Review

Communication masking in marine mammals: A review and research strategy

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ABSTRACT

Underwater noise, whether of natural or anthropogenic origin, has the ability to interfere with the way in which marine mammals receive acoustic signals (i.e., for communication, social interaction, foraging, navigation, etc.). This phenomenon, termed auditory masking, has been well studied in humans and terrestrial vertebrates (in particular birds), but less so in marine mammals. Anthropogenic underwater noise seems to be increasing in parts of the world's oceans and concerns about associated bioacoustic effects, including masking, are growing. In this article, we review our understanding of masking in marine mammals, summarise data on marine mammal hearing as they relate to masking (including audiograms, critical ratios, critical bandwidths, and auditory integration times), discuss masking release processes of receivers (including comodulation masking release and spatial release from masking) and anti-masking strategies of signalers (e.g. Lombard effect), and set a research framework for improved assessment of potential masking in marine mammals.

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List of terms and abbreviations

Ambient noise   The background level of sound in the environment other than the signal(s) of interest (see American National Standards Institute, 2013).

Audiogram   Graph of hearing threshold level as a function of frequency (American National Standards Institute, 2008).

Auditory evoked potentials (AEP)   Electrical potential emanating from the auditory nervous system upon presentation of an acoustic stimulus. AEPs can be obtained from electrodes placed on the head (American National Standards Institute, 2008).

Auditory integration time   A measure of the time interval beyond which the detectability of a signal by an animal does not improve with increasing duration.

Comodulation masking release (CMR)   A decrease in expected masking (i.e., release) that occurs for coherently modulated sound (sound with amplitude fluctuations that are consistent across a range of frequencies).

Critical band (CB)   The frequency band of sound, being part of a continuous-spectrum noise covering a wide band, that contains sound power equal to that of a pure tone centred in the CB and just audible in the presence of the wideband noise (American National Standards Institute, 2008).

Fletcher critical band   An estimate of bandwidth computed from critical ratios (American National Standards Institute, 2008), $CB = 10^{CR/10}$. Fletcher critical bands tend to be narrower than critical bandwidths measured by more direct (e.g. white noise band widening) methods.

Critical bandwidth   The bandwidth of white noise at which the detection threshold of a tone at the centre of the white noise band ceases to increase with increasing width of the noise band. The critical bandwidth is determined in masked hearing experiments where the white noise band is progressively widened, and is commonly used as an estimate of the bandwidth of the auditory filter at the same centre frequency (Fletcher, 1940; Moore, 1995).

Critical ratio (CR)   The difference between the sound pressure level of a pure tone just audible in the presence of a continuous noise of constant spectral density and the sound pressure spectrum level for that noise expressed in dB (American National Standards Institute, 2008).

Masking   The process by which the threshold of hearing for one sound is raised by the presence of another (masking) sound; and the amount by which the threshold of hearing for one sound is raised by the presence of another (masking) sound, expressed in dB (American National Standards Institute, 2008).

Masking release   A decrease (release) from expected masking, mediated by a specific mechanism, e.g., comodulation masking release.

Noise   An unwanted disturbance within a useful frequency band (American National Standards Institute, 2013); with regards to acoustic masking, noise is the masking sound.

1/3 octave band level   Level of sound contained within a frequency band that is 1/3 of an octave wide (American National Standards Institute, 2004, 2013).

Power spectral density (PSD)   Sound power divided by bandwidth. The PSD describes how the power of a sound is distributed with frequency. In this article, it is computed as the mean square pressure within 1 Hz frequency bins and expressed in dB re 1 μPa^2/Hz.

Received level (RL)   The level of sound (e.g., in terms of SPL_{rms}) at the position of the listener (i.e., receiver).

Root-mean-square sound pressure level (SPL_{rms})   20 times the logarithm to base 10 of the root of the average (over some duration T) of the squared pressure time series,

$$SPL_{rms} = 20\log_{10}\left(\sqrt{\tfrac{1}{T}\int_T P(t)^2 dt / P_{ref}}\right), \text{ where } P_{ref} = 1 \,\mu Pa \text{ in water.}$$

Signal-to-noise ratio (SNR)   The difference between the signal level (dB) and the noise level (dB).

Source level (SL)   Level (e.g., in terms of SPL_{rms}) referenced to a distance of 1 m from a given source (expressed in dB re 1 μPa at 1 m). Because many anthropogenic underwater sources have dimensions greater than 1 m, the sound spectrum is typically measured in the far field, and a sound propagation model applied to compute what the spectrum would have been at 1 m if the source could have been collapsed into a point source. Source levels determined this way are also called far-field equivalent source levels, as they are useful to predict the received level in the far field (in combination with appropriate sound propagation models), but do not adequately describe (in fact, overestimate) the received level near the source.

Spatial release from masking (SRM)   A decrease (release) from expected masking that occurs when signal and noise sources are located at different positions.

Within-valley listening   A decrease (release) from expected masking that occurs when a listener detects the presence of a target signal within quieter gaps in fluctuating background noise; also known as dip listening.

1. Introduction

Sound plays an important role in the lives of marine mammals. All marine mammal species produce sound, and sound production has been associated with a variety of behaviours including those related to mating, rearing of young, social interaction, group cohesion, and feeding. For example, dolphin sounds specific to social interactions, courtship, agonistic behaviour, travel and foraging have been identified (Díaz López, 2011; Dudzinski, 1996; Herzing, 1996). The songs of fin whales (*Balaenoptera physalus*, Croll et al., 2002), bowhead whales (*Balaena mysticetus*, Johnson et al., 2015) and humpback whales (*Megaptera novaeangliae*) play a role in mating (Darling et al., 2006; Payne and McVay, 1971; Winn and Winn, 1978). Mother-and-pup recognition calls have been described in seals, sea lions, and walrus (Charrier et al., 2010; Insley et al., 2003). Bottlenose dolphins (*Tursiops truncatus*) use signature whistles identifying individuals (Caldwell and Caldwell, 1965; Janik and Sayigh, 2013). Killer whales (*Orcinus orca*, Ford, 1989, 1991) and sperm whales (*Physeter macrocephalus*, Weilgart and Whitehead, 1997) have dialects by which populations living in the same geographic region can be told apart. Communication is crucial in cultural social learning (Noad et al., 2000; Rendell and Whitehead, 2003) in some marine mammal species. Odontocete cetaceans have a biosonar system (Au, 1993), producing high-frequency clicks and utilizing their returning echoes to find and identify swimming prey and discern environmental structure. Furthermore, there is evidence that marine mammal species—with and without specialized biosonar capabilities—rely on biological sounds to find prey and to avoid predators (Cure et al., 2013; Deecke et al., 2002; Gannon et al., 2005), and likely use environmental sounds to support spatial orientation and navigation in three-dimensional marine habitats. Underwater noise, whether of natural or anthropogenic origin, may interfere with the abilities of marine mammals to receive and process relevant sounds

and could potentially impact individual fitness. Thus, noise-generating activities in marine mammal habitats, including those related to oil and gas exploration and production, military operations, and transportation, require careful consideration with respect to their possible auditory effects.

Of all the ways in which noise can affect the lives of marine mammals, auditory masking is perhaps the most pervasive. Masking occurs when the ability to detect or recognise a sound of interest is degraded by the presence of another sound (the masker). Quantitatively, masking refers to the amount in decibels by which an auditory detection threshold is raised in the presence of a masker (American National Standards Institute, 2013). While masking is a common, if not universal, feature of natural communication systems, predicting masking is difficult given the variety of factors that must be accounted for.

Fig. 1 illustrates the factors that play a role in acoustic communication in natural environments. The sender emits a call with certain spectral characteristics at a given source level. This call travels through the underwater habitat, where it experiences propagation losses, including scattering and absorption. The acoustic characteristics of the call that the listening animal receives depend on the location of both the sender and the receiver, as well as the propagation environment. The ocean is naturally noisy with sounds from physical sources such as wind, waves, ice, precipitation, and earthquakes, and biological sources such as snapping shrimp, chorusing fish, and singing whales. Anthropogenic operations further add to underwater noise. At the location of the listening individual, noise—whether of anthropogenic or natural origin—can mask the sender's signal. Apart from the spectral characteristics of signal and noise at the receiver's location, certain characteristics of the listener's auditory system also affect the potential for and the degree of masking. These auditory features include the absolute sensitivity of the auditory system, the frequency tuning, temporal integration of acoustic energy, and various kinds of masking release that are known to occur. Further, the perception of noise can elicit anti-masking responses in the sender, who may alter vocal behaviour by changing calling parameters such as level, repetition rate, or frequency—collectively known as a Lombard effect (Lombard, 1911). Not only acoustic communication is at risk of masking (as in the present example), but also echolocation and the detection of environmental, predator and prey sounds.

Masking is a complex phenomenon and masking levels are difficult to predict for any particular combination of sender, environment, and receiver characteristics. There is no species for which a complete masking model exists; however, certain models have proven to be effective for some species in many listening situations. More research is needed to understand the process of masking, the risk of masking by various anthropogenic activities, the biological significance of masking, and anti-masking strategies, before masking can be incorporated into regulation strategies or approaches for mitigation. In this review article, we focus on auditory masking under water (as opposed to in air, which would also be important for the amphibious marine mammals that spend significant time on land), discuss our understanding of masking in marine mammals, highlight information gaps, and present a research strategy to fill these gaps.

2. The power spectrum model of masking

Fletcher (1940) described hearing experiments with humans in which a pure tone was masked by broadband white noise of varying bandwidth. For narrow bands of noise centred at the tone frequency, masking increased with increasing noise bandwidth. For wide bands of noise, masking was independent of noise bandwidth. The bandwidth at which this trend changed was termed the *critical bandwidth*, and was conceptually related to the width of auditory filters operating within the listener's auditory system. Noise within the critical bandwidth was assumed to be able to mask a signal at its centre; noise outside the critical bandwidth was not. Based on these early experiments, the power spectrum model of masking was developed (Moore, 1995). In this model, the auditory periphery of a listener acts as a series of overlapping bandpass filters. When attempting to detect a signal in noise, the listener attends to the filter that encompasses the signal, or to the filter that has the highest signal-to-noise ratio (SNR). The SNR is computed as the ratio of time-averages of signal and noise power. According to the power spectrum model of masking, above a certain SNR, the signal can be reliably detected, but below this SNR, it cannot.

Given observations with human listeners, Fletcher (1940) postulated that at detection threshold, the SNR was equal to 0 dB; i.e., the signal power equalled the noise power within the critical band (CB). This is called the *equal-power assumption*. Fletcher (1940) further proposed to approximate the shape of the auditory filter as rectangular, in which case the width of the CB could be computed as the ratio of the power of the tonal signal P_t and the power per Hertz (power spectral density) of the broadband white noise PSD_n at the threshold of detection. This ratio, expressed in logarithmic terms, is called the *critical ratio* (CR). It is the difference between the tonal signal sound pressure
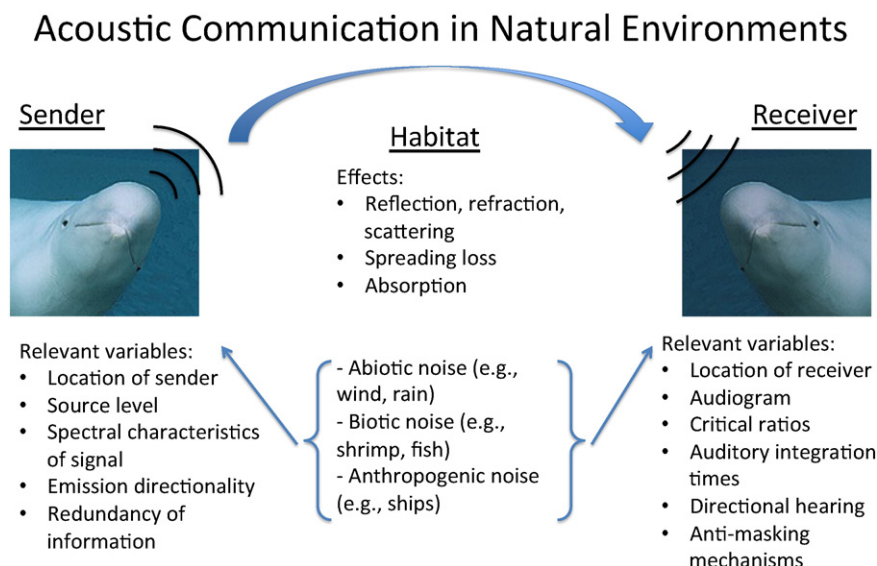

Fig. 1. Factors of the habitat, sender and receiver, which are relevant to effective acoustic communication in marine environments.

level and the surrounding noise power spectral density level at detection threshold.

In Fig. 2, the frequency spectrum of a 1 kHz tone is shown, together with the spectrum of masking noise. To be more 'realistic', the tone does not have infinite sharpness, but rather a 3 dB (half-power) width of 3 Hz, and the noise PSD has some 'jitter'. The CR of the listener in this illustration is 20 dB; i.e., at detection threshold, the power level of the tone is 20 dB above the PSD level of the noise. Assuming rectangular shape of the auditory filter and equal power (at detection threshold) of tone and noise within the auditory filter surrounding the tone (Fletcher, 1940), one estimate of the width of the filter can be computed as $CB = 10^{CR/10} = 10^2 = 100$ Hz, in this case extending from 950 to 1050 Hz. The CB computed this way (i.e. from CR) is also called the Fletcher critical band. We now know that a number of early assumptions including the shape of the filter and the equal-power assumption were incorrect. For humans, critical bandwidths measured directly via progressive noise band-widening experiments are about 2.5 times the Fletcher critical band. For animals, the situation is more challenging as the relationships between CR and CB estimates can vary greatly by species (e.g. Yost and Shofner, 2009). Nevertheless, the concept of a band of frequencies over which the ear sums energy is very helpful in understanding masking. This is because it provides a guide to the size of the band over which one should calculate a received SNR.

The power spectrum model of masking, combined with the CR concept as illustrated in Fig. 2, has been used to predict masking levels of noise for several vertebrate species (e.g., Cunningham et al., 2014b; Dooling et al., 2013; Erbe, 2002; Erbe and Farmer, 2000a, 2000b; Jensen et al., 2009). The general approach is to measure the noise PSD in a band surrounding the signal of interest, and add the CR to reach the predicted level where the signal would be just detectable. In cases where the relevant bandwidth of the surrounding noise is not known, one-third octave bands are commonly used to estimate the noise power within a given signal. While this approach is effective at predicting the masking potential of many noise types, there are exceptions.

There are several known natural listening situations in which the amount of masking produced by continuous background noise is actually less than predicted by the power spectrum model of masking—in other words, a release from masking occurs that makes a signal easier for a listener to separate from noise (e.g., Branstetter and Finneran, 2008; Cunningham et al., 2014b; Holt and Schusterman, 2007). The two best-studied forms of masking release are spatial release from

Fig. 2. Illustration of Fletcher's (1940) equal-power assumption. The listener receives a 1 kHz tone of 130 dB re 1 μPa root-mean-square sound pressure level (SPLrms) in the presence of white masking noise of 110 dB re 1 μPa²/Hz power spectral density (PSD). The listener's critical ratio (CR) is 20 dB at 1 kHz. In the illustrated example, the tone is predicted to be just at the detection threshold, because its level is one CR above the noise PSD level. Assuming rectangular filters of width $CB = 10^{CR/10}$, the band levels of tone and noise are equal at detection threshold (equal-power assumption). The orange box indicates the width of the band (CB) and the band level.

masking (SRM) and comodulation masking release (CMR). In SRM, the signal and the noise arrive at the listener from different directions, and directional hearing abilities enhance the listener's ability to detect and process the signal. In CMR, the noise is amplitude modulated across multiple frequency bands, and the listener can correlate information from multiple bands to help determine when the signal occurs (Hall et al., 1984). Further, in the case of intermittent or pulsed noise, the power spectrum model is insufficient, as it does not account for any temporal variability within signal and noise and associated masking release through within-valley or "dip" listening during minima in the noise.

Given some fundamental concepts like the source-path-receiver framework (Fig. 1), and the power spectrum model of masking including CRs and critical bandwidths (Fig. 2), the challenges and complexities associated with predicting the masking effects of underwater noise can be more thoughtfully considered. The following two sections of this article (Sections 3 and 4) discuss key biological aspects of marine mammals—as they relate to masking—in more detail. These include the auditory characteristics of the listeners themselves, and the auditory and behavioural strategies that the animals may employ to counter the masking effects of noise.

3. Hearing characteristics relevant to masking

Sounds are processed within listeners' auditory systems, which vary in structure and function across marine mammal species. Among the many parameters used to describe hearing capabilities, three are particularly relevant to assessing the potential for masking in a given species. These are the absolute sensitivity of the auditory system, the frequency tuning characteristics of the system, and the manner in which acoustic energy is processed over time.

3.1. Absolute hearing sensitivity: the audiogram

A signal that is undetectable to a listener in quiet conditions cannot be masked. Similarly, a noise that is not detectable in quiet or ambient noise conditions can be ignored as a potential masker. An audiogram can be used to estimate whether an animal will be able to hear a given sound based on the measured hearing capabilities of the species. The audiogram is composed of a series of detection thresholds for narrowband signals obtained across a range of sound frequencies, and is generally depicted as a continuous sensitivity curve. Mammalian audiograms exhibit a characteristic U-shape, with a frequency region of best sensitivity that rolls off at distal frequencies, both lower and higher (Masterton et al., 1969). In practice, audiograms are measured in quiet conditions, i.e., conditions that allow the absolute (best) sensitivity of the auditory system to be measured without interference from noise. While such conditions rarely exist in nature, this approach allows the hearing sensitivity of different types of animals to be directly compared.

Audiograms are obtained from individuals using either behavioural or neurophysiological methods. Behavioural hearing thresholds are measured from captive marine mammals trained to report the detection of auditory cues, while physiological hearing thresholds are estimated from auditory evoked potentials (AEPs) recorded from the nervous system. Behavioural audiograms provide reliable information about the sounds an individual can perceive. However, obtaining hearing data using behavioural methods is time and resource intensive, limiting studies to small sample sizes and species that can be trained and studied in captivity. Physiological audiograms do not actually describe the sounds an individual animal can perceive, but they do provide a neurological correlate to hearing that can be expressed as auditory thresholds. Physiological measurements tend to yield supra-threshold estimates of hearing (e.g., Houser and Finneran, 2006; Mulsow and Reichmuth, 2010; Schlundt et al., 2007; Szymanski et al., 1999; Wolski et al., 2003; Yuen et al., 2005), but these data can be obtained more quickly and
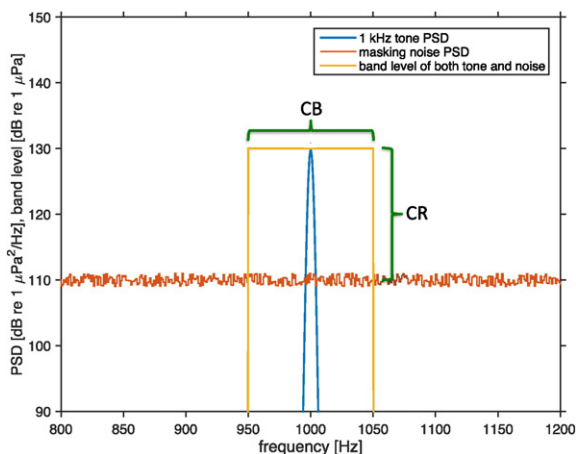
from untrained, uncooperative, or temporarily restrained subjects. AEP data are easiest to measure from odontocetes, which show hypertrophy of the auditory system and best sensitivity to high-frequency sounds that are not commonly significant components of external (background) noise or internal (biological) noise. AEPs are most difficult to obtain from large animals with low-frequency hearing sensitivity such as elephant seals (Houser et al., 2008a), and presumably, mysticete whales. At low frequencies, AEPs show large discrepancies with behavioural hearing data and AEPs are generally not used to obtain reliable hearing thresholds below ~10 kHz in odontocetes (Mooney et al., 2012; Supin et al., 2001), or below ~1 kHz in pinnipeds (Mulsow et al., 2012b). While hearing thresholds obtained using behavioural and physiological methods are not interchangeable—especially for non-odontocete marine mammals and low-frequency sounds—both can provide useful information about marine mammal hearing (Mooney et al., 2012).

Hearing measurements from multiple individuals can be combined to estimate species-typical audiograms (Fig. 3) that are useful to determine the masking potential of different types of noise. It is important to note that while such audiograms can be incorporated into masking models, they do not accurately represent the hearing abilities of all conspecifics. Hearing sensitivity may differ even among similar individuals of a given species. For example, the audiograms of 14 relatively young (3–15 year-old) bottlenose dolphins tested with neurophysiological

methods under similar conditions varied by up to 10 dB (Popov et al., 2007). Further, as with humans, hearing demographics are influenced by both age and sex. Younger animals have better hearing sensitivity, while older individuals exhibit presbycusis, or age-related hearing loss. Presbycusis has been shown in cross-sectional studies of bottlenose dolphins, progressing from high to low frequencies, and being worse in males than females (Brill et al., 2001; Houser et al., 2008b). Longitudinal studies of single individuals also reveal progressive hearing loss that follows similar patterns (Brill et al., 2001; Finneran and Schlundt, 2010; Kloepper et al., 2010; Schusterman et al., 2002). Hearing loss occurs frequently in wild as well as captive individuals, and can be explained by advancing age (Mulsow et al., 2011b; Ridgway and Carder, 1997), disease processes (Ketten et al., 2001), and congenital defects (Mulsow et al., 2011b; Reichmuth and Ghoul, 2012; Ridgway and Carder, 1997). In the case of some captive marine mammals, hearing loss may also be attributed to the administration of ototoxic medications (Finneran et al., 2005). For this reason, behavioural audiograms of young, healthy individuals should be used when generating representative audiograms for marine mammal species, and wherever possible, data from multiple individuals should be considered.

Another factor that may influence hearing sensitivity is depth for diving animals. While most audiograms are measured in relatively shallow water, hearing sensitivity may change as a function of depth. Hearing sensitivity generally worsened with depth in a diving California
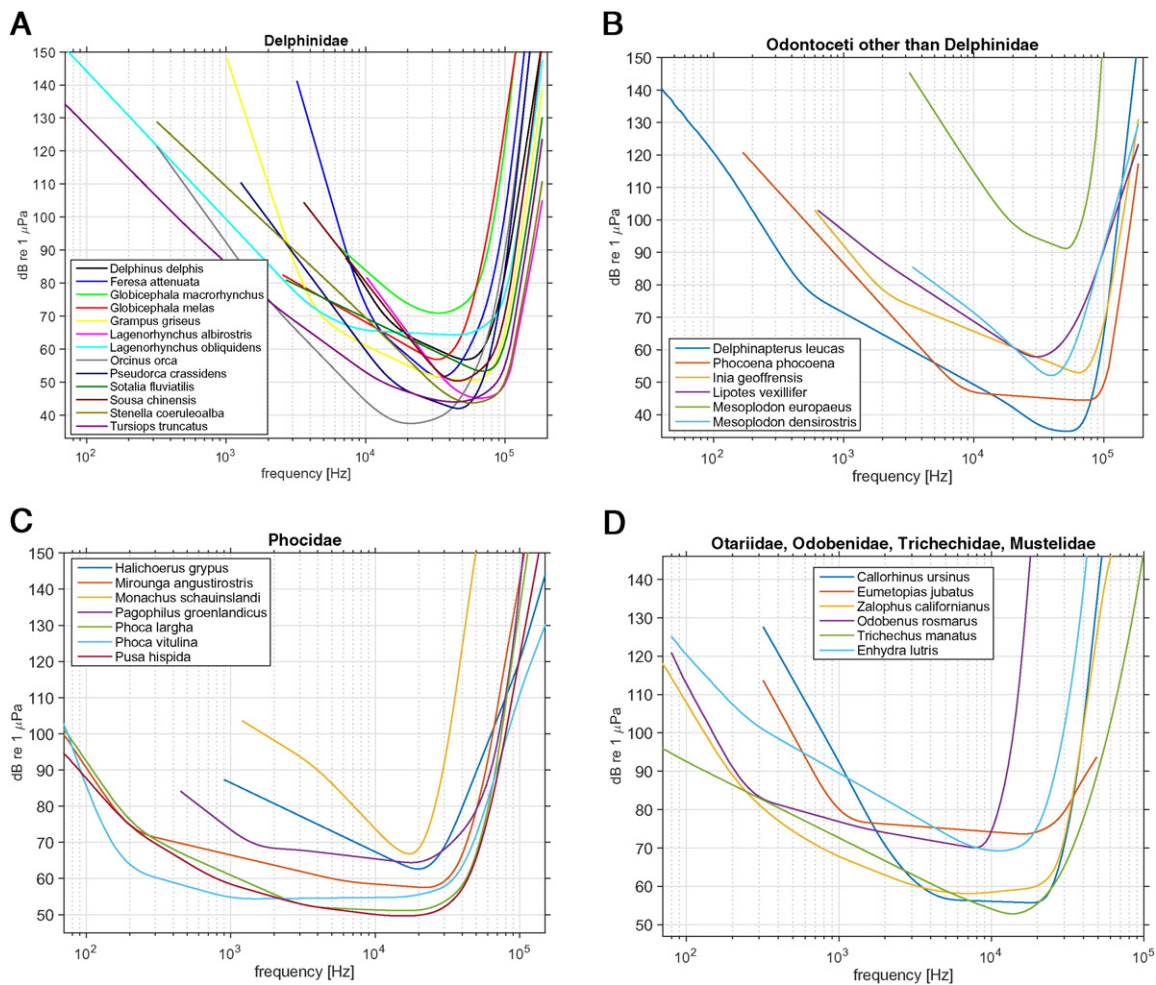
Fig. 3. Minimum underwater audiogram levels measured for various marine mammal species. For each species, measured hearing thresholds were pooled from all individuals and both AEP and behavioural methods (based on the underwater studies cited in Table 1). A mostly convex curve was fitted through the minimum hearing thresholds requiring exactly one stationary point (a single local extremum that is the absolute minimum) and allowing for maximally one inflection point (where the curvature changes towards the lower frequencies, see e.g. Hawaiian monk seal (*Monachus schauinslandi*)). Note that for most species, sample sizes are small, and for some species only AEP data are available. Auditory thresholds below 1 kHz are not often available, but all marine mammals are likely to hear below 1 kHz.

Table 1
Audiogram data is available for the following species.

Family Delphinidae		
Common dolphin (*Delphinus delphis*)	Popov and Klishin (1998)	5–150 kHz (physiological, water)
Pygmy killer whale (*Feresa attenuata*)	Montie et al. (2011)	5–120 kHz (physiological, water)
Short-finned pilot whale (*Globicephala macrorhynchus*)	Greenhow et al. (2014)	5–120 kHz (physiological, water)
	Schlundt et al. (2011)	5–160 kHz (physiological, water)
Long-finned pilot whale (*Globicephala melas*)	Pacini et al. (2010)	4–100 kHz (physiological, water)
Risso's dolphin (*Grampus griseus*)	Nachtigall et al. (1995)	1.6–110 kHz (behavioural, water)
	Nachtigall et al. (2005)	4–150 kHz (physiological, water)
	Mooney et al. (2015)	4–150 kHz (physiological, water)
White-beaked dolphin (*Lagenorhynchus albirostris*)	Nachtigall et al. (2008)	16–215 kHz (physiological, water)
Pacific white-sided dolphin (*Lagenorhynchus obliquidens*)	Tremel et al. (1998)	0.75–150 kHz (behavioural, water)
Killer whale (*Orcinus orca*)	Hall and Johnson (1972)	0.5–31 kHz (behavioural, water)
	Szymanski et al. (1999)	1–100 kHz (behavioural, water)
		1–100 kHz (physiological, water)
False killer whale (*Pseudorca crassidens*)	Thomas et al. (1988)	2–85 kHz (behavioural, water)
	Yuen et al. (2005)	4–45 kHz (physiological, water)
Tucuxi (*Sotalia fluviatilis*)	Liebschner et al. (2005)	2–31.5 kHz (behavioural, air)
	Sauerland and Dehnhardt (1998)	4–135 kHz (behavioural, water)
Indo-Pacific humpback dolphin (*Sousa chinensis*)	Li et al. (2012)	5.6–152 kHz (physiological, water)
Striped dolphin (*Stenella coeruleoalba*)	Kastelein et al. (2003)	0.5–160 kHz (behavioural, water)
Bottlenose dolphin (*Tursiops truncatus*)	Brill et al. (2001)	10–120 kHz (behavioural, water)
	Finneran and Houser (2006)	10–150 kHz (behavioural, water)
		10–150 kHz (physiological, water)
	Finneran and Houser (2007)	10–40 kHz (physiological, water)
	Finneran et al. (2008)	10–160 kHz (physiological, water)
	Finneran et al. (2010)	1–160 kHz (behavioural, water)
	Finneran and Schlundt (2007)	1–100 kHz (behavioural, water)
	Houser and Finneran (2006)	10–150 kHz (behavioural, water)
		10–150 kHz (physiological, water)
	Houser et al. (2008b)	10–180 kHz (physiological, water)
	Johnson (1966)	0.075–150 kHz (behavioural, water)
	Ljungblad et al. (1982)	2–135 kHz (behavioural, water)
	Popov and Supin (1990a)	5–150 kHz (physiological, water)
	Popov et al. (2007)	8–152 kHz (physiological, water)
	Schlundt et al. (2007)	10–150 kHz (behavioural, water)
		10–150 kHz (physiological, water)
	Turl (1993)	0.05–0.3 kHz (behavioural, water)
Family Monodontidae		
Beluga whale (*Delphinapterus leucas*)	Awbrey et al. (1988)	0.125–8 kHz (behavioural, water)
	Castellote et al. (2014)	4–150 kHz (physiological, water)
	Erbe and Farmer (1998)	0.5–10 kHz (behavioural, water)
	Finneran et al. (2002b)	0.4–30 kHz (behavioural, water)
	Finneran et al. (2005)	2–130 kHz (behavioural, water)
	Johnson et al. (1989)	0.04–125 kHz (behavioural, water)
	Klishin et al. (2000)	8–128 kHz (physiological, water)
	Mooney et al. (2008)	8–128 kHz (physiological, water)
	Popov and Supin (1990b)	15–110 kHz (physiological, water)
	Ridgway et al. (2001)	0.5–100 kHz (behavioural, water)
	White et al. (1978)	1–130 kHz (behavioural, water)
Family Phocoenidae		
Harbour porpoise (*Phocoena phocoena*)	Andersen (1970a)	1–150 kHz (behavioural, water)
	Kastelein et al. (2010a)	0.25–160 kHz (behavioural, water)
	Kastelein et al. (2002a)	0.25–180 kHz (behavioural, water)
	Kastelein et al. (1997)	0.5–4 kHz (behavioural, air)
Family Iniidae		
Amazon river dolphin (*Inia geoffrensis*)	Jacobs and Hall (1972)	1–105 kHz (behavioural, water)
	Popov and Supin (1990b)	8–130 kHz (physiological, water)
Family Lipotidae		
Chinese river dolphin (*Lipotes vexillifer*)	Wang et al. (1992)	1–200 kHz (behavioural, water)
Family Ziphiidae		
Blainville's beaked whale (*Mesoplodon densirostris*)	Pacini et al. (2011)	5.6–160 kHz (physiological, water)
Gervais' beaked whale (*Mesoplodon europaeus*)	Cook et al. (2006)	20–160 kHz (physiological, water)
	Finneran et al. (2009)	5–80 kHz (physiological, water)
Family Phocidae		
Grey seal (*Halichoerus grypus*)	Ridgway and Joyce (1975)	2–150 kHz (physiological, water)
	Ruser et al. (2014)	1–20 kHz (physiological, air)
Leopard seal (*Hydrurga leptonyx*)	Tripovich et al., 2011	1.0–4 kHz (physiological, air)
Northern elephant seal (*Mirounga angustirostris*)	Kastak and Schusterman (1998)	0.1–6.4 kHz (behavioural, air)
		0.075–6.3 kHz (behavioural, water)
	Kastak and Schusterman (1999)	0.075–20 kHz (behavioural, air)
		0.075–55 kHz (behavioural, water)
	Reichmuth et al. (2013)	0.1–32.5 kHz (behavioural, air)
Hawaiian monk seal (*Monachus schauinslandi*)	Thomas et al. (1990a)	2–48 kHz (behavioural, water)

Table 1 (continued)

Family Phocidae		
Harp seal (*Pagophilus groenlandicus*)	Terhune and Ronald (1971)	1–32 kHz (behavioural, air)
	Terhune and Ronald (1972)	0.76–100 kHz (behavioural, water)
Spotted seal (*Phoca largha*)	Sills et al. (2014)	0.075–51.2 kHz (behavioural, air)
		0.1–72.4 kHz (behavioural, water)
Harbour seal (*Phoca vitulina*)	Kastak and Schusterman (1998)	0.1–6.4 kHz (behavioural, air)
		0.075–6.4 kHz (behavioural, water)
	Kastelein et al. (2009a)	0.2–80 kHz (behavioural, water)
	Kastelein et al. (2009c)	0.125–100 kHz (behavioural, water)
	Mohl (1968a)	1–22.5 kHz (behavioural, air)
		1–180 kHz (behavioural, water)
	Terhune (1988)	1–64 kHz (behavioural, water)
	Terhune (1989)	1–16 kHz (behavioural, air)
	Terhune (1991)	0.1–16 kHz (behavioural, air)
	Wolski et al. (2003)	0.25–30 kHz (behavioural, air)
		2–22 kHz (physiological, air)
	Reichmuth et al. (2013)	0.1–32.5 kHz (behavioural, air)
		12.8–72.408 kHz (behavioural, water)
	Cunningham et al. (2014a)	69 kHz (behavioural, water)
Caspian seal (*Pusa caspica*)	Babushina (1997)	0.5–20 kHz (behavioural, air)
		1–40 kHz (behavioural, water)
Ringed seal (*Pusa hispida*)	Terhune and Ronald (1975)	0.1–90 kHz (behavioural, water)
	Sills et al. (2015)	0.1–72.4 kHz (behavioural, water)
		0.075–51.2 kHz (behavioural, air)
Family Otariidae		
Northern fur seal (*Callorhinus ursinus*)	Babushina et al. (1991)	0.1–25 kHz (behavioural, air)
		0.5–40 kHz (behavioural, water)
	Moore and Schusterman (1987)	0.5–32 kHz (behavioural, air)
		0.5–42 kHz (behavioural, water)
Steller sea lion (*Eumetopias jubatus*)	Kastelein et al. (2005b)	0.5–32 kHz (behavioural, water)
	Mulsow et al. (2011b)	1–32 kHz (physiological, air)
	Mulsow and Reichmuth (2010)	1–32 kHz (physiological, air)
		0.125–34 kHz (behavioural, air)
California sea lion (*Zalophus californianus*)	Reichmuth et al. (2013)	0.1–32.5 kHz (behavioural, air)
		0.1–43.054 kHz (behavioural, water)
	Finneran et al. (2011)	0.5–32 kHz (physiological, air)
	Kastak and Schusterman (1998)	0.1–6.4 kHz (behavioural, air)
		0.075–6.4 kHz (behavioural, water)
	Kastak and Schusterman (2002)	2.5–35 kHz (behavioural, water)
	Moore and Schusterman (1987)	1–32 kHz (behavioural, air)
	Mulsow et al. (2011a)	2–32 kHz (physiological, air)
	Mulsow et al. (2012a)	1–38 kHz (behavioural, water)
	Mulsow et al. (2014)	0.5–32 kHz (physiological, air)
	Mulsow et al. (2011b)	0.5–32 kHz (physiological, air)
	Schusterman (1974)	4–32 kHz (behavioural, air)
	Schusterman et al. (1972)	0.25–64 kHz (behavioural, water)
	Reichmuth and Southall (2012)	6.4–37.2 kHz (behavioural, water)
	Cunningham et al. (2014a)	69 kHz (behavioural, water)
Family Odobenidae		
Walrus (*Odobenus rosmarus*)	Kastelein et al. (1996)	0.125–8 kHz (behavioural, air)
	Kastelein et al. (2002b)	0.125–15 kHz (behavioural, water)
	Kastelein et al. (1993)	0.25–4 kHz (behavioural, air)
Family Trichechidae		
Brazilian manatee (*Trichechus inunguis*)	Klishin et al. (1990)	5.0–70 kHz (physiological, air)
West Indian manatee (*Trichechus manatus*)	Bullock et al. (1982)	0.75–40 kHz (physiological, air)
	Gaspard et al. (2012)	0.25–90.5 kHz (behavioural, water)
	Gerstein et al. (1999)	0.4–46 kHz (behavioural, water)
	Popov and Supin (1990b)	5–160 kHz (physiological, water)
Family Ursidae		
Polar bear (*Ursus maritimus*)	Nachtigall et al. (2007)	1–22.5 kHz (physiological, air)
	Owen and Bowles (2011)	0.125–31.5 kHz (behavioural, air)
Family Mustelidae		
Sea otter (*Enhydra lutris*)	Ghoul and Reichmuth (2014)	0.125–40 kHz (behavioural, air & water)

sea lion (*Zalophus californianus*) (Kastak and Schusterman, 2002) but remained mostly unchanged in beluga whales (*Delphinapterus leucas*) (Ridgway et al., 2001). More information is needed about diving and hearing in marine mammals, but until such information is available, auditory thresholds measured in relatively shallow water are used to predict hearing at all depths in the water column.

Audiograms obtained in acoustically controlled conditions are available for a limited number of marine mammal species. The most reliable data are from representative species that have been routinely studied in captivity, including the bottlenose dolphin, beluga whale, California sea lion, and harbour seal (*Phoca vitulina*). While individuals of several species within the Family Delphinidae have been tested (Fig. 3, Table 1), audiograms for over 20 delphinid species are still lacking. Out of the Family Monodontidae, comprising the beluga whale and the narwhal (*Monodon monoceros*), the latter remains to be tested. Out of the Family Phocoenidae, only the harbour porpoise (*Phocoena*

phocoena) and none of the other six species have had an audiogram measured. Also, some of the river dolphin species are untested. Only two beaked whale species have been accessible (using AEP methods only), with the hearing abilities of nearly 20 other beaked whale species unknown. In the case of pinnipeds, eight of 18 phocid species and three of 14 otariid species have been studied. There is no audiogram for the West African manatee (*Trichechus senegalensis*), the marine otter (*Lutra felina*), or sperm whales (Families Physeteridae and Kogiidae), nor any of the mysticete whales (Families Balaenidae, Neobalaenidae, Balaenopteridae, and Eschrichtiidae), although multiple attempts have been made to model mysticete hearing sensitivity based on anatomy and physiology (e.g., Cranford and Krysl, 2015; Houser et al., 2001; Tubelli et al., 2012).

Table 1 provides citations to studies reporting audiometric data for marine mammals. Note that while most studies of odontocete hearing have emphasized the reception of waterborne sounds, two studies have measured sensitivity to sounds received in air (Kastelein et al., 1997; Liebschner et al., 2005). In contrast, the hearing of some pinnipeds and the sea otter (*Enhydra lutris*) has been examined for both airborne and waterborne sounds. A few of the amphibious carnivores (pinnipeds, polar bear) have only been tested in one of the two media (air or water). It is important to consider that hearing sensitivity measures, including the frequency range over which sounds are audible, are strongly influenced by the media through which sounds are transmitted to the receiving animal. Therefore, audiograms can only be applied for the medium in which they were obtained (Reichmuth et al., 2013).

Table 1 also provides the frequency ranges over which audiometric data have been measured for each marine mammal species. Of note here is the observation that behavioural studies of most pinnipeds and some odontocete cetaceans extend on the low end to a few hundred Hz, while AEP audiograms are typically constrained above 5–10 kHz for odontocete cetaceans, and above 1 kHz for pinnipeds. This is due to methodological constraints associated with testing trained animals in pools, and conducting AEP measurements at relatively low frequencies. The lack of low-frequency hearing data available for many marine mammals does not imply that low-frequency sounds are inaudible to these animals. Rather, it is likely that most—if not all—marine mammals can hear sounds extending below 100 Hz. The more gradual low-frequency roll-off visible in all the audiograms (see e.g., bottlenose dolphin) indicate that hearing sensitivity declines below the range of best sensitivity into frequency regions lower than those commonly tested. This is an important consideration for masking studies given the prevalence of low-frequency sound sources and natural contributors to ambient noise.

Hearing thresholds used to construct audiograms are typically obtained for narrowband (tonal) signals in order to provide frequency-specific measures of sensitivity. However, animal signals and anthropogenic sounds tend to have energy distributed over wider frequency bands. A few studies have used behavioural auditory testing methods to directly measure detection thresholds for specific broadband and complex sounds, e.g., from sonars (Kastelein et al., 2011a, b), acoustic deterrents (Kastelein et al., 2014), acoustic tags (Cunningham et al., 2014a), oceanographic experiments (Au et al., 1997), construction noise including pile driving (Kastelein et al., 2012, 2013a, b), and conspecific calls (Erbe and Farmer, 1998). Comparisons of detection thresholds measured for complex sounds to audiograms generated with simple tones indicate that audiograms cannot always predict the audibility of complex sounds (Cunningham et al., 2014b; Erbe and Farmer, 1998), especially when they have strong broadband or harmonic components.

3.2. Frequency tuning: critical bands and critical ratios

In mammals, the auditory periphery functions in a manner similar to a series of bandpass filters that separate a sound into its individual frequency components for higher level processing. The bandwidth and shape of these filters (i.e., the sharpness of frequency tuning), largely determine a listener's ability to extract acoustic signals from coincident noise. This is because a filter with a narrower bandwidth can improve the SNR by removing noise energy that extends beyond the signal frequency. For example, the narrower auditory filters in beluga whales likely explain why a beluga whale consistently outperformed a bottlenose dolphin during biosonar target detection tasks in various levels of broadband noise (Turl et al., 1987). Knowledge of the frequency tuning of the auditory system is therefore essential for masking models.

Frequency tuning is most often quantified using the key metrics of critical bandwidths and critical ratio (CR). Critical bandwidths provide a direct estimate of the width of an auditory filter and are traditionally measured using experiments that progressively alter the frequency bandwidth of noise surrounding a given signal (Fletcher, 1940; Moore, 1995). Within such an experimental paradigm, the detection threshold for a tone embedded in broadband noise is measured as a function of noise bandwidth. As the noise bandwidth is progressively increased, the threshold gradually increases. The slope of threshold increase, however, eventually decreases and approaches zero. At this point, further widening the noise band no longer increases the threshold. Fitting two lines (an upward sloping one through the smaller bandwidths and a horizontal one through the larger bandwidths) identifies a break point at their intersection. This break point is used to approximate the critical bandwidth. Critical bandwidths typically vary with signal frequency, and tend to widen as signal frequency increases.

Directly measuring critical bandwidths is challenging and time-intensive, particularly with marine mammals. The CR is logistically easier to measure and provides an indirect and rough measure of the listening bandwidth (Scharf, 1970). To review, the CR is the difference between the sound pressure level of a tonal signal at detection threshold and the power spectral density level of a coincident flat-spectrum masker that encompasses the tone frequency. Under Fletcher's equal-power-assumption, the Fletcher CB at a given frequency is computed from the corresponding CR: $CB = 10^{CR/10}$. While it is convenient to estimate critical bandwidths from CR data in this manner, Fletcher CBs can range from the same size to considerably narrower or wider than critical bandwidths measured with direct experimental methods across different species and therefore Fletcher CBs are considered to be an unreliable approximation of filter bandwidth (Hamilton, 1957; Langemann et al., 1995; Southall et al., 2003; Yost and Shofner, 2009). Fletcher's (1940) equation implies that auditory filters are of rectangular shape; however, deviations from this are shown by direct studies of filter shape (e.g., Finneran et al., 2002a; Lemonds et al., 2012).

Among marine mammals, direct measurements of critical bandwidths have been completed for bottlenose dolphins, California sea lions, harbour seals, and northern elephant seals (*Mirounga angustirostris*). Auditory filter shapes have been further investigated using complementary methods in bottlenose dolphins, beluga whales, harbour porpoises, finless porpoises (*Neophocaena phocaenoides*), and harbour seals. CRs have been directly measured in a larger number of marine mammals. The odontocetes tested include bottlenose dolphins, false killer whales (*Pseudorca crassidens*), beluga whales, and harbour porpoises. The pinnipeds tested include harbour seals, spotted seals (*Phoca largha*), ringed seals (*Pusa hispida*), northern elephant seals, northern fur seals (*Callorhinus ursinus*), and California sea lions. CRs are also available for the West Indian manatee, and the recently tested southern sea otter. Table 2 provides citations to the published studies reporting critical bandwidths, auditory filter shapes and CR in marine mammals, as well as the frequency ranges for which these data are available. Again, note that more data for pinnipeds and fewer data for cetaceans are available at low frequencies.

Fig. 4 shows CR measurements obtained for marine mammals under water. The CR mostly increases with frequency, except at low frequencies. Taking CRs as a measure of frequency tuning and an estimate of bandwidth (Fletcher CB, American National Standards Institute, 2008, $CR = 10 \log_{10}(CB)$), the relationship between Fletcher CB and centre

Table 2
Frequency tuning information is available for the following species.

Family Delphinidae		
False killer whale (*Pseudorca crassidens*)	Thomas et al. (1990b)	CRs (8–115 kHz)
Bottlenose dolphin (*Tursiops truncatus*)	Johnson (1968a)	CRs (5–100 kHz)
	Au and Moore (1990)	CRs (30–140 kHz)
		Critical bandwidths (30–120 kHz)
	Popov et al. (1996)	Auditory filter shape (16–128 kHz)
	Popov et al. (1997)	Auditory filter shape (64–108 kHz)
	Finneran et al. (2002a)	Auditory filter shape (20, 30 kHz)
	Lemonds et al. (2011)	CRs (40–120 kHz)
	Lemonds et al. (2012)	Auditory filter shape (40 kHz – 100 kHz)
	Supin et al. (1993)	Auditory filter shape (16–128 kHz)
	Johnson (1971)	Auditory filter shape & CRs (70 kHz)
Family Monodontidae		
Beluga whale (*Delphinapterus leucas*)	Johnson et al. (1989)	CRs (0.40–125 kHz)
	Finneran et al. (2002a)	Auditory filter shape (20, 30 kHz)
	Klishin et al. (2000)	Auditory filter shape (32–108 kHz)
Family Phocoenidae		
Finless porpoise (*Neophocaena phocaenoides*)	Popov et al. (2006)	Auditory filter shape (22.5–140 kHz)
Harbour porpoise (*Phocoena phocoena*)	Bibikov (1992)	Auditory filter shape (120 kHz)
	Popov et al. (2006)	Auditory filter shape (22.5–140 kHz)
	Kastelein and Wensveen (2008)	CRs (4 kHz)
	Kastelein et al. (2009b)	CRs (315 Hz - 150 kHz)
Family Phocidae		
Northern elephant seal (*Mirounga angustirostris*)	Southall et al. (2000)	CRs (0.1–2.5 kHz, water)
	Southall et al. (2003)	CRs (0.2–8 kHz, air)
		Critical bandwidths (2.5–8 kHz, air)
Harp seal (*Pagophilus groenlandicus*)	Terhune and Ronald (1971)	CRs (2–8.6 kHz, air)
Spotted seal (*Phoca largha*)	Sills et al. (2014)	CRs (0.1–25.6 kHz, air & water)
Harbour seal (*Phoca vitulina*)	Renouf (1980)	CRs (2–15 kHz, air)
	Turnbull and Terhune (1990)	CRs (4–32 kHz, water)
		CRs (2–16 kHz, air)
		Critical bandwidths (4–32 kHz, water)
		Critical bandwidths (2–8 kHz, air)
	Turnbull and Terhune (1993)	CRs (2–16 kHz, water)
	Terhune (1991)	CRs (0.25–1 kHz, air)
	Southall et al. (2000)	CRs (0.1–2.5 kHz, air)
	Southall et al. (2003)	CRs (0.2–8 kHz, air)
		Critical bandwidths (2.5–8 kHz, air)
Ringed seal (*Pusa hispida*)	Terhune and Ronald (1975)	CRs (4–32 kHz, water)
	Sills et al. (2015)	CRs (0.1–25.6 kHz, water)
Family Otariidae		
Northern fur seal (*Callorhinus ursinus*)	Moore and Schusterman (1987)	CRs (2–32 kHz, water)
California sea lion (*Zalophus californianus*)	Southall et al. (2000)	CRs (0.2–2.5 kHz, water)
	Southall et al. (2003)	CRs (0.2–8 kHz, air)
		Critical bandwidths (2.5–8 kHz, air)
Family Trichechidae		
West Indian manatee (*Trichechus manatus*)	Gaspard et al. (2012)	CRs (4–32 kHz, water)
Family Mustelidae		
Sea otter (*Enhydra lutris*)	Ghoul and Reichmuth (2014)	CRs (0.250–22.6 kHz, air)

frequency corresponds to a constant-Q bank of filters at most frequencies, indicated by a linear (in a logarithmic plot) increase in Fletcher CB as a function of centre frequency. Q is the ratio of centre frequency to bandwidth of a filter, and is called the quality factor. In other words, in a constant-Q bank of filters, the ratio of centre frequency to bandwidth is constant, and the logarithm of the bandwidth plotted against the centre frequency on a logarithmic scale is upward sloping. Fractional octave bands are constant-Q bands, and the widths of 1/3, 1/6 and 1/12 octave bands are shown in Fig. 4 as well. Most Fletcher CBs in Fig. 4 show a constant-Q trend, except at low frequencies (e.g., beluga whale and harbour porpoise at frequencies <3 kHz). Here, Fletcher CBs approach a bank of constant-bandwidth filters, where the CB levels off and no longer changes with decreasing frequency, i.e., CBs as a function of centre frequency are constant, independent of frequency, and hence distributed horizontally in the plot.

Fig. 5 shows direct estimates of critical bandwidth obtained from marine mammals using experimental methods (band-widening, notched-noise or tone-tone masking techniques). In the case of bottlenose

dolphins, critical bandwidths measured in band-widening experiments yielded the largest estimates. In notched-noise and tone-tone masking experiments, the 10 dB bandwidth (i.e., the width measured at 10 dB below the peak of the estimated filter shape) is obviously wider than the 3 dB bandwidth. Equivalent rectangular bandwidths (ERB, defined as the width of a rectangular filter with the same peak amplitude and area under the curve as the estimated filter shape) tend to be the narrowest measures of filter width. Comparing with Fig. 4, Fletcher CBs (calculated from CR data) underestimate the critical bandwidths measured in band-widening experiments. In humans and some terrestrial vertebrate animals, critical bandwidths are about 2.5 times as wide as Fletcher CB. A factor 2.5 in bandwidth is the same as an additional 4 dB in Fletcher CB ($10\log_{10}(2.5) = 4$), which brings all of the measurements in Fig. 4 close to the 1/3 octave line. It is therefore that 1/3 octave bands are often used in masking models as a conservative bandwidth over which to compute the noise PSD.

Fig. 5 combines data from pinnipeds tested in air and underwater. In contrast to measures of auditory sensitivity that depend on pathways of
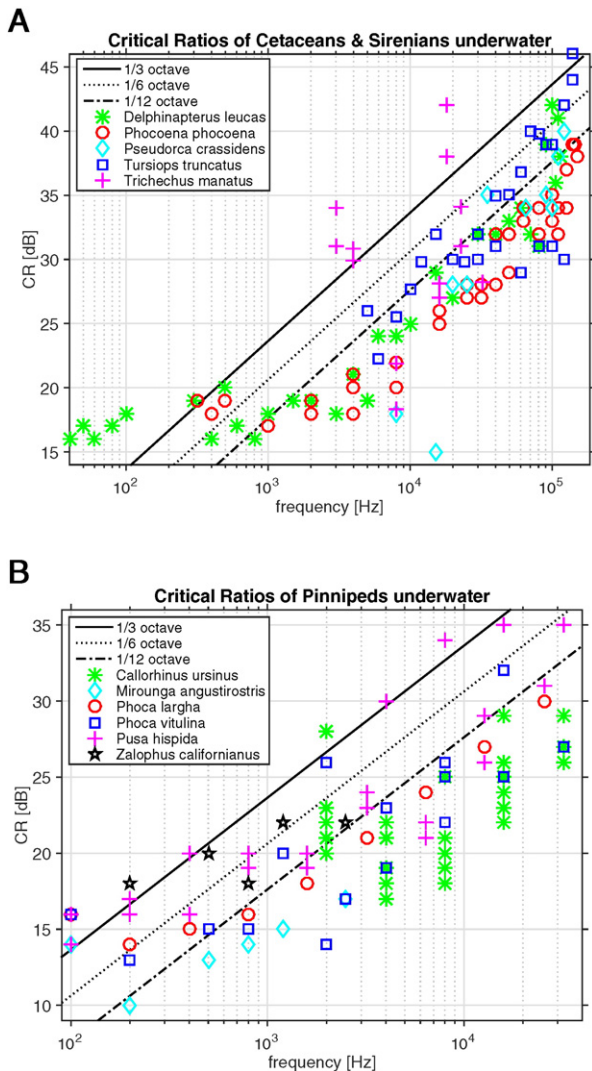
Fig. 4. Critical ratios (CR) of marine mammals. Shown are all of the CR data available. Fractional-octave bandwidths of 1/3 octave, 1/6 octave, and 1/12 octave are shown for comparison. While some of the CR data fall below the 1/12 octave constant-Q line, the actual critical bandwidth is expected to be significantly wider. In the absence of direct critical bandwidth measurements, 1/3 octave bands are commonly used to estimate the frequency span of noise surrounding a given signal that may contribute to masking. See source material in Table 2.

Fig. 5. Estimated critical bandwidths for bottlenose dolphin (Au and Moore, 1990; Finneran et al., 2002a; Lemonds et al., 2012; Popov et al., 1996, 1997; Supin et al., 1993), beluga whale (Finneran et al., 2002a; Klishin et al., 2000), finless and harbour porpoises (Popov et al., 2006), northern elephant seal and California sea lion (Southall et al., 2003), and harbour seal (Southall et al., 2003; Turnbull and Terhune, 1990). Critical bandwidths determined by noise band widening are marked '*'. Bandwidths estimated in notched-noise or tone-tone masking experiments are symbolized 'l' in the case of reported equivalent rectangular bandwidths (ERB), '+' for 3 dB bandwidths and 'o' for 10 dB bandwidths. Note that some of these data were collected using behavioural paradigms, others using AEP. Both in-air and underwater data of pinnipeds are included.

sound transmission to the inner ear, CRs and critical bandwidths appear to be related to cochlear processes and are the same whether measured in air or in water, as confirmed in several studies of amphibious seals and sea lions (Renouf, 1980; Sills et al., 2014; Southall et al., 2003; Turnbull and Terhune, 1990).

As is obvious from Figs. 4 and 5, ignoring methodological differences in measurement, auditory filter characteristics vary across taxonomic groups and within species. In most animals, it is probably the case that the smaller the CR, the narrower the critical bandwidth. While CRs do not provide reliable approximations of CBs, they do provide important information about an animal's ability to detect signals in noise and can serve as an indirect measure of frequency tuning in the auditory periphery.

Beyond the simplicity of the CR, the extent to which the auditory filters are peaked (or "sharpened") influences a listener's ability to detect sounds in noise, as well as discriminate sounds from one another (e.g., Saunders et al., 1979). For the modelling of masking by anthropogenic noise, knowledge of auditory filter shape is very valuable. However, this data is mostly lacking for marine mammals. Critical bandwidths and CRs provide one estimate of the amount of noise surrounding a
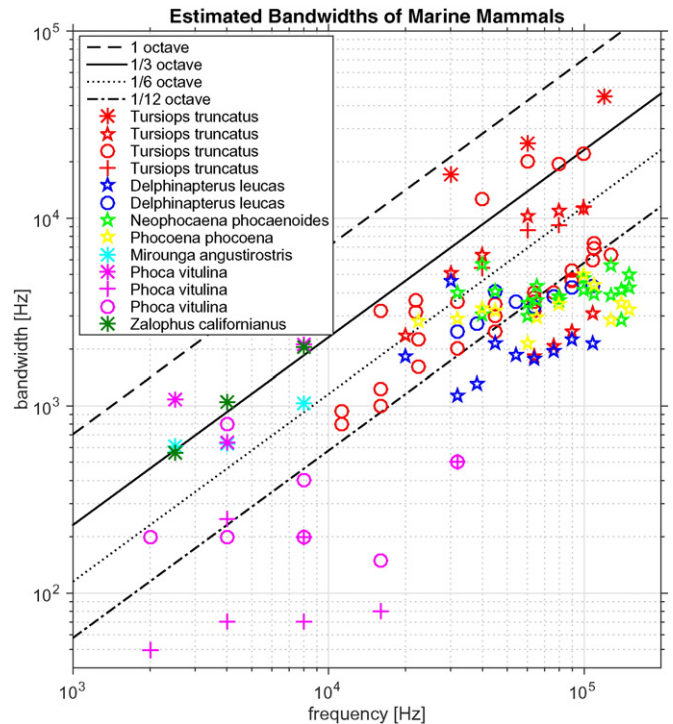
narrow-band signal that is effective at masking. In the absence of species-specific information on frequency tuning, 1/3 octave bands are commonly used as an estimate (see Figs. 4 and 5) of the noise power within the auditory filter encompassing a given signal (e.g., Clark et al., 2009; Cunningham and Mountain, 2014; Jensen et al., 2009; Payne and Webb, 1971). As with audiogram measurements, it is not yet apparent to what extent extrapolation of CR and critical bandwidth data to unstudied species (within a family, or larger taxonomic group) is appropriate. However, it is reasonable to assume that species groupings showing similar hearing sensitivity will also show similar trends in measures of frequency tuning.

3.3. Auditory integration times

The duration of an acoustic signal influences its detectability by a listener. Auditory thresholds for short-duration signals improve with increasing signal duration up to a certain value, usually a few hundred milliseconds in vertebrates. Increasing duration beyond this value does not further improve a listener's ability to hear a given signal. This temporal processing characteristic of the auditory system is expressed as *integration time*. Auditory integration times depend on signal frequency, with longer integration times for lower-frequency signals and shorter times required for higher-frequency signals.

Auditory integration times have been measured for seven marine mammal species thus far (Table 3). Integration times for narrowband signals in marine mammals are of the order of tens to hundreds of milliseconds, depending on the signal frequency. Integration times for broadband clicks, such as those used by odontocetes for echolocation, are not as well studied and require further investigation. There is some evidence from both behavioural (Au et al., 1988) and neurophysiological

Table 3

Auditory integration studies with marine mammals. All studies listed were completed with behavioural methods, with the exception of Popov and Supin (1990a).

Family Delphinidae			
Bottlenose dolphin (*Tursiops truncatus*)	Johnson (1968b)	Narrowband (0.25–100 kHz)	35–220 ms
	Au et al. (1988)	Broadband (click echoes)	264 μs
	Popov and Supin (1990a)	Broadband (clicks)	0.5 ms
Family Monodontidae			
Beluga whale (*Delphinapterus leucas*)	Johnson (1991)	Narrowband (60 kHz)	20 ms
Family Lipotidae			
Chinese river dolphin (*Lipotes vexillifer*)	Wang et al. (1992)	Narrowband (10–96 kHz)	> 5000 ms
Family Phocoenidae			
Harbour porpoise (*Phocoena phocoena*)	Kastelein et al. (2010a)	Narrowband (0.25–150 kHz, water)	134 ms
Family Phocidae			
Harbour seal (*Phoca vitulina*)	Terhune (1988)	Narrowband (1–64 kHz, water)	13–104 ms
	Holt et al. (2004b)	Narrowband (2.5 kHz, air)	134 ms
	Kastelein et al. (2010b)	Narrowband (0.2–40 kHz, water)	14–3624 ms
	Reichmuth et al. (2012)	Narrowband (0.2 kHz, air & water)	< 500 ms
Family Otariidae			
California sea lion (*Zalophus californianus*)	Ghoul et al. (2009)	Narrowband (2.5–10 kHz, air)	98–176 ms
	Holt et al. (2012)	Narrowband (2.5–10 kHz, air)	120–167 ms
Northern elephant seal (*Mirounga angustirostris*)	Ghoul et al. (2009)	Narrowband (5 kHz, air)	134 ms

(Supin et al., 2001) hearing experiments that integration times for these pulsed sounds are much shorter and of the order of hundreds of microseconds.

Audiometric studies that measure absolute sensitivity (audiograms) and frequency tuning (critical bandwidths and CRs) intentionally use test signals with durations that are greater than the expected integration time. Signals shorter than the integration time would require higher sound pressure levels for detection than would be predicted from extrapolation of audiogram data. Therefore, if predicting an animal's ability to detect a signal of interest in quiet conditions, the tone level (SPL$_{rms}$) should be computed over a fixed window of a few 100 ms length, rather than the potentially shorter pulse duration, before comparing to the audiogram. In masking models that use SNR as a decision metric, auditory integration times must be taken into account when deciding the time window over which SNR is calculated, in order for the results to be biologically meaningful. For example, auditory integration times have been applied to acoustic data from behavioural response studies to more accurately estimate the received sensation levels of brief target signals (Miller et al., 2014).

3.4. Other parameters

Additional parameters indicative of an animal's hearing capabilities also play a role in auditory masking, but at present, it is unknown how these factors might best be included in predictive models or assessments of masking. Such factors include the time difference limen (the minimum difference in duration between two signals that can be discerned by a listener; Yunker and Herman, 1974), the frequency difference limen (Popov et al., 1986; Thompson and Herman, 1975), the intensity difference limen (Bullock et al., 1968; Dubrovskiy, 1990; Johnson, 1971, 1986; Moore and Schusterman, 1976; Popov et al., 1986), the modulation rate transfer function (Klishin et al., 2000; Mooney et al., 2009, 2011; Mulsow and Reichmuth, 2007), and the length of temporal gaps between signal and noise, across which forward and backward masking can occur (also called the "critical interval"; Bibikov, 2004; Moore et al., 1984; Supin and Nachtigall, 2013; Supin et al., 2008, 2009, 2011; Vel'min and Dubrovskii, 1976).

Other parameters related to spatial hearing capabilities may be important to consider with respect to masking. The *minimum audible angle* is the smallest angle that can be resolved if two signals come from slightly different directions. These angles typically increase with decreasing frequency and are smaller for broadband clicks than for pure tones. Minimum audible angles <1° have been reported in

bottlenose dolphins (Renaud and Popper, 1975). Minimum audible angles have also been measured for harbour porpoises (Andersen, 1970b; Dudok Van Heel, 1959), northern elephant seals in air (Holt et al., 2004a, 2005), harbour seals in air and in water (Holt et al., 2004a, 2005; Mohl, 1968b; Terhune, 1974), California sea lions in air and in water (Gentry, 1967; Holt et al., 2004a, 2005; Moore, 1975; Moore and Au, 1975), and northern fur seals in air and in water (Babushina and Polyakov, 2004). Due to the manner in which sounds travel through water, minimum audible angles are larger in water than in air.

The *receiving beam pattern* expresses the hearing threshold as a function of angle about the midline of the animal, and can be expressed in logarithmic terms as the ratio of the actual received intensity and that of an omnidirectional receiver. As a result of spatial hearing abilities, two sounds coming from different directions will differ in perceived intensity. The receiving beam pattern has been measured for the harbour porpoise (Kastelein et al., 2005a), beluga whale (Klishin et al., 2000; Popov and Supin, 2009), bottlenose dolphin (Au and Moore, 1984; Popov and Supin, 2009), and Amazon river dolphin (*Inia geoffrensis*) (Supin and Popov, 1993). Spatial hearing capabilities (as described by the metrics of minimum audible angle and receiving beam pattern) contribute to masking release mechanisms discussed in the next section.

4. Masking release and anti-masking strategies

So far, we have been primarily concerned with estimating the average signal and noise energy within specific time and frequency windows. This is only part of the challenge in understanding masking as marine mammals, like other animals, have evolved mechanisms that enhance the detectability of signals in the presence of masking noise. These are both mechanisms at work in the auditory system of the receiver that exploit additional acoustic information not captured by SNR measurements, and strategies employed by signallers to increase the probability that a signal will be detectable when it reaches a listener.

4.1. Masking release processes of the receiver

Spatial release from masking (SRM) occurs when signal and noise are received from different directions, allowing a listener to utilize binaural effects to enhance signal detectability and reduce the expected amount of masking. Binaural cues arise from comparison of the sounds received from the same source at two ears, and include perceived differences in sound phase and level (see Yost and Dye, 1997). SRM has been investigated in bottlenose dolphins and killer whales listening under

water (Bain and Dahlheim, 1994; Zaitseva et al., 1975, 1980), in harbour seals listening under water (Turnbull, 1994), and in harbour seals and California sea lions listening in air (Holt and Schusterman, 2007). Although other marine mammals have not been studied with respect to SRM, it is likely that they also have the ability to utilize binaural hearing capabilities to enhance the detection of signals in noise, given their acute underwater sound localization capabilities. This view is supported in part by the prominent asymmetry of odontocete skulls, a feature that is thought to aid in sound localization (Mooney et al., 2012).

An interesting observation was made during biosonar target detection experiments with a beluga whale and a bottlenose dolphin. When a noise source was placed in the direct echolocation path between the animal and the target, the beluga was able to enhance its target detection performance by using a surface-reflected path for its emitted and received biosonar signal. This implies that the animal actively employed a SRM, as the target echo and masking noise would have arrived from different directions. The dolphin did not make use of the surface-reflected signal (Penner et al., 1986). There have been no studies investigating whether such multi-path propagation can enhance the detection of communication calls.

Comodulation masking release (CMR) occurs when the masker is amplitude modulated across a wider frequency range than the auditory filter around the signal. In other words, the masker exhibits similar amplitude modulation patterns across a broad range of frequencies, and hence is coherently modulated. For example, the propeller cavitation spectrum of ship noise is often strongly comodulated by the propeller blade rate, leading to a nearly pulsed pattern where the spectral energy content of each pulse likely spans multiple critical bands. Spectrograms of noise types with different degrees of comodulation (including sounds from snapping shrimp, rain, boats, pile saws and ice) have been described elsewhere (Branstetter et al., 2013a). CMR has been well studied in humans where the presence of comodulated bands outside of the critical band aid signal detection, likely via the listener's ability to compare amplitude fluctuations across multiple auditory filters and detect the change that occurs in the coherent pattern when the signal is present (Hall et al., 1984). CMR has recently been shown experimentally in bottlenose dolphins (Branstetter and Finneran, 2008; Branstetter et al., 2013b; Trickey et al., 2010), beluga whales (Erbe, 2008), harbour seals and California sea lions (Cunningham et al., 2014b).

The effect of CMR can be quite dramatic. A masking release of up to 17 dB has been measured from a trained dolphin detecting signals in comodulated noise versus flat-spectrum white noise (Branstetter and Finneran, 2008). In another study, two bottlenose dolphins were tasked to detect a 10 kHz tone in the presence of natural and anthropogenic noises, as well as synthetic, Gaussian white noise and synthetic, comodulated white noise (Branstetter et al., 2013b). Natural noises included snapping shrimp, rain, and ice squeaks. Anthropogenic noises included pile saw noise and boat noise. A progressive band-widening paradigm was used and indicated that, when the spectrum level of the noise was kept constant, detection thresholds for the dolphin were comparable for all noise types up to a certain bandwidth, beyond which they diverged, as would be expected in the case of CMR. CRs were lower for signals embedded in noise that was comodulated, making the signals easier to detect. This finding suggests that CRs traditionally measured using Gaussian white noise may not be reliable in all masking scenarios, and CMR must be accounted for.

Masking release was also observed in the study by Erbe and Farmer (1998), in which a beluga whale was trained to detect a beluga whale vocalization in naturally-occuring thermal ice-creaking noise, and in two types of anthropogenic noise: propeller cavitation noise and bubbler system noise, both from an icebreaking vessel. The signal and the noises were recorded in the Arctic. The three types of noise were broadband (32 Hz – 22 kHz), occupied similar frequency bands and were normalised to the same total power, but differed in the finer distribution of power versus frequency and temporal structure. The amount of masking observed differed by up to 11 dB from the strongest masker

(bubbler system noise) to the weakest masker (thermal ice-cracking noise). Synthetic, Gaussian white noise was also used in the masking trials for comparison (Erbe, 2000). CMR likely eased the masking effects of propeller cavitation noise, which was more strongly modulated than the bubbler system noise. Within-valley (or "dip") listening let the animal detect the call in the quieter parts of the ice-cracking noise. Multiple yet brief looks at the call (Erbe, 2008; Holt and Carney, 2005; Viemeister and Wakefield, 1991) allowed the beluga whale to perceive the call within the non-continuous noise, and no matter the number and width of the gaps, the animal responded whenever 75% of the call emerged through the gaps (Erbe, 2008).

Cunningham et al. (2014b) measured detection thresholds in quiet and masked conditions using complex signals and noise in two pinnipeds—one California sea lion and one harbour seal. Signals were designed to isolate three common complex features of natural sounds: frequency modulation (FM), amplitude modulation (AM), and the presence of multiple harmonics. To test the accuracy of threshold predictions based on audiograms and CRs, detection thresholds were compared to power-spectrum-type hearing models based on psychophysical data for the two pinniped subjects. The study found that subjects were able to detect harmonic signals at lower than predicted levels in both quiet and masked conditions (as in Buus et al., 1986), and that masking release occurred for FM signals and for recorded shipping noise that exhibited comodulation. Maximum sensitivity differences from predicted were 8 dB in both quiet and masked conditions, leading the authors to conclude that marine mammal hearing models based solely on audiograms and CRs must be used with caution.

In summary, both the structure of signals (e.g., tonal, FM, AM, harmonic) and the structure of noise (e.g., time-varying, comodulated), as well as their spatial segregation, are known to provide some release from the amount of masking expected by CRs determined with more spectrally even (Gaussian) noise. In addition to masking relief provided by auditory processing, an animal's behaviour can also influence whether a signal can be detected from background noise. For example, the listener might orientate towards the sender, move to a different position to improve SNR or the availability of binaural cues, and/or reduce its self-noise (e.g., remain still). These active listening strategies will also affect signal detection abilities in the presence of noise within the limitations imposed by the auditory system.

4.2. Anti-masking strategies of the sender

Marine mammals may alter the characteristics of their vocalizations in the presence of noise (Lombard effect, Lombard, 1911) as an anti-masking strategy that originates at the sender rather than at the receiver (Hotchkin and Parks, 2013). Killer whales have been shown to raise the amplitude of their communication signals in the presence of ship noise (Holt et al., 2011); as have beluga whales (Scheifele et al., 2005). Humpback whales increased the source level of their songs proportionately to increases in wind-dependent ambient noise (Dunlop et al., 2014). In a non-social context, bottlenose dolphins were found to raise the amplitude of their outgoing echolocation clicks when masking noise was added to the environment (Au et al., 1974). A beluga whale adapted its echolocation clicks, shifting to higher intensities and higher frequencies after being moved to a different ambient noise environment (Au et al., 1985).

Certain marine mammals have been reported to alter the frequency content of their calls in the presence of interfering noise, potentially as a way to minimize spectral overlap. Right whales (*Eubalaena glacialis*) (Parks et al., 2007), beluga whales (Lesage et al., 1998), and common dolphins (*Delphinus delphis*) (Ansmann et al., 2007) apparently shifted the frequency of their calls away from the environmental frequencies containing the most noise energy. These observations, however, were not made in controlled conditions and more research is needed on the usage and effectiveness of this Lombard response in marine mammals. There is also evidence that odontocetes shift the main energy of their

echolocation signals outside of the band of masking noise (Au et al., 1974, 1985; Moore and Pawloski, 1990; Romanenko and Kitain, 1992; Thomas and Turl, 1990), another observation that should lead to more systematic investigation of the extent to which frequency-shifting, as an anti-masking strategy, may occur in marine mammals.

Increasing repetition rate or redundancy of calls reduces the potential for masking and improves the odds of detection by a listener. Many marine mammals display high redundancy in calling behaviour in typical conditions, presumably as a strategy for increased detectability by conspecifics. Increases in call repetition rates have been documented for bottlenose dolphins (Buckstaff, 2004) and beluga whales (Lesage et al., 1998) in the presence of ship noise. Similarly, the redundancy within the calls of harp seals (*Pagophilus groenlandicus*) is highest in noisy conditions (Serrano and Terhune, 2001). Furthermore, increases in call duration have been reported for killer whales in the presence of masking noise (Foote et al., 2004).

Finally, some call types appear more resistant to masking as a function of their structure. For example, downsweeps had lower detection thresholds than equivalent upsweeps in a harbour seal (Turnbull and Terhune, 1994). While the underwater signals of marine mammals might have design features to support transmission and detection in ambient noise conditions, less is known about the extent to which they can modify their calling behaviour in response to the addition of anthropogenic noise. Most of the evidence of active usage of anti-masking strategies by marine mammals stems from opportunistic observations, and more research is needed in controlled and/or comparable settings.

5. Sources of underwater noise and the role of the acoustic environment in masking

In Sections 3 and 4, we reviewed the biological parameters playing a role in masking, such as the hearing abilities of the listener (e.g., audiogram, CRs, critical bandwidths, auditory filter shapes), masking release phenomena, and anti-masking strategies employed by the sender. To understand acoustic communication in natural environments, these biological parameters need to be considered in a framework that also includes physical parameters, such as the acoustic characteristics of the sound propagation environment, ambient noise and, last but not least, the acoustic characteristics of the masker (e.g., an anthropogenic source of noise).

5.1. Examples of anthropogenic underwater noise

Several summaries of underwater noise characteristics have been published (e.g., Richardson et al., 1995), and more recently of the sounds emitted by offshore petroleum operations (Wyatt, 2008), naval, fisheries and hydrographic sonars (Ainslie, 2010), pile driving (Illinworth and Rodkin Inc., 2007), dredging (Reine et al., 2014; Robinson et al., 2011), and ships (e.g., Hatch et al., 2008; McKenna et al., 2012). Noise that is produced in air, such as by airplanes and helicopters (Wyatt, 2008), is generally transmitted into the water only within a 26° cone. Fig. 6 shows a few examples of underwater noise expressed as far-field equivalent source levels (in 1/3 octave bands). Such source levels are useful for the prediction of received levels far from the source using common sound propagation models. They do not adequately represent what would be measured very near the source, in the so-called near-field.

While Fig. 6 gives some indication of the frequency bands and levels emitted by the various sources, the temporal characteristics can be vastly different, ranging from continuous, to continuous and amplitude-modulated, to pulsed (Fig. 7). It is this temporal and spectral structure of realistic underwater noise (as opposed to continuous Gaussian noise) that can dramatically reduce the amount of masking observed relative to the expected amount. This is because the power spectrum model of masking uses time-averages of band levels, ignoring finer
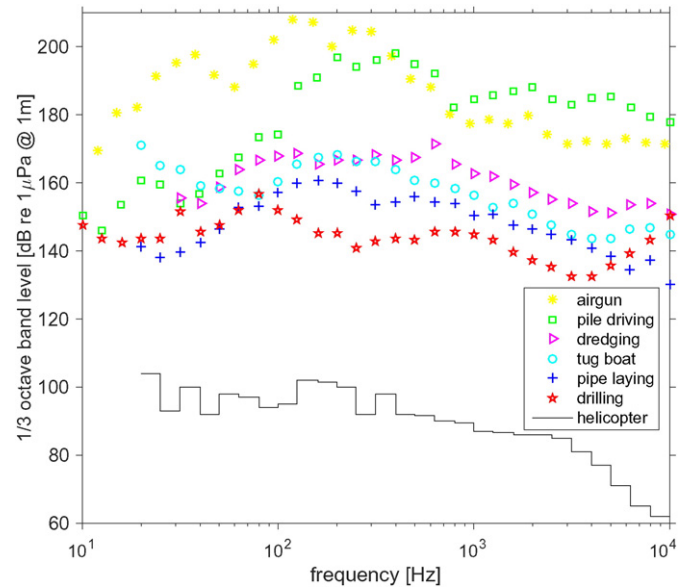

Fig. 6. One-third octave source spectra of selected anthropogenic activities. The seismic airgun array spectrum was recorded from a 2800 in³ array at 400 m range, and back-propagated to 1 m. The pile driving spectrum was recorded at 14 m range (Erbe, 2009) and similarly back-propagated. For these pulsed sounds, the mean-squared pressure was calculated over the duration from the 5% to the 95% cumulative energy points of the pulse. The dredge *JFJ de Nul*, the tug *Fujisan Maru*, the pipelay barge *Castoro* and the drilling platform *Molikpaq* were recorded at less than 100 m and back-propagated by Hannay et al. (2004, cited in Wyatt, 2008). The helicopter was flying at 305 m height above water and recorded underwater. One-third octave band levels were back-propagated to the water surface (Greene, 1985; Richardson et al., 1995).

temporal structure and multiple-band phenomena such a CMR. The spectrogram in Fig. 7 shows a ship's broadband propeller cavitation noise, which is strongly amplitude-modulated by the propeller blade-rate (the product of the number of blades and the rotations per second, in this case 11 Hz). A signal consisting of four 100 ms upsweeps from 5.2 to 5.6 kHz occurs at the same time. While the noise has slightly higher PSD at the signal frequencies, bits of the signal are detectable acoustically through the quieter gaps in the noise by within-valley listening. Even if the gaps in the noise were much shorter and weaker, the signal might
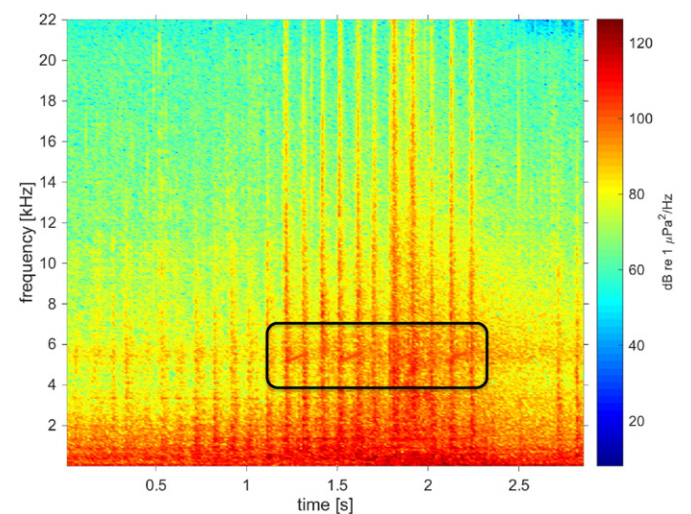

Fig. 7. Spectrogram of ship noise, amplitude-modulated by the propeller blade-rate, and a signal consisting of four upsweeps which are partially masked so that only bits of the signal emerge through the quieter gaps in the noise.

be detected at the times of the noise pulses by CMR, i.e., by a correlation of outputs at multiple auditory filters.

5.2. Sound propagation effects

Masking does not happen at the noise source. Rather, masking is a phenomenon that occurs at the receiver, some distance away from the source. The source characteristics, such as level, source spectrum and source spectrogram therefore are not sufficient to predict masking effects on animals, and an understanding of the features of the noise that a given listener receives at some distance from the sound source is required. The spectral and temporal characteristics of sound change as the sound propagates through the ocean. Therefore, the masking potential of a noise source changes as it radiates from the sound source—not just because of changes in level but also because of changes in temporal and spectral structure. Fig. 6 shows that close to the source, many types of anthropogenic noise are broadband with significant energy over at least three decades in frequency (10 Hz–10 kHz). However, energy at high frequencies is absorbed readily by vibration of seawater molecules (François and Garrison, 1982a,b), losing about 0.1 dB/km at 1 kHz, increasing to 1 dB/km at 10 kHz and 35 dB/km at 100 kHz. Also, in shallow water, energy at low frequencies doesn't propagate through the water. As a result, the spectrum of the noise at the position of the receiver is typically very different from the spectrum near the sound source.

Fig. 8 shows the spectrogram measured from a vessel passing by a recorder over a five-minute period. Due to propeller cavitation, the noise emitted by this vessel is broadband from 30 Hz to >20 kHz and continuous. At the recorder, however, multi-path arrivals (most dominantly the direct and the surface-reflected paths) lead to repeated constructive and destructive interference at certain frequencies as the vessel passes. This results in a U-shaped interference pattern called the Lloyd Mirror effect. The received noise has relatively quieter gaps in frequency and time, through which potential signals might be detected by a listener at the same position as the recorder.

Apart from such multi-path effects, frequency dispersion during propagation also leads to spectral changes. Most strikingly, brief and broadband pulses can transform into narrow-band, longer-duration, frequency-modulated tonal sounds. For example, the signals of seismic airguns near the source are typically <1 s in duration and cover a frequency band of several kHz. Several km from the source, these signals can transform into frequency-modulated sounds of the order of seconds in length, yet limited to a restricted band of low frequencies (typically <100 Hz) (Gedamke and McCauley, 2010; Guerra et al., 2011). Fig. 9
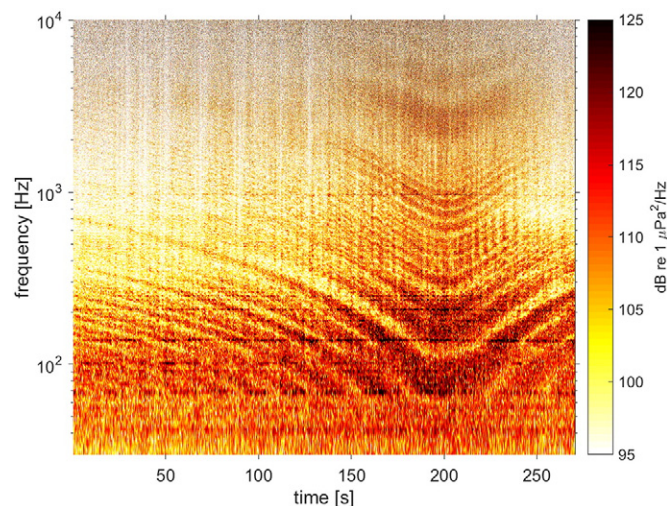
shows spectrograms of received seismic array signals in different environments. Whether the seismic pulses transform into up- or down-sweeps with propagation depends primarily on the seafloor properties and sound speed profile. The top panel of Fig. 9 shows broadband pulses received at 1.5 km range from a seismic survey. Reverberation is obvious at 5–100 Hz for about 5 s following each pulse. The middle panel depicts a typical modal arrival pattern of airgun signals measured in a shallow-water sound channel over a soft (fluid) bottom (at 80 km range) that can be characterized by a Pekeris model (Tolstoy and Clay, 1987). The bottom panel of Fig. 9 shows the modal arrival pattern of the same seismic survey as in the top panel, but measured in shallow water over an elastic seabed at 40 km range. In this environment, the intra-modal frequency dispersion is stronger and has an opposite sign than that in a Pekeris waveguide (Duncan et al., 2013).

5.3. Ambient noise

Ambient noise refers to the background level of sound in the environment. It can have contributions of abiotic (wind, waves, precipitation, ice break-up), biotic (snapping shrimp, fish or whale choruses) or anthropogenic (distant shipping) origin. Summaries of ambient
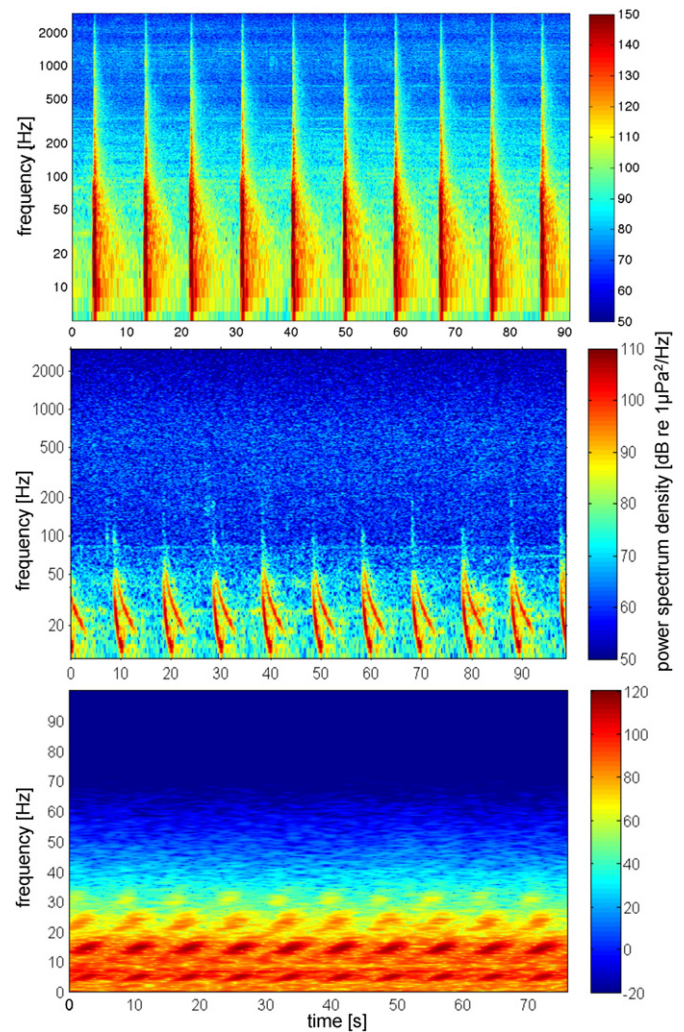
Fig. 9. Spectrograms of seismic airgun signals received at three locations around Australia at a range of 1.5 km (top), 80 km over a soft seabed in shallow water (middle) and 40 km over a hard seabed in shallow water (bottom). The top and bottom recordings are of the same seismic survey. As can be seen, pulses that are brief and broadband near the source, can turn into frequency-modulated, narrowband sounds at some range.

Fig. 8. Lloyd Mirror pattern of a vessel passing by a recorder in water of 34 m depth.

noise in different parts of the world's oceans have been published (e.g., Cato, 1978, 1997; Erbe et al., 2015; Wenz, 1962) showing a wide range of variability in acoustic habitats used by marine mammals. Ambient noise needs to be considered in masking models to determine whether the detection of sounds (signals and noise) is audiogram or ambient-noise limited. In the latter case, ambient noise can reduce the range over which anthropogenic sounds are expected audible and potentially relevant as maskers. As such, ambient noise not only reduces the range of audibility of anthropogenic noise but also the range and amount of masking. Natural sources of ambient noise can sometimes mask anthropogenic sources of noise, potentially reducing animal responses to anthropogenic noise that would be expected from received levels alone. For example, a captive harbour porpoise showed behavioural responses to playbacks of naval sonar. They swam further away from the transducer, surfaced more often, swam faster, and breathed more forcefully. However, such responses were reduced by the presence of additional continuous background noise, in this case wind-generated noise at various sea states (Kastelein et al., 2011b). The effects of naval sonar systems on harbour porpoises appeared to be determined not only by the received levels of signal and anthropogenic noise and the hearing sensitivity of the animals, but also by other sources of background noise.

5.4. The SONAR equation

The SONAR equation was originally developed to assess the performance of SONAR (SOund Navigation And Ranging) systems. It is useful for estimating signal detection in noise. It takes the source level of a sound, accounts for propagation or transmission loss, considers the ambient noise level at the receiver and compares the resulting signal-to-noise ratio to the receiver's detection threshold. Different forms of the SONAR equation include different source, transmission and receiver parameters and hence apply to different scenarios.

The received level (RL) of a sound can be computed as the source level (SL) minus the transmission loss (TL):

$$RL = SL - TL.$$

In deep water, where sound can propagate uniformly in all directions, transmission loss can be modelled as geometric spreading over range r:

$$TL_{sph} = 20 \log_{10}(r/1m).$$

In shallow water, propagation is bound by the sea floor and the sea surface and can be modelled as cylindrical spreading:

$$TL_{cyl} = 10 \log_{10}(r/1m).$$

Molecular vibration (absorption) loss can be accounted for as:
$TL_{abs} = \alpha r$, where α specifies the amount of absorption in dB/km and is a function of frequency.

Transmission loss is commonly modelled as a combination of spherical and cylindrical spreading, and absorption:
$TL = 20 \log_{10}(h/1\,m) + 10 \log_{10}(r/h) + \alpha\, r$, where h is the range at which propagation transitions from spherical to cylindrical.

Considering a simple listening scenario (see Fig. 1) where one animal emits a signal, another animal at some range r will be able to detect this signal if the received level is above the receiver's detection threshold (DT):

$$RL = SL - TL; RL > DT.$$

In the case of a tonal signal and in the absence of ambient noise, DT is simply the threshold given by the audiogram.

In the presence of broadband ambient noise, the received level of the tone has to be at least one critical ratio (CR) above the noise power-spectral-density (PSD_n) for the tone to be detectable:

$$RL > CR + PSD_n.$$

6. Estimating the masking potential of underwater noise

In the previous sections, we developed a framework to conceptualise acoustic communication in natural environments (see Fig. 1) and reviewed the acoustic parameters of the sender, habitat and receiver. This information can be used to construct models of masking to determine potential limitations of communication in natural environments.

6.1. The power spectrum model + CR

The first step in estimating the masking potential of anthropogenic activities is identifying the noise sources of interest, the acoustic environment (i.e., ambient noise and sound propagation conditions), and the marine mammal species that may potentially be affected. Further assessment requires identifying the range of signals that are biologically relevant to these species (e.g., sounds from conspecifics, predators, prey, or the environment). If there is no overlap between the frequency bands of signals and noises, the masking potential is minimal, and non-masking effects (such as behavioural disturbance) should be considered. If there is spectral overlap between important signals and anthropogenic noise, sound propagation models need to be built for both signals and noises, and received levels need to be compared at the location of a hypothetical listener or listeners.

Ambient noise at the listener location needs to be considered to determine whether the detection of signal and noise is limited by the listener's hearing threshold (audiogram) or by ambient noise. In Fig. 10a, the PSD of wind-dependent noise is shown at four sea states (SS 0.5, 1, 2 and 4). At frequencies >40 kHz, thermal noise (molecular agitation) affects the ambient spectrum, apparent at low sea states as the up-sloping PSD for increasing frequency (Wenz, 1962). For comparison, a beluga whale audiogram is shown in the figure. The audiogram consists of the minimum thresholds over all individuals tested (see Fig. 3). The vertical green lines indicate the critical ratios (CR), subtracted from the audiogram. Note that CR depends on frequency, and therefore the lengths of the green lines increase with frequency (see Fig. 4). If the PSD of ambient noise is more than a CR below the audiogram, hearing will likely be audiogram limited, otherwise likely ambient noise limited. In Fig. 10a, at SS 0.5, hearing will likely be ambient noise limited only between 10 kHz and 100 kHz. At SS 4, hearing will likely be ambient noise limited between 400 Hz and 100 kHz.

In Fig. 10b, only the PSD of wind-dependent noise at SS 1 is shown for simplicity. In addition, the propeller cavitation spectrum of a large vessel with a SL of 180 dB re 1 µPa @ 1 m is plotted at five ranges. Applying a geometrical transmission loss model (spherical spreading to 100 m range, cylindrical thereafter) and molecular absorption, the received spectrum is plotted at 20 m, 100 m, 1 km, 10 km, 100 km. While the overall level decreases with increasing range, the loss is greater at high frequencies due to molecular absorption. (For scenarios where the physical environment is known, more specific complex propagation models can be employed.) The same concept applies as in Fig. 10a, i.e., if the PSD of the received ship noise is more than a CR below the audiogram, then the detection of signals will be audiogram limited, otherwise ship noise limited.

Fig. 10c adds three example signals: tones at 1 kHz, 10 kHz and 40 kHz. The tone at 40 kHz is exactly one CR above the ship noise PSD received at 100 m range. It is considered to be just at the detection threshold in this type of noise. A stronger tone would also be audible; a weaker tone would be masked. The 10 kHz tone, at its level indicated, would be masked by ship noise at 100 m range, but not by ship noise at
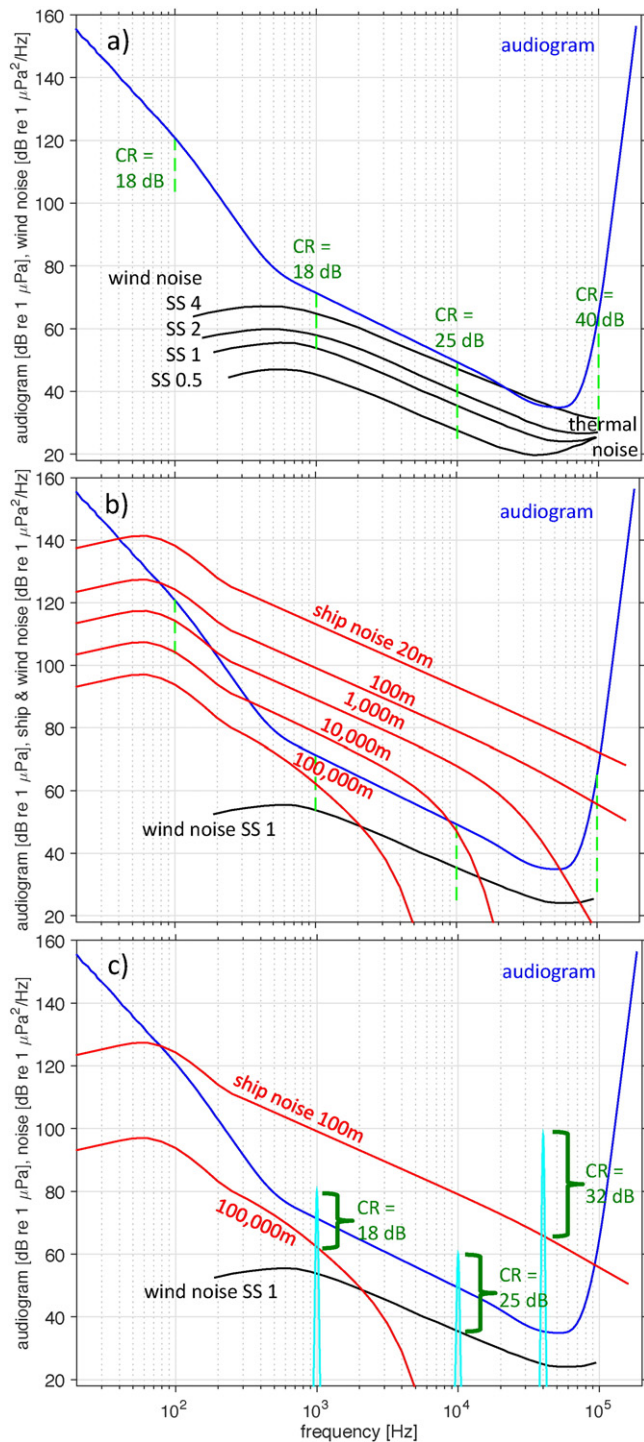
Fig. 10. The role of ambient noise in masking. The audiogram is the smoothed minimum beluga whale audiogram (see Fig. 3). The PSD of wind-dependent ambient noise is shown at various sea states (SS). Critical ratios (CR) are indicated as vertical green lines. Whenever the PSD of ambient noise is more than 1 CR below the audiogram, hearing is threshold (audiogram) limited rather than ambient noise limited. In panel (a), hearing would be ambient noise limited at SS 0.5 between 10 kHz and 100 kHz, and at SS 4 between 400 Hz and 100 kHz. The same argument applies in the presence of ship noise, i.e., whenever the PSD of the received ship noise is more than 1 CR below the audiogram, hearing is audiogram limited, otherwise ship noise limited. The propeller cavitation spectrum of a potential vessel is shown at five ranges in panel (b), based on a transmission loss model that accounted for geometrical spreading and molecular absorption. In this model, ship noise at 100 km range would mostly be unable to mask except for tones at about 300 Hz-2 kHz. Three example tones are shown in panel (c). The 1 kHz tone is at the detection threshold in ship noise at 100 km range. The 10 kHz tone is shown at the detection threshold in wind noise at SS 1. The 40 kHz tone is shown at detection threshold in ship noise at 100 m. Any tone whose level is below the audiogram would be inaudible even in the absence of noise.

100 km range, as the noise PSD is much more than 1 CR below the tone level. In the absence of ship noise, the 10 kHz tone would be masked by wind noise at SS >1. It is drawn at the detection threshold in SS 1. The 1 kHz tone is not masked by wind noise at SS 1, but is masked by ship noise at <100 km range. The level of the 1 kHz tone is drawn just at the detection threshold in this type of ship noise at 100 km range.

The power spectrum model of masking combined with the CR has been shown to successfully predict the masking of bird calls in many natural listening scenarios (Dooling et al., 2009a). While this approach was developed for masking assessments in terrestrial systems, it can be similarly applied in underwater environments. The approach is conservative in that it ignores the temporal relationship between signal and noise, directionality of either, binaural hearing effects, comodulation of the noise across multiple bands, and anti-masking strategies that can reduce the potential for masking. There is not enough data at this stage to include this information in general masking models for situations (animal species, received signal type, received masker) other than the few that have been tested. One way might be the addition of a comodulation index to quantify the masking potential of the noise as suggested by Branstetter et al. (2013a). Erbe (2008) applied masking metrics (CR data) only to the valleys within her specific types of noise. In the case of pulsed signal and noise, and with information on temporal integration times, the power spectrum model can be used to provide a statistical representation of the SNR, accounting for the variation of time lag between signal and noise. For example, if signal and noise have similar pulse and gap lengths, the signal pulses might coincide with the noise pulses leading to maximum masking; whereas if the pulses of signal and noise arrived out of sync, masking would be minimal; and a statistical assessment would account for the various cases.

6.2. The critical ratio plus additional signal excess

The power spectrum model of masking with CR estimates when a signal is just detectable in noise. The mere detection of a conspecific's call, however, might not be "useful" to the listener. From human studies we know that a higher SNR is needed for comfortable communication than for signal detection (Franklin et al., 2006). This has been corroborated in some species of birds, where a signal excess (SE) of 2–3 dB above the CR is needed for call discrimination instead of mere detection, and an additional signal excess of 2–3 dB is needed for call recognition (Dooling and Blumenrath, 2014; Dooling et al., 2009a, b; Lohr et al., 2003). The signal excess needed for comfortable communication is difficult (if not impossible) to measure in animals, but can be estimated by assuming comparable signal excess to that required by human subjects (Franklin et al., 2006).

Dooling et al. (2009b) computed the received level (RL(r)) of a bird vocalization as a function of range r, by subtracting a transmission loss (TL(r)) from the vocalization's source level (SL): RL(r) = SL − TL(r). TL(r) was computed as a combination of geometrical spreading and an environment-dependent attenuation term. The call was considered masked when the received level was less than the measured CR above the average noise PSD in the critical band surrounding the signal: RL(r) − CR < PSD_n (masking criterion). As mentioned previously, if the critical bandwidth is unknown, then a 1/3 octave band of the noise surrounding the signal is used to identify the portion of noise that will most influence detection. Fig. 11 illustrates the application of this model for two hypothetical birds in an open field in varying levels of background noise. The red curve shows the term RL(r) − CR as a function of range from the caller to the listener, and the dotted line at 245 m indicates where this term intersects the noise PSD of 30 dB re 20 μPa²/Hz. At r > 245 m, the call can no longer be detected by the receiver. In Fig. 11, the curves for discrimination, recognition and comfortable communication are computed as RL(r) − CR − SE as a function of range, where an additional signal excess is subtracted before comparison to the noise PSD. Note that as the zones move beyond detecting
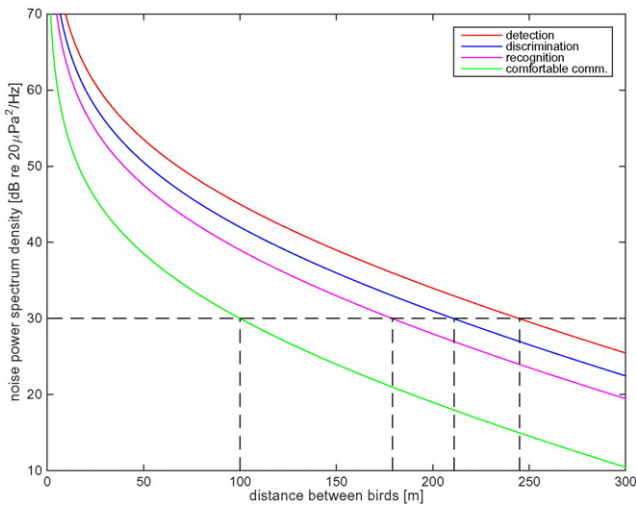
Fig. 11. Ranges over which a bird might experience comfortable communication (100 m), call recognition (180 m), call discrimination (210 m) and call detection (245 m) in white ambient noise of 30 dB re 20 µPa²/Hz. The source level of the call was 100 dB re 20 µPa zero-peak; the open habitat attenuation was set to 5 dB/100 m; the CR was chosen at 20 dB. The SNR excess for signal discrimination was set to 3 dB above the CR, for signal recognition 6 dB above the CR, and for comfortable communication 15 dB above the CR in this example (modified from Dooling et al., 2009b).

the mere presence of a call, the minimum distance that separates caller and receiver is significantly reduced.

Fig. 11 can be translated into a listener-centric, spatial view of masking effects (Fig. 12). Obviously, in real-world settings, the environment will likely not have circular symmetry, and therefore the zones will be of irregular shape. It is worth noting that underwater, sound typically travels over very long ranges, and at very little loss in certain conditions. While the difference of a few dB between signal detection and signal recognition might translate to a few tens of metres in air, this might become orders of magnitude farther underwater. In other words, one would expect the zones to be much farther apart underwater than in air. Also, reflection, diffraction, scattering and multi-path arrivals will typically generate an intricate pattern of constructive and destructive interference in depth, range and azimuth, quite different from the monotonic decrease in received levels implied by Fig. 11.
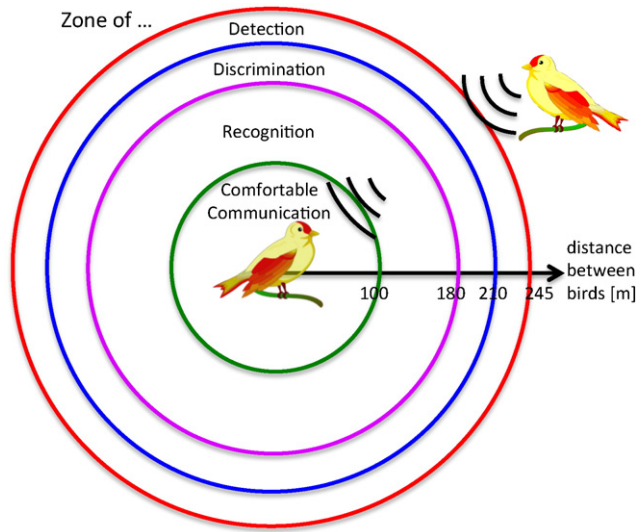
6.3. Illustrating zones of masking

The power spectrum model of masking plus CR can be applied to any spatial arrangement of caller, listener and noise source. Sound propagation in 3D space yields different received spectra as a function of range, depth and azimuth about a noise source. Zones of masking are commonly plotted as a function of range (Fig. 11) or range and azimuth (Fig. 12, Dooling et al., 2009b). Zones of masking as a function of range and depth have also been modelled (Erbe and Farmer, 2000b). An alternative illustration is provided by a so-called 'maskogram' (Erbe, 2015). An example of a maskogram is given in Fig. 13, which is based on masked hearing experiments with a beluga whale (Erbe, 2000; Erbe and Farmer, 1998). In this illustration, a ship is located along the y-axis. The x-axis points into the direction of increasing range from the ship. The broadband (32 Hz–22 kHz) received levels of the ship (with a source level of 172 dB re 1 µPa @ 1 m) are shown on a colour scale from 90 to 150 dB re 1 µPa, based on recordings in the Arctic and subsequent sound propagation modelling (Erbe and Farmer, 2000a). A calling beluga whale is positioned along the diagonal (red line), i.e., at different ranges from the ship. A listening beluga whale (white face) can be located anywhere in the plot. In the top left part (i.e., in the triangle formed by the left and the top edges of the plot and the diagonal), the listener is located between the ship and the caller. In the bottom right part of the plot, the caller is located between the ship and the listener. The ship-to-listener distance (indicated by a black arrow) can be read off the x-axis and is the sum of the ship-to-caller distance (white arrow) and the caller-to-listener distance (pink arrow) in this example, where the listener is on the far side of both caller and ship. The modelled broadband received levels of the call are plotted along the diagonal using the same colour scale (90–150 dB re 1 µPa) as for the ship. The call received level is plotted where ever the call is audible in the absence of ship noise, based on its detection threshold measured in quiet conditions (Erbe and Farmer, 1998). In the black areas, the call is predicted to be masked by ship noise, i.e., the received signal-to-noise ratio is less than the "critical" SNR measured behaviourally.

The maskogram provides a noise source-centred view of the masking scenario highlighting the zone of masking as a function of both the ship-to-caller distance and the ship-to-listener distance. At the location of the white face in Fig. 13, the listening whale is 350 m from the ship and 200 m from the calling whale. It is predicted to hear only ship noise at a received level of 113 dB re 1 µPa. If the listener
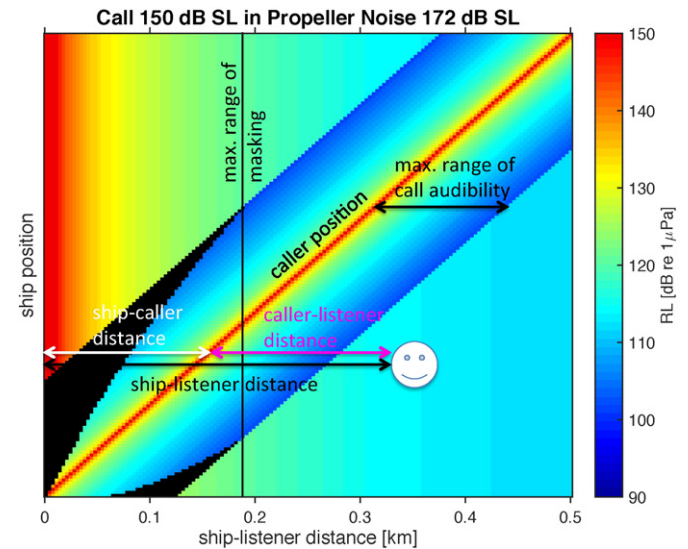

Fig. 12. Zones of detection, discrimination, recognition and comfortable communication around a listening bird (modified from Dooling et al., 2009b). Ranges are indicative only. For birds with larger CRs, the radii of the various zones will be less. In louder ambient noise conditions, the radii will also be less.

Fig. 13. Maskogram for a beluga whale call with a source level of 150 dB re 1 µPa in propeller cavitation noise with a source level of 172 dB re 1 µPa. The maximum range of masking is 188 m.

moves to the left, i.e., closer to both ship and caller, it is estimated to start to hear both ship and caller at about 260 m from the ship. Here, the ship noise is not predicted to mask the call. The animal is believed able to detect enough portions of the call through the quieter gaps in the amplitude-modulated ship noise. In addition, some of the broadband energy of the ship noise is outside of the critical band around the call. As the listener gets even closer to both ship and caller, the levels of both ship and caller increase. At 150 m range from the ship, the listener is at the same location as the caller; the call received level is maximum, 150 dB re 1 μPa. At this position, the listener is expected to still hear both call and ship. As the listener moves even closer to the ship, it leaves the caller behind, i.e., the listener is now in between the ship and the caller. With decreasing distance to the ship, the noise level rises, the call level decreases. When the listener is about 70 m from the ship and 80 m from the caller (the caller is 150 m from the ship), the listener is assumed to only hear the ship. At this position, the call is deemed masked, i.e., it would be detectable in the absence of the ship but not in the presence of the ship. If the caller is closer to the ship, less than 60 m, then the model predicts two zones of masking, one in between and one on the far side of caller and ship.

The maskogram visualizes various spatial ranges: the maximum range of audibility of the ship (17 km, if the x-axis were zoomed out in Fig. 13), the maximum range of call audibility (210 m), the maximum range of masking by the ship (190 m), and the change of the range of masking as a function of caller, ship and listener positions. Ambient noise can be added to the maskogram and would limit the range of audibility of the ship and the range of audibility of the call, hence reducing the zone of masking (i.e., the black areas in Fig. 13). As the maskogram in Fig. 13 is based on behavioural measurements where realistic signals (beluga whale calls) were played randomly in continuous ship noise, it accounts for inherent masking release mechanisms, such as CMR and within-valley listening. As a result, the zone of masking is less than what would be predicted by the power spectrum model and CR alone. While SRM was not tested in the beluga whale experiment, the spatial separation of signal and noise sources can be accounted for by including a directivity index (DI; from experimental data) of the receiver in the SONAR equation, which enhances the SNR. If a listening animal orientates towards the signal source, the received signal spectrum can be assumed optimal for detection, whereas the noise might arrive from the side or behind, where its spectrum is not optimally received, but 'degraded'. In killer whales, a SRM of up to 12 dB was observed at 4 kHz, when the signal was presented from the front, and the noise from behind (Bain and Dahlheim, 1994). SRM depends on frequency. It can be included in masking models as a spectral level difference between the received signal and noise as a function of angle about the listening animal. Maskograms as a function of angular separation between the caller and the masker are shown in Erbe (2015) highlighting the potential reduction of the zone of masking as a result of SRM.

6.4. Habitat-wide assessments

The above steps outlined how masking can be assessed for specific spatial arrangements of caller, listener and masking noise. In the field, caller, listener and noise sources move. In an attempt to incorporate these movements into a simple model of masking, Clark et al. (2009) estimated the effect of the time-varying distribution of ships on the communication space of baleen whales. Hypothetical calling whales and listening whales were distributed uniformly across the species' habitat in this modelling effort, and actual ship positions as a function of time were used to estimate anthropogenic noise levels across the study area. Recordings of ambient noise made at the site were used to determine natural ambient conditions. Sound propagation was modelled from every caller to every listener. The volume of space over which the listeners could hear each caller in quiet conditions was compared to the reduced volume of space as multiple ships passed through the habitat simultaneously. The loss of communication space for all callers

was integrated into a masking index as a function of time. This model can account for directional sources and directional hearing capabilities of the animal (via a directivity index), if this information is known for the target species. No information about directivity was available for this scenario with baleen whales. In the absence of CR information for baleen whales, Clark et al. (2009) used 1/3 octave bands combined with an equal energy hypothesis to approximate auditory processing by the whales. Equal-energy in each band determined signal detection; a higher SNR was used to model signal recognition. The outcome of this effort illustrated the potential loss of communication space in this ship noise scenario as a result of masking. However, given the lack of knowledge about hearing in mysticetes, it relied heavily on a number of assumptions.

An agent-based (animat) model (e.g., Donovan et al., 2012; Frankel et al., 2002; Mountain et al., 2013; Shyu and Hillson, 2006) can be incorporated into other habitat-wide assessments, that allow movement of callers and listeners according to behavioural rules. Such rules might include behavioural responses to noise. In theory, these models could keep track of the amount of masking each listener experiences over time. However, a large knowledge base is needed to support such a model. This includes knowledge of the propagation environment, the types of signals that are biologically relevant, the species that live in the area, the hearing capabilities of these species, their physical and acoustic behaviour etc. While some of this information is available, much is not, and for this reason, further work is needed to provide data for successful masking models for anthropogenic noise.

7. Information gaps and research needs

In order to accurately predict the auditory effects of anthropogenic noise on marine mammals, researchers must continue to develop and refine masking models that are both practical and accurate. To be practical, a model must be computationally efficient, as well as generalizable to a large class of individual animals. To be accurate, a model must account for the relevant auditory and behavioural phenomena that can significantly affect predicted masking amounts. The need for practicality and the need for accuracy are often in conflict when modelling complex natural phenomena, and auditory masking is no exception. In order to effectively balance these two needs, a research strategy must be developed that targets the information gaps most likely to degrade accuracy, and addresses these gaps in the most efficient and practical way possible.

The power-spectrum model of masking combined with CRs is a relatively simple and often effective approach. By comparing the signal level and the noise level in a narrow band of noise surrounding the signal, we can generate practical and accurate estimations of masking in a subset of natural listening scenarios (Dooling et al., 2013). However, as discussed earlier, it is likely that the numerous types of masking release that occur in natural listening scenarios make threshold predictions based on this approach overly conservative in many situations. If we can identify and quantify the forms of masking release most likely to cause inaccurate predictions, we can amend the power spectrum model using additive correction factors. This would allow accuracy to improve over time, while allowing for working models as research develops.

We have established that mammalian auditory systems are able to compare information from multiple auditory filters, and exploit the temporal properties of sound to enhance detection. These two auditory abilities have been shown to lead to several forms of masking release in mammalian species: comodulation release from masking (Branstetter and Finneran, 2008; Hall et al., 1984; Klink et al., 2010), enhanced detectability of harmonic stimuli (Buus et al., 1986; Cunningham et al., 2014b), within-valley listening and multiple looks (Erbe, 2008; Holt and Carney, 2005; Viemeister and Wakefield, 1991), and enhanced detectability of inseparable signals in separable noise (Cunningham et al., 2014b; Nelken et al., 1999).

In order to incorporate additive factors to improve the power spectrum model, these forms of masking release must be quantified and then parameterized. An example of how this can be achieved comes from Branstetter et al. (2013a), who calculated a "comodulation index" based on systematic studies of CMR in odontocetes. Such an index could serve to help generate better masking predictions when considered in addition to the power spectrum. Such efforts should be expanded to include other forms of masking release in representative marine mammal species. These research efforts can build on behavioural studies with trained animals using well-controlled experiments to determine how variations in signal and noise alter detection thresholds relative to predictions from a basic power spectrum model. The studies described in Cunningham et al. (2014b) began investigation along these lines by systematically exploring the role of FM, AM, and harmonic signal structure in detectability. However, more work needs to be done to determine how variations in modulation functions and harmonic structure influence detection before these complex features can be parameterized for inclusion in masking models.

Further, such an approach can be developed to incorporate release from masking due to spatial segregation of signals and noise (SRM), given improved experimental data to better describe this auditory phenomenon. Incorporating spatial factors into masking models may also refine predictions of expected hearing effects. The power spectrum model typically does not consider aspects of binaural hearing. Therefore, the gain in signal detectability due to the spatial separation of sounds is not accounted for in most masking models—one exception is the communication space approach that does include directivity terms (Clark et al., 2009), but there is a lack of experimental data to quantify these terms. SRM in general may or may not be an important consideration depending on the amount of spatial masking release expected in typical marine mammal listening scenarios. Lower-frequency communication sounds of marine mammals can be directional (Au et al., 2006; Blackwell et al., 2012; Lammers and Au, 2003; Miller, 2002). High-frequency echolocation clicks are highly directional (Au, 1993; Au et al., 1995; Beedholm and Mohl, 2006). Many types of anthropogenic and environmental noise can be directional (Arveson and Vendittis, 2000; Baggeroer et al., 2005; Deane, 2000; Erbe and King, 2009; Zakarauskas and Thorleifson, 1991), with directionality resulting from a combination of the emission beam pattern and sound propagation effects. Sources near the water surface (ships, seismic arrays, rain etc.) have strong vertical directivity. Studies should be conducted to identify whether or not spatial masking release is likely to be a relevant factor in estimating masking from E&P sources. After the magnitude of potential spatial effects have been experimentally evaluated, decisions can be made as to whether and how to incorporate such effects into more accurate masking models.

In addition to research on masking release that occurs within the auditory system of a listener, research must be also be continued on the anti-masking strategies adopted by various marine mammals. These studies, which focus on sound production rather than sound reception, require study of how different species alter their vocalizations in response to increasing levels of background noise. Such studies are likely to continue to be opportunistic in nature, capitalizing on situations where changes in sound production are correlated with changes in natural and anthropogenic noise. An advantage of this approach is that—in addition to providing information about whether plasticity in acoustic communication is sufficient to counter the masking effects of noise—they serve to indicate situations in which changes in the acoustic environment alter the acoustic behaviour of marine mammals (e.g., Buckstaff, 2004; Parks et al., 2007). While the absence of these effects does not necessarily indicate that masking effects are not significant, the presence of these effects underscores the apparent biological importance of call transmission to the adaptive signallers in those situations. There have been fewer laboratory studies of anti-masking strategies in marine mammals (e.g., Au et al., 1985). New approaches should be considered to improve understanding of this phenomenon. Once

such data have been generated, additive components to the power spectrum model can be developed to include increases in source level, call rate and the shifting of frequency content.

While the power spectrum model combined with CR may provide conservative estimates of masking because it does not account for the types of masking release discussed above, such a model may be liberal in other ways. By defining masking in terms of the detectability of a signal, this type of model effectively ignores the fact that animal listeners need to process the information encoded in acoustic stimuli, which often requires a higher SNR than simple detection. Psychoacoustic studies in some species of birds and humans suggest that a 2–3 dB increase in SNR is needed for discrimination of two sounds relative to the SNR needed for simple detection, a 5–6 dB increase for recognition of a known sound, and about 15 dB increase for comfortable communication (Dooling and Blumenrath, 2014; Franklin et al., 2006). These are significant values, as each 6 dB increase in signal SPL required by a listener halves the estimated communication range in a spherical spreading environment. Whether comparable increases in SNRs are required for signal discrimination and recognition in marine mammals should be experimentally confirmed for representative species. When such data become available, they can be readily added to an expanded power spectrum model to more reasonably reflect the true nature of acoustic communication and the masking effects of noise.

Finally, it is important to note that basic hearing data—such as audiograms and CRs—are of poor quality or missing for many species, including all baleen whales. Efforts must continue to provide more foundational hearing data for the modelling of potential noise effects. As understanding of auditory specializations in marine mammals develops, so will our ability to appropriately extrapolate among species groupings (see e.g., Mulsow and Reichmuth, 2010). For better-studied species, we now have the opportunity to expand on such basic auditory research by attempting to conduct more complex research with real signals (e.g., animal calls) and noise (e.g., ship noise, pile driving or seismic airgun noise), as done by Erbe and Farmer (Erbe and Farmer, 1998). While such studies provide more realistic scenarios, they also raise a number of difficulties and complexities. The challenges of addressing these applied research questions have already been broached for marine mammals (Branstetter et al., 2013b; Cunningham et al., 2014b), and additional progressive research will move the field forward as has been shown for both birds (Lohr et al., 2003) and humans.

There are additional factors that could be included in a masking model. However, a more complex model is not necessarily a more accurate model, depending on how generalizable the additional factors are. It is important to identify the most relevant of these and then to implement the correction efficiently. Further, it is possible that the inclusion of additional factors may lead to improvement in certain areas while degrading model performance in others. It is also possible that trying to account for too many factors may lead to models that are overly complex computationally. By focusing on integrating the major auditory and behavioural phenomena that are most likely to improve masking predictions, we can strike a balance between model complexity and accuracy. Because mammalian auditory systems tend to share many general features, new research with marine mammals should be based on the existing literature on auditory masking in humans and other terrestrial mammals, which is much more complete than the literature for marine mammals.

The real impetus for supporting the development of refined models of auditory masking for marine mammals confronted with—in some areas—increasing levels of anthropogenic noise comes from concern for the biological consequences of masking on these animals. The quantitative assessment of such consequences requires long-term study of acoustic exposure and individual fitness, which may be evident only over an animal's lifetime, and even then, is difficult to link to given environmental disturbances. Such modelling efforts are ongoing (e.g., Costa, 2012) and beyond the scope of this review. Here, we assume that—given the importance of sound to many marine mammals—masking is worthy

Table 4
Summary of research recommendations.

Research need	Priority	Probable cost
Masking studies investigating the effects of complex features of signal and noise	High	Medium
Masking studies investigating the effects of spatial segregation of signal and noise	High	Medium
Improved hearing data for marine mammals including new species	Medium	Medium
Studies of anti-masking strategies in wild and captive marine mammals	Medium	Variable
Studies on signal excess required for signal detection versus discrimination, recognition and comfortable communication	Medium	High
Studies of masking effects on wild animals	Low	High
Integrating new data into masking models	Medium	Low

of further study and that research needs can be identified, prioritized, and evaluated to improve understanding of the auditory effects of anthropogenic sounds on marine mammals. Our research recommendations are summarised in Table 4.

Acknowledgement

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