

Review

Focusing on the receiver – Hearing in two focal cetaceans exposed to Ocean Economy developments

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ABSTRACT

Plans for large-scale economic developments in the Indian Ocean, including increased shipping, oil and gas exploration and offshore mining, have resulted in concerns about potential impacts on cetaceans. Two species of particular interest are the resident, coastal Indian Ocean humpback dolphin *Sousa plumbea* and the migratory humpback whale *Megaptera novaeangliae*. As the two species belong to different hearing groups (high-frequency odontocetes vs low-frequency mysticetes), we review the available literature on their differing hearing mechanisms (physiology), specialities and sensitivities here as there is a lack of data available for these two species in the Indian Ocean region. The reviewed information included audiogram data, species-specific frequencies and sensitivity ranges, ear morphology and adaptations for hearing in their respective groups where available. For odontocetes, most information stems from animals under human care, while for mysticetes bioacoustic measurements, like audiograms, are more difficult to access, resulting in a lack of data on hearing for *M. novaeangliae*. Our review highlights an absence of baselines upon which to measure future impacts from anthropogenic developments in the Indian Ocean and we suggest future work to address this.

Our work is not only timely in view of the planned anthropogenic developments in the Indian Ocean, but also has wider implications in the global context as cumulative impacts on cetaceans grow due to increased international demand for resources and associated Ocean Economy developments.

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1. Introduction

Cetaceans currently face a myriad of threats in this age of global change [1] and impacts from anthropogenic developments are increasingly being documented globally, with anthropogenic noise presenting the number one pollution problem in the world's oceans today [2,3]. However, in some regions, important baseline data upon which to measure impacts from anthropogenic developments are missing. One such area is the Indian Ocean [4,5]. The current Ocean/Blue Economy drive in the region is accelerating [6,7] and includes plans for large-scale economic development, such as increased shipping [8], oil and gas exploration and offshore mining [9]. Several maritime trade routes are found in the region and currently 30% of global tanker traffic passes through the Mozambique Channel [10]. In addition, most states are actively expanding their own offshore oil and gas production efforts, which will further increase shipping and noise [10]. This is of significant concern, particularly as the cumulative effects of multiple noise- and ship-related stressors remain largely unassessed for the region [10] and ambient noise levels in the Indian Ocean have already been documented to be increasing [11]. However, the impact that noise poses to marine life is rarely considered in management or development plans [10], which raises concerns about its potential effect on the marine fauna of the region, particularly cetaceans [12,13].

Documented impacts from marine noise pollution on cetaceans include displacement of animals [14], increase in physiological stress levels [15], communication interference [16], disruption of foraging behaviour [17], and damage of auditory systems [18,19]. Two species of particular interest in the Indian Ocean are the Indian Ocean humpback dolphin (*Sousa plumbea*) and the humpback whale (*Megaptera novaeangliae*). The Indian Ocean humpback dolphin (*S. plumbea*) is a very coastal species found throughout the Western Indian Ocean from Cape Point (South Africa) to the southern tip of India and is currently listed as 'Endangered' [20,21]. In contrast, the humpback whale (*M. novaeangliae*), which is migratory and present in the Indian Ocean from June to October [22], except for the non-migratory population in the Arabian Sea, which is present year-round [23], is currently listed as 'Least Concern' as its populations are increasing; however, it is a cosmopolitan species and thus of relevance to industry globally [24]. Both species are likely to be present in the area of planned developments throughout the Indian Ocean region and thus of particular concern to all stakeholders.

Differences in frequency-specific hearing sensitivity among different marine mammal groups influence how they are affected by noise exposure [25]. Southall et al. [18,19] provide a comprehensive review of methods used to evaluate and quantify noise exposure levels for different anthropogenic sources expected to cause (1) behavioural responses of varying severity and (2) reductions in auditory sensitivity changes, including both temporary threshold shifts (TTS) and permanent threshold shifts (PTS) in marine mammals. The two species our review is focussed on are representatives of different hearing groups as defined by Southall et al. [19] – the Indian Ocean humpback dolphin *S. plumbea* is an odontocete (toothed whales, dolphins, and porpoises) representative of high-frequency (HF) cetaceans, and the humpback whale *M. novaeangliae* is a mysticete (baleen whales) and representative of low-frequency (LF) cetaceans.

Anthropogenic sound, and vessel traffic in particular, is increasingly recognised as an important influencer of marine soundscapes [2,3,26,27], likely masking marine mammal sounds [28], potentially changing the animals' behaviour [18,19] and raising the risk of ship strike [29,30]. To date, there has been little analysis of static versus moving sound sources and often overlooked in noise mitigation is the hearing frequency of the receiver i.e., the animals

exposed to the anthropogenic noise. Ships, for example, are moving sound sources and thus soundscapes are of a dynamic nature due to differing environmental conditions [13,29]. A recent review assessing the ocean soundscapes throughout the Anthropocene era describes in detail just how anthropogenic noise (anthrophony) has interfered with the communication abilities of marine mammals (biophony) and calls for anthropogenic noise to be recognised in cumulative impact assessments conducted on marine ecosystems [3]. While many developed countries have made statutory commitments to guarantee underwater noise levels are kept below levels that are harmful to marine ecosystems [31], these are lacking in the Indian Ocean, leaving species with high site fidelity, such as *S. plumbea*, at risk [32], and creating a reduction in listening space for cetaceans [33]. In view of the planned anthropogenic developments in the region, there is a clear need to review the hearing mechanisms (physiology), specialities, and sensitivities of these two focal cetacean species relevant to the Indian Ocean.

2. Materials and methods

We started our review with a broad literature search in the Google Scholar database using keywords relevant to our review purpose, including hearing frequencies, sensitivity ranges, ear morphology, adaptations for hearing, audiograms, passive acoustic recordings, behavioural studies, high-frequency cetaceans, low-frequency cetaceans, *Sousa plumbea*, *Megaptera novaeangliae*.

We conducted a systematic and standardised review of the scientific literature, published from 1959 to 2021. For this we reviewed over one hundred published accounts for both species, including journal articles, reviews, and reports, and subsequently narrowed our search down to key literature sources for the two species containing some or all of the keywords previously listed (e.g., hearing frequencies, sensitivity ranges, ear morphology, adaptations for hearing, audiograms, passive acoustic recordings, etc.) for the species of interest. From these key literature sources, we cross-checked citations relevant to our review and obtained additional literature sources this way until we started seeing a repetition of references. However, only the English literature was reviewed, possibly creating a bias regarding the total number of publications. In addition, as relevant literature for *Sousa plumbea* remains scarce, available information for other species in the genus *Sousa* was included. The available information on odontocete vocalizations (which can aid in the inference of hearing capabilities) is presented by geographical region, with consideration for potential population-level differences. Similarly, for humpback whales, little is known about the movement of individual humpback whales between populations, and therefore further information is presented by ocean basin.

3. Indian Ocean humpback dolphin (*Sousa plumbea*) as a representative for odontocetes

Hearing in marine mammals in general, and cetaceans in particular, is not well understood as studies on the topic are, for obvious reasons, difficult to conduct on wild animals. Thus, the majority of information stems from animals under human care (captive scenarios) and is restricted to the smaller odontocetes. However, caution should be employed when interpreting and extending such data, which are often obtained from one individual to the species as a whole or to wild populations as many factors, including the physical situation, medical administration and the background noise environment (i.e. reflection of sound off the walls in a captive facility) can influence hearing measurements [34]. Potential differences with age may also need to be considered due to the still

developing biosonar-relevant structures in young animals [35,36] or age-related hearing loss in older individuals [37].

Audiograms have only been conducted on around 20 marine mammal species [38] and usually only on a few individuals per species, thus audiogram variability remains little understood [39]. Audiograms in animals are usually conducted by studying the auditory evoked potential (AEP) response or behaviourally. AEPs are a type of electroencephalogram (EEG) signal generated from the brain stem by an acoustical stimulus and thus the AEP response is taken to reflect the auditory ability (or hearing threshold levels) of an individual. The available information to date suggests a large diversity in hearing sensitivities and ranges among odontocetes due to a combination of individual variation and species differences [25]. There have also been many instances of hearing loss associated with both age and sex when sample sizes within a species are increased [25,40]. It is generally assumed that a species' frequency of best hearing sensitivity overlaps to a large degree with the frequency of their vocalizations (Fig. 1) [38]. The best frequency of hearing for odontocetes is between 20 and 150 kHz [41,42,43,44].

Both terrestrial and marine mammals generally have a U-shaped audiogram, showing the best hearing sensitivity frequency band, and the decreased sensitivity at lower and higher frequencies (Fig. 2) [19]. Odontocetes are able to hear unusually high frequencies, with some ranging as high as 180 kHz [25]. Nearly all odontocete species can process sounds very quickly, because they possess

fine scale frequency discrimination, which not only compensates for faster underwater sound speed, but also for the complex requirements of echolocation. For this, anatomical and post-mortem investigations have revealed that odontocetes have developed a distinct method of receiving sound which is unique in mammals. These studies have shown that odontocetes use specialized acoustic fats in their lower jaws [48] to transmit sound to uniquely structured ear and skull configurations [49]. Here, the high frequency sounds (such as those originating from echolocation) are better detected along the lower jaw, while low frequency sounds (such as those originating from vocalizations) are best detected near the opening to the ear canal [50,51]. Adding to this knowledge, X-ray computed tomography (CT) has provided a means for examining the auditory anatomy of cetaceans *in situ* without the need for anatomical or post-mortem investigations. Subsequent studies have revealed alternative pathways of sound reception in marine mammals, such as the finite element modelling (FEM) conducted by Cranford et al. [52]. Using CT data sets and various measurements of sound-propagation characteristics, the simulated head of an adult male Cuvier's beaked whale (*Ziphius cavirostris*) was produced, revealing likely sound propagation pathways into and out of the head [52]. The most interesting FEM results were the discovery of a previously undescribed 'gular pathway' for sound reception in *Ziphius*, whereby sound enters the head from below, passes between the mandibles and is propagated by the acoustic fat toward the bony ear complexes. More recent studies investigating the function of the external ear canal in cetaceans [53] revealed the presence of lamellar corpuscles. Each corpuscle was made up of a central axon with surrounding lamellae of Schwann receptor cells and encapsulated by a thin cellular layer. The authors explain that these corpuscles appeared to be mechanoreceptors that formed part of the sensory system. These features were absent in the terrestrial mammals included in the study and may represent a unique phylogenetic feature of cetaceans. Thus, it is generally accepted that a specialized sound reception system has been developed by dolphins [54].

The ear morphology of cetaceans generally differs from that of other mammals in that their pinnae (external part of the ear) are absent [49]. Furthermore, odontocetes transduce sounds through the lower jaw to the auditory ossicles, the three bones in the middle ear that serve to transmit sounds to the cochlea. Describing the outer, middle, and inner ear morphology (i.e. the peripheral auditory system) of odontocetes is key for the further evaluation of acoustic pollution effects [55,56,57]. The morphology of the external ear canal of odontocetes has received little attention in comparison to the middle and inner ear [58,59,60,61] and there is a debate on whether the canal still serves any function [49,53,58,62]. While the middle ears of all cetaceans are adapted to withstand extreme pressures, other potential characteristics that determine hearing in the middle ear include the mass and stiffness of the ossicular chain [49,62]. According to Ketten [62], lower frequencies are favoured by increased mass and volume of the ossicular chain, while high frequency transmissions are aided by its stiffness. The tympano-periotic complex and the middle ear of 18 odontocete species are extensively described by Nummela et al. [59]. The inner ear is made up of a membranous labyrinth housing the cochlea (auditory organ) and the vestibular system (acceleration and position organs) [49,62]. The auditory organ present in all odontocetes can be divided into three conventional mammalian divisions, which include the *scala media*, the *scala tympani* and the *scala vestibuli* [62]. The structure and function of the inner ear of various species of odontocetes has been described in detail in numerous studies including earlier ones by McCormick et al. [58] and Wever et al. [63,64,65,66] as well as more recent studies by Racicot et al. [60,61] and Morell et al. [67,68,69].

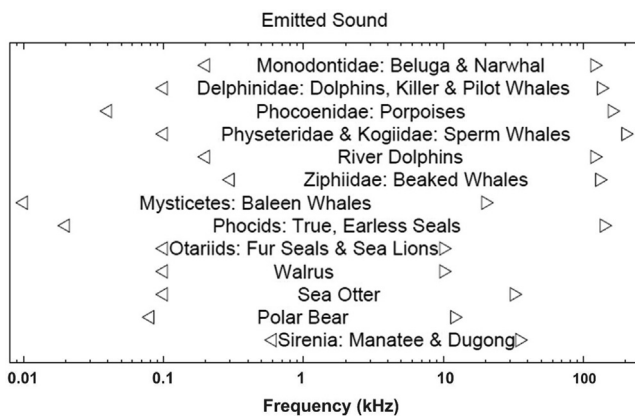


Fig. 1. Different frequency bands, including echolocation, of various marine mammals (adapted with permission from Erbe [38], based on data from Richardson et al. [45], Erbe [46], Perrin et al. [47]).

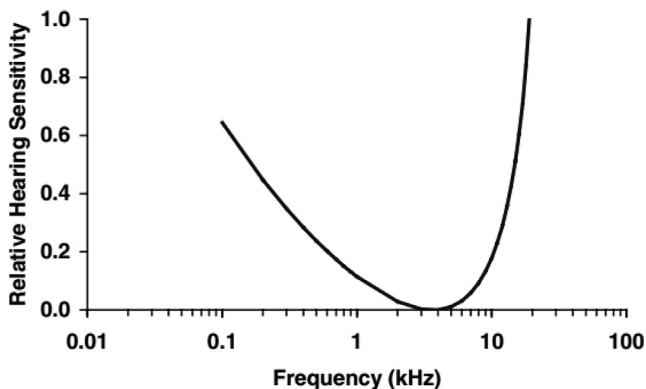


Fig. 2. Relative hearing sensitivity function determined by integrating humpback whale frequency-position functions with cat and human audiometric and anatomic data (reproduced with permission from Houser et al. [116]).

Standard measurements, such as bullae lengths/volumes and cochlear volumes, were obtained from the ears of various odontocete species. Computerized tomography (CT) scans were used to create 3D reconstructions and the relations of these variables to the respective species' hearing specificity were investigated; unfortunately, *Sousa* was not amongst the species investigated [56]. Results indicated that all measurements could be used to classify species as they all appeared to be reliable species indicators. In all species, a strong linear correlation ($r > 0.9$) was found for all the length measurements and many of the volumes, while also indicating a constant ratio between the tympanic and periotic bones. This constant ratio could be used as a morphological basis for further species-specific acoustic comparison as it implies a functional relationship between the structures and offers information on the sound reception mechanism of odontocetes [56].

To date there is little data available on the hearing of the Indian Ocean humpback dolphin (*S. plumbea*). One study investigated passive acoustic recordings of a pod of 5 wild animals from Puttalam Lagoon, Sri Lanka [70]. Vocalisations of the animals were classified as broadband click trains, whistles, grunts and burst pulses like those of several other delphinid cetaceans. The highest intensity of broadband click pulses was around 38 kHz, while the range was between 8 and >48 kHz and a range of 5.5–17 kHz was obtained for narrow banded, frequency modulated whistles. Low frequency, narrow band grunt vocalisations were also detected, with the highest intensity around 1 kHz and a range of 0.4 to 2.5 kHz. Comparisons to previous vocalisations of humpback dolphins from eastern Australian waters (*Sousa chinensis*) [71,72] showed similar patterns, except for the absence of quacks (low frequency). Another study using passive acoustic monitoring (PAM) of 4 groups of *S. plumbea* and 8 groups of *Tursiops aduncus* in Menai Bay, Zanzibar, indicated that clicks of *T. aduncus* had significantly lower peak, centroid, higher –3 and higher –10 dB frequencies compared to *S. plumbea*, whereas the two species had similar bandwidth and duration parameters [73]. This study indicates the first steps of acoustically describing and classifying *S. plumbea* and *T. aduncus* in the western Indian Ocean region while also highlighting the potential of using acoustic monitoring in future species-specific studies for identifying the temporal and spatial distribution of these sympatric species [73]. The analysis of 2260 whistles of *S. plumbea* documented off the Sindhudurg coast of Maharashtra, India, also provided a comprehensive description of humpback dolphin whistles, detailing its acoustic features and qualitative properties [74]. Seven contour classes could be categorised based on aural-visual (AV) classification; whistle durations ranged from 0.01 s to 1.60 s and spanned a broad frequency range of 2.3 to 33.0 kHz [74]. CT imaging and standard gross dissection techniques were used to describe the sound generating structures of the Indian Ocean humpback dolphin *S. plumbea*, using the Indo-Pacific bottlenose dolphin (*T. aduncus*) as a comparative model [36]. In both species, the overall arrangement of the sound generating structures, such as the air sacs and muscles, were similar. The main difference between the two species is that *S. plumbea* has a small left posterior branch of the melon that is not present in *T. aduncus*. This may reflect an adaptation that *S. plumbea* possesses for changing the direction of high frequency communication sounds which is seen in several other delphinids, such as *Lagenorhynchus* sp. and *Grampus griseus*. Additionally, the longer rostrum in *S. plumbea* might indicate a more directional echolocation beam compared to *T. aduncus* [75,76].

3.1. *Sousa chinensis*

In comparison to *S. plumbea*, more data are available for its sister-taxon *S. chinensis*. However, while hearing ranges of Delphinids are generally similar, little is known about individual

(within-species) variation (especially according to age and health status) or between populations (due to differing social structures and/or different soundscapes), with the exception of one study by Houser and Finneran [77]. Thus, a summary of the available information on vocalizations (and potential hearing capabilities) of *S. chinensis* from a series of studies of wild populations is presented by geographical region due to potential population-level differences (Table 1). Literature relating to acoustics and hearing in HF cetaceans tend to focus on the sound produced by the animal (e.g. whistles [78,79,80] and/or clicks [81]) as well as the soundscape of the habitat of the animal (e.g. Caruso et al. [82,83]; Dong et al. [84]; see Table 1).

Most studies on *S. chinensis* vocalizations and hearing originate from Chinese waters (Table 1), which is also true for the only audiogram available for the species. This data, obtained from a healthy adult animal under human care in Nanning Zoo, China, estimated to be 13 years old, may be considered as a baseline of hearing information for *S. chinensis* [34]. The audiogram (a function of hearing threshold versus stimulus frequency) of the single *S. chinensis* individual produced a U-shape depicting an area of high hearing sensitivity between approximately 20 and 120 kHz [34]. Another study of six *S. chinensis* under human care from *Under-Water World Singapore Pte. Ltd.* indicated that from 1166 whistles produced, most were for a short period (with the majority being <1 s) and of a lower frequency, with centre frequencies mostly being around 3.8 kHz [85]. Individual 'signature whistles' could not be established, but the data could be classified into 5 classes. However, this low number of whistle classes may not be surprising as members of the group exhibited family ties and were living together for several years [85].

Generally, noise components in the mid- to high-frequency ranges may have potential impacts for dolphins vocalizing in similar frequencies, such as members of the genus *Sousa*, which is of concern [86]. Information related to the characteristics of species-specific vocalizations and their related active communication space (i.e. "the effective range over which a communication signal can be detected by a conspecific", [87]) is of utmost importance in order to recognise impacts of underwater noise pollution as well as other threats [87].

4. Humpback whale (*Megaptera novaeangliae*) as a representative for mysticetes

A range of factors, such as the species, the context, the properties of the stimuli, and the former exposure of the animal, influence the behavioural responses of marine mammals to acoustic stimuli, which can vary widely [97]. Thus, odontocetes generally have a higher maximal hearing frequency and higher maximal sensitivity than mysticetes (Fig. 1). Unlike odontocetes, mysticetes cannot be held in aquaria, which makes it more difficult to obtain bioacoustic measurements, such as audiograms. Consequently, there is a lack of data on hearing for humpback whales (*M. novaeangliae*).

For odontocetes and pinnipeds, absolute detection threshold ranges from 40 to 70 dB re 1 μ Pa at the best sensitivity frequencies. It is therefore often presumed that mysticetes have comparable absolute thresholds at their best hearing frequencies [98]. Each animal can hear their own vocalisations and typically, the vocalisation frequency bandwidth coincides with the best hearing sensitivity frequency range [98]. The best sensitivity range resembles the range of recorded calls of the humpback whale. However, maximum sensitivity does not correspond with what one would assume from humpback whale calls and ear anatomy but occurs at slightly higher frequencies [98].

To gather information about hearing in mysticetes, indirect methods have been used, with one such method using vocalisation

Table 1
Summary of select literature reviewed on hearing and sound production in *S. chinensis* by geographic region.

Region	Location	Study focus	Main results	Citation
Hong Kong	Lantau Island	Vocalisations	Vocalizations described as burst pulses, broadband click trains, and narrowband frequency modulated sounds, including whistles which were generally like those of other delphinids.	Sims et al. [88]
China	Zhuhai	Echolocation clicks and hearing (via AEP's) in young (~13-year-old) and old (~40-year-old) dolphin	Echolocation clicks emitted by older dolphin had lower hearing range and lower click peak and centre frequencies compared with younger dolphin, probably due to age-related hearing loss (presbycusis).	Li et al. [34] Li et al. [37]
	Pearl River Estuary and Beibu Gulf	Whistles with active communication spaces (ACS)	Various whistle contour types exhibited significant differences in ACSs; small ACS were attributed to elevated ambient noise levels, indicating a certain degree of individual variation.	Wang et al. [87]
	Pearl River Estuary	Examination of sound scape	Dolphin sounds were mostly identified when ambient sound levels were low and when fish vocalisations were absent, leading to the suggestion of noise avoidance and passive eavesdropping by dolphins on prey.	Wang et al. [89]
	Sanniang Bay	Echolocation signals	Clicks produced were comparable to other similar body-sized whistling dolphins, with clicks being of short durations, broadband and ultrasonic pulses although source levels appear to be lower.	Fang et al. [90]
	Sanniang Bay	Apparent source level (ASL) for recordings of dolphin groups	ASL estimates in this study appear to be conservative, but comparable to other similar-sized dolphins.	Kimura et al. [91]
	Sanniang Bay	Whistle characterization	Whistles characterised by short duration, broad frequency range, and two harmonics.	Wang et al. [92]
	Zhanjiang	Whistle comparisons	Intraspecific differences were significant for all dolphin whistle duration and frequency parameters between this location and Malaysia (Hoffman et al. [93]), while whistle parameters differed significantly to those obtained from the study in Sanniang Bay, China, with the exception of start frequency, maximum frequency and harmonic counts (Wang et al. [92]). Potential geographic isolation between populations of <i>S. chinensis</i> was suggested as reason for differences.	Dong et al. [94]
Malaysia	Western Malaysian Peninsular	Whistles	The duration of the whistles was found to differ significantly between locations, which could be attributed to local soundscape adaptations.	Hoffman et al. [93]
Australia	Moreton Bay	Indirect effects of boat traffic on the acoustic behaviour (species has since been re-assigned as <i>Sousa sahalensis</i> [95])	Boat passages had no effect on vocalization rates, but dolphin whistling rates increased significantly immediately afterwards, which was not detected when boats were more than 1.5 km away from the dolphin groups. Increased whistling in response to boats was detected in groups containing mother-calf pairs, while significantly less whistling was detected by groups with no calves, suggesting that noise produced by transiting vessels altered the cohesion of the group.	Van Parijs & Corkeron [96]

data under the assumption that frequencies of vocalisations produced by animals are usually audible to conspecifics [25]. Vocalisation recordings of mysticetes carried out since 1951 by Watkins & Wartzok [99] suggested that low frequency sounds are used and heard by baleen whales. Another indirect method is the examination of ear anatomy, which allows deductions to be made about a species' hearing capabilities. Dissected ears of dead or stranded animals have also been used to study the anatomy of the baleen whale inner ear. While odontocete ears show specialisations for high frequency hearing, their absence within the inner ear of mysticetes (cochleae) were noted by Yamada & Yoshizaki [100]. Pathological examinations of the temporal bones from dead humpback whales following a 5000 kg explosion were harvested and examined using both histology and a CT scan [101]. In all four ears, authors found signs of mechanical trauma; with no indication that these results were caused by repeated barotrauma or chronic infection as there were no signs of similar abnormalities discovered in ears from control animals that were not exposed to blasts. Therefore, like other mammals, the results indicated that whales are susceptible to severe blast trauma. Ketten [49,102,103,104,105] and Ketten et al. [106] concluded that baleen whale sensitivity was highest at frequencies in the low sonic to infrasonic range (<20 Hz). Compared to the high-frequency hearing odontocetes, humpback whales have a much broader, thinner and less rigidly supported basilar membrane of the cochlea. While odontocetes have two channels of acoustic fat that direct sound to the ear [107,108], mysticetes likely also use bone to conduct

sound [109]. Odontocetes have features consistent with hearing above 150 kHz, such as basal ratios of >0.6 and bony membrane support of 20–60%, whereas acute infrasonic hearing is implied in mysticetes by the <0.002 apical ratios and the absence of bony lateral support.

The hypothesis that species can hear and distinguish vocalisations made by conspecifics is supported by playback studies even though these studies are not specifically designed to test hearing in mysticetes [110–113]. A study near Cape Cod showed that the majority of whales, including *M. novaeangliae*, reacted to sounds made by humans which ranged from 15 Hz to 28 kHz, but reactions were not detected at higher frequencies between 36 and 60 kHz [114].

Behavioural reactions of baleen whales to biological and industrial sounds were assessed in the field based on the assumption that animals react to the sounds they hear, providing absolute suprathresholds of hearing [98]. However, sounds that are barely audible may not trigger a reaction from the animals, they may only react to sounds that are louder than a certain level. Reaction thresholds may also vary due to a number of factors, some of which include the animals age, sex, and health status; the current behavioural state of the animal; its prior experience with a specific (similar or other) sound (habituation versus sensitization); the group composition (responses are more likely in groups with calves); the habitat and geographic location (close to shore versus offshore); as well as the season and the time of day [98]. Behavioural thresholds between 80 and 90 dB re 1µPa received level

from pingers at 4 kHz were the lowest behavioural thresholds reported for humpback whales (Todd et al. 1992 in Erbe [98]). Under the assumption that audibility thresholds likely lie somewhere under the response threshold, absolute sensitivity at 4 kHz may be close to the upper range of best sensitivity, possibly around 70 dB re 1 μ Pa, for other marine mammals [98].

Ambient noise levels are rather high in the ocean and this overlaps with the best hearing sensitivity frequencies of humpback whales. The ambient noise levels below 1 kHz are, on average, above 70 dB re 1 μ Pa (one-third octave band levels), even when the environment is quiet (up to Beaufort sea state 1) and there are no nearby industrial activities. Consequently, ambient noise may be the limiting factor of acoustic detection thresholds with regards to biological and industrial sounds, instead of the baleen audiogram at those frequencies [98]. Clark & Ellison [115] claim that it is likely that the oceans' historical ambient noise levels (without industrial sources like shipping) played an evolutionary role in the development of the marine mammal audiogram. The authors also assumed that the highest sensitivity in mysticetes should be at the frequency of their own vocalisations. Clark & Ellison [115] postulated that through evolutionary forces the audiogram should have been located in such a manner that the auditory systems' dynamic range would have been used most efficiently. For other mammals, the critical ratio ranges from 16 to 24 dB re 1 Hz.

Houser et al. [116], building on work by Moore et al. [117], produced a modelled audiogram for humpback whale relative hearing sensitivity using data that combined anatomical studies (basilar membranes of humpback whales), psychoacoustic records and the anatomical hearing indices from two land mammals that are well-studied (human and cat). The resulting audiogram (Fig. 2)

formed a U-shape typical of mammals, while also indicating sensitivity to frequencies that ranged from 700 Hz to 10 kHz and a maximum relative sensitivity range (values close to 0) of 2–6 kHz. The first predicted audiogram for humpback whales was developed through this integrated approach, which resulted in the first band-pass model of the humpback ear.

Using the limits of the absolute detection thresholds (i.e. 40 dB re 1 μ Pa and 70 dB re 1 μ Pa), Erbe [98] re-plotted the data in such a way that the frequency of best hearing displayed a 40 dB re 1 μ Pa minimum threshold for the first curve and a 70 dB re 1 μ Pa minimum threshold for the second curve. The humpback whale audiogram range was created under the assumption that the absolute detection thresholds of humpback whales fall within the range of other non-mysticete marine mammal species.

Further computer modelling of the audiogram of *M. novaeangliae* was developed by making use of a finite element (FE) model of the middle ear in an effort to evaluate the middle ear transfer function (METF) and calculate the transmission of acoustic energy to the cochlea [118]. An anatomically accurate model, featuring both bone and soft tissues, was produced. The resultant finite element transfer function revealed a frequency range between approximately 15 Hz and 3 kHz when the tympanic membrane was stimulated, and a range between approximately 200 Hz to 9 kHz when the thinner region of the tympanic bone next to the tympanic membrane was stimulated. The known species vocalisations corresponded well with these predicted ranges of best sensitivity hearing. Recently, Southall et al. [19] also investigated low-frequency cetaceans, producing an estimated group audiogram using extensive extrapolations and assumptions in the absence of direct data from *in vivo* hearing studies.

Table 2

Summary of select literature reviewed on hearing, vocalisations, and effects of noise exposure in *M. novaeangliae* by ocean basin.

Ocean basin	Location	Study focus	Main results	Citation
North Pacific	Hawaii	Sound playback techniques	A "rapid approach" response was the strongest reaction recorded and this reaction was initiated as far as 28 km from the source of the sound. Estimated responses to a feeding call were received at a very low broadband level (102 dB re 1 μ Pa), while synthetic sounds received responses at about 106 re 1 μ Pa.	Frankel et al. [125]
	Hawaii (in the Auau channel)	Song sounds	Variations in the maximum source level were found between individual units of song, with values ranging from 151 to 173 dB re 1 μ Pa. A high upper frequency limit of 24 kHz for hearing has been suggested for humpback whales due to the high frequency harmonics of their songs. Periods of low frequency pulses (ca. 40 Hz) were recorded. Although pulse organization varied, the average peak and centre frequencies (range of 39 to 40 Hz) as well as the bandwidths (13 Hz) were comparable between the two groups. Social sounds, bubble trains, song components, and other species were excluded as possible reasons for this sound.	Au et al. [126]
	Hawaii	Underwater recordings	Vocalizations were found to have a simple arrangement with low frequencies (mean of 220 Hz), while lasting short intervals (mean of 170 ms) and having comparatively narrow bandwidths (mean of 2 kHz). Two types of communication signals were produced: vocal and non-vocal sounds. No significant changes in the frequencies or time intervals of the two common vocal sounds were recorded when either noise type (wind or vessel) was increased. Increased wind-dominated noise caused groups to increase their vocal source levels, while replacing vocal sounds with sounds generated by surface behaviours. Groups showed neither behaviour in response to increased vessel noise. Significant correlation was found between the amount of non-vocal sounds and wind speed (and thus also wind noise), indicating that their response was specific to an increase in wind noise. Vocal source levels were lower than expected in response to vessel noise, implying possible signal masking.	Darling [127]
Southwest Pacific	Hawaii (off southwest Maui and Kauai)	Vocalisations of calves	Modelled communication space decreased with an increase in vessel noise with significantly fewer social interactions between groups (likely in response to a reduced communication network). However, this difference in social behaviour was not fully explained by signal masking, indicating that both the signaller and receiver's behaviour was also altered by some other effect caused by the physical presence of the vessel.	Zoidis et al. [128]
	Australian east coast	Behavioural observations and underwater recordings	DTAGs were used to record and define the non-song sounds produced by foraging whales with eight sound groups produced by cluster analysis, and all sounds having similar acoustic properties.	Dunlop [129]
North Atlantic	Australian east coast	Communication space measured		Dunlop [130]
	Stellwagen Bank National Marine Sanctuary	Digital Acoustic Tags (DTAGs)		Stimpert et al. [131]

Additional information on the hearing capacity of *M. novaeangliae* is summarised in Table 2. Literature relating to acoustics and hearing in LF cetaceans, such as *M. novaeangliae*, tend to focus on sound produced by the animal (e.g. song [119,120]) and behavioural studies (e.g. Thompson et al. [121]; Stimpert et al. [122]; see Table 2).

Little is known about the movement of individuals between humpback whale populations; thus, no information exists on population-level differences in vocalizations and hearing. Therefore, further information from behavioural response studies is presented by ocean basin, although there appears to be a general absence of studies examining hearing and vocalizations of humpback whales off Africa in general, both in the South Atlantic (with the exception of Cerchio et al. [123,124]) and in the Indian Ocean (Table 2).

5. Conclusion and future recommendations

Our review highlights the need to investigate hearing in two focal species from the Indian Ocean to establish baselines upon which to measure potential impact from the planned anthropogenic developments in the region.

Particularly, data on the overlap of acoustic habitats of humans and cetaceans is required [25]. For this, management of the cumulative levels of noise pollution, either through risk maps [132] and/or by modelling possible changes in the growth of the population in response to noise disturbance [133–135] are needed. In addition, information on audiograms and ear morphology for *S. plumbea* and *M. novaeangliae* is lacking. No consensus has been reached concerning the functioning of the baleen whale auditory system [25]. The hearing abilities of mysticetes have been predicted by a number of studies [136], but to date no audiograms have been established. While measuring AEPs in adult mysticetes poses challenges, the approach could potentially be employed in juvenile whales [25]. It has been suggested that practical test scenarios may be offered by situations involving stranded or entangled animals, which would not only empirically test the current auditory models for future applications to other species, but also verify mysticete sound sensitivity [25]. Additionally, further research into the perception of sound by cetaceans is required as recent results from the BRAHSS study (<https://www.brahss.org.au>) raised questions regarding unexpectedly subtle changes of humpback whales to sounds from seismic air guns. To advance our knowledge on the basic hearing abilities for *S. plumbea*, AEP's are required, and additional focus should be placed on auditory health as other factors, besides anthropogenic noise, may adversely affect hearing [137,138]. We suggest that an integrated approach of combining studies on live (e.g., AEP's in the case of odontocetes, recordings of vocalizations and behavioural observations) and dead, stranded animals (e.g., examinations of ear anatomy in both odontocetes and mysticetes) is required to obtain baselines upon which to measure impact as this is vital for good governance [139].

In view of global trends on anthropogenic underwater noise [3], the Ocean Economy developments in the Indian Ocean appear in another light. Furthermore, 'harnessing' the blue economy forms part of the larger continental discussion on sustainable development seen in the African Union's Agenda 2063 [140], where 38 out of the 54 African States are coastal [139,141]. In addition, similar Ocean Economy developments are currently underway worldwide in other ocean basins, for example, in South African waters [5], the South Atlantic [140], and in European Seas [142], aiming to be sustainable to differing degrees [7]. However, a recent review on Brazilian environmental licensing legislation indicated that none of the reviewed environmental licensing reports assessed the potential impacts of anthropogenic noise related to the con-

struction of shipping facilities and seismic activity on cetaceans [143], despite the existing evidence on the effects of this type of noise pollution justifying responsible management and environmental legislation. This is not an isolated case, as many developing countries have lax environmental legislation and/or poor law enforcement [143].

Anthropogenic ocean noise may be the most prevalent factor of all the cumulative impacts that marine mammals globally, and the Indian Ocean humpback dolphin in particular, are currently facing [3,144,145,146]. As these mammals are increasingly reflecting the overall health of our oceans [146], the Indian Ocean humpback dolphin can be viewed as a good regional indicator and flagship species for Ocean Health due to its coastal, non-migratory lifestyle and its distribution throughout the Indian Ocean, making it particularly prone to the local cumulative impacts from anthropogenic developments, including anthropogenic ocean noise [146]. This would not only increase awareness of this little known, endangered dolphin and the myriad of anthropogenic threats it faces, but it may also facilitate increased research on impacts from anthropogenic developments in the region.

CRedit authorship contribution statement

Stephanie Plön: Conceptualization, Methodology, Supervision, Writing – review & editing, Project administration, Funding acquisition. **Natasha Roussouw:** Methodology, Visualization, Writing – original draft.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Stephanie Plön reports financial support was provided by AECOM.

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