservative rule for calls with a high signal-to-noise ratio (SNR), matching the SNR range of the tag data (Raven Pro 1.6 parameter SNR NIST Quick > 14 dB). This rule assigns FM calls to fin whales when Duration90% < 0.6 s and to blue whales when Duration90% > 0.7 s. However, as this rule may be useful for manual inspection of spectrograms, its applicability is limited. Calls falling between the Duration90% thresholds cannot be attributed, resulting in a substantial proportion of detected FM calls that may remain unclassified in PAM datasets. I achieved a more robust approach using deep learning (DL) features, which have proven effective for call classification across various taxa (Calonge et al., 2024; Frazao et al., 2020; Jung et al., 2021; Stowell, 2022; Stowell et al., 2019a; Waddell et al., 2021). By combining DL feature extraction using pre-trained models with non-linear dimensionality reduction, FM calls from long-term mooring recordings could be projected into an embedding space defined by tag-derived calls with confirmed species identity, with the reference ground-truth data being constrained into species-specific clusters. All calls from the long-term PAM dataset were subsequently projected into this embedding space and assigned unambiguously to one of the two tag-based species-specific clusters. While this approach is restricted to high SNR calls (Raven Pro 1.6 parameter SNR NIST Quick > 14 dB), it demonstrates that integrating ground-truthed tag data into PAM analyses represents a promising avenue for improving species attribution when call types are poorly separable using conventional acoustic parameters. However, the DL-based approach presented here is generally more computationally and methodologically demanding than manual inspection. Nevertheless, combining the classification framework with a prior implementation of an automated FM call detector (e.g., Schall et al., 2024) would substantially improve analytical efficiency and reliability, particularly for large, long-term and multi-site PAM datasets.

Limitations related to transmission loss

The approaches I employed to distinguish between species' upcalls and FM calls, including both parameter-based methods and DL features, face one inevitable limitation with regard to their applicability. Transmission loss, the attenuation and degradation of acoustic signals due to environmental conditions and propagation effects during transmission from the sender to the receiver (Forrest, 1994), likely further reduces the reliability of call classification in long-term datasets, particularly for low SNR calls. Such signal deterioration includes the shortening of the signal due to decreasing acoustic intensity with increasing distance from the source. Inevitably, this also results in alterations of other call parameters, including possible shifts in frequency limits, potentially reducing interspecific separability and thereby complicating classification. Consequently, the parameters used to distinguish upcalls in Chapter 1, duration and slope (with slope being inherently dependent on duration and bandwidth), are particularly sensitive to transmission loss effects. For FM calls, complete separation into species categories remains challenging even in the absence of transmission loss, as demonstrated by the substantial overlap in call parameters observed in acoustic tag recordings at the source (see Chapter 2). Transmission loss, especially the induced signal shortening, therefore further complicates an already limited interspecific separability. As a result, the application of the Dur90% threshold is strongly constrained to high-quality FM calls. Beyond parameter-based approaches, DL features are also sensitive to transmission loss related changes in call structure. Although the supervised embedding process enforces separation between fin and blue whale FM calls a slight overlap between the clusters is still observed when the data are not constrained to species-specific clusters. This cluster overlap reflects the overlap observed in call parameters. Because DL features are computed from the full audio input and thus implicitly include call characteristics, changes in call parameters such as call duration or bandwidth are likely to influence the extracted DL features and, therefore, classification performance. Consequently, both FM call classification approaches, call parameters and DL features, are effectively restricted to high-quality calls (SNR NIST Quick ≥ 14 dB). A similar constraint applies to upcalls, where low-quality calls may not be classified correctly due to signal degradation. When studies require confident species confirmation, analyses therefore need to be restricted to high-quality calls. While this restriction improves confidence in species attribution, it substantially limits the proportion of calls, particularly FM calls, for which reliable classification is currently feasible.

Methodological limitations in deep learning feature extraction and pathways forward

As with any methodological framework, the approach I present in Chapter 2 has limitations with respect to both correctness and applicability. One limitation arises from the DL feature extraction itself. While DL approaches can achieve high detection and classification accuracy for species-specific signals (Stowell et al., 2019a, 2019b), they are also widely used for soundscape analysis (Stowell, 2022), since DL features are computed for the full audio input. Using these methods only one cannot directly determine which aspects of the audio snippet, whether specific call characteristics or elements of the surrounding acoustic context, are depicted as important and drive the separation observed in the embedding space. Consequently, while the supervised embedding approach assigns calls unambiguously to species-specific clusters, I cannot verify the correctness of individual call attributions. Explainable artificial intelligence (AI) methods present a promising approach to overcome this limitation (Ahmed et al., 2022; Das and Rad, 2020; Minh et al., 2022). Techniques such as layer-wise relevance propagation (Bach et al., 2015) or DeconvNet (Noh et al., 2015) can provide insights into the spectrograms pixel contribution to a model's internal representations. Applied to the FM call classification, such approaches could help to disentangle and understand clustering outcomes. A systematic explainable AI analysis was beyond the scope of Chapter 2, but represents a valuable direction for future work to increase interpretability and confidence in DL–based acoustic classification. Since the DL features capture all acoustic information in the snippet, they may partially reflect recording site-specific characteristics rather than purely species-specific call properties (Darias-O'Hara et al., 2026; Mesaros et al., 2018; Szegedy et al., 2014), possibly introducing uncertainty into species attribution. Evidence for such effects was observed in my applied approach, in which some clustering outcomes appeared to be driven primarily by recording location. One potential strategy to mitigate this effect would be to perform classification separately for individual recording locations rather than combining data across sites. However, this would require multiple parallel clustering analyses and would reduce analytical efficiency in large multiple site datasets. Alternatively, soundscape-driven biases could be reduced at the data collection stage. Soundscapes are defined as the combined contribution of abiotic, biotic, and anthropogenic sound sources, representing the assemblage of sounds received at a given location (Erbe et al., 2025). Recorded soundscapes and their diversities vary therefore with geographic location, season and recorder depth. Recordings obtained from different locations may exhibit similar soundscapes, while recordings from the same location may differ substantially with depth (Mattmüller, 2025). Deploying recorders in acoustically similar soundscapes could therefore help minimise the bias of soundscape variability. However, current knowledge of soundscape similarity across the Southern Ocean remains limited (Cazau et al., 2017; Haver et al., 2017; Mattmüller, 2025).

The most robust, yet least feasible, solution would be to collect ground-truth recordings from animal-borne tags simultaneously with passive acoustic data from moored recorders. The tag data provided the essential reference that enabled both parameter-based and deep-learning approaches, making their integration central to the methodological advances presented in Chapter 2. Consequently, the collection of ground-truth tag recordings in close proximity to moored recorders across seasons would allow the construction of embedding spaces using species-specific calls recorded within the same local soundscapes as long-term PAM data. This approach would serve to minimise potential soundscape biases when projecting long-term PAM detections. In this scenario, the ground-truth dataset would provide the most representative reference possible for species attribution. However, to the best of my knowledge, no acoustic tag recordings are currently available for fin or blue whales in the Southern Ocean. The remoteness of the region, combined with strong seasonal limitations on fieldwork, makes such data collection particularly challenging. As a result, Chapter 2 relied on tag recordings from fin whales off Chile and blue whales off California. While FM calls have been reported for fin and blue whales globally across populations and are not generally described as exhibiting pronounced population-specific differences (e.g., McDonald et al., 2001; Miller et al., 2021; Oleson et al., 2007; Ou et al., 2015; Romagosa et al., 2021; Schall et al., 2020; Širović et al., 2013), population- or hemisphere-specific variation cannot be excluded. This population mismatch between tag data and long-term PAM recordings may therefore have contributed to uncertainty in FM call attribution. Together, the aforementioned points emphasise the critical importance of tag data for advancing acoustic classification, as well as the need to interpret DL-based results in the context of geographical variability of recordings.

Despite the discussed limitations, I can present a substantial methodological advance by directly leveraging ground-truthed acoustic tag recordings to inform FM call classification in long-term PAM data. I could also demonstrate that only a small fraction of contextually assumed FM call labels were consistent with confirmed tag-based DL feature classifications. This finding highlights the limited reliability of context-based labelling for fin and blue whale FM calls and underscores the need for non-contextual, standardised classification approaches in baleen whale acoustics, such as those developed in Chapters 1 and 2 of this thesis. While the FM call classification approaches presented here remain subject to constraints related to signal quality and data availability, this work deliberately prioritises classification reliability over sample size. More generally, I argue that such prioritisation is essential when addressing questions of species occurrence and distribution. In this context, analysing a smaller subset of confidently attributed calls may be preferable to including a larger number of uncertain classifications, although the appropriate balance ultimately depends on the specific research question.

How can we extend this method to classify other baleen whales' FM-calls?

In this synthesis, I focus on Antarctic blue and Southern Hemisphere fin whale FM calls, primarily due to data availability (i.e., Miller et al., 2021). However, other baleen whale species, such as humpback, right, sei, and minke whales also produce FM calls that overlap strongly in frequency (approximately 35–200 Hz) and duration (approximately 200 ms to 5 s; see supplementary material Figure S1 for call comparisons; e.g., Dominello and Širović, 2016; Edds-Walton, 2000; Miller et al., 2021; Nikolich and Towers, 2020; Ou et al., 2015; Pivari et al., 2024; Schall et al., 2021a; Webster et al., 2016). Moreover, their global habitats greatly overlap (Horwood, 2009; IWC SORP, 2016, 2019; Risch et al., 2019; Würsig et al., 2017). In current PAM studies, right whale FM calls are generally distinguished by their harmonic structure (Webster et al., 2016), whereas humpback whale FM calls are often produced as part of structured songs, providing contextual cues that aid in species attribution (Schall et al., 2021a). Similarly, sei whale FM calls are often distinguished based on the context of call repetition (Baumgartner et al., 2008; Romagosa et al., 2020). They are generally thought to be produced in more repeated patterns, typically occurring in pairs or triplets (Baumgartner et al., 2008; Romagosa et al., 2020; Tremblay et al., 2019; Wang et al., 2016). Antarctic minke whales also produce series of clustered FM calls, referred to as bioduck calls (Filún and van Opzeeland, 2023; Risch et al., 2014a). Yet, minke whales are also known to produce single FM calls (Dominello and Širović, 2016; Filún and van Opzeeland, 2023), which are often distinguished based on differences in frequency or duration relative to fin and blue whale calls (Dominello and Širović, 2016; Edds-Walton, 1997). However, the results I discuss here demonstrate that such context- and parameter-based distinctions are not necessarily reliable. Therefore, FM calls produced by humpback, right, sei and minke whales should be incorporated into the DL feature-based framework developed in Chapter 2. For this to be effectively implemented, confirmed reference data is required, either from moored PAM recordings where species identity is certain, or from animal-borne tag recordings. While FM call classification could be restricted to Southern Ocean baleen whale populations, the framework could also incorporate data from other ocean basins, given that these species hold global distributions (Horwood, 2009; NOAA, 2020; Risch et al., 2019; Würsig et al., 2017). In addition to ground-truth data, long-term PAM datasets containing high-quality FM calls to be assigned to species-specific clusters are required. Again, ideally both datasets, the ground-truth and long-term, would originate from the same populations. While some acoustic tagging efforts have been conducted on humpback (Parks et al., 2014; Stimpert et al., 2020), right (Parks et al., 2011), sei (Cusano et al., 2023), and minke whales (Casey et al., 2022; Risch et al., 2014b), to my knowledge, no extended acoustic tagging effort or large, well-curated long-term datasets of baleen whale FM calls currently exist that are comparable to those available for fin and blue whales (Miller et al., 2021). However, for both, ground-truth and long-term datasets, a sufficiently large number of high-quality FM calls is essential to provide adequate reference information for clustering, currently limiting the integration of more species.

Ultimately, the framework I presented here offers a first step towards a more general approach for FM call identification and classification approach. When combined with an automated call detector (Kowarski and Moors-Murphy, 2021; Miller et al., 2021; Schall et al., 2024), such a framework should be ideally trained on sufficiently large and diverse datasets, including high-quality FM calls from multiple Southern Ocean baleen whale species and populations, to provide a standardized method for Southern Ocean baleen whale classification. Extension to a global scale is also possible, but would require substantially more data. The development of open-access acoustic datasets spanning multiple species and call types would therefore be a critical step towards improving automated detection and classification methods.

Possible future challenges in call classification

Changes in the acoustic environment can interfere with animal acoustic signals, leading to masking, altered vocal behaviour, or shifts in call characteristics (Clark et al., 2009; Fournet et al., 2018; Holt et al., 2011; Melcón et al., 2012; Parks et al., 2007; Scheifele et al., 2005). Increasing ambient noise, particularly due to anthropogenic noise (which is projected to intensify over the coming decades; Jalkanen et al., 2022), or climate-induced environmental noise alterations, such as sea ice loss and increasing storms (Duarte et al., 2021), are especially problematic for baleen whales, as the dominant energy of their vocalisations overlaps strongly with low-frequency noise below 150 Hz (Clark et al., 2009; Dominello and Širović, 2016; Romagosa et al., 2020; Širović et al., 2004). As a result, the likelihood of signal masking increases, reducing effective communication space for whales while simultaneously limiting the number of high-quality calls available for PAM. For the FM call classification approach, I developed in Chapter 2, increased masking poses a particular challenge. The classification framework is already constrained to high-quality calls (SNR NIST Quick > 14 dB), a criterion that currently excludes approximately 80% of FM calls in the available datasets. Future increases in ambient noise are therefore likely to substantially reduce the number of calls that can be reliably classified further. Beyond masking, elevated ambient noise has also been shown to alter vocal behaviour, including reduced calling rates and shifts in call characteristics (Melcón et al., 2012; Parks et al., 2007; Slabbekoorn and den Boer-Visser, 2006). Such changes are especially problematic for call classification, as they may increase overlap among already similar call types. Noise-induced shifts in call characteristics have been documented across taxa. For example, increases in the low-frequency limits of calls have been observed in great tits (*Parus major;* Slabbekoorn and den Boer-Visser, 2006), striped dolphins (*Stenella coeruleoalba*; Papale et al., 2015), and right whales (Parks et al., 2007, 2009, 2016) when ambient noise interferes with communication. Shifts of this kind could further reduce separability between call types that already overlap strongly in frequency and duration. In Chapter 1, I observed notably higher low-frequency limits in southern right whale upcalls compared to those reported in previous studies (Calderan et al., 2021; Dombroski et al., 2016; Parks et al., 2007; Webster et al., 2016), resulting in greater similarity to low-frequency limits of analysed humpback whale upcalls. While the parameters mainly driving species differentiation, slope and bandwidth (Chapter 1), remained sufficiently distinct to allow reliable classification, further upward shifts in low-frequency limits will alter both parameters, possibly reducing interspecific separability, thereby complicating classification. Similar effects may be expected for FM calls, which are already more difficult to distinguish.

The observed shift in southern right whale upcall characteristics in Chapter 1 is unlikely to be driven by anthropogenic noise, as anthropogenic noise levels in the Southern Ocean remain comparatively low (Haver et al., 2017; Mattmüller, 2025). However, ambient noise can also be of biological origin. Off Elephant Island the southern right whale upcalls are most likely adjusted to the high intensity fin whale calls, which are masking the lower frequencies of southern right whale upcalls (80–90 Hz; Burkhardt et al., 2021; Dombroski et al., 2016; Parks et al., 2011; Širović et al., 2004). Competition for acoustic space can lead animals to adjust signal characteristics to occupy a different acoustic niche, thereby reducing interference. Adjustments to acoustic niches may also be forced by regime shifts, whereby species invade into new habitats and acoustic environments, occupying already established acoustic niches. Such processes have been documented across taxa (e.g., birds, amphibians, marine mammals; Both and Grant, 2012; Hopkins et al., 2022; Medeiros et al., 2017; Mossbridge and Thomas, 1999; Sueur et al., 2019). Climate change is increasingly driving shifts in species distributions and community composition (Simmonds and Eliott, 2009; Sueur et al., 2019), which can result in both increased or decreased competition for acoustic space between species. As mentioned before, species distribution can assist signal classification by constraining the range of possible species. However, distributional shifts could further reduce the reliability of such contextual approaches, by causing previously non-overlapping species to co-occur, or leading to unrecognised shifts out of known habitats or species replacements. Similarly, behavioural cues, such as call repetition patterns as in sei whale FM calls, may become less reliable, as ambient noise has been shown to alter calling rates in baleen whales (Melcón et al., 2012; Parks et al., 2016). The mentioned factors influencing species distribution and acoustic behaviour form a highly dynamic system, often limiting the utility of context-based classification and underscoring the need for non-contextual, standardised approaches. The same dynamic nature also highlights the necessity of continuous monitoring and periodic manual inspection by bioacousticians, to detect emerging changes and adjust automated analyses accordingly. Summing up, increasing ambient noise, climate-driven community shifts, and the resulting changing soundscapes are likely to make acoustic classification more difficult, while simultaneously reducing the number of calls that can be reliably analysed. These developments must be explicitly considered when designing PAM studies and analytical frameworks. If call characteristics continue to shift, approaches based on DL features may become increasingly important. However, this also highlights the need to better understand which signal properties drive classification decisions. For approaches such as the parameter-based upcall classification in Chapter 1, continued manual inspection and periodic reassessment of call characteristics may be necessary to detect and account for long-term shifts. For the FM call classification framework, I developed in Chapter 2, ensuring that long-term PAM detections are projected onto reference clusters derived from tag data collected during similar time periods and regions may become increasingly important. Spatio-temporal mismatches between reference and target datasets could otherwise introduce additional uncertainty if call characteristics change over time, but at different rates. Finally, increasing acoustic masking not only reduces classification reliability but also decreases the number of calls detected by recorders, potentially reducing the overall effectiveness of PAM. This may require adjustments in long-term PAM deployment strategies. In the Southern Ocean, the HAFOS network spans multiple recording locations across the Atlantic Sector of the Southern Ocean (ASSO; Rettig et al., 2013). While this broad spatial coverage is currently valuable for long-term and multi-site analyses on baleen whale acoustic presence (e.g., Filún and van Opzeeland, 2023; Schall et al., 2020b; Thomisch et al., 2016; Van Opzeeland et al., 2013), future PAM deployment strategies may need to become more localized. In the context of potentially reduced effective communication spaces, focusing on areas of known high whale presence, such as off Elephant Island, may be more effective for recording individual high-quality calls required for reliable species-level classification. Overall, acoustic research frameworks will need to adapt to ongoing changes in soundscapes driven by anthropogenic noise, climate change, and changes in species distribution, both in analytical methods and in PAM deployment design.

What drives the similarity of call types among baleen whales?

When discussing the reliable classification of acoustically similar call types, an inevitable question arises: why do different baleen whale species produce calls so similar in their acoustic characteristics? As outlined earlier in this thesis, acoustic signals evolve through an interplay of anatomical, environmental, and social factors (Clark, 1990; Clark and Gagnon, 2022; Croll et al., 2002; Elemans et al., 2024). For both call types discussed in this thesis, the species groups examined (those producing upcalls and FM calls, respectively) exhibit similarities in preferred habitats (Branch, 2025), as well as in their social and acoustic complexity (e.g., Branch, 2025; Clapham, 1996; Dunlop et al., 2007; Rossi-Santos et al., 2022; Shabangu et al., 2020; Tyack, 2022). I suggest that these shared ecological and social factors likely favour the similar acoustic solutions, with each species converging on call structures that are most effective for their communicative function within comparable habitats.

Both, the upcall and FM call, are widely described as contact calls used to maintain contact among conspecifics (Casey et al., 2022; Dominello and Širović, 2016; Dunlop et al., 2007; Edds-Walton, 1997; Oleson et al., 2007; Parks et al., 2011; Pivari et al., 2024; Wiggins and Hildebrand, 2020). For such a function, their relatively simple and short nature in lower frequencies is of advantage, as this maximises transmission range and facilitates perception by conspecifics (Titus 1998, Edd-Walton 1997, Clark1982). In particular, pelagic baleen whales, that are producing FM calls, predominantly vocalise below 150 Hz, to maximise transmission efficiency or to avoid predation risk (Branch, 2025; Cusano et al., 2023; Dominello and Širović, 2016; Edds-Walton, 1997; Filún and van Opzeeland, 2023; Payne and Webb, 1971). As a consequence, the frequency ranges and species-specific call repertoires are relatively constrained, likely contributing to the substantial overlap in call characteristics observed among FM-producing baleen whales. Compared to pelagic species, humpback and right whale exhibit non-song vocalisations with a higher frequency range (up to 2.3 kHz and 1 kHz, respectively; Clark, 1982; Dunlop et al., 2007, 2008; Vanderlaan et al., 2003). This raises the question of why their upcalls nevertheless remain acoustically similar, despite the apparent potential to avoid overlap. In both species, upcalls function as contact calls across a variety of social contexts and habitats (Dombroski et al., 2016; Dunlop et al., 2008). I therefore suggest that the upcall represents a call structure that is particularly robust and effective across environmental conditions and behavioural contexts. The social interactions where upcalls are produced by both species also include the use in mother-calf communication in shallow water nurseries

(Pack et al., 2017; Zeh et al., 2022). North Atlantic right whale calves (<1 year) are known to produce calls that are shorter and more variable than those of adults, likely reflecting progressing vocal learning and physical development (Root-Gutteridge et al., 2018). From this perspective, relatively simple call structures may be easier to learn and more reliable for communication during early vocal development, providing an additional hypothesis for the exhibition of similar upcall characteristics across species.

To my knowledge, FM calls have not been linked to mother-calf interactions, although such a function cannot be excluded. Instead, FM calls are generally described as contact calls used for long-range or surface communication between conspecifics (Dominello and Širović, 2016; Edds-Walton, 1997), but have also been associated with foraging behaviour and prey biomass (Nikolich and Towers, 2020; Oleson et al., 2007; Pivari et al., 2024; Romagosa et al., 2021). In the Southern Ocean, blue, fin, humpback, right, sei and minke whales all feed on Antarctic krill (*Euphausia superba;* Buss et al., 2022; Calderan et al., 2023; Friedlaender et al., 2014, 2015; Miller et al., 2019; Santora et al., 2010, 2014), occasionally leading to sympatric feeding events (Friedlaender et al., 2015; Herr et al., 2022b), where interspecific call types could be advantageous. In birds, heterospecific eavesdropping on acoustic signals has been documented, where individuals use calls produced by other species, often similar in call characteristics, to gain ecological advantages such as reduced predation risk (Fallow et al., 2011; Magrath et al., 2009). Similarly, I cannot exclude that FM calls may be detected and used by other baleen whale species, as cues related to feeding activity or prey presence, either by chance or as part of intentional interspecific signalling. One line of evidence supporting an interspecific function is that the only ocean basin where blue and fin whales do not occur sympatrically is the Mediterranean Sea, where, to my knowledge, FM calls have not been reported (pers. com. Virginia Sciacca). However, several observations argue against a generalised interspecific function of FM calls across baleen whale species. Studies have shown that sympatric baleen whales exhibit resource partitioning by exploiting krill patches that differ in location, depth, or prey size composition (Buss et al., 2022; Santora et al., 2010). Furthermore, although FM calls are produced globally by blue, fin, humpback, right, sei, and minke whales, prey preferences can vary substantially among species and populations (e.g., Burkhardt-Holm and N'Guyen, 2019; Mizroch et al., 2009; Notarbartolo-Di-Sciara et al., 2003; Tamura and Konishi, 2009; Watanabe et al., 2012). These differences make it rather unlikely that FM calls serve as an interspecific signal for prey availability. Shared use of FM calls as indirect cues may be more plausible among species with overlapping prey targets and foraging strategies (Santora et al., 2010), such as blue and fin whales, for which joint feeding events have been documented (Friedlaender et al., 2015). Another possible explanation for the similarity of FM calls might be the close phylogenetic (evolutionary) relationship between species, particularly between blue and fin whales, which are able to produce fertile hybrids (Árnason and Gullberg, 1993; Bérubé and Aguilar, 1998; Fioravanti et al., 2022; Pampoulie et al., 2021). Although hybridization could theoretically contribute to call similarity among offspring, evidence from vocal learning species suggests that hybrids typically acquire vocalisations from present conspecifics rather than producing intermediate calls (Ivanitskii and Marova, 2025). As blue and fin whales are both vocal learners (Garland and Carroll, 2022) and share close evolutionary relationships and habitats, vocal influences from the closely related species may also contribute to similarities in call structure.

Finally, I cannot conclusively explain the drivers of call similarities across species. It is also possible that baleen whales perceive acoustic differences that are so subtle that they cannot be captured by the parameters and representations used in current analyses, allowing them to reliably identify conspecifics despite the apparent similarity of call types.

Population specific song characteristic in fin whales

Baleen whale song represents a topic of extensive research and ongoing interest. While blue and humpback whales have been extensively studied with regard to their song and its population specificity, as well as the species' population structure (e.g., Cato, 1991; Garland et al., 2013; McCauley et al., 2018; McDonald et al., 2009, 2006; Miller et al., 2014; Schall et al., 2020b, 2021; Shabangu and Kowarski, 2022; Širović et al., 2004), southern right and sei whales are classified as non-song species (Clark, 1982; Crance et al., 2019; Tremblay et al., 2019). Southern Hemisphere fin whales produce song, yet they are comparatively under-investigated with respect to song characteristics and population specificity, and remain data-deficient regarding population structures (IWC SORP, 2019). Therefore, they are the focal species for examining baleen whale song characteristics in this synthesis.

The high-frequency component: a simple and robust cue for acoustic fin whale populations in the Southern Ocean

The presence of a high-frequency (HF) component in fin whale song has been suggested as a valuable characteristic for identifying acoustic populations in the Southern Ocean

(Gedamke, 2009; Simon et al., 2010; Wood and Širović, 2022). The results presented in Chapters 3 and 4 support this hypothesis, by showing that these features remain distinct and recognizable across regions and years. The analysed HF components show inter- and intra-annual variabilities in their peak frequencies, as it has been observed across multiple baleen whale species (Gavrilov et al., 2011; Leroy et al., 2018a; Malige et al., 2020; Rice et al., 2022; Romagosa et al., 2024), indicating that this signal is not entirely stable. However, the current variability in peak frequencies is minimal and occurs at a slow and predictable rate. As a result, the signals remain spectrally recognizable and distinguishable, key requirements to be considered as a reliable acoustic cue for population differentiation (Delarue et al., 2009).

In general, this approach to identify acoustic populations is particularly user-friendly, as it can rely on straightforward inspection of the HF component in spectrograms. The presence of a given population can be rapidly evaluated by the simple method of checking the peak frequency or frequency range of the HF component. It is therefore also well suited for preliminary data checks of acoustic population presence, e.g., in long-term spectrograms or power spectral density calculations, and can also be easily incorporated into automated detection approaches (Schall and Parcerisas, 2022). Yet the reported shifts in call characteristics may affect the accuracy of population monitoring. Automated detection methods will require regular adjustments to ensure long-term accuracy. Given the stable nature of the shift in the HF components call characteristics, synthetic call models that evolve over time could support the adaptation of automated detection methods. However, manual revision of a subset of detections might be crucial for identifying unexpected changes. This kind of adaptive approach would ensure that shifts in call characteristics, whether gradual or abrupt, do not affect the accuracy of population monitoring. Compared to other population-specific characteristics, such as inter-note intervals (INIs), which require precise calculation of the time between pulses, the HF component offers a simpler and more efficient alternative. Nevertheless, this approach is currently limited to the Southern Hemisphere. In the Northern Hemisphere, HF components have been reported for fin whales but these do not exhibit population-specific differences. Accordingly, INIs remain the preferred method for distinguishing populations in this region. Overall, the results of Chapters 3 and 4 indicate that HF components of Southern Hemisphere fin whale song provide a reliable and simple acoustic cue for distinguishing populations across the Southern Ocean, with potential relevance for informing management and conservation efforts in a region where genetic and morphological data for defining smaller management units remain limited (Clapham et al., 2008). For this purpose, it would be ideal to analyse all available recordings for the presence of the HF components to obtain a circumpolar perspective. Conducting such analyses across multiple years would also allow for a more robust assessment of temporal stability as well as potential shifts over time in acoustic population distributions.

Alternative song characteristics for identifying acoustic fin whale populations

Inter-note Intervals

Inter-note intervals (INIs) are the most commonly used acoustic characteristic to describe fin whale acoustic populations across ocean basins, particularly in the North Atlantic and North Pacific (Best et al., 2022; Guazzo et al., 2024; Helble et al., 2025; Romagosa et al., 2024; Wood and Širović, 2022). Following the identification of distinct HF components in Southern Ocean fin whale song in Chapters 3 and 4, I analysed INIs across ASSO recordings to assess whether they correspond to the same acoustic populations.

INIs were calculated for fin whale songs recorded at two locations: Elephant Island (EI, or Western South Atlantic, WSA) and the Greenwich Meridian (GM, or Eastern South Atlantic, ESA; see supplementary material Figure S1 for recorder locations). These locations were chosen as they were the only sites where high-quality pulses could be reliably detected and where distinct acoustic populations can be observed. The recordings represent songs with distinct high-frequency (HF) components: 86 Hz off EI (WSA-86 Hz HF component) and 99 Hz at GM (ESA-99 Hz HF component). INI analysis was conducted using cepstrogram analysis, a method that has previously been developed to quantify echoes arising from multipath propagation in the water column (Trabattoni et al., 2020, 2023), and subsequently applied to identify INIs in multiple cetacean species, including Antarctic blue, pygmy blue, fin, Antarctic minke and sperm whales (Dréo et al., 2025; Szesciorka et al., 2025). In this approach, the quefrency (s) represents the time lag between repetitive signals in a recording; thus, peaks in the cepstrum correspond to the INIs of fin whale 20-Hz pulses (Dréo et al., 2025). A detailed description of the cepstrogram analysis, performed on high-quality song sequences persisting for ≥2 minutes, is provided in the Methods section of the supplementary material.

The analysis revealed clear differences in INIs between EI and GM songs, visible in Figure 6. At EI, a dominant quefrency peak occurred at 14.8 s (WSA-15s INI displayed in purple), with a secondary peak at 11.8 s, INI values that agree with previous measurements at the

Western Antarctic Peninsula (Wood and Širović, 2022), and corresponding to songs with the WSA-86Hz HF component. In contrast, songs recorded at GM, associated with the ESA-99Hz HF component, showed a shorter dominant INI of 10.5 s (ESA-11s INI displayed in orange).

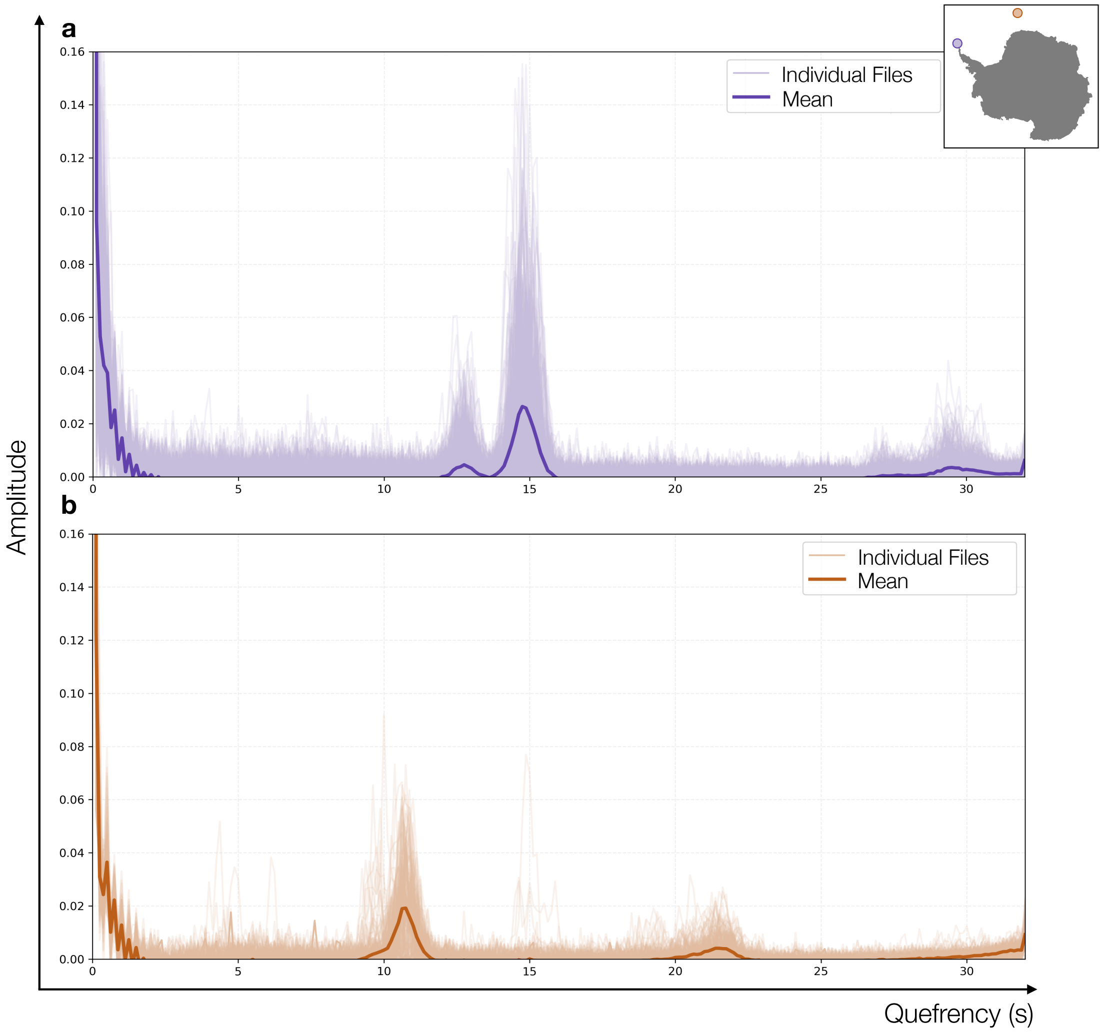

Figure 6. Mean cepstra computed for each individual file, with the overall mean across recordings. Showing a) two dominant quefrency peaks at around 11.8 s and 14.8 s in the song of EI recordings, and b) one dominant quefrency peak at around 10.5 s for detected song at GM. The data comprised a total of 432 files (2160 min) from EI and 164 files (1640 min) from GM.

These differences indicate that both, HF components and INIs, can be used to distinguish Southern Hemisphere fin whale acoustic populations, although the secondary peak at EI (approximately 12 s) is close to the ESA-11s INI, which could reduce the clarity of population separation based on INIs alone. However, it is important to note that the respective INI peaks remained consistently visible in annual analyses at both recording locations (Figure 7). In accordance with global gradual increases in fin and blue whale song INIs (e.g., Helble et al., 2025; Malige et al., 2020; Romagosa et al., 2024), the INIs in the ASSO exhibit a smilar trend. Linear regression analyses indicated an increase in INI duration of the WSA-15s INI of approximately 0.55 s per year between 2013 and 2020. At GM, a slight decrease in the ESA-11s INI (−0.01 s per year) was observed between 2009 and 2013; however, this trend is likely driven by outliers in 2009 recordings, which exhibited longer INIs (approximately 15 and 17 s) more similar to the WSA-15s INI. When these outliers are excluded, the ESA-11s INI also shows a slightly increasing INI trend, as illustrated in Figure 7.

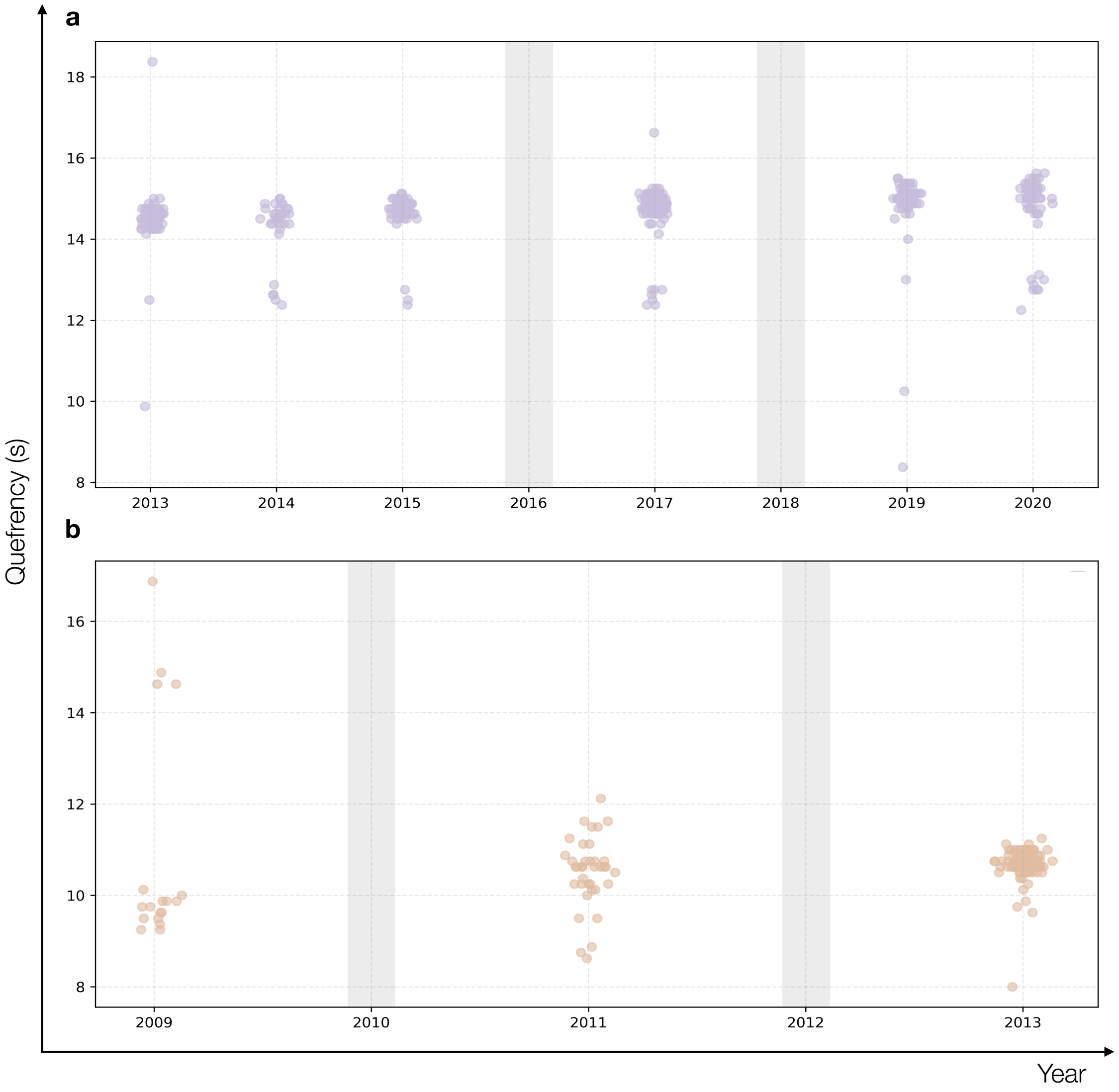

Figure 7. Scatter plots showing annual trend in mean quefrency of each individual file at a) EI (2013 – 2020) and b) GM (2009 – 2013). Grey shaded bars represent years with no data available. The data comprised a total of 432 files (2160 min) from EI and 164 files (1640 min) from GM.

Outliers were also observed in EI recordings from 2019, where INIs matched durations typically associated with GM songs. Given the high mobility of fin whales (Aulich et al., 2019; Herr et al., 2022a; Mizroch et al., 2009), one possible explanation is the presence of individuals from one acoustic population within the detection range of recorders located in the other population's habitat. Alternatively, whales may have been in acoustic contact with the other population and partially adapted their song characteristics. Support for song convergence through cultural transmission comes from GM recordings in 2009 (Figure 8), which exhibit mixed song characteristics: Figure 8 a) displays a WSA-15s INI (purple) typical of EI songs but lacks a HF component, while b) shows a combination of a WSA-15s INI (purple) with an ESA-99Hz HF component (orange). The latter, exhibiting truly mixed characteristics, cannot be explained solely by the movement of a WSA-song producing individual to GM, as it reflects partial adoption of elements from another population's song rather than a typical population-specific song. Song learning and cultural horizontal transmission have been documented in other vocal learners, including humpback whales and birds (Garland et al., 2013; Garland and Carroll, 2022; Garland and McGregor, 2020), suggesting that partial song adoption through acoustic exposure is likely.

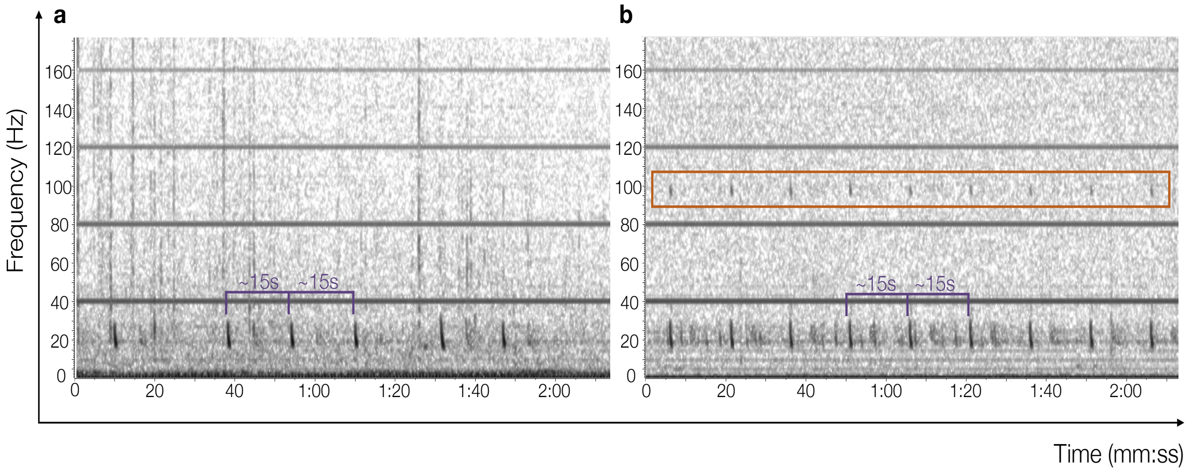

Figure 8. Spectrogram showing fin whale song with a typical WSA-15s INI (purple) recorded at GM in 2009. a) shows recording from the 21.01.2009 and b) from 28.05.2009, including the typical ESA-99Hz high frequency component (orange box) at this recording site. Smoothed spectrograms were calculated using a Hanning window with a 512-point FFT/DFT and 80% overlap.

Aside from these outliers, differences between the WSA-15s and ESA-11s INIs were sufficiently large and non-overlapping across the analysed years. Similar to the HF component, inter-annual shifts in INIs were relatively small and appeared predictable, supporting their utility as a population-specific song characteristic in the Southern Ocean. INIs therefore represent a valuable alternative or complementary metric to HF components, particularly in situations where HF components are not detectable, or where INI estimation is challenged by overlapping calls from multiple individuals. Together, these song characteristics provide flexible and robust tools for identifying fin whale acoustic populations, and their combination can also offer insights into the connectivity among populations in the Southern Ocean.

Song variants

Song variant composition, defined by the temporal patterning of 20-Hz pulses, has also been shown to vary geographically and has been proposed as an indicator of population identity (Constaratas et al., 2021; Širović et al., 2017; Wood and Širović, 2022). A singlet song variant consists of the regular repetition of single 20-Hz pulses with a consistent INI (see Figure 9 a). Doublet variants are characterised by an alternating pattern of long and short INIs (e.g. short–long–short-long), while triplet variants exhibit repeating sequences of three INIs, typically comprising two long and one short interval or vice versa (e.g. short–short–long; see Figure 9 b; Oleson et al., 2014; Wood and Širović, 2022). Importantly, identification of these variants requires sequences of at least three pulses for doublets and four pulses for triplets, as shorter sequences cannot be distinguished from short sequences of a singlet pattern.

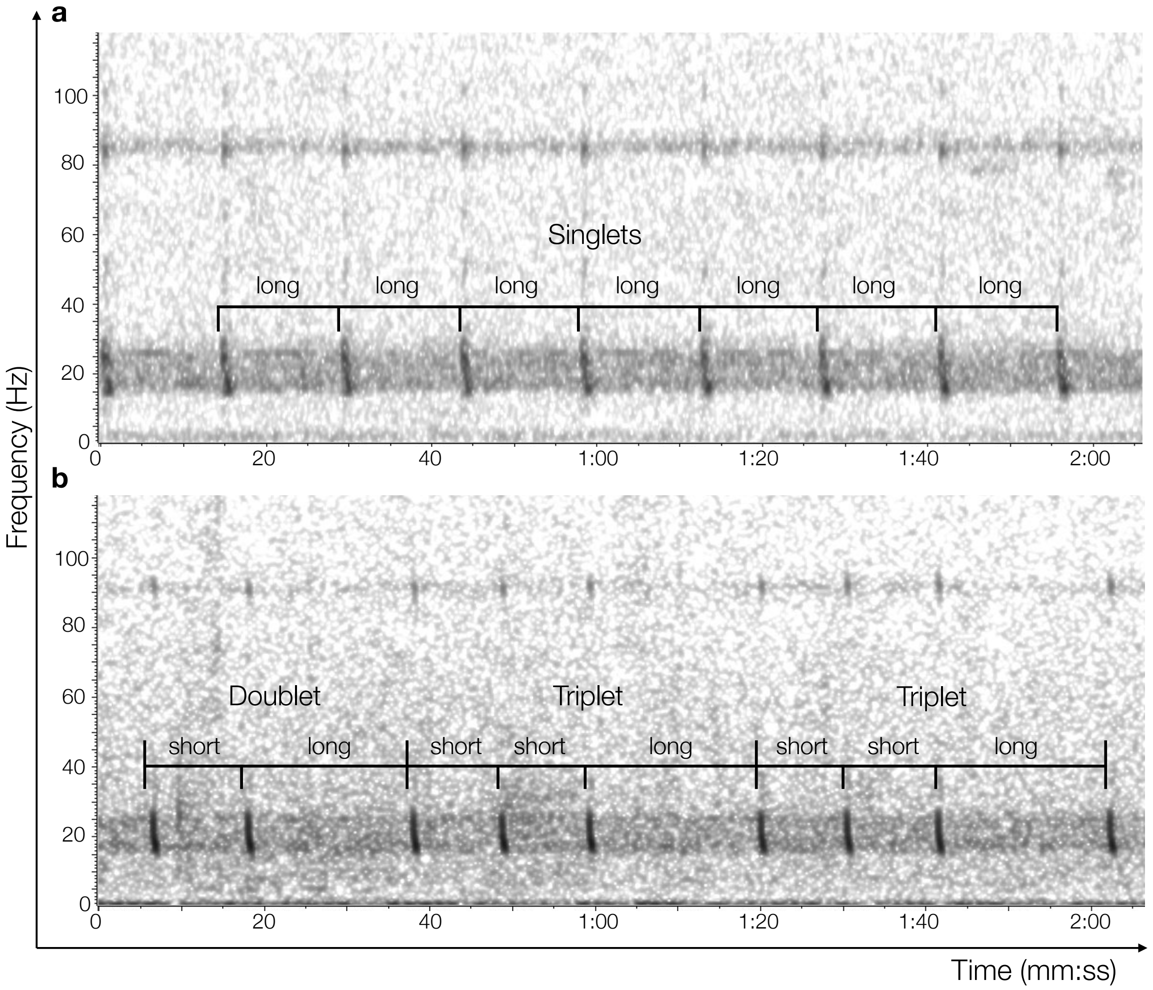

Figure 9. Spectrograms showing fin whale song variants. a) displays singlet song recorded off EI on 27.05.2014 and b) displays doublet and triplet variants recorded at GM on 22.03.2011. Smoothed spectrograms were calculated using a Hanning window with a 512-point FFT/DFT and 80% overlap.

To provide a comprehensive review on song structures that might serve acoustic population identification, song variants were analysed for fin whale song recorded off EI and the GM, respectively. Song structure differed between locations with respect to song variant composition. EI song was predominantly composed of singlet song (approximately 85%), with only approximately 15% consisting of more complex song variants (Figure 10).

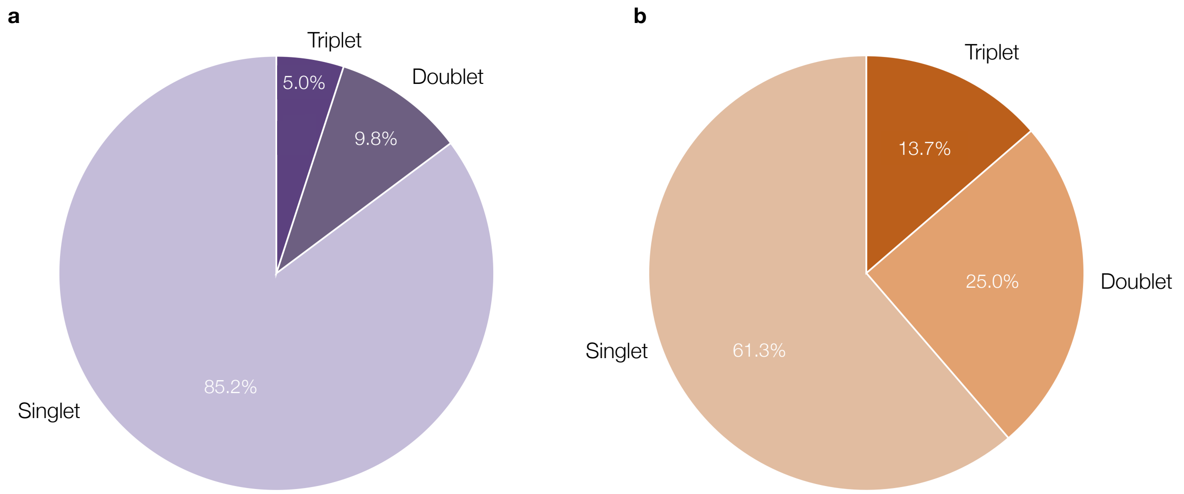

Figure 10. Percentage of analysed pulses assigned to each song variant in the INI analysis. (a) EI (2013–2020) and (b) GM (2009–2013). Only pulses from the analysed files are included. The data comprised a total of 432 files (2160 min) from EI and 164 files (1640 min) from GM.

In contrast, song recorded at the GM generally exhibits higher complexity, with approximately 25% doublets, 14% triplets and 61% singlets (Figure 10). Analyses across recording years and seasons further revealed that the relative proportion of song variants remained relatively stable over time, with only small inter-annual variability, suggesting that song variant composition represents another potential cue for acoustic population identification (Figure 11). However, song variants exhibit relatively high intra-annual variabilities. Data from GM in 2009 and EI in 2014 were excluded from this interpretation due to limited and poorly seasonally distributed song presence, as was the dataset from November 2017, which consisted of only a single recording. For the remaining years, EI (2017, 2019, 2020) and GM (2011, 2013) showed consistent seasonal patterns. During this period at EI, the proportion of singlet song decreased to around 70%, while doublet and triplet song variants each increased to approximately 15%. At GM, singlet song decreased to below 20%, with doublets accounting for around 20% and triplets increasing to up to 50% of the analysed song. At both locations, song structure changed substantially over the course of the season, differing markedly from the overall song variant composition observed across years. A similar intra-annual pattern of decreasing song structure complexity was observed at the western Antarctic Peninsula (Wood and Širović, 2022), although greater inter-annual variability was reported there, potentially reflecting differences in data availability or temporal coverage. Notably, despite this variability, songs recorded at the Greenwich Meridian consistently exhibit a higher overall song complexity than those recorded at Elephant Island. However, the pronounced intra-annual variability may still lead to increased similarity between songs from different populations at certain times of the year, thereby reducing the reliability of song variant composition as a population identifier when based on short-term recordings. Instead, this metric is likely most informative when derived from long-term datasets that capture annual song variant proportions, which more clearly reflect persistent, population-specific differences. Consequently, song variant composition alone may not represent an indicator for population identification as robust as the HF component or INI.

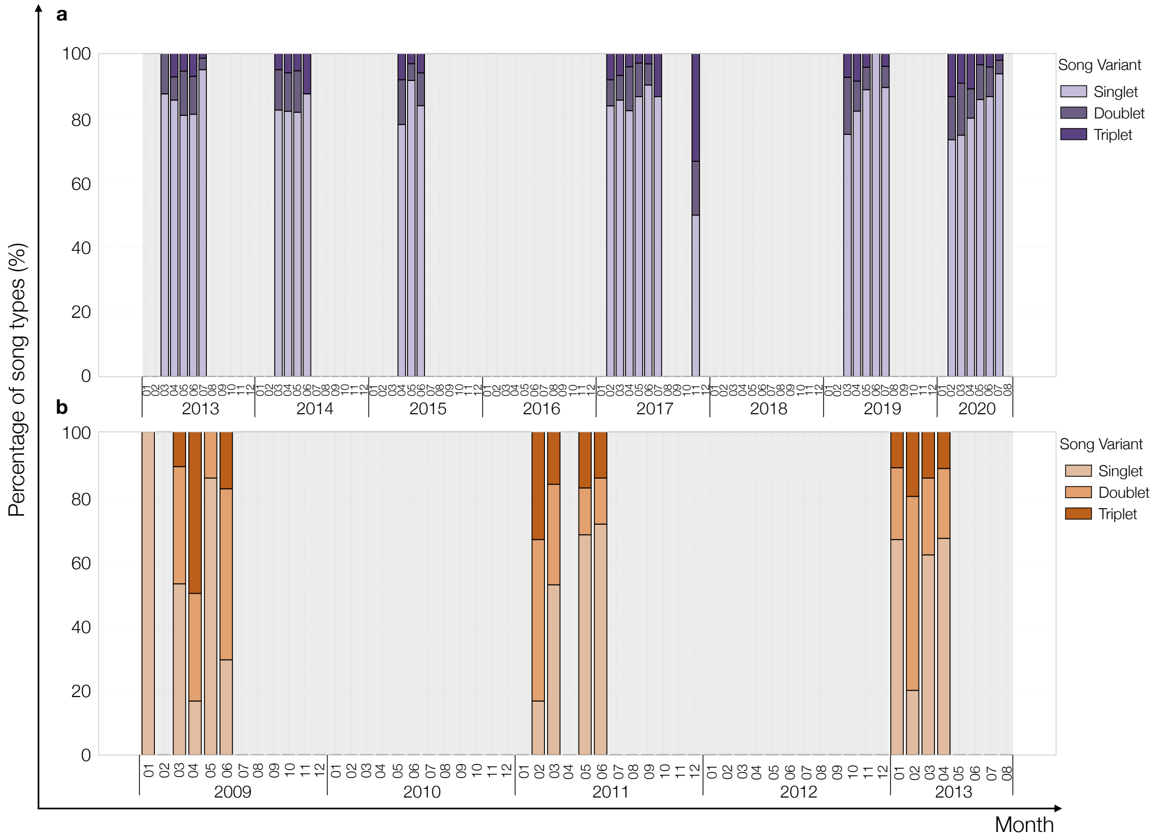

Figure 11. Monthly percentage of analysed pulses belonging to each song variant. a) EI (2013 – 2020) and b) GM (2009 – 2013). Grey shaded areas represent months with no data available.

Song characteristics across global fin whale acoustic populations

While the different song characteristics, especially the HF component and the INI, can support the understanding of the presence of acoustic populations and provide important insights with implications for conservation, their applicability is region dependent. Figure 12 presents an attempt to summarise the global distribution of known fin whale acoustic populations based on HF components and INIs. Since this overview is necessarily simplified it focuses on dominant INIs only. Data from multiple years were combined when

HF components and INIs were similar, accounting for known inter- and intra-annual variabilities.

In the Southern Hemisphere, five acoustic fin whale populations can currently be distinguished based on HF components. Although occasional spatial overlap in HF component occurrence has been reported, for example off the west coast of Australia, HF components generally show clear geographical distributions. In the Atlantic Sector of the Southern Ocean, two distinct HF components (WSA-86Hz and ESA-99Hz) are consistently observed. The two corresponding populations can additionally be identified using INIs, with WSA-15s and ESA-10s, respectively. In contrast, the identification of acoustic populations in the Northern Hemisphere relies almost exclusively on INIs. Although HF components have been reported in the North Atlantic (but not in the Mediterranean; Castellote et al., 2012), their frequencies typically range between 130 and 140 Hz and do not exhibit consistent geographic differentiation (Castellote et al., 2012; Clark and Gagnon, 2022; Garcia et al., 2019; Hatch and Clark, 2004; Simon et al., 2010). Consequently, HF components cannot be used reliably for population differentiation in this region. Based on INIs, three acoustic populations have been proposed in the North Atlantic, including one in the Mediterranean, one in the broader North Atlantic, and one further north in the Barents Sea (Castellote et al., 2012; Garcia et al., 2019; Romagosa et al., 2024; Simon et al., 2010). In the wider North Pacific, fin whale song exhibits greater diversity, with approximately five reported dominant INIs. Two INIs dominate in the North Pacific, while additional more regional INIs have been described in the California Bight, the Chukchi Sea, and the Aleutian region (see Figure 12). The two latter of these INIs are also present in the Bering Sea alongside the main North Pacific INI (Archer et al., 2019; Helble et al., 2025; Oleson et al., 2014; Širović et al., 2017; Weirathmueller et al., 2017).

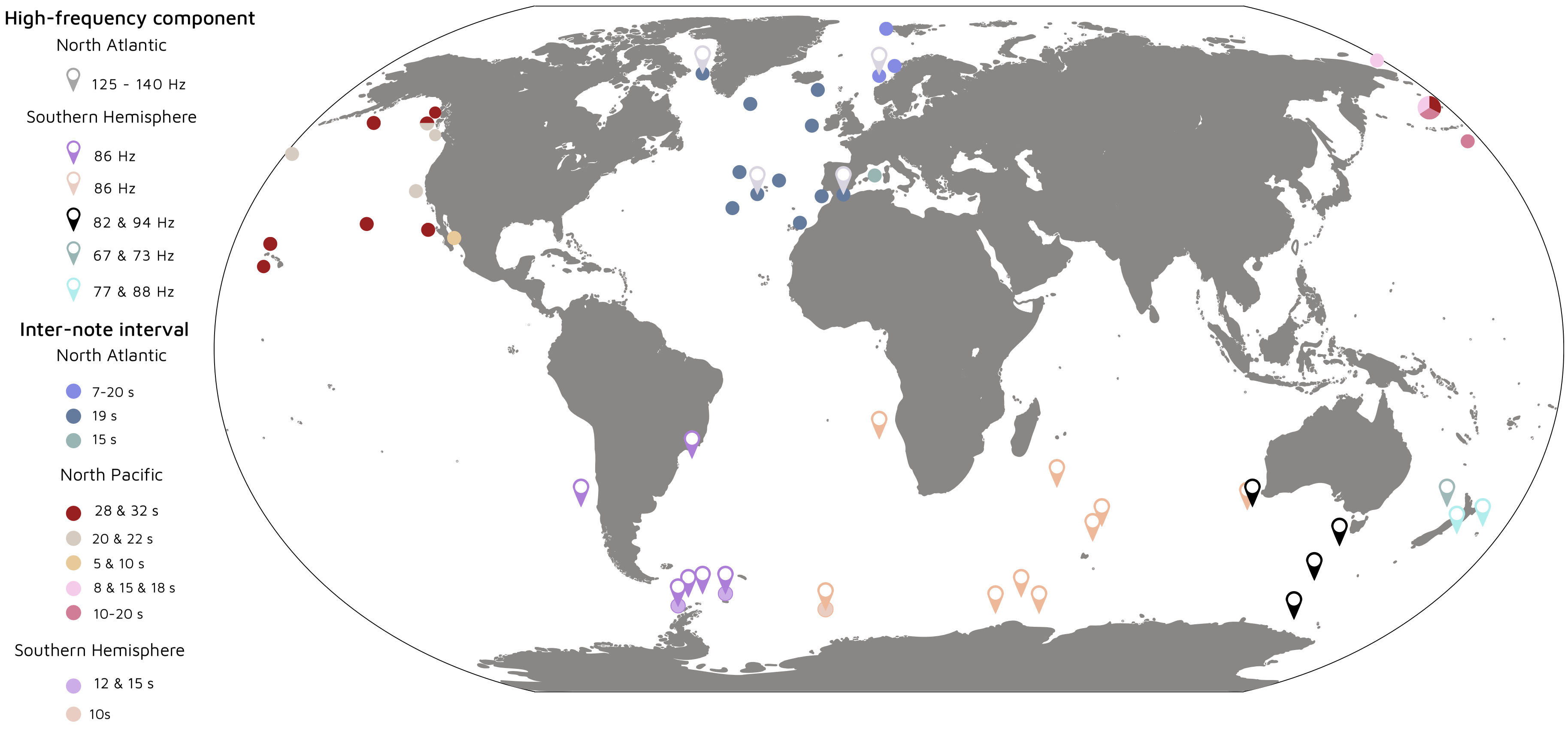

Figure 12. Map illustrating a global but simplified overview on two fin whale characteristics, the high-frequency (HF) components and the inter-note intervals (INIs), based on data from this and previous studies. Each marker represents a recording location, with matching colors indicating similar HF components and dominant INIs. For the North Atlantic and North Pacific, only dominant INIs are shown. Data from multiple years were combined where INIs and HF components were similar, accounting for known inter- and intra-annual variability and minor frequency differences. This map was created on Canva.com as a visual aid in understanding the spatial distribution of fin whale HF components; thus, the accuracy of coordinates of the data points is limited. The data underlying this map are listed in the supplementary material Tables S2 and S3.

However, this INI representation is necessarily simplified, as the interpretation of INIs is not straightforward and strongly depends on analytical choices, including the timing of recordings and the temporal scope of the analysed datasets. Inter- and intra-annual variability in fin whale song can result in markedly different INI estimates depending on temporal coverage (Romagosa et al., 2024; Weirathmueller et al., 2017). Correct interpretation of INIs is also particularly relevant in regions where fin whale songs include two distinct 20-Hz note types, commonly referred to as the A (main note) and B (backbeat) notes, which differ in their acoustic characteristics, with B notes typically exhibiting a narrower bandwidth. The presence of two note types is very common in the North Pacific, but has also been reported in the North Atlantic and off New Zealand (Archer et al., 2019; Castellote et al., 2012; Constaratas et al., 2021; Helble et al., 2025; Širović et al., 2017). When calculating INIs, results therefore depend on whether intervals are measured simply between consecutive notes (e.g. A–B or B–A; Castellote et al., 2012; Romagosa et al., 2024; Širović et al., 2017), or whether all possible note-pair combinations (A–A, A–B, B–B, B–A) are included (Guazzo et al., 2024; Helble et al., 2020, 2025). These different approaches may result in different INI estimates and may capture varying information about population structure at smaller or more local scales. In such cases, INI alone is insufficient to characterise song patterns, and both INI and note-pair composition must be considered jointly (Guazzo et al., 2024). While approaches that analyse all song note pairs may reveal finer-scale population patterns within ocean basins, differences in note-pair composition do not necessarily indicate distinct populations. Individual fin whales with similar dominant INIs can produce different note-pair combinations, and note-pair usage can also vary seasonally (Helble et al., 2020).

It is likely that song complexity differs among the North Pacific, North Atlantic, and the Southern Hemisphere, since fin whales present in these regions are recognised as genetically distinct populations (Buss et al., 2023). Therefore, different song characteristics may be more or less informative for population analyses in each ocean basin, and analytical frameworks need to account for this complexity. Rather than applying a single method globally, comparable and standardised approaches should be developed that incorporate the dominant song structures present within each ocean basin. Such spatially specific yet comparable approaches will allow more robust population assessments and ultimately provide a clearer and more consistent picture of fin whale acoustic population structure at global scales.

Outlook: Towards a more standardised and reliable acoustic research

This thesis contributes methodological approaches aimed at improving the reliability of passive acoustic analyses in the Southern Ocean, addressing key challenges in call classification and acoustic population identification. The frameworks developed here can support more standardised analyses in future research, facilitating greater comparability across studies and improving confidence in acoustic inferences. At present, passive acoustic monitoring is characterized by substantial methodological diversity (Baumgartner and Mussoline, 2011; Bittle and Duncan, 2013; Huang et al., 2016; Michel et al., 2025; Rasmussen and Širović, 2021; Usman et al., 2020; Zhang et al., 2019). Individual research groups often employ distinct recording systems, data collection protocols, and analysis workflows. While many of these approaches are effective, this diversity can limit comparability among studies. At the same time, the rapid growth of large acoustic datasets provides valuable opportunities to investigate underwater soundscapes, but also poses significant challenges for efficient and reproducible data processing and interpretation (Wall et al., 2025). These developments highlight the increasing importance of establishing core tools, workflows, and best practices that support standardised, reliable, and open acoustic research. Standardisation efforts should best span multiple levels of the analytical pipeline, such as file formats, recorder settings and calibration, data pre-processing, and analytical workflows (Wall et al., 2025; Wood, 2026). Developing and adopting standardised approaches will be essential for enabling robust comparisons across regions, time periods, and research programs.

As acoustic datasets continue to grow, artificial intelligence and machine learning approaches are becoming increasingly important for detection and classification tasks across species (Gibb et al., 2019; Huang et al., 2016; Kahl et al., 2021; Schall et al., 2024; Stowell, 2022; Stowell et al., 2019a). While these methods offer powerful solutions, they are often implemented as ‘black boxes’, which limits interpretability and can obscure sources of error. Future research should therefore incorporate explainable AI approaches that allow insight into how detections and classifications are generated (Ahmed et al., 2022; Das and Rad, 2020; Minh et al., 2022). Importantly, standardised analytical frameworks must also account for potential variability in call and song characteristics, including gradual inter- and intra-annual shifts, as well as more abrupt changes driven by song revolutions or increasing ambient noise levels. Consequently, a human-in-the-loop approach, involving regular manual revision of subsets of automated detections, is critical for validating results, identifying unexpected changes in call structure, and informing necessary adjustments to analytical pipelines. Manual inspection also enables a more holistic understanding of acoustic signals, including call structure, context, and concurrent soundscape features (Wood and Kahl, 2024). However, manual approaches also require standardisation. Distinct manual analysis workflows across individual reseach groups can result in differences in software settings and analytical choices that can influence call visualisation and, consequently, the derived call characteristics. Such variability arises not only from differing parameter settings but also from analyst experience and subjective bias (Leroy et al., 2018b). Even experienced analysts may draw slightly different selection boxes when analysing the same call repeatedly. As a result, manual measurements can be affected by these factors, posing challenges for the comparability and reproducibility of results across studies and datasets. To minimise such biases, the bioacoustic research community would benefit from greater conformity in manual analysis protocols, including clear guidelines for tasks such as drawing selection boxes for call measurements or manually analysing inter-note intervals. The development and coordination of such standardised procedures would be well suited to international initiatives such as the Southern Ocean Research Partnership (SORP), which focuses on advancing circumpolar research on baleen whale populations, including fin and blue whales. Establishing shared analytical frameworks and harmonised workflows, for example through shared workspaces such as APLOSE (https://osmose.ifremer.fr/doc/), which facilitate standardised annotation and review of passive acoustic data with predefined settings for specific data types or analyses, would represent an important step towards more reliable and comparable acoustic research. The ongoing difficulties in call identification and the analytical frameworks proposed to address these could also benefit from being integrated into platforms such as the Global Library of Underwater Biological Sources (GLUBS; www.glubs.org). Such platforms can help make persistent challenges and emerging solutions more transparent to the wider research community by connecting underwater sound repositories, analysis tools, and reference libraries through a single access point.

Ultimately, the effectiveness of any analytical framework depends not only on technical choices but also on the expertise and collaboration of the research teams implementing them (Wood, 2026). While it is no longer feasible to keep pace with expanding acoustic datasets without automated tools, human expertise remains indispensable for guiding analyses, interpreting results, and ensuring biological relevance. The future of acoustic research will therefore rely on an integrated approach, combining standardised workflows, transparent and interpretable AI methods, and expert-driven validation to ensure reliable and meaningful insights from passive acoustic monitoring.

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Publications and Author Contributions

Chapter 1

Wöhle, S., Burkhardt, E., Van Opzeeland, I., and Schall, E., (2023). Exploring and verifying the acoustic presence of southern right whales (*Eubalaena australis*) off Elephant Island, Antarctica Journal of the Acoustical Society of America; 153 (6): 3301–3311. https://doi.org/10.1121/10.0019633

Author contribution statement

S.W.: conceptualization, data curation, formal analysis, investigation, methodology, visualization, writing—original draft, writing—review and editing; E.B.: conceptualization, resources, supervision, writing—review and editing; I.V.O.: conceptualization, resources, supervision, writing—review and editing; E.S.: conceptualization, methodology, project administration, supervision, writing—review and editing. All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Chapter 2

Wöhle, S., Parcerisas, C., Buchan, S., Calambokidis, J., Stafford, K. M., and Schall, E. Searching for separation between frequency-modulated calls of blue and fin whales. Under review in Nature Scientific Reports.

Author contribution statement

S.W. conceived the study and was responsible for all data analysis, methodology, visualization, and writing—original draft, as well as reviewing and editing the manuscript. C.P. contributed to methodology, supervision, and manuscript review and editing. S.B. developed the Chile tag project, participated in field campaigns, and is the owner of the Chile tag dataset. Assisted with manuscript review and editing. J.B. developed the California tag project, participated in field campaigns, and is the owner of the California tag dataset. Assisted with manuscript review and editing. K.M.S. helped develop the Chile tag project, contributed to funding acquisition, participated in field campaigns for the Chile tag data, and assisted with manuscript review and editing. E.S. contributed to conceptualization, methodology, project administration, supervision, and manuscript review and editing. All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Chapter 3

Wöhle, S., Thomisch, K., Burkhardt, E., Van Opzeeland, I., Schall, E. (2025) Geographical distribution of two acoustic fin whale (*Balaenoptera physalus*) populations across the Weddell Sea. Royal Society Open Science. 12: 241866. https://doi.org/10.1098/rsos.241866

Author contribution statement

S.W.: conceptualization, data curation, formal analysis, investigation, methodology, visualization, writing—original draft, writing—review and editing; K.T.: software, writing—review and editing; E.B.: conceptualization, resources, supervision, writing—review and editing; I.V.O.: conceptualization, resources, supervision, writing—review and editing; E.S.: conceptualization, methodology, project administration, supervision, writing—review and editing. All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Chapter 4

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Author contribution statement

S.W.: conceptualization, data curation, formal analysis, investigation, methodology, visualization, writing—original draft, writing—review and editing; L.P.: formal analysis, writing—review and editing; E.B.: conceptualization, resources, supervision, writing—review and editing; I.V.O.: conceptualization, resources, supervision, writing—review and editing; E.S.: conceptualization, methodology, project administration, supervision, writing—review and editing. All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Supplementary Material

Supplementary Material – Chapter 1

Table SI. Rave Pro 1.6 settings for acoustic data analysis, and calculated time (TAR) and frequency analysis resolution (FAR).

Recording sites	Sample frequency	Window size	Time analysis resolution (s)	Frequency analysis resolution (Hz)	TAR error (%)	FAR error (%)
BSA	4000	560	0.14	7.143	10.769	10.504
GM	5333	350	0.065	15.237	10.938	7.619
EI	5333	740	0.141	7.111	10.818	10.457

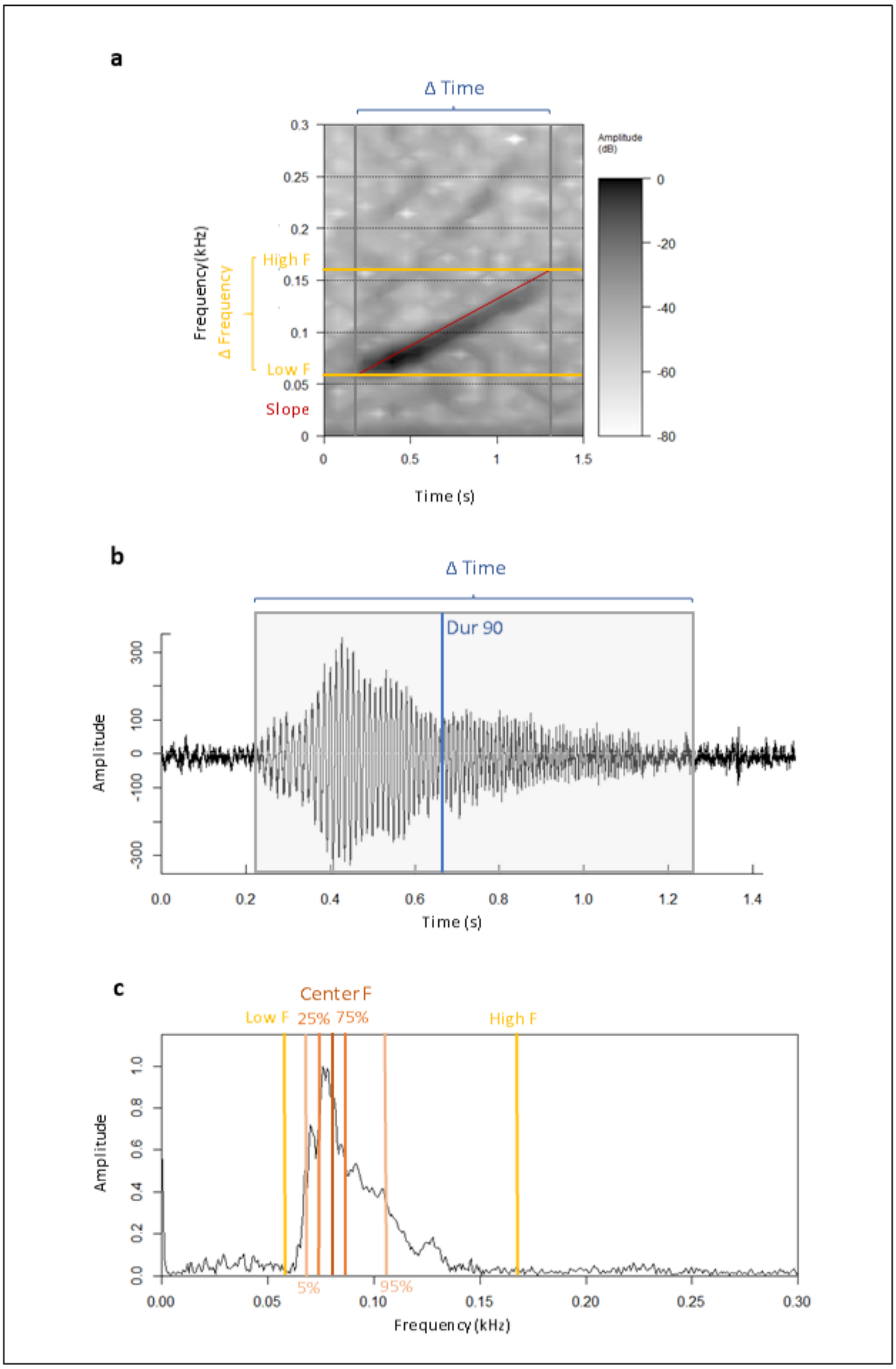

Figure SI. Visualization of performed measurements in Raven Pro 1.6. (a) Spectrogram of a confirmed southern right whale upcall (recorded on 25 August 2013 at 11:07:54 pm at BSA) showing low and high frequency limits (Low F and High F), bandwidth (Δ F) and duration (Δ Time), (b) waveform of the same upcall displaying the selected duration (Δ Time) and the duration 90% (Dur 90) measurements, and (c) associated frequency spectrum showing low and high frequency limits (Low F and High F), and the division into frequency intervals of 5%, 25% (1st quartile), 50% (Center F), 75% (3rd quartile) and 95% of the energy contained in the signal. Spectrogram and frequency spectrum calculated with a FFT of 740 in Hanning window.

Table SII. Overview of the R functions used for the statistical testing and automated classification. com = community matrix, df = data frame and G = Groups of the different upcall classes used in this study.

Source	Test	Function	Parameter
Oksanen *et al.*, 2020	ANOSIM	‘anosim’	(com, df$G, distance = "bray", permutations = 10000)
Oksanen *et al.*, 2020	PERMANOVA	‘adonis’	(com~G, data = df, permutations = 10000)
Martinez Arbizu, 2020	Pairwise Comparison	‘pairwise.adonis’	(com, factors = df$G)
Oksanen *et al.*, 2020	SIMPER	‘simper’	(df, simper (com, G))
Liaw and Wiener, 2002	Random Forest	‘randomForest’	(G ~ ., data = df, importance = T, ntree = 500, mtry = 3)
Kursa and Rudnicki, 2010	Boruta	‘Boruta’	(Location ~ ., data = df)

Table SIII. Temporal distribution of detected unconfirmed upcalls off Elephant Island (EI). In total 1125 upcalls were detected on 27 days. Recordings took place from 15 January to 9 November 2013; lighter grey shading of cells indicates that data are available for only parts of the months. White fields indicate no data available.

Month	**Jan**	**Feb**	**Mar**	**Apr**	**May**	**June**	**July**	**Aug**	**Sep**	**Oct**	**Nov**	**Dec**
Recordings	░	▓	▓	▓	▓	▓	▓	▓	▓	▓	░	
Number of detected vocalizations	46	80	145	775	74			5				

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Supplementary Material – Chapter 2

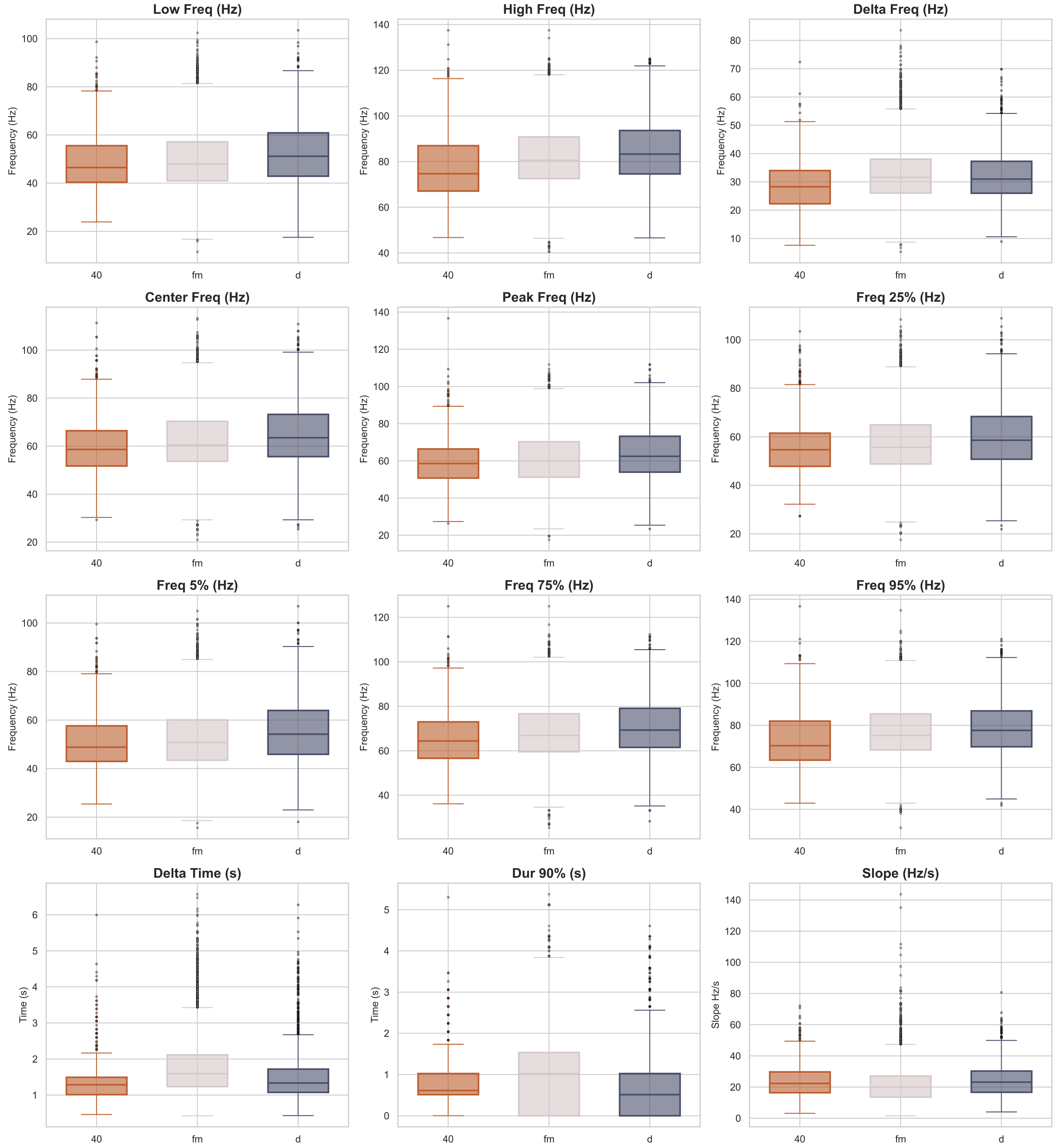

Figure S1. Boxplots representing the 12 quantitative acoustic measurements from the *high SNR dataset* for the three groups of labelled FM calls: 40Hz-calls of fin whales (*40 - orange*), D-calls of blue whales (*d - blue*), and frequency-modulated (FM) calls of uncertain attribution (*fm - lightgrey*).

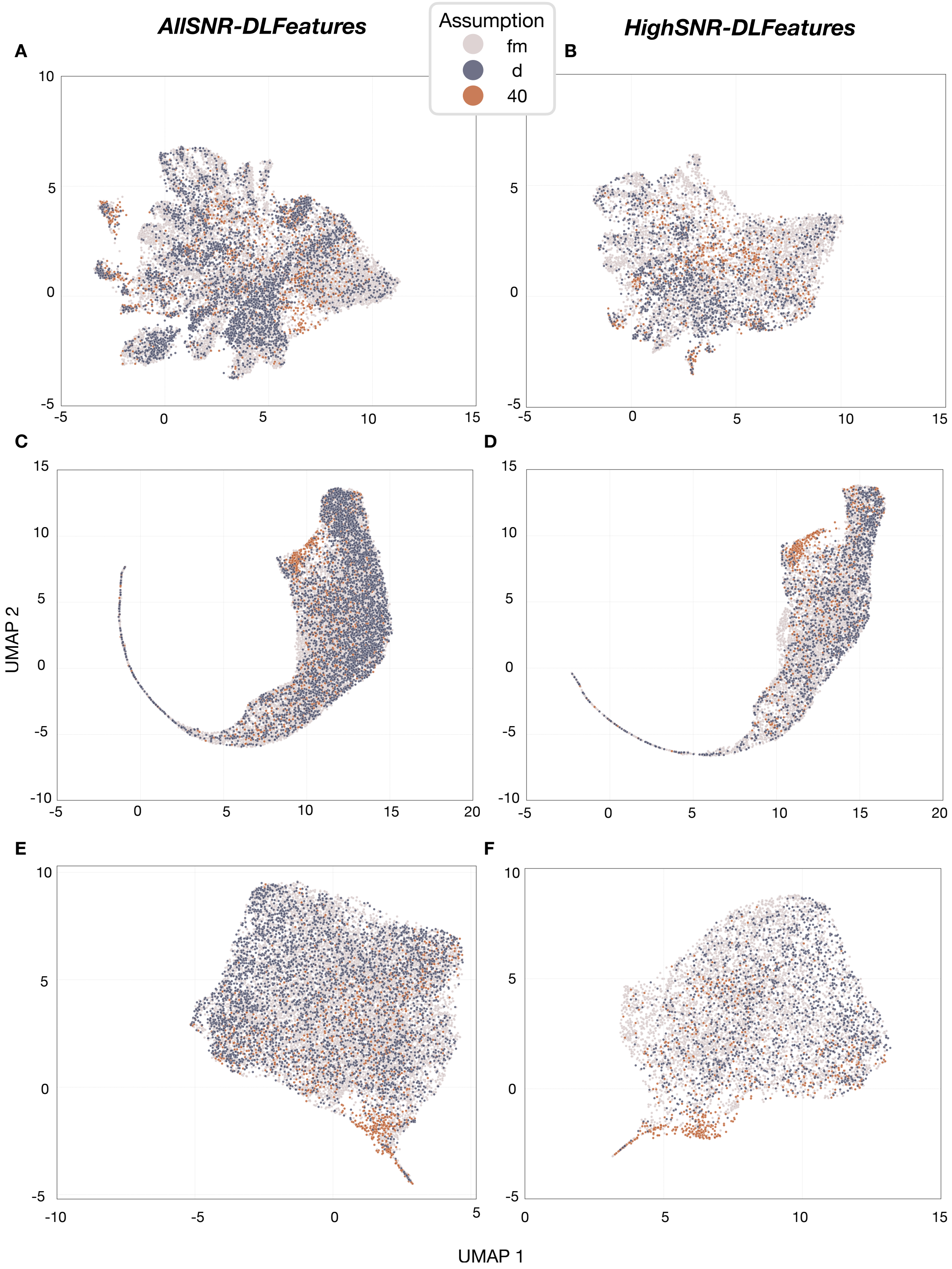

Figure S2. Dimension reduction using UMAP on the deep learning feature extraction across the various model embeddings GoogleWhale (A, B), Perch (C, D), and Surfperch (E, F) on the *AllSNR-* and *HighSNR*-datasets. Panels show UMAP projections generated using an unsupervised approach. 40Hz-calls of fin whales (*40 - orange*), D-calls of blue whales (*d - blue*), and frequency-modulated (FM) calls of uncertain attribution (*fm - lightgrey*).

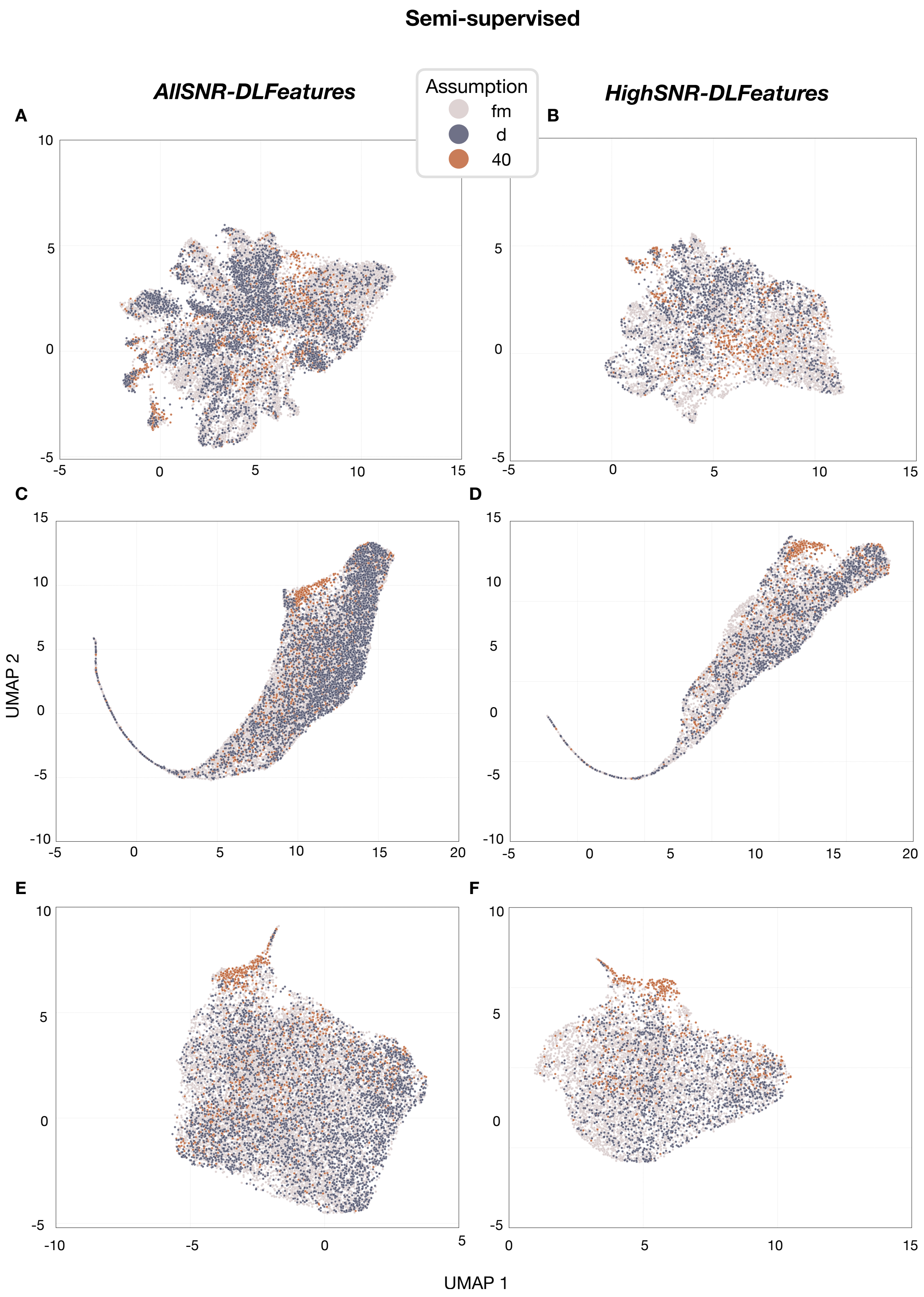

Figure S3. Dimension reduction using UMAP on the deep learning feature extraction across the various model embeddings Googlewhale (A, B), Perch (C, D), and Surfperch (E, F) on the *AllSNR*- and *HighSNR*- datasets. Panels show UMAP projections generated using a semi-supervised approach. 40Hz-calls of fin whales (*40 - orange*), D-calls of blue whales (*d - blue*), and frequency-modulated (FM) calls of uncertain attribution (*fm - lightgrey*).

Table S1. Number and proportion of FM calls per cluster based on the three groups of assumed call types - 40Hz-calls of fin whales (*40*), D-calls of blue whales (*d*), and FM calls of uncertain attribution (*fm*) - across the various model embeddings (Perch, GoogleWhale, and Surfperch) on the *AllSNR*- and *HighSNR*-datasets as determined by the HDBSCAN algorithm. Each entry shows the count of FM calls belonging to a given assumed call type within a cluster, followed by the corresponding percentage (in parentheses) relative to the total number of FM calls in the respective cluster. Noise points are labeled as *unassigned*. Clustering was performed using a min_cluster_size of n = 50.

Dataset	**Cluster**	**No. of '40' (%)**	**No. of 'd' (%)**	**No. of 'fm' (%)**	**No. total**
Perch AllSNR	unassigned	530 (8.6)	1620 (26.3)	4010 (65.1)	6160
	1	4 (6.3)	8 (12.7)	51 (81)	63
	2	582 (5)	2442 (20.9)	8668 (74.19	11692
	3	1 (1.1)	20 (22)	70 (76.9)	91
Perch HighSNR	unassigned	271 (11.7)	547 (23.6)	1501 (64.7)	2319
	1	348 (5.8)	1096 (18.3)	4539 (75.9)	5938
	2	2 (3.9)	10 (19.6)	39 (76.5)	51
Google Whale AllSNR	unassigned	1063 (7)	3685 (24.1)	10526 (68.9)	15274
	1	1 (0.7)	27 (19.3)	112 (80)	140
	2	3 (0.7)	53 (13.1)	350 (86.2)	406
	3	50 (2.3)	325 (14.9)	1811 (82.8)	2186
Google Whale HighSNR	unassigned	621 (7.4)	1653 (19.8)	6079 (72.8)	8353
Surfperch AllSNR	unassigned	1117 (6.2)	4090 (22.7)	12799 (71.1)	18006
Surfperch HighSNR	unassigned	621 (7.4)	1653 (19.8)	6079 (72.8)	8353

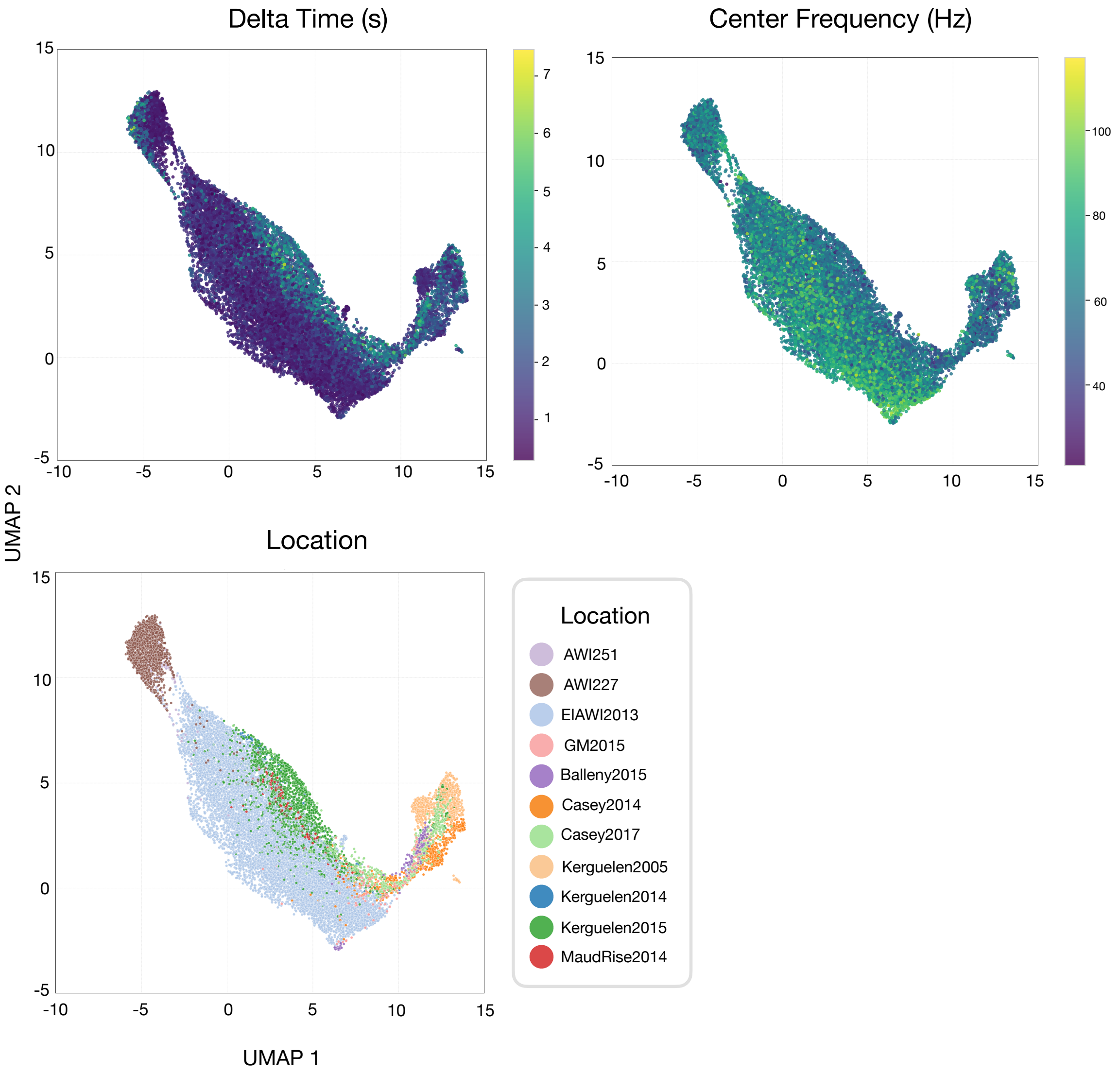

Figure S4. Dimension reduction using UMAP on the *AllSNR-DLFeatures-Bioloingual*. Panels show UMAP projections generated using an unsupervised approach, and representing the acoustic parameters Delta Time (s) and Center Frequency (Hz), as well as the recording locations.

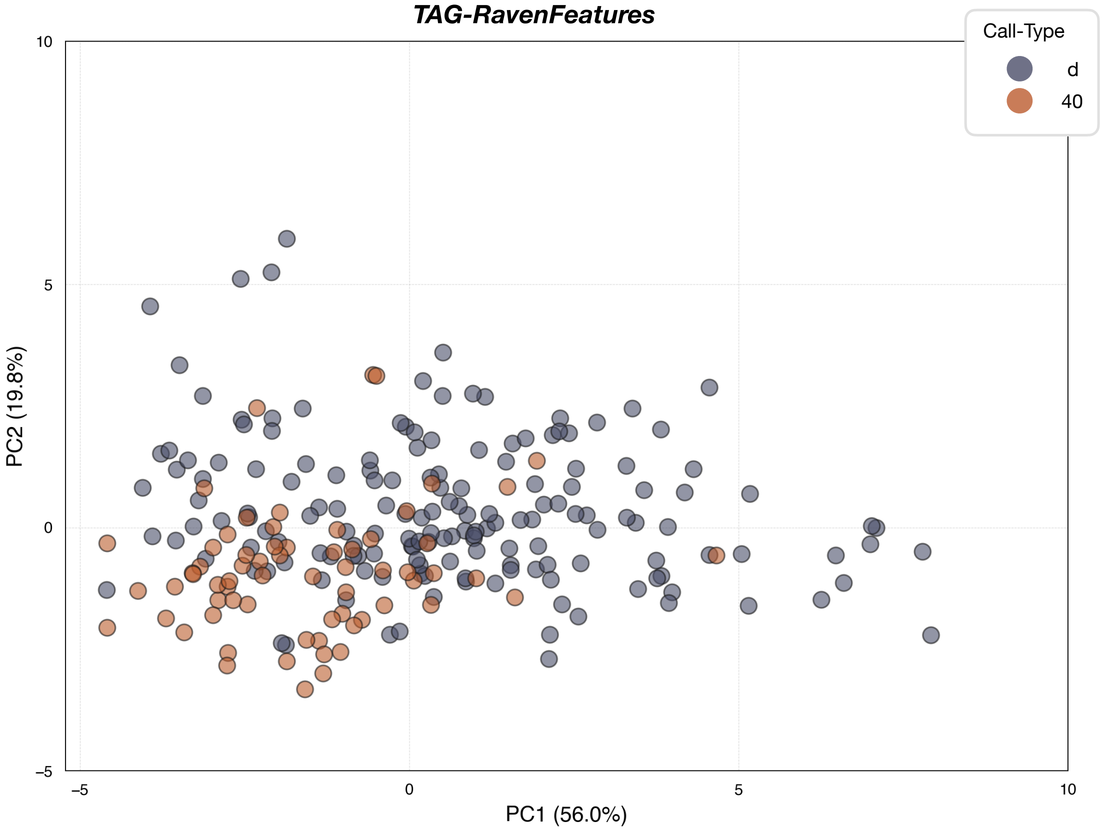

Figure S5. Principal Component Analysis (PCA) on the *Tag-RavenFeatures*, showing the two-dimensional distribution of the two confirmed call types: 40Hz-calls of fin whales (*40 - orange*), and D-calls of blue whales (*d - blue*).

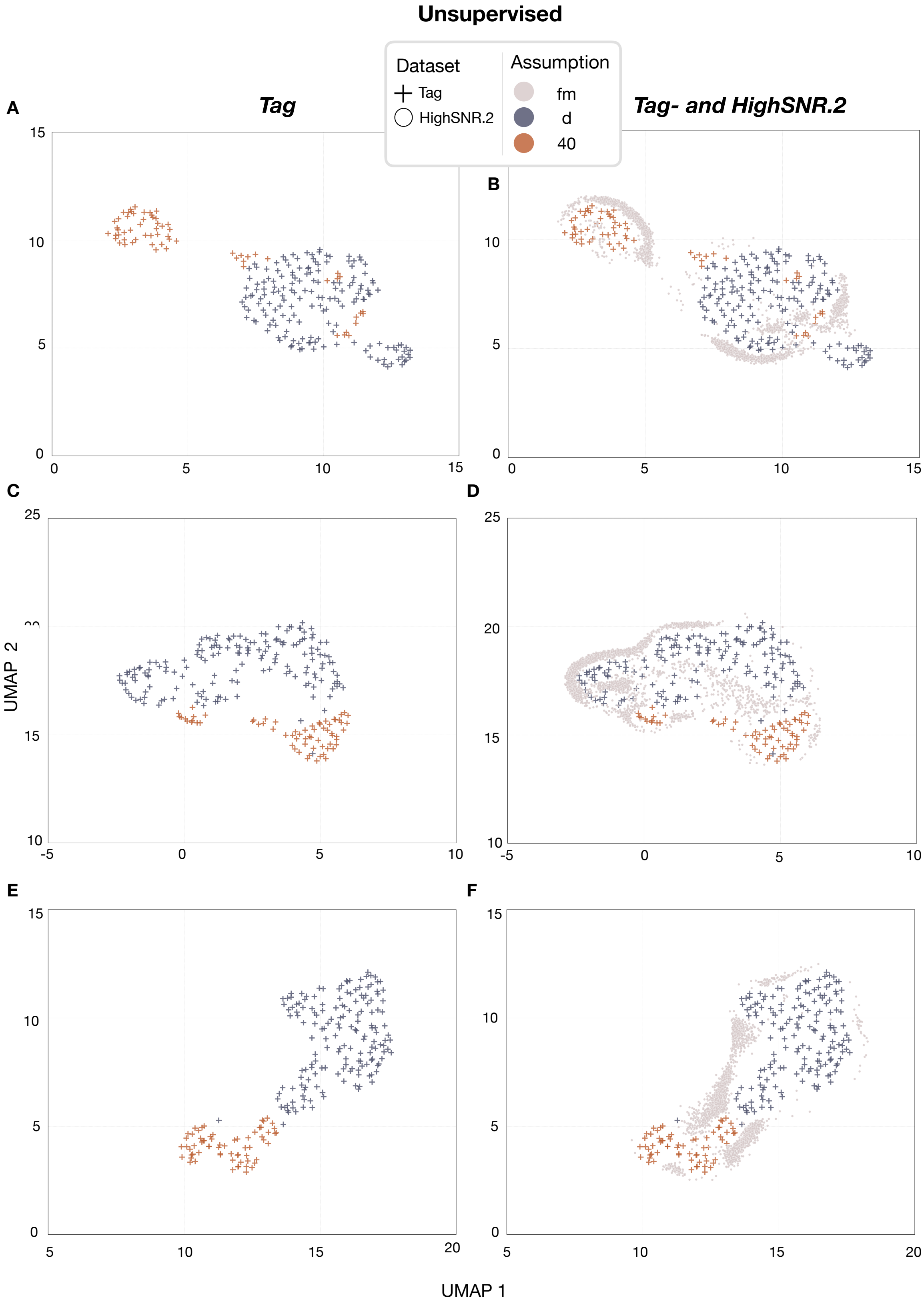

Figure S6. Dimension reduction using UMAP on the deep learning feature extraction across the various model embeddings Biolingual (A, B), Perch (C, D), and Surfperch (E, F) on the *Tag*- dataset. Panels show UMAP projections generated using an unsupervised approach. The *HighSNR.2*-embeddings are projected onto the *Tag*-embedding UMAP space and their source is assumed unknown (*fm - lightgrey*). 40Hz-calls of fin whales (*40 - orange*), and D-calls of blue whales (*d - blue*) from the tag data are shown accordingly.

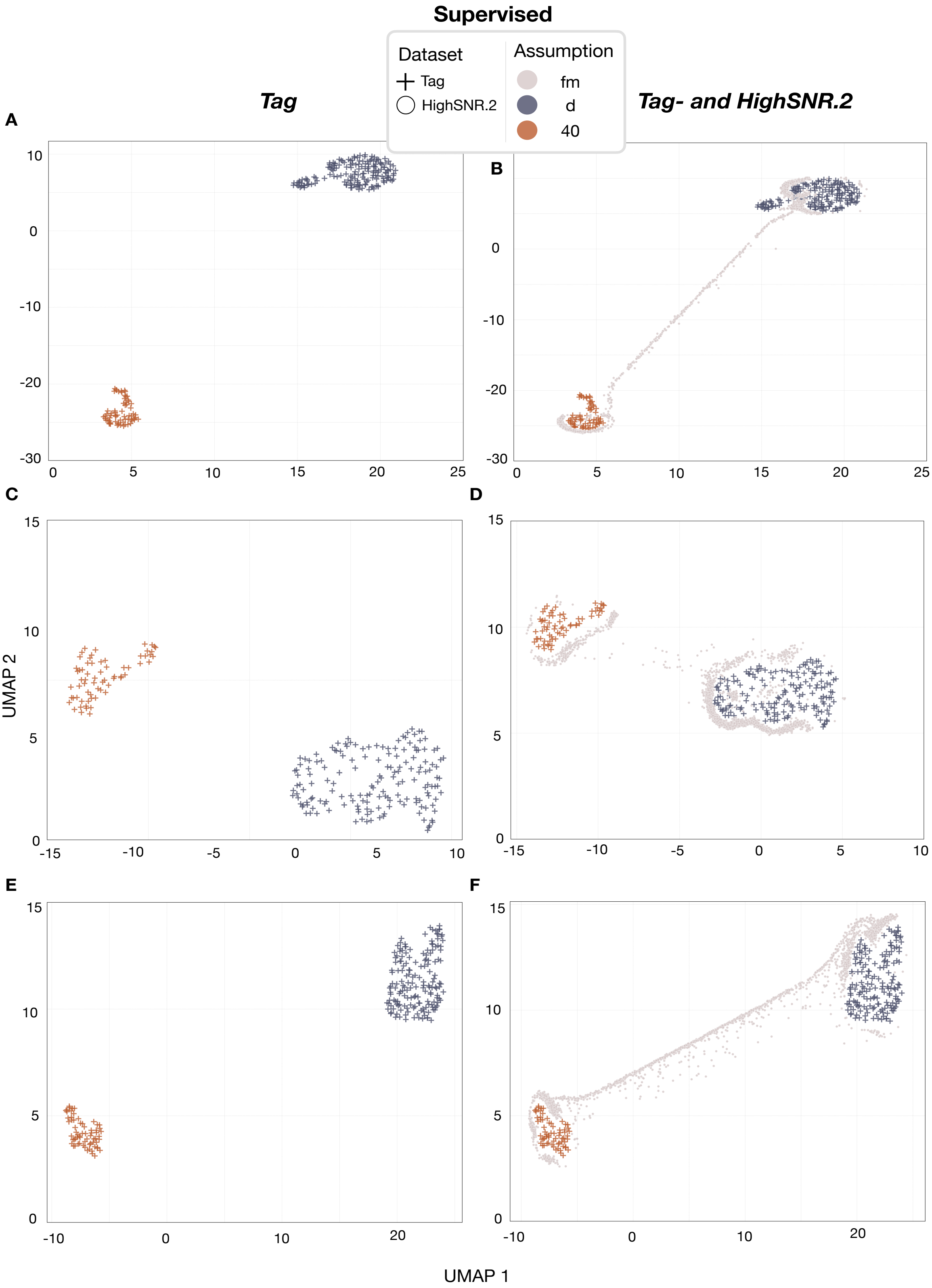

Figure S7. Dimension reduction using UMAP on the deep learning feature extraction across the various model embeddings Biolingual (A, B), Perch (C, D), and Surfperch (E, F) on the *tag* dataset. Panels show UMAP projections generated using a supervised approach. The *HighSNR.2*-embeddings are projected onto the *Tag*-embedding UMAP space and their source is assumed unknown (*fm - lightgrey*). 40Hz-calls of fin whales (*40 - orange*), and D-calls of blue whales (*d - blue*) from the tag data are shown accordingly.

Table S2. Number and proportion of FM calls per cluster based on the two confirmed call types - 40Hz-calls of fin whales (*40*), and D-calls of blue whales (*d*) in the *Tag-DLFeatures*, across the various model deep learning features (Biolingual, Perch, and Surfperch) as determined by the HDBSCAN algorithm. Each entry shows the count of the confirmed FM calls belonging to a given assumed call type within a cluster, followed by the corresponding percentage (in parentheses) relative to the total number of FM calls in the respective cluster. Noise points are labeled as *unassigned*. Clustering was performed independently on each dataset with HDBSCAN using different min_cluster_size values: Biolingual and Surfperch (min_cluster_size = 10), and *Perch* (min_cluster_size = 5).

Dataset	**Cluster**	**No. of '40' (%)**	**No. of 'd' (%)**	**No. total**
Tag-DLFeaturesBiolingual	unassigned	24 (48)	26 (52)	50
	1	41 (100)	0 (0)	41
	2	1 (0.8)	129 (99.2)	130
	3	0 (0)	10 (100)	10
Tag-DLFeaturesPerch	unassigned	26 (41.9)	36 (58.1)	62
	1	9 (6.5)	129 (93.5)	138
	2	31 (100)	0 (0)	31
Tag-DLFeaturesSurfperch	unassigned	19 (20.4)	74 (79.6)	93
	1	47 (83.9)	9 (16.1)	56
	2	0 (0)	82 (100)	82

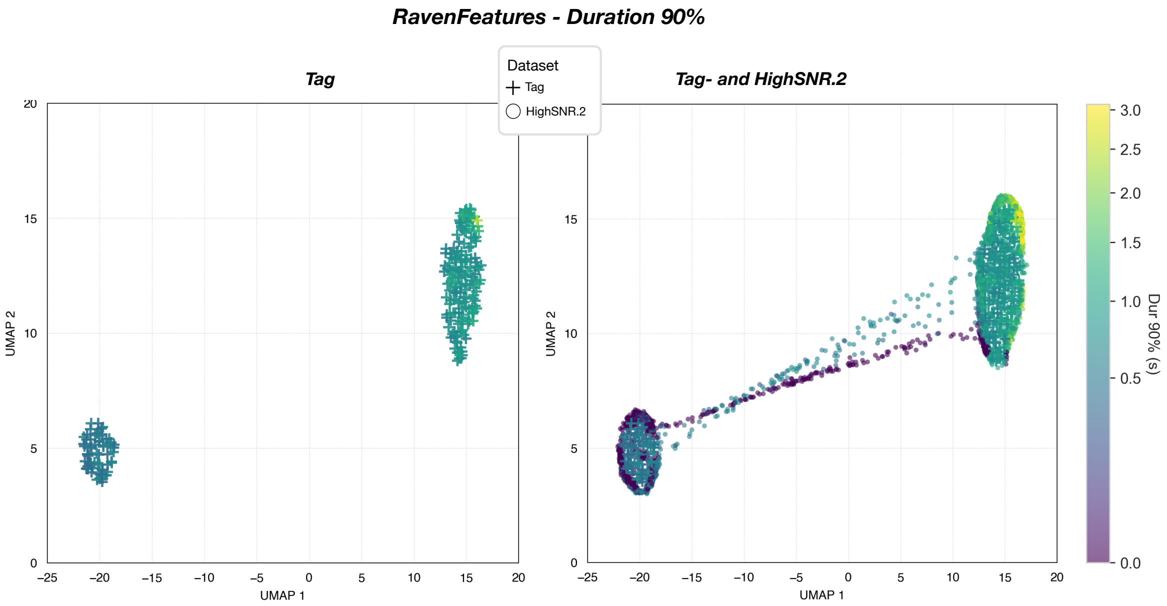

Figure S8. Dimension reduction using a supervised UMAP on the *Tag-RavenFeatures* and *HighSNR.2-RavenFeatures* projected onto the tag UMAP space. Both panels represent the acoustic parameter Duration 90% (s).

Table S3. Number and proportion of assumed labels (40Hz, d, or fm) per cluster in the *HighSNR.2-RavenFeatures* and *-DLFeatures* datasets, projected onto the according *Tag* UMAP spaces. Classification was performed using a k-nearest neighbor (kNN) approach to assign each assumed *HighSNR.2* FM call label to the closest tag-defined call type cluster (40Hz, D, or unassigned). kNN was applied to the projected *HighSNR.2* data only, with *min_distance* = 2, calls that did not fall within the selected distance threshold of 2 to any tag neighbors were considered unassigned.

Dataset	**Cluster**	**No. of '40' (%)**	**No. of 'd' (%)**	**No. of 'fm'**	**No. total**
HighSNR.2-RavenFeatures	unassigned	49 (18.35)	66 (24.72)	152 (56.93)	267
	40	177 (14.79)	262 (21.89)	758 (63.32)	1197
	d	168 (7.16)	372 (15.86)	1806 (76.98)	2346
HighSNR.2-DLFeatures_GoogleWhale	unassigned	0 (0)	0 (0)	0 (0)	0
	40	31 (10.6)	66 (22.6)	195 (66.8)	292
	d	351 (10.4)	587 (17.4)	2441 (72.2)	3379

Supplementary Material – Chapter 3

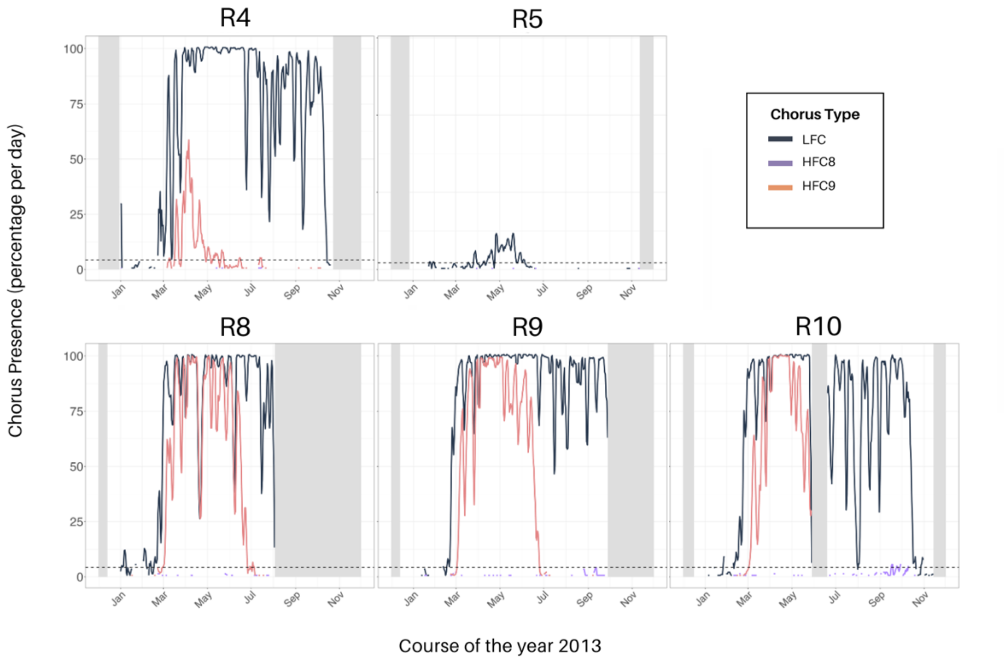

Figure S1. Line plots representing the percentage of files containing LFC and HFC per day over the course of the year 2013. Recordings consisted of 144 10-minute files per day. LFC is displayed in dark-grey, HFC8 in purple and HFC9 in orange. The lines were computed with a three-day running mean to smooth out the lines for a better overview. Dashed horizontal lines indicate the false positive rate of 3%, representing 4.3 recording files per day, as calculated by Schall and Parcerisas (2022). The grey bars indicate time periods where no data was available.

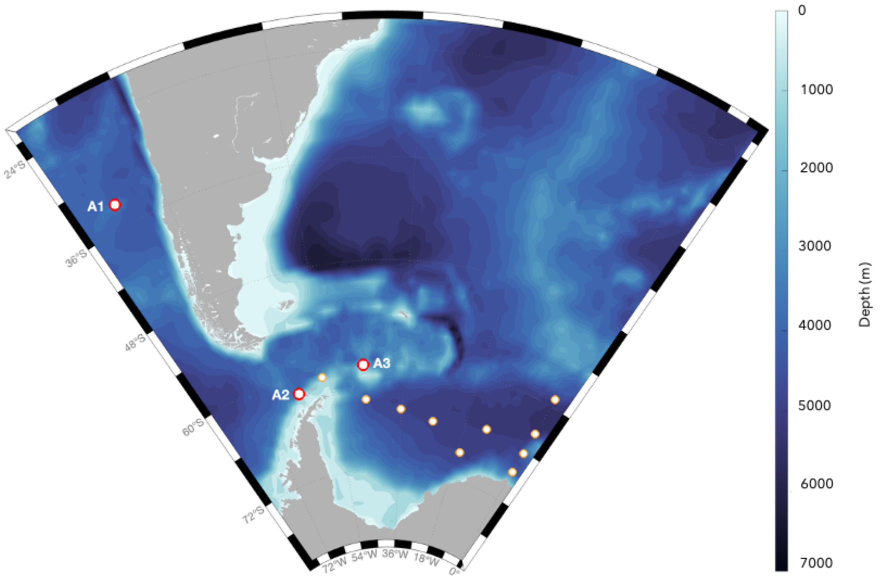

Figure S2. Bathymetric map of the ASSO and part of the southern Pacific indicating the geographical locations of the additionally used acoustic recorders (A1-A3, in red), as well as the ten recording positions of this study (represented in orange). Map was generated with M-MAP in MATLAB.

Table S1. Deployment information on additional passive acoustic recordings included in this study.

Recorder	Site	Latitude	Longitude	Recording Year	Sample Frequency (Hz)
A1	Juan Fernandez	61 00.88 S	55 58.53 W	2014	250
A2	Western Antarctic Peninsula	62 16.69° S	62 07.80° W	2002	500
A3	South Orkney Islands	60 24.297° S	45 57.58° W	2016	32800

Table S2. Results of the High-frequency (HF) component analysis of all passive acoustic recordings included in this. Values reflect the median, mean and standard deviation (SD) of assessed peak frequencies.

Site	Median	Mean	SD
R1 (2013)	86.92	86.48	1.25
R1 (2019)	84.96	85.26	1.5
R7	96.68	96.82	0.86
Juan Fernandez	85.94	85.79	0.37
Western Antarctic Peninsula	88.87	88.45	0.85
South Orkney Islands	86.92	86.58	1.26

Table S3. Results of the Dunn's post-hoc test for pairwise comparisons. The table lists pairwise comparisons of locations, associated Z- and p-values. p-values adjusted for multiple comparisons. A p-value smaller than 0.05 indicates a statistically significant difference between the locations being compared.

Comparison	Z-value	p-value
R7 - R1 2019	22,89797458	2,4336E-116
R7 - R1 2013	16,25099552	1,09883E-59
R7 - South Orkney Islands	14,63811714	8,02251E-49
R1_2013 - R1_2019	6,837172412	4,03858E-12
R1_2019 - WAP	-6,614434015	1,86488E-11
R1_2019 - South Orkney Islands	-6,531355925	3,25885E-11
R7 - Juan Fernandez	5,070461474	1,98426E-07
R1_2013 - WAP	-3,779742307	7,84954E-05
South Orkney Islands - WAP	-3,598146448	0,000160247
R7 - WAP	3,0293636	0,001225348
Juan Fernandez - WAP	-2,875124767	0,002019339
Juan Fernandez - South Orkney Islands	-1,088700741	0,138142938
R1_2013 - Juan Fernandez	1,022325588	0,153313413
R1_2019 - Juan Fernandez	-0,666525939	0,252537495
R1_2013 - South Orkney Islands	-0,270952306	0,393213857

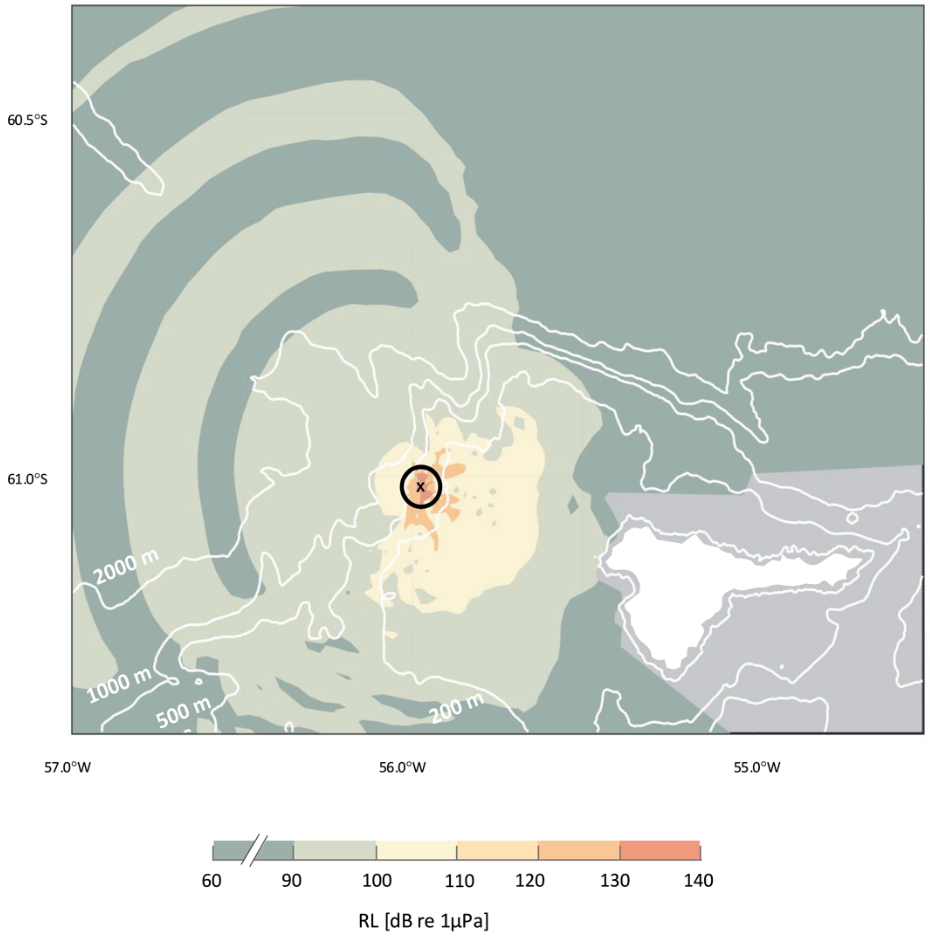

Figure S3. Sound pressure levels calculated for location R1 off Elephant Island with silt bottom as implemented in Burkhardt et al., (2021) based on Diekmann and Kuhn, (1999). Calculations represent the sound pressure levels at a depth of 10.7 m as received from a virtual source placed at the recorder's position 215 m depth (SL = 180 dB between 18 and 22 Hz). This set-up serves as a model proxy for the real, reverse situation, i.e. a source situated at 10.7 m and the recorder deployed at 215. Map created using Arndt et al., (2013) and Greene et al., (2017).

Fin whale HF components detected in previous publications

Table S4. High-frequency (HF) components of fin whales from different studies conducted in the southern hemisphere. Values reflect the peak frequencies that were (re-)assessed in the course of this study (marked in italics) or given mean values from previous studies.

Study	HF Component values	Area	Year of Recording
This study	86.48 ± 1.25 Hz	R1,2	2013
	96.82 ± 0.86 Hz	R 3-10 (except 5)	2013
	85.26 ±1.4 Hz	R1	2019-2020
Buchan et al., 2019	85.79 ± 0.37 Hz	Chilean Waters 33 27.28.8° S, 78 56.2.8° W	2007 - 2009, 2014 - 2016
Širović et al., 2009	88.45 ± 0.85 Hz	Western Antarctic Peninsula 62 16.69° S, 62 07.80°W, Scotia Sea 60 00.02° S, 51 53.88° W	2003 - 2004
Åsvestad et al., 2024	86.58 ± 1.26 Hz	South Orkney Islands 60 24.297° S, 045 57.548° W	2016
Širović et al., 2009	~99 Hz	Eastern Antarctica 66 44.24° S, 69 48.72° E	2003 - 2004
Burkhardt et al., 2021	85.6 ± 1.5 Hz	Elephant Island 61 00.88° S, 55 58.53° W	2013 – 2016
Leroy et al., 2018	~99 Hz	Indian Ocean (Multi Recorder Array)	2010 - 2016
Gedamke, 2009	~99 Hz	Kerguelen Plateau 62.6° S, 81.3° E, Prydz Bay 66.2° S, 74.5° E, Cape Leeuwin 34.4° S, 115.1° E, waters of eastern Antarctica (30°-80°E	2004 - 2007
	~82 and ~94 Hz (backbeat)	Line from Tasmania to Antarctica, center recorder at 53.7° S, 141.8° E	2016
Constaratas et al., 2021	78.4 ± 1.85 and 67.8 ± 1.72 Hz (backbeat)	Gisborne, New Zealand	2014 - 2015
	77.6 ± 1.36 and 88.2 ± 2.32 Hz (backbeat)	Cook Strait, New Zealand	2017

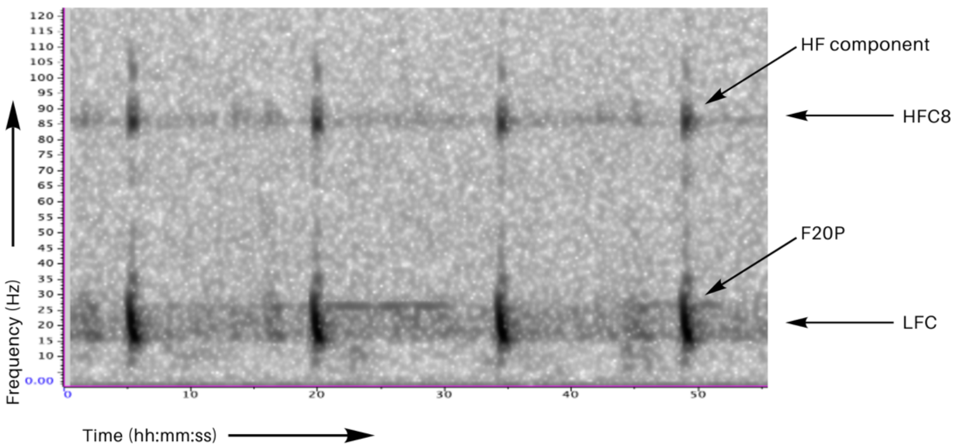

Figure S4. Fin whale call spectrograms of recordings off Elephant Island (R1) from this study, recorded on the 5th July 2013. Spectrogram is showing F20P, the resulting Low Frequency Chorus (LFC), as well as the simultaneous HF component centered at ~86 Hz, resulting in the High Frequency Chorus HFC8. Spectrogram parameters: Hanning window with a window size of 5000, DFT size of 8192 and an 80% overlap.

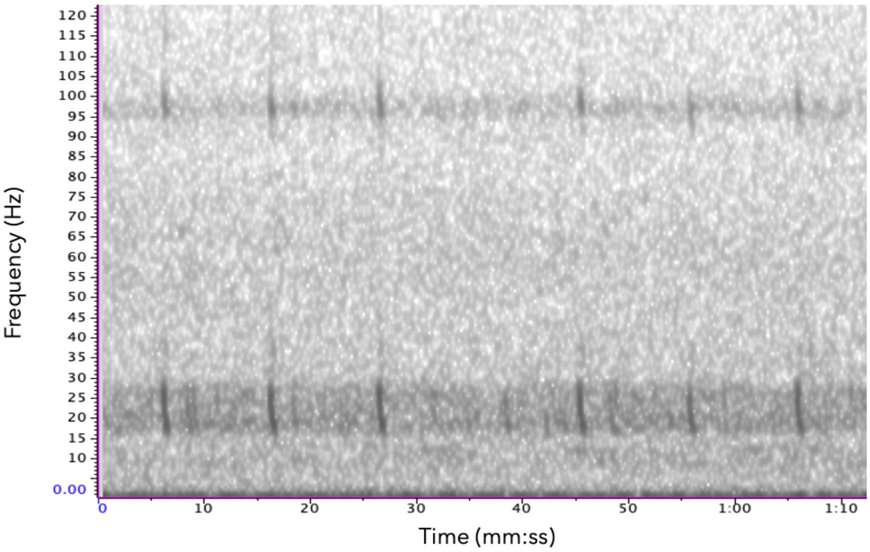

Figure S5. Fin whale call spectrograms of recordings at the Greenwich Meridian (R7) from this study. Spectrogram is showing F20P with the simultaneous high-frequency component centered at ~99 Hz. Spectrogram parameters: Hanning window with a window size of 5000, DFT size of 8192 and an 80% overlap.

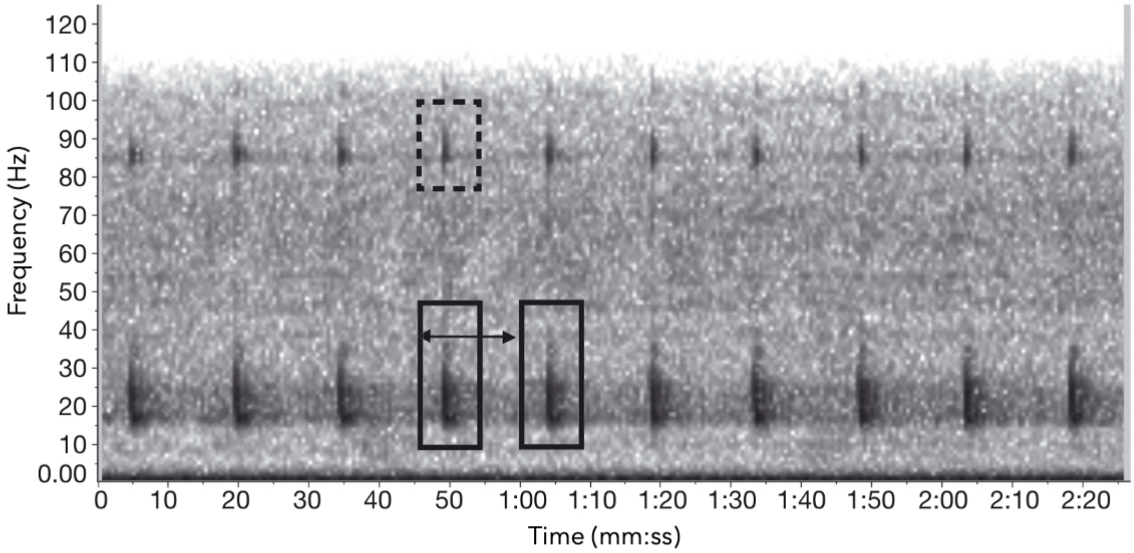

Figure S6. Screenshot of a spectrogram from recordings in Chilean waters from Buchan et al., 2019. Spectrogram shows F20P and a simultaneous high-frequency component centered at ~86 Hz (dashed rectangle). Spectrogram parameters: Hann window, FFT: 256 samples, 25% overlap.

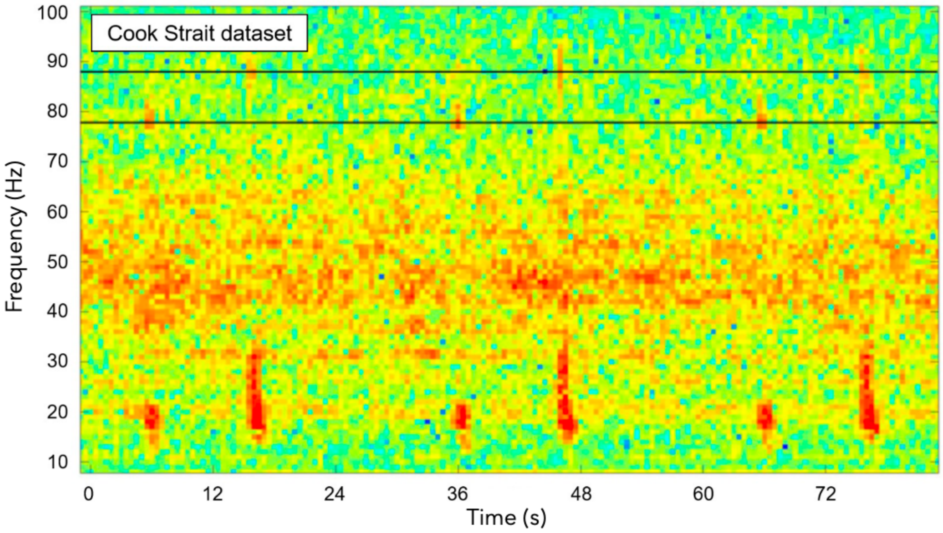

Figure S7. Screenshot of a spectrogram from recordings in the Cook Strait, New Zealand during 2017 from Constaratas et al., 2021. Spectrogram shows F20P and two simultaneous high-frequency components centered at ~78 and ~88 Hz. Spectrogram parameters: Hann window, FFT: 256 samples, 25% overlap.

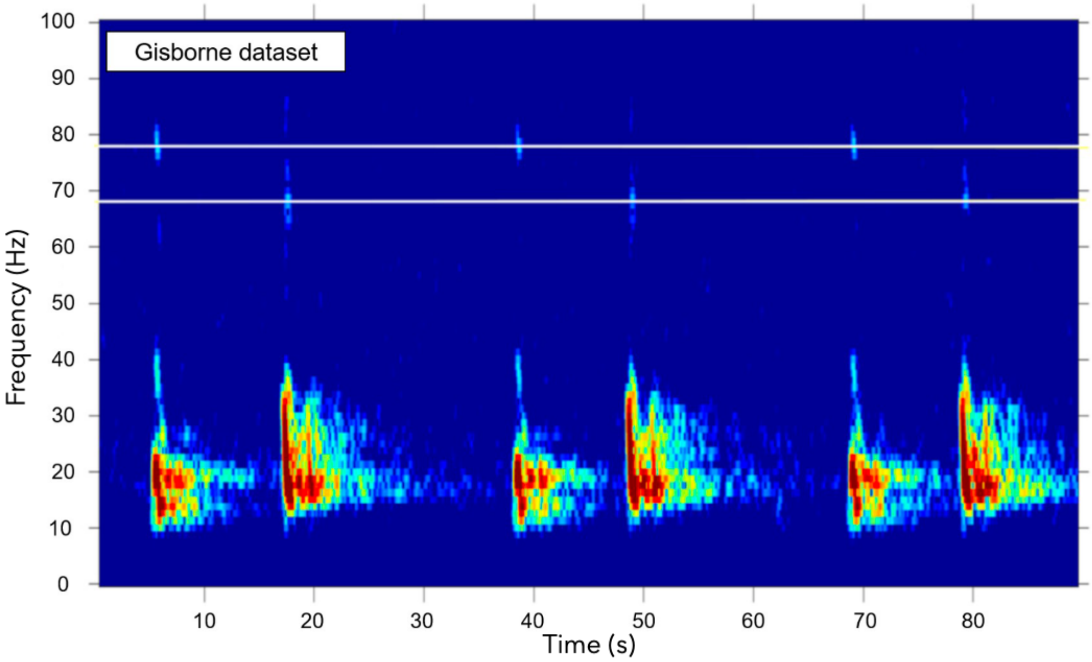

Figure S8. Screenshot of a spectrogram from recordings offshore Gisborne, New Zealand during 2014-2015 from Constaratas et al., 2021. Spectrogram shows F20P and two simultaneous high-frequency components centered at ~78 and ~68 Hz. Spectrogram parameters: Hann window, FFT: 256 samples, 25% overlap.

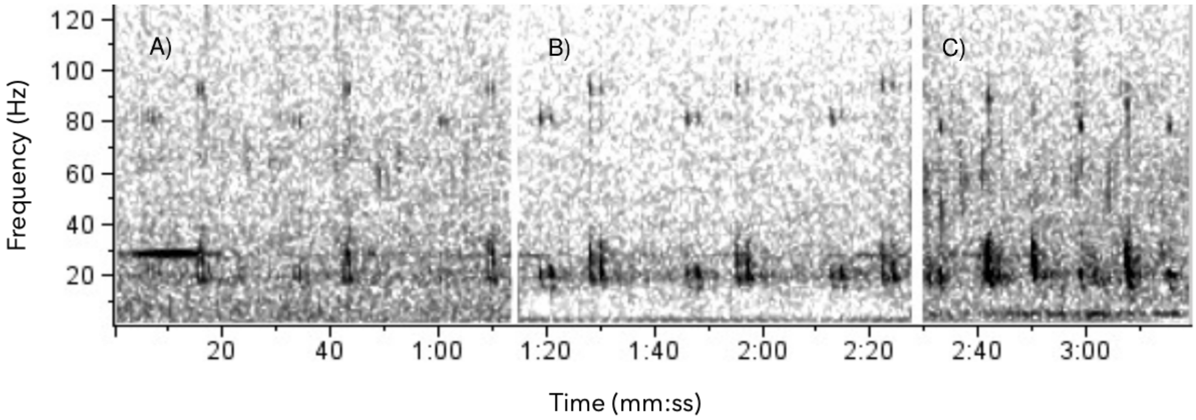

Figure S9. Screenshot of a spectrograms from a recorder transect from Tasmania towards Antarctica from Gedamke, 2009. A) nearest Tasmania, B) central position, and C) near Dumont d'Urville. Spectrogram shows F20P and dual high-frequency components centered at ~82 and ~94 Hz. Spectrogram parameters: Hanning window, FFT: 4096 samples, 50% overlap.

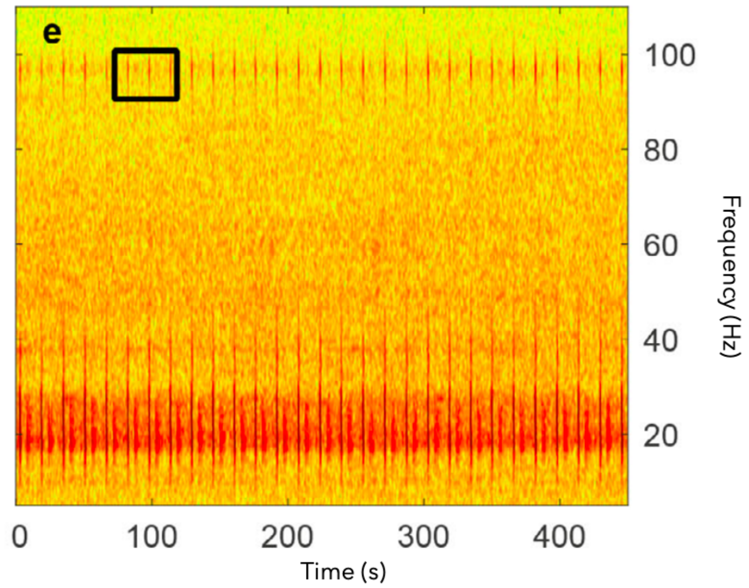

Figure S10. Screenshot of a spectrogram from recordings in the Indian Ocean from Leroy et al., 2018. Spectrogram shows F20P and a high-frequency component centered at ~99 Hz (black rectangle).

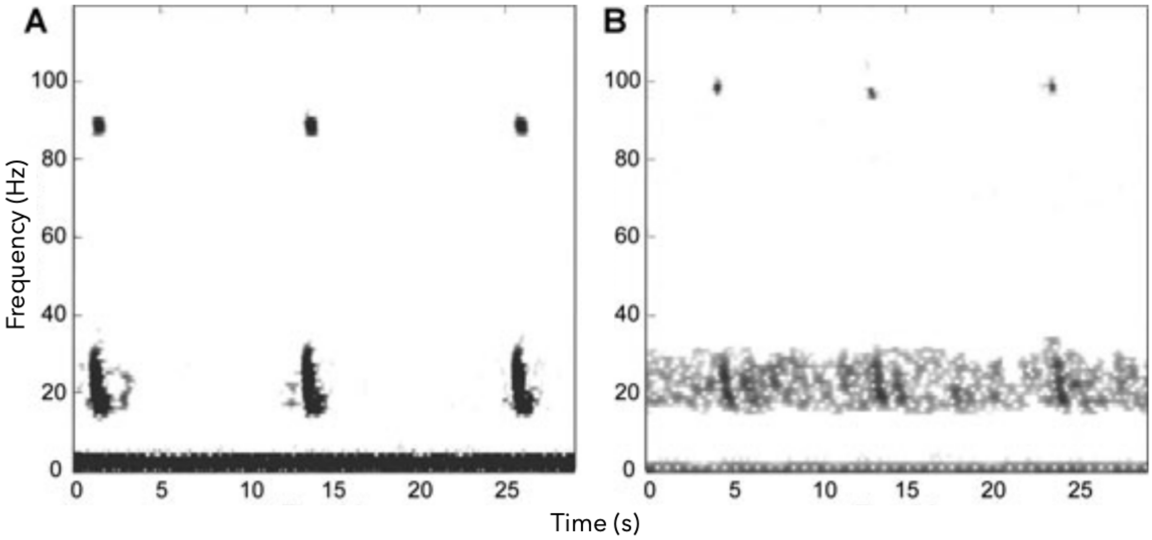

Figure S11. Screenshot of two spectrograms showing fin whale call characteristics of A) the Western Antarctic Peninsula and the Scotia Sea, and B) Eastern Antarctica (Širović et al., 2009). Spectrogram A) shows F20P and a high-frequency component centered at ~89, while B) shows a high-frequency component at ~99 Hz. Spectrogram parameters: Hanning window, FFT: 500 samples, 90% overlap.

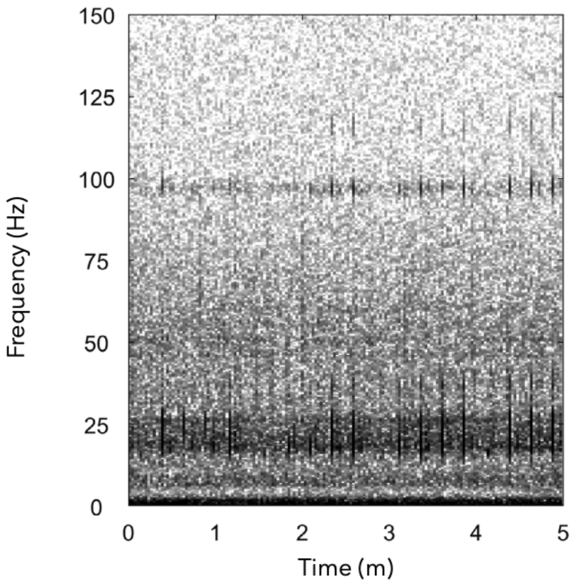

Figure S12. Screenshot of a spectrogram from recordings at the north-west of Walvis Ridge, Namibia during 2011 – 2012 from Thomisch et al., 2019. F20P are accompanied by a simultaneous high-frequency component centered at ~99 Hz. Spectrogram parameters: Hanning window, FFT size of 20 000 points, and a 90% overlap.

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Supplementary Material – Chapter 4

Table SI. Threshold values for the respective signal detection methods and corresponding true positive rates (TPR), when allowing for the stated false positive rates (FPR) as estimated by Schall and Parcerisas (2022). Signal types are abbreviated as follows: F20P – 20-Hz pulse, LFC – low-frequency chorus, HFC – high-frequency chorus. Detection methods differ depending on signal type. For the choruses (LFC and HFC), two metrics are used: signal-to-noise ratio (SNR), and power spectral density area (PSD Area). These metrics are compared against predefined thresholds to identify the presence of low- and high-frequency choruses.

For 20-Hz pulse (F20P) detection, the algorithm evaluates kurtosis, temporal and spectral SNR, and signal bandwidth, using a decision tree approach with multiple thresholds to filter potential detections. A multi-step decision process allows for detecting fainter 20-Hz pulses within a chorus (i.e., lower TST.2 than TST) if a certain bandwidth (TBW) is exceeded and the pulse exhibits high kurtosis (TK1.2), indicating a clear 20-Hz pulse.

Signal Type	**Detection method**	**Threshold value**	**TPR**	**FPR**
LFC	SNR	4	0.89	0.03
HFC8	PSD Area	0.3	0.93	0.03
HFC9	PSD Area	0.35	0.76	0.03
F20P	signal’s kurtosis (TK1)	3.25	0.8	≤0.01
F20P	kurtosis product (TK2)	40		
F20P	spectral SNR (TSF)	9		
F20P	temporal SNR (TST)	-2		
F20P	temporal SNR (TST.2)	-7		
F20P	signals’ bandwidth (TBW)	75		
F20P	signal’s kurtosis (TK1.2)	4		

Table SII. Deployment information on passive acoustic recordings. Acoustic data were obtained using two types of acoustic recording devices: The SonoVault autonomous recorders (Develogic GmbH, Hamburg, Germany, Reson TC4037-3 hydrophone) continuously recording at a sampling frequency of 5,333 Hz, and the Autonomous Underwater Recorder for Acoustic Listening (AURAL; Model 2, Multi-Électronique) recording at a sample frequency of 32,777 Hz. The acoustic recorders were deployed at different depths and set to different duty cycles, tailored to each recorder's specific depth rating, battery life, and data storage limitations. Dataset of AWI227-14_SV1004 is only made available upon request, as the data quality decreases over the recording period.

Location	**Deployment ID**	**Recorder Type**	**Latitude**	**Longitude**	**Depth (m)**	**Recording Period**	**Data Availability**
EI	AWI251-01_SV1008	SonoVault	61 0.88° S	55 58.53° W	212	2013-01-15 – 2013-11-09	https://doi.org/10.1594/PANGAEA.973191
	AWI251-01_AU0231	AURAL	61 0.13° S	55 97.78° W	210	2013-01-16 – 2016-02-10-	https://doi.org/10.1594/PANGAEA.966766
	AWI251-02_AU0231	AURAL	61 0.20°S	55 97.79°W	212	2017-01-29 - 2018-02-04	https://doi.org/10.1594/PANGAEA.981214
	AWI251-03_AU0085	AURAL	61 0.22° S	55 98.81° W	179	2019-02-01 - 2021-02-04	https://doi.org/10.1594/PANGAEA.982321
GM	AWI227-11_SV0002	SonoVault	59 0.50°S	000 1.10° E	1007	2010-12-11 - 2011-08-22	https://doi.pangaea.de/10.1594/PANGAEA.983645
	AWI227-12_SV1025	SonoVault	59 2.82° S	000 5.78° E	1020	2012-12-11 – 2013-07-13	https://doi.org/10.1594/PANGAEA.966612
	AWI227-14_SV1004	SonoVault	59 0.50°S	000 1.07°E	1070	2016-12-22 - 2018-09-18	data set can be made available upon request

Table SIII. Results of the applied linear regression model exploring yearly decrease rates of HF components at the Greenwich Meridian (GM) and off Elephant Island (EI).

Location	Group	Estimate	Standard Error	t-value	Significance
GM	Intercept	300.25796	60.71618	4.945	***
	Year	-0.10108	0.03017	-3.351	***
EI	Intercept	458.68542	22.12843	20.73	***
	Year	-0.18491	0.01097	-16.86	***

Table SIV. Information on High Frequency Components analyzed at the Greenwich Meridian (GM) and Elephant Island (EI).

Location	Year	Median of Peak Frequency (Hz)	Number of Calls
GM	2011	97.168	295
	2013	96.680	1134
	2017	96.191	59
EI	2013	85.938	257
	2014	86.426	134
	2015	85.938	125
	2017	85.449	559
	2019	85.449	285
	2020	84.473	423

Table SV. Results of the applied linear mixed-model analyzing seasonal variation in peak frequency. Random effects include YearMonth, accounting for variation between years, and Residual Variance, representing unexplained within-group variation. The Intercept represents the estimated peak frequency at the reference level (March). Month L captures the linear seasonal trend, while Month Q, Month C, and Month^4 represent higher-order polynomial terms that test for more complex seasonal fluctuation.

Random Effects		
Group	**Variance**	**Standard Deviation**
YearMonth	0.3251	0.5702
Residual	1.1036	1.0505

Fixed Effects			
Group	**Estimate**	**Standard Error**	**t-value**
Intercept	85.73571	0.11622	737.732
Month L	-0.93394	0.26698	-3.498
Month Q	-0.18917	0.26502	-0.714
Month C	0.20170	0.25245	0.799
Month^4	0.01814	0.25471	0.071

Supplementary Material – Synthesis

1.Non-Song signals and acoustic separation of baleen whales

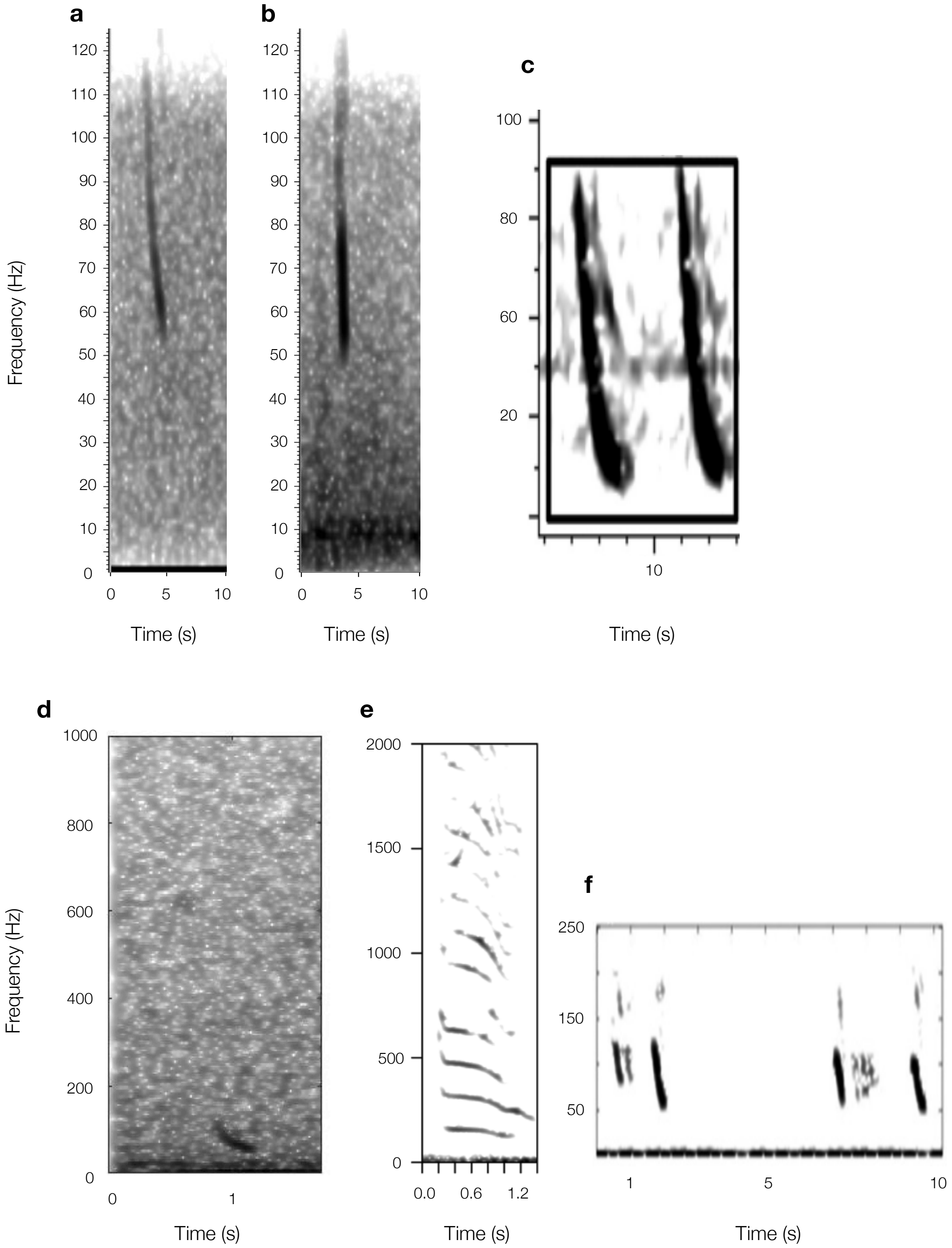

Figure 4. Spectrograms of baleen whale frequency-modulated (FM) calls illustrating their characteristic frequency contours and ranges. (a) Blue whale and (b) fin whale FM calls from this thesis. (c) Sei whale, (d) humpback whale, (e) southern right whale, and (f) Antarctic minke whale FM calls, adapted from Tremblay et al., (2019), Schall et al., (2021), Webster et al., (2016) and Dominello and Širović, (2016), respectively. Note that x- and y-axis scales differ among panels.

2. Population specific song characteristic in fin whales

Methods

Song characteristics were investigated using passive acoustic data from two recording positions, Elephant Island (EI) and the Greenwich Meridian (GM), over several years within the ASSO (see Figure S1 and Table S1).

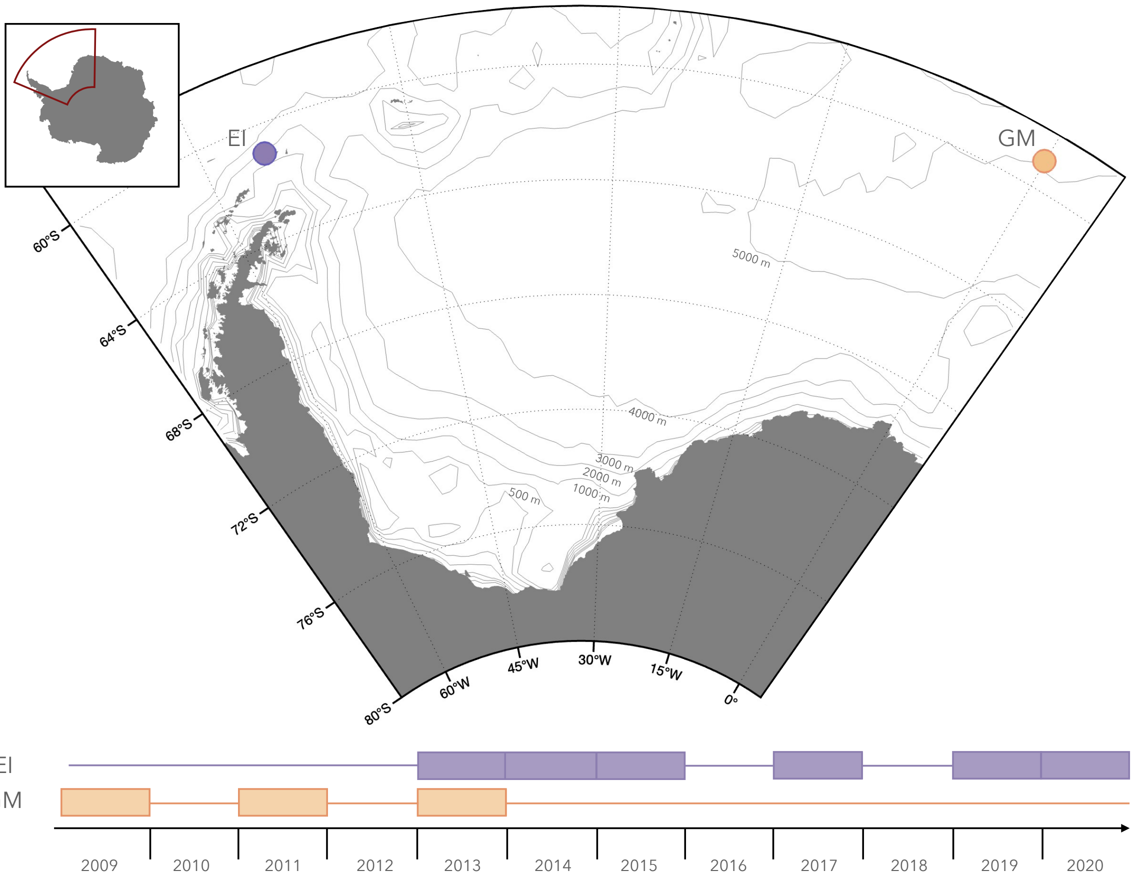

Figure S1. Map of the ASSO indicating the two acoustic recording sites: Elephant Island (EI) and the Greenwich Meridian (GM). Timeline indicates recording availability for each year and site. Map generated in MATLAB using M-MAP (Pawlowicz, 2020; The MathWorks Inc., 2022). Data were prepared following standard procedures of the Ocean Acoustics Group at the Alfred Wegener Institute in Bremerhaven, Germany (Thomisch et al., 2023).

All passive acoustic data were pre-analysed using the automated detector developed by Schall and Parcerisas (2022). The detector identifies fin whale 20-Hz pulses, and was optimized for a subset of the present dataset, yielding true positive rates above 80% and false positive rates ≤ 0.01%. The pulse detection relies on signal-specific features, which are compared against predefined thresholds to identify presence of 20-Hz pulses.

Table S1. Number of analysed recording files per month and year at EI and GM. In total, 2160 min (432 files) from EI and 1640 min (164 files) from GM, were included in the song analyses.

Site	Year	Month	FileCount
EI	2013	3	1
		4	12
		5	25
		6	20
		7	13
	2014	3	4
		4	9
		5	20
		6	1
	2015	4	16
		5	24
		6	30
	2017	2	4
		3	15
		4	25
		5	51
		6	35
		7	2
		11	1
	2019	3	16
		4	12
		5	23
		6	2
		7	6
	2020	2	2
		3	10
		4	11
		5	23
		6	10
		7	9
GM	2009	1	1
		3	12
		4	1
		5	1
		6	3
	2011	2	1
		3	27
		5	7
		6	2
	2013	1	1
		2	2
		3	61
		4	45

For analysis of fin whale song characteristics, inter-note interval (INI) and song variants, recordings were selected based on the presence of song. Here, ‘song’ was defined as sequences of 20-Hz pulses persisting for ≥2 minutes, following an established definition (Sirovic, 2017; Oleson, 2014; Wood & Sirovic, 2022). Pulse detections were first filtered for signal quality, selecting pulses with a temporal signal-to-noise ratio (SNRT) of >3 dB at GM and >10 dB at EI, these thresholds were determined during manual inspection of site-specific SNRT distributions. Pulse trains of ≥120 s were then filtered for SNRT consistency, allowing a maximum SNRT difference of 4 dB between consecutive pulses. Pulse train quality was verified through manual inspection of 10 randomly selected files per recorder in Raven Pro 1.6 (The Cornell Lab of Ornithology, Center for Conservation Bioacoustics, Ithaca, NY). Filtered recordings were decimated to 500Hz and processed to compute cepstra following Dréo et al., (2025). The cepstrum, expressed in quefrency (seconds), represents the time lag between repetitive signals in a recording, regardless of the signals' source. Consequently, any sufficiently regular periodic biological or non-biological signal could also produce cepstral peaks. Here, such ambiguity was avoided by analysing only the cepstrograms of filtered song sequences. Cepstrogram analysis has previously been applied to quantify echoes arising from multipath propagation in the water column. More recently, this method has been proposed for estimating INIs in baleen whale song and sperm whale click trains (Caruso et al., 2015; Dréo et al., 2025; Szesciorka et al., 2025), where peaks in the cepstrum correspond to the dominant INIs of e.g., fin whale 20-Hz pulse sequences.

Mean cepstra were calculated for each recording file (each 5 or 10 minutes of recordings), as well as across all files. To assess inter-annual variation in quefrency, the mean values per file from both locations were plotted chronologically by year, and a linear regression was fit with "year" as the explanatory variable and peak quefrency as the response, assuming Gaussian distribution. Model assumptions were checked via QQ plots of residuals for normality and homogeneity of variance.

Results

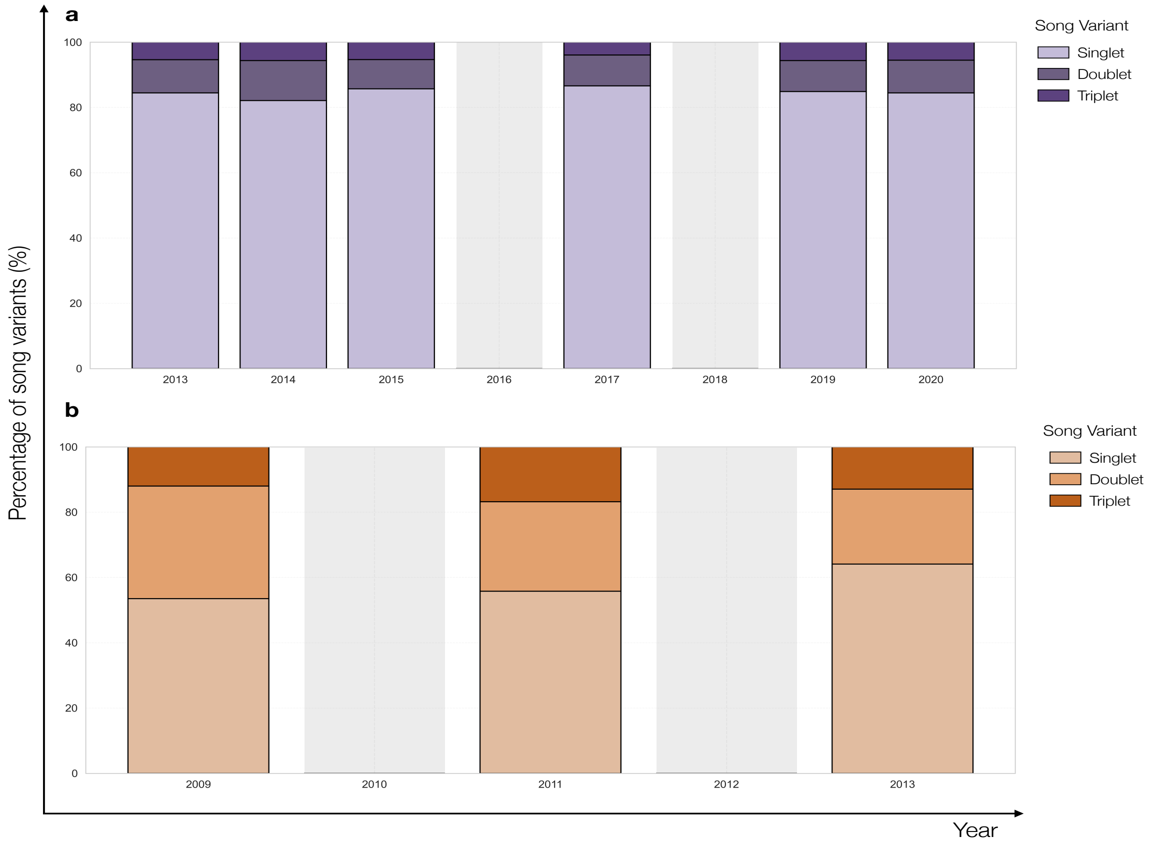

Figure S2. Annual percentage of analysed pulses belonging to each song type. a) EI (2013 – 2020) and b) GM (2009 – 2013). Grey shaded bars represent years with no data available.

Table S2. Global fin whale song INIs. Review is simplified, and restricted to studies after 2010. INIs are rounded for general comparison; ranges are indicated with a dash (–), and additional INIs arising from song structure (e.g., doublets or triplets) are indicated with an ampersand (&).

Region	Location	Approximate INI (s)	Recording Years	Reference
North Pacific	Hawaii	21 & 26 - 28 & 34	2000 & 2005	Oleson et al., (2014)
		17 & 24, 28 & 33	2010-2017	Helble et al., (2020)
		30 & 34	2017-2023	Helble et al., (2025)
		25 & 35	2000-2014	Archer et al., (2019)
	North West Pacific	25	2000-2014	Archer et al., (2019)
	Chuckchi Sea	8 & 15 & 18	2000-2014	Archer et al., (2019)
	Aleutian	10-20	2000-2014	Archer et al., (2019)

	Bering Sea	8 & 15-18, 10-20	2000-2014	Archer et al., (2019)
		23 & 28 - 29 & 34	2000-2001, 2005	Oleson et al., (2014)
	Western Gulf of Alaska	15, 28 & 34	2000-2014	Archer et al., (2019)
	Eastern Gulf of Alaska	20 & 22	2000-2014	Archer et al., (2019)
	Langaran Island	20 & 22	2000-2014	Archer et al., (2019)
	Bowie Seamount	13 & 17, 20 & 22	2000-2014	Archer et al., (2019)
	Vancouver Island	13 & 17, 20 & 22	2006-2012	Koot, (2015)
	Central Pacific	15 & 28	2000-2014	Archer et al., (2019)
	Northeastern Pacific	25-28, 11-16 & 14-18	2003-2014	Weirathmueller et al., (2017)
	Montery Bay	25	2000-2014	Archer et al., (2019)
	Southern California	18 & 24 - 27 & 33	2000-2002	Oleson et al., (2014)
	Southern California	16 & 22	2001-2012	Širović et al., (2017)
	Gulf of California	4 & 11	2004-2010	Širović et al., (2017)
	Gulf of California	5 & 10, 25	2000-2014	Archer et al., (2019)
Southern Ocean	Antarctic Peninsula	12 & 14	2000-2014	Archer et al., (2019)
	Antarctic Peninsula	12 & 14	2001-2003, 2014-2016	Wood and Širović, (2022)
	Antarctic Peninsula	12 & 15	2013-2020	This study
	Greenwich Meridian	11	2009-2013	This study
North Atlantic	Davis Strait, Western Greenland	13.5	2007	Simon et al., (2010)
	Norwegian Sea	15	2014	Garcia et al., (2019)
	Svalbard Islands	7-20	2014-2020	Papale et al., (2023)
	Southeast Iceland	13	2007	Romagosa et al., (2024)
	Southeast Greenland	13-19	2007-2020	Romagosa et al., (2024)
	Celtic Sea	15	2016-2017	Romagosa et al., (2024)

	Portugal	13-16	2008-2016	Romagosa et al., (2024)
	Canary Islands	15	2015	Romagosa et al., (2024)
	Barents Sea	8-18	2015-2018	Romagosa et al., (2024)
	Azores	13	2006-2009	Castellote et al., (2012)
	Strait of Gibraltar and Alboran Sea	13	2006-2009	Castellote et al., (2012)
	Western Mediterranean	15	2006-2009	Castellote et al., (2012)
	New York Bight and Boston	9,16	2008-2009	Morano et al., (2012)

Table S3. Global fin whale song high-frequency (HF) components. Values are rounded for general comparison.

Region	**Location**	**Approximate HF component (Hz)**	**Recording Years**	**Reference**
North Atlantic	Norwegian Sea	130	2014	Garcia et al., (2019)
	Davis Strait	131	2006-2007	Simon et al., (2010)
	Azores	135-140	2006-2009	Castellote et al., (2012)
	Strait of Gibraltar	135-140	2006-2009	Castellote et al., (2012)
	Alboran basin	135-140	2006-2009	Castellote et al., (2012)
Southern Hemisphere	Chile	86	2007-2016	Buchan et al., (2019)
	Antarctic Peninsula	86	2013-2020	Chapters 3 & 4 (Wöhle et al., 2025b, 2025a)
	Antarctic Peninsula	86	2013	Burkhardt et al., (2021)
	Antarctic Peninsula	89	2003-2004	Širović et al., (2009)
	Namibia	99	2011-2013	Thomisch et al., (2019)
	Greenwich Meridian	99	2010-2013	Chapters 3 & 4 (Wöhle et al., 2025b, 2025a)
	Greenwich Meridian	99	2003-2004	Širović et al., (2009)
	Kerguelen Plateau	99	2004-2006	Gedamke, (2009)
	Indian Ocean	99	2011-2015	Leroy et al., (2018)

	Western Australia	99	2004-2006	Gedamke, (2009)
	Eastern Australia	82 & 94	2004-2006	Gedamke, (2009)
	New Zealand (Cook Strait)	67 & 73	2016-2017	Constaratas et al., (2021)
	New Zealand (Gisborne)	77 & 88	2014	Constaratas et al., (2021)

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Eidesstattliche Erklärung

Hiermit versichere ich, Svenja Kathleen Wöhle, dass ich vorliegende Dissertation mit dem Titel:

‘Acoustic signals of Southern Ocean baleen whales: assessing methods to reliably identify species- and population-specific vocalisations in passive acoustic monitoring data’

selbstständig verfasst und keine anderen als die angegebenen Hilfsmittel und Quellen benutzt und die allgemeinen Prinzipien wissenschaftlicher Arbeit und Veröffentlichungen, wie sie in den Leitlinien guter wissenschaftlicher Praxis der Carl von Ossietzky Universität Oldenburg festgelegt sind, befolgt habe.
Zudem versichere ich, dass diese Dissertation noch keiner anderen Fakultät oder Universität zur Prüfung vorgelegen hat und, dass diesem Promotionsverfahren keine endgültig gescheiterten Promotionsverfahren vorausgegangen sind. Diese Dissertation ist, abgesehen von den angegebenen Teilpublikationen (Kapitel 1, 3, und 4), noch nicht veröffentlicht worden.
Die von mir vorgelegte Dissertation ist von Prof. Dr. Gabriele Gerlach, Dr. Elena Schall, Dr. Ilse Van Opzeeland und Elke Burkhardt betreut worden.

Bremen, den 28. Januar 2026

Svenja Kathleen Wöhle