

HOW HARBOUR PORPOISES UTILISE THEIR NATURAL ENVIRONMENT AND RESPOND TO NOISE

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Abstract:	The harbour porpoise is thought to be in decline in Danish waters and is a protected species in European waters. Effective protection requires information not only on the threats present, but also their impacts, which in turn relies upon sufficient knowledge of the normal behaviour of the species. Tagging studies have begun to provide some of the needed information, but datasets remain small and are often inconsistent due to high individual variation between animals. Accordingly, this Ph.D. thesis provides further insight into natural behaviour of the porpoise in Danish waters, in addition to which it considers how acoustic impacts may influence that behaviour. The work consisted of several different approaches. Firstly, as tagging studies are currently the only method to obtain some of the needed information, combined acoustic-behavioural loggers were deployed on porpoises with satellite transmitters and the possible impacts of such methodology were assessed. Subsequently, established behavioural criteria for the identification of sleeping activity were used to identify potential sleeping behaviour from the resulting data and investigate any daily patterns that were present. Secondly, this Ph.D. thesis also presents a new tag-release system for lower-impact attachment of the larger combination fastloc GPS-biologger tags. The main advantage of these units is that they can provide 3-dimensional movement and location information with greater accuracy than previous units. This will not only facilitate more detailed analysis of habitat use in the porpoise, but also permit assessment of various acoustic impacts in this species in situ. Finally, acoustic impacts are discussed in this Ph.D. thesis. Such impacts can be quite subtle and likely interact with other pressures on porpoises in their natural environment, as discussed here with regards to a mass stranding of porpoises in North-West Denmark in 2005. This Ph.D. thesis concludes with a review of current advice regarding management criteria for acoustic exposure in marine mammals in general.
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Marine mammal acoustic exposure criteria revisited

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Abstract

The fact that noise in the ocean from anthropogenic activities can interfere with marine life interacting with their environment has been realised gradually over the last 4 decades, with an associated rise on the political agenda. A number of assessments over this period eventually led to the extensive review by Southall et al. (2007), who also offered initial scientific guidance regarding noise exposure criteria. While that review emphasised that current scientific understanding remains imperfect and that much information is incomplete or lacking at best, the proffered criteria filled a large policy vacuum, thus quickly becoming the *de facto* standard. In the present paper we undertake a critical, but constructive review of these criteria with the intention of adapting them for wider relevance. Specifically we address the assumptions upon which the criteria are based, as it is here that the greatest risk of misinterpretation of the guidance lies. This treatise thus assesses the fundamentals behind the exposure criteria through the consideration of: permanent threshold shift as a metric for onset of injury; the theory behind the M-weighting; the severity of behavioural responses as a reliable indicator for non-injurious impact; and the concept that a lack of response can indicate a lack of impact. Finally, we offer advice in the continual process forward on the issue of acoustic impacts, suggesting a more fitness-based approach.

Key words: Underwater noise, temporary threshold shift, impact assessment, behavioural response, hearing.

1 Introduction

Hearing is the primary sense for most marine life to interact with their environment, including detecting signals from prey and predators, signals from conspecifics and competitors, and for toothed whales also echoes of their own signals. Noise introduced into the environment by human activities thus has the potential to interfere with this interaction, in addition directly affecting exposed animals (e.g., NRC 1994, 2003, 2005, Richardson et al. 1995, Hildebrand 2005, MMC 2007, Nowacek et al., 2007). This fact has been realised gradually over the last 4 decades and as a consequence underwater noise has gradually moved up on the political agenda. A seminal review was made by (Richardson et al. 1995). In this review the focus was primarily descriptive; a collection of all available information on relevant noise sources and studies of their impact on marine mammals. A decade later (Southall et al. 2007) made an updated review of much of the available literature and offered initial scientific guidance regarding noise exposure criteria. Although scientifically based, this paper is heavily influenced by, and targeted to, policy in the United States because the suggested criteria are based on the legal definitions of injury and behavioural harassment under the U.S. Marine Mammal Protection Act (MMPA). As a consequence of this, the scientific recommendations provided by (Southall et al., 2007) may not be fully appropriate for direct application in other countries, or even under other domestic legislation in the United States, such as the Endangered Species Act (ESA). Several non-U.S. legal frameworks, such as the European Habitats Directive (92/43/EC) and the Marine Strategy Framework Directive (2008/56/EC) focus more on sustaining populations, the habitats that support them and the ecosystems of which they are a part, rather than accounting for takes of individual animals.

Nevertheless, even though Southall et al. (2007) emphasises that current scientific understanding remains imperfect and that much information is incomplete or lacking completely, the criteria suggested by Southall et al. (2007) filled a policy vacuum. The urgent need for someone to step forward and propose actual exposure criteria meant that the suggestions of Southall et al. (2007) quickly has acquired status as the *de facto* standard in many political processes around the world, despite limitations and caveats inherent to an issue as complex as that of noise effects on marine mammals. There has been surprisingly little constructive debate over the contents of their initial recommendations and no substantive alternative have still yet been offered (but see Ellison et al., 2011).

Southall et al. (2007) deserves much credit for suggesting actual exposure criteria, although such a move inevitably attracts criticism. Some sources claiming that the criteria are too restrictive on particular industries, some that they are not nearly restrictive enough and still others criticising the criteria for simply being premature, based on insufficient knowledge and incapable of capturing all the intricate but yet relevant differences among the many species of marine mammals and the many different contexts wherein potential conflicts occur.

In attempt to further the process of identifying meaningful approaches to mitigate noise effects on marine mammals we here undertake a critical, but constructive review of the guidance and recommendations presented by (Southall et al., 2007) with the intention of adapting them for wider relevance, hopefully beyond the consideration of any specific legislative standards. Although we do consider some new concepts that were not included in the review by Southall et al. (2007), the discussion that follows does not represent a comprehensive updated review of all the available literature. Rather we attempt to constructively critique not so much the original conclusions, but more the assumptions which underlie the conclusions.

Often the greatest dangers in transfer of scientific guidance to legislation is not misinterpretation of the guidance itself but failure to realise the limitations given by the implicit and explicit assumptions underlying the recommendations. The treatise below fall in two sections following discussions in Southall et al. (2007); exposure criteria for injury and exposure criteria for behavioural disturbance.

2 Exposure criteria for injury

Southall et al. (2007) develops the first general exposure criteria for marine mammals. In doing this, they make a number of principal and necessarily simplifying assumptions. Of these, three are considered by us as being key assumptions: 1) that a signal must be audible, in order to be capable of inflicting damage, 2) that risk of impact scales with loudness-weighted sound exposure level (signal energy), and 3) that permanent threshold shift (PTS) should serve as the basis for defining safe exposure limits. These assumptions will be discussed and challenged in the following.

2.1 Audibility as prerequisite for impact

Marine mammals in general have acute underwater hearing, and for that reason, the auditory system is considered to be the first to suffer from injuries when exposed to increasingly powerful noise (Southall et al., 2007). Specifically, permanent threshold shift (PTS) is considered by Southall et al. (2007) to be the lowest received levels that can be expected to cause direct injury to the animal.

Sound exposure, however, may also induce other, potentially injurious effects that are more subtle or hard to measure, and hence be overlooked, particularly in marine animals. One such parameter is physiological discomfort, which is very hard to quantify unless it is extensive enough to materialize in the forms of increased levels of stress hormones or reduced fitness over long periods of time. Several studies on human divers indicate that sound exposures can cause long term physiological effects with consequences for fitness that may not be reliably detected through elevated levels of stress hormones or reduced auditory capabilities in the form of temporary threshold shift (TTS).

Steevens et al. (1999) report two cases of what appears to be noise-induced neurological disturbances in two navy divers. The first diver was exposed to 160 dB re 1 μ Pa (rms) for 15 min (190 dB SEL) at 240 Hz, causing no measurable TTS. However, at the end of the exposure he reported light-headedness, somnolence, blurred vision and a vibratory feeling in his extremities, and he was unaware that the sound source had been turned off. Half an hour after the exposure and after being decompressed from 3 ATA, the diver again reported to experience nausea and only responded to strong verbal stimuli. These symptoms abated within 30 min and none of physiological variables measured during or after the exposure could explain his response. Three weeks later he again suffered from an episode of light-headedness, memory loss and nausea and, despite an intense neurological workup, no cause could be established. After 9 months he subjectively assigned continued impairments in the forms of insomnia and memory loss to the sound exposure. Sixteen months after the exposure he was undergoing anti-seizure and anti-depressant therapy.

In the second case study of Steevens et al. (1999), a diver was exposed to 181 dB re 1 μ Pa (rms) for 15 min (210 dB SEL) at 1000 Hz. That caused along with a TTS of 19.2 dB, a feeling of light-headedness, inability to concentrate, agitation, blurred

vision and head vibrations. The following day the diver reported an increased sensitivity to noise. Two weeks after the exposure, he still experienced heightened sensitivity to noise, increased irritability and concentration problems. A year later he reported that he still felt that he had not recovered fully having concentration problems and mood swings.

Similar conditions were also reported over the short-term by Montague & Strickland (1961), who asked 23 divers to turn up the level of a 1500 Hz pure tone until it became unbearable. The level at which 50% felt that to be the case was 200 dB re 1 uPa (rms), but the paper provides no information on the duration of the exposure at those levels. At exposure levels of some 190 dB re 1 uPa (rms) all divers reported to feel the sound and that their visual fields were rotated and distorted. This oculo-gyral motion coincided with the onset of the tone and was maintained until the tone stopped. All divers displayed a TTS of 6-7 dB five minutes after the exposures which is comparable to the TTS induced in most marine mammal studies (Schlundt et al., 2000; Finneran et al., 2002a; Lucke et al., 2009).

While correlation does not equate causality, these studies nevertheless suggest that exposures with SELs around or even below those shown to cause TTS may under some circumstances lead to long term neurological disturbances. The consistent effects on the visual system suggest that the mechanism behind these neurological disturbances relate to over-stimulation of the vestibular system that has a strong oculocomotor feedback (Parker et al., 1978). There are to our knowledge no dedicated studies of this in marine mammals, but during intense sound exposures some navy dolphins have displayed behaviours, such as biting the experimental setup or refusing to return to the bit plate that may perhaps be indicative of some level of discomfort (Schlundt et al., 2000; Finneran et al., 2002a). It is presently unknown if such responses are short term and merely reflect annoyance on the part of the animal or if they in fact are tell-tale sign of similar neurological disturbances and discomfort indicated for some human divers at similar or lower sound levels.

The methodology currently in use during intense sound exposure experiments in marine mammals is in our opinion unable to uncover such effects. It is therefore possible that marine mammals may, in at least some cases, suffer from noise-induced neurological disorders that go undetected, but which are potentially much more problematic than TTS. Such neurological effects may not only be problematic from an animal welfare point of view, but they are also likely to have fitness effects in the form of reduced vigilance if induced in the wild. We argue that the human diver studies suggests that marine mammals may, at least under some circumstances, suffer from neurological disorders induced by acoustic over-stimulation of the vestibular system at levels at or below those reported to cause TTS. This possibility calls for specific investigations on this issue for marine mammals. The fact that an air adapted ear and vestibular apparatus of humans does suffer from these effects lend weight to the supposition that an acutely adapted ear to water such as that of whales would prone to suffer from the same effects at comparable or lower levels.

2.2 Scaling of impact with loudness-weighted energy

For obvious reasons it is impossible to develop exposure criteria for all possible sound sources and thus there is a fundamental need for a common metric, which can be used to assess several types of sounds and also sounds for which no experimental data are available. As pointed out by Southall et al. (2007) and many others, it is essential to take the hearing of the animal into account when evaluating the impact of a particular sound. This follows implicitly from the assumption of

audibility as a prerequisite for impact and thus the most fundamental feature in this respect is audibility: can the animal hear the sound and if so, how loud is the sound perceived to be (i.e., loudness)? From this stems the method of frequency weighting of sound.

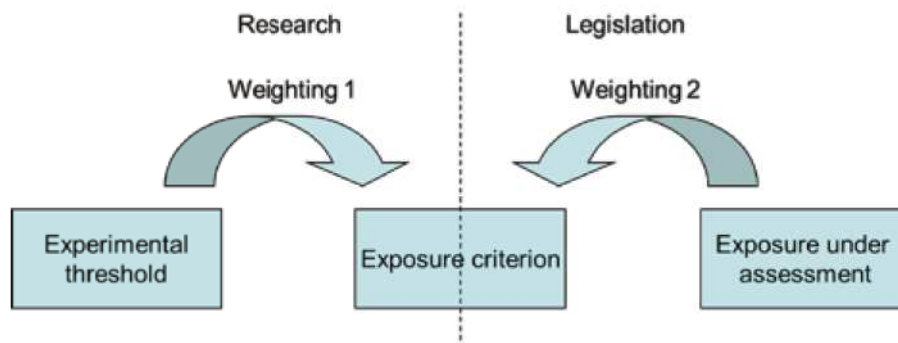
Conceptually, frequency weighting is straightforward by consisting of a band pass filter that fully or partially remove those parts of the signal which fall outside the range of best hearing for a given group of animals with similar hearing. In human audiology this is done through a series of weighting curves, developed to suit different types of sound. Two of these are discussed by Southall et al. (2007): the A-weighting curve and the C-weighting curve. The differences between these weighting functions are found in the steepness of the curves towards low and high frequencies and the extent of the flat pass band in the centre.

Most routinely used in human noise assessments is the A-weighting filter (Anonymous, 2004). The A-weighting is close to being an inverted human audiogram, meaning that sounds are weighted according to their audibility by humans. The justification for the A-weighting is straight-forward: when evaluating the effect of a sound it makes sense to include only the part of the sound which is audible to humans. C-weighting then, is an alternative to A-weighting that is intended to better reflect human sensitivity to louder sounds. Two additional weighting curves, the B-weighting and the D-weighting are no longer used and are not discussed.

Southall et al. (2007) introduce and discuss an analogue to C-weighting for marine mammals, the M-weighting. The M-weighting is subdivided into five functional and taxonomic groups (low frequency, mid frequency and high frequency cetaceans, pinnipeds in water and pinnipeds in air). It is debatable if the used frequency limits are correct and whether there ought to be more groups, but these discussions must await better hearing data from baleen whales in particular. Here we will only consider the fundamental assumption, that an analogue to the less known and little used C-weighting from human audiometry should be used as model, rather than the ubiquitous A-weighting. Both A- and C-weighting functions are based on equal loudness contours for humans, reflecting the fact that how loud a sound is perceived by a human is not directly related to the sound pressure, but a function of both frequency and sound pressure. Loudness is measured in Phon and the A-weighting curve is based on the 40 Phon iso-loudness curve, which corresponds to the sound pressure level at different frequencies where a sound is perceived as being as loud as a pure tone at 1 kHz at 40 dB SPL. The 40 Phon iso-loudness curve roughly parallels the shape of the human audiogram, but is offset with 40 dB. C-weighting on the other hand was introduced to quantify the loudness of more intense sounds and is modelled to roughly follow the 80 Phon iso-loudness curve, the argument being that this weighting would be better at capturing the loudness and presumably also better reflect the impact of loud noise. This assumption, however plausible it may seem, is nevertheless essentially without experimental support and C-weighting, even of loud sounds have been replaced by A-weighting in almost all human community noise regulations (e.g. 2000/14/EC; 2002/49/EC). Even for short impulsive sounds, such as gunshots, where the C-weighting is still recommended when recording peak levels, A-weighted levels correlate significantly better with annoyance, as rated by human observers, than does the C-weighted levels (Vos, 2003; Meloni & Rosenheck, 1995). There is thus a need for a second look at the justification for using C-weighting-based M-weighted levels in marine mammals.

A second argument put forward by Southall et al. (2007) for a C-weighting analogue for marine mammals is that the weighting curve is wider than the audiogram and hence results in conservative criteria (i.e. providing stricter than needed pro-

Figure 1. Frequency weighting must be performed twice; first when establishing the criterion from data (left), then when exposures are subsequently compared to the criterion (right).



tection of the animals), as weighted sound levels are, if anything, overestimated. In reality, this reasoning is potentially flawed, as it depend upon if the frequency weighting is being used to establish exposure criteria, or if it is being used to compare a sound to already established criteria. In a situation with scarcity of data each of the two steps should be to the precautionary side to allow for conservative judgements to the benefit of the human or animal to be exposed. However, what may not be immediately evident is that a clearly conservative approach in the first step will be the direct opposite in the second step and vice versa. This is due to the fact that the first step deals with determining the lowest level of sound capable of producing a response/damage (establishing an exposure criterion), whereas the second step is the reverse: determining whether a given sound exceeds the exposure criterion (Figure 1).

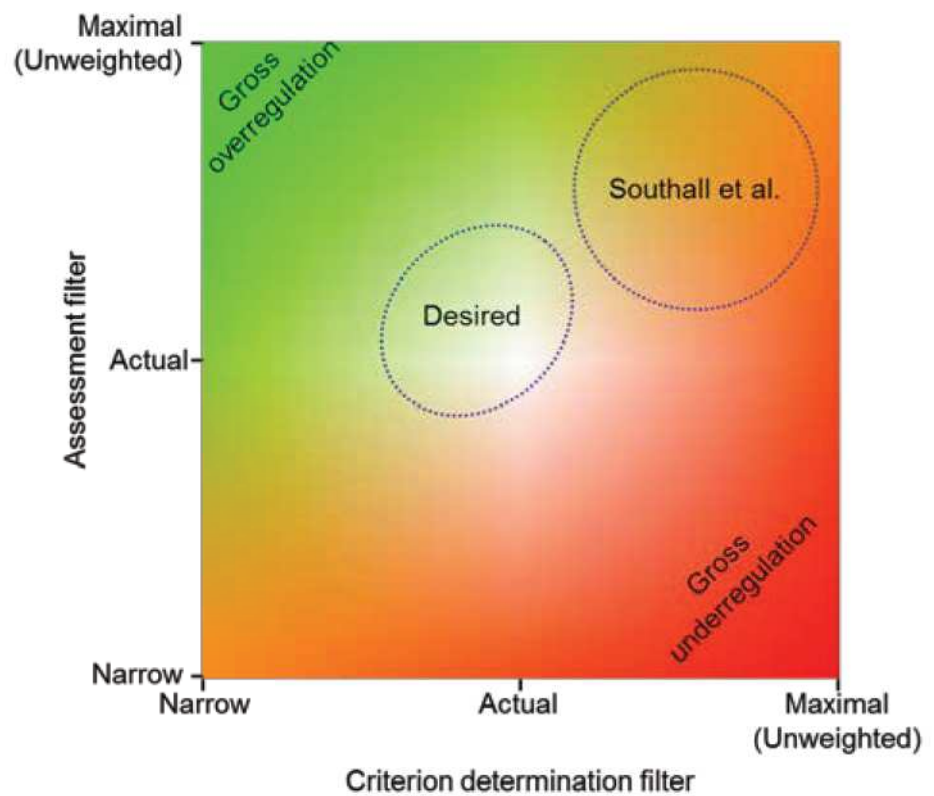
No matter how limited information is available, an exposure criterion must be based on some experimental data. Thus, there are two sides to an exposure criterion (Figure 1): establishment of the criterion from data (research or establishment side) and use of the criterion in assessments (legislation or application side). Frequency weighting can (and should) be performed on both sides: when establishing the criterion (establishment of the weighting function) and again when assessing impact of a particular sound, i.e. comparing the sound to the established criterion (application of the weighting function). Ideally, the two weighting functions are identical and match the actual weighting function of the ear. This is by and large commonly agreed to be the case for A-weighting in humans as this function is based on an overwhelmingly large experimental and clinical evidence. However, the two functions need not be identical. Realising how little we know about hearing and effects of noise in marine mammals, it makes sense to be conservative if there is doubt about the true form of the function, i.e. deliberately select a weighting function that is more likely to lead to tighter regulation of activities than actually needed (the precautionary principle). However, it turns out that errors committed on the establishment and application sides are not reciprocal. A conservative weighting for one side turns out to be the opposite on the other side. Why is that? Consider the following relationships:

$$L_{unweighted} \geq L_{wide} \geq L_{actual} \geq L_{narrow}$$

where L denotes sound pressure level of any sound weighted by different weighting functions, of which one corresponds to the actual weighting in the ear, one is too wide and one is too narrow.

The unweighted (broadband) sound pressure level will always be equal to or greater than any weighted sound pressure level. The more restrictive (or the narrower) a weighting function is, the more sound energy is filtered out and the lower the weighted sound pressure will be. When going from data to criterion (the establishment side of the criterion, on the left in Figure 1) the precautionary principle

Figure 2. Consequences of using different combinations of weighting functions in establishing criteria (horizontal axis) and assessing noise against criteria (vertical axis). Green indicates conservative areas, red indicates liberal areas. White spot in centre is optimal point.



would dictate using a filter not wider than the actual weighting in the ear of the animal, i.e. to the narrow side. This will lead to an underestimate of the criterion, i.e. the criterion will be below the level where effects actually incur. In contrast, when assessing impact (the application side of the criterion, on the right side in Figure 1), and a given sound is compared to the established criterion, the precautionary principle dictates the use of a filter that is at least as wide as the actual filter. This will lead to an overestimation of the potential impact of the assessed sound, i.e. the sound will be regulated to the criterion at a level below the actual level at which effects incur.

Figure 2 illustrates the consequences of selecting different combinations of weighting filters. The white spot in the centre illustrates the desirable point where frequency weighting actually conforms to the physiology of the ear. To the upper left is the point where a narrow filter (or weighting) is used in establishing the criterion and a wide filter (or weighting) used in assessments. This leads to certain over-regulation, which is not desirable, but it is at least safe to the animals. Opposite this point, in the lower right, is the least desired combination, leading to certain under-regulation, but also conferring the least protection to the animals. Along the lower left to upper right diagonal are the combinations with uncertain outcomes. In the best cases biases will cancel out, leading to the most appropriate level of regulation, but it is much more likely they will lead to errors to either side.

Now, returning to the suggested criteria of Southall et al. (2007), they discuss only the right (application) side of figure 1, comparing sounds to the established criterion. When doing so, they deliberately selected the shape of the weighting function to be wider than they actually believe it is, in correspondence with the precautionary principle, as described above. However, by doing this they introduce an underestimation on the left (establishment) side of figure 1. The result of this is that their criteria fall somewhere into the upper right part of figure 2, with an uncertain outcome.

A few examples will illustrate the problem. First the simplest situation, where an exposure criterion is established for a particular sound, for example an air gun pulse, and this criterion is later used to evaluate exposure to the very same sound in a different context. In this case it does not matter if the weighting function is too wide, as the error committed on the left side cancels out completely with the error with opposite sign committed on the right side. A second example would be a criterion based on exposure to a sound well within range of best hearing of the animal, but used to assess potential impact of a second sound which is on either the upper or lower end of the hearing range. The weighted level of the sound used to establish the criterion will be virtually identical to the unweighted level, as it falls within range of best hearing, even if the weighting function used is too wide ($L_{\text{wide}} = L_{\text{actual}}$). The weighted level of the sound being assessed against the criterion will be too high, however ($L_{\text{wide}} > L_{\text{actual}}$), because energy outside range of best hearing is included. What does this mean? This means that the sound under assessment will be considered to have an impact at lower levels than is actually the case, i.e. a conservative (protective) regulation. The third example is the reverse, where a sound at the edge of best hearing is used to establish a criterion which is then later used to assess potential impact of a second sound well within range of best hearing. Here the signs switch and an under-regulation is the result. The signal under assessment is compared to a criterion which is set too high, because a weighting function too wide was used. From these examples follows that care should be taken when using a criterion established with one type of sound to assess impact on other sounds, in particular if the sound used to establish the criterion is outside range of best hearing and the sound under assessment is within range of best hearing.

2.3 PTS as basis for definition of exposure limits

Once a weighting standard is defined and accepted, exposure criteria need to then be based on some threshold of impact. For reasons of U.S. legislation, Southall et al. (2007) selected the occurrence of injury and behavioural responses. While we discuss the appropriateness of the use of behavioural responses as a threshold for exposure criteria below, we generally agree that use of injury as one threshold for impact is appropriate. However, the determination of what exactly constitutes injury is up for debate as we will outline below.

Injury may be defined as the temporary or permanent impairment of a body function inflicted by events in the environment. In the case of noise induced injuries in marine mammals, they can be divided into direct and indirect injuries. Indirect injury involves sound induced behavioural and physiological changes that can subsequently lead to injury or death. This can either happen as a consequence of a flight response where animals strand themselves or through noise induced changes in behaviour that lead to changes in physiological regulation of the body with fatal or near fatal consequences (Hooker et al., 2012). Prominent examples of that are mass strandings of beaked whales where one or more animals have been injured or died following exposures to intense mid frequency sonar pulses that by themselves are not causing direct injuries (Hooker et al., 2012). It still remains unclear whether beaked whales die because they strand themselves as a consequence of a flight response to the sonar sounds or if they suffer from a lack of fatal or near fatal mitigation of nitrogen loading, leading to decompression sickness and secondarily also strandings. Either way, both modelling (Zimmer & Tyack, 2007) and play back experiments (Tyack et al., 2011) strongly indicate that beaked whales may suffer from indirect injury or death from exposure to mid frequency sonars at levels that are orders of magnitude lower than those that would be required to cause direct injury.

Direct injury involves sound exposures that are high enough to impair the function of some parts of the body of the exposed animals. In extreme cases such exposures may directly cause fatal injuries, but available data suggest that requires levels of exposure well in excess of 230 dB re 1 uPa (peak) (Richardson et al., 1995). Such high sound levels are really only realized when using explosives in, for example, ship shock trials or very close to pile driving. The zone around the source at which fatal injuries will occur is small enough (less than 1000 meters even for larger charges) that this is one of the impacts of noise that can be effectively avoided through careful monitoring prior to the blast. However, non-fatal injuries can be generated at much lower received levels that may have long-term animal welfare and fitness consequences for the exposed animal, calling for a conservative assessment of when such injuries should be expected.

TTS is not considered by Southall et al. (2007) to be an injury as the hearing threshold of the animal by definition recovers. That line of reasoning may seem a little peculiar as animals and humans suffer from a range of injuries (such as a broken leg) that they may recover from without permanent problems, and yet they are considered injuries. However, in most cases, TTS disappears over minutes or hours, so the effect of elevated hearing threshold from noise exposure is indeed reversible over shorter time periods than most other common non-fatal injuries. Nevertheless, there are, in our view, several problems with using sound exposures required to generate PTS as onset for concern about injury in marine mammals. For good reasons, PTS has not deliberately been generated in marine mammals. Rather it is assumed that PTS will occur at SELs for pulses 12 dB higher than those that generate TTS as is the case for terrestrial mammals (e.g., Ahroon et al., 1996). Southall et al. (2007) use 6 dB as onset for concern for onset of PTS, but then also use 6 dB poorer hearing as onset for TTS, so the PTS is proposed to happen at SELs 12 dB higher than the SEL that starts to change the hearing thresholds for TTS.

To estimate onset of PTS for free ranging animals, it is required that the onset of TTS can be measured reliably and in a way that is representative for a young, healthy animal with good hearing in the wild. Despite very careful and meticulous experimental approaches (Finneran et al., 2002b; Nachtigall et al., 2003), the TTS studies so far made on toothed whales are, at least to some degree, potentially affected in two ways that may lead to an overestimation of levels required to generate TTS. One potential problem pertains to the issue that at least earlier studies were conducted under noisy conditions in sea pens that lead to derivation of masked hearing thresholds set by the ambient noise (Au et al., 1999; Nachtigall et al., 2003, 2004) or by an introduced masker to stabilize noise levels (Finneran et al., 2000; Schlundt et al., 2000). This means that the onset for TTS will be overestimated because the true baseline hearing threshold is never established. That problem has been partly alleviated more recently by doing TTS experiments in quieter tanks (Finneran et al., 2002a). But that does not preclude a potential second problem; that the dolphins used in the Finneran et al. (2002a) TTS experiment both had hearing thresholds in the relevant frequency band that are some 10 dB above the lowest thresholds measured for that species in younger animals (Johnson et al., 1968a). It is therefore at present debatable if the TTS levels derived are in fact representative for young bottlenose dolphins and Belugas. Three recent studies (Lucke et al., 2009; Popov et al., 2011; Kastelein et al., 2012) on porpoises have generated TTS at SELs considerably lower than reported for the two larger toothed whale species. Future studies will hopefully elucidate if such differences are indeed species specific or at least in part related to different methodologies, masking levels or age classes of animals. The critical point for the consideration here is that the onset for concern of injury for a given marine mammals species is currently viewed to happen 12 dB for pulses and 26 dB for continuous noise above SELs that just evoke TTS whatever those levels may be. Hence if the TTS levels are overestimated so will the SEL thresholds for injury.

Another and perhaps more fundamental problem related to defining the onset of injury is that injury may in fact occur at levels that are considerably below those estimated to cause PTS. The threshold for concern of injury of $PTS = TTS + \text{a scaling value dB}$ hinges critically on the assumption that the auditory system is by far the most sensitive system in the body, and that the hearing at large is unharmed if the hearing threshold returns to normal. There are data from other species that question both these fundamental assumptions of Southall et al (2007) as we will outline below.

TTS is by definition a temporary elevation of hearing threshold that returns to normal after a period that relate to the intensity and duration of the noise exposure. TTS does not involve the destruction of hair cells, but is instead caused by swelling of cochlear nerve terminals similar to that resulting from excitotoxicity (Kujawa & Liberman, 2009). Recently, it has been shown that levels causing reversible TTS will in fact also lead to permanent degeneration of cochlear afferent nerves (Kujawa & Liberman, 2009). So while the thresholds are intact, this degeneration may compromise more complex auditory processing and lead to a reduction of stimulus encoding under noisy conditions, tinnitus and hyperacusis. Thus, while TTS is reversible in terms hearing sensitivity, these revealing recent data very much question the notion that TTS, no matter how severe, is associated with benign sound exposure levels when considering functions that are vital for auditory scene analysis and hence ultimately fitness for many aquatic mammals that rely on sound for navigation, communication and foraging.

We acknowledge that TTS plus some dB value to approximate PTS is a convenient metric for injury assessment because it is well defined and because it is, at least for smaller marine mammals, possible to measure with evoked potential techniques. However, based on the examples outlined above, we argue that there is mounting circumstantial evidence to suspect that injury in the form of damage to cochlear afferents or neurological disturbances induced by acoustic over-stimulation of the vestibular system may occur at sound levels lower than those expected to cause PTS. Consequently, the claim that the onset for concern about injury may be conservatively placed at a level of sound exposure that is 12 dB higher than that required to elevate hearing thresholds at the onset of TTS (as per Southall et al., 2007) is in our view not necessarily conservative nor correct. The fact that there are strong indications of neurological disturbances and permanent damage to cochlear afferents at sound exposure levels at or just above those required to generate moderate TTS in other mammals should, in our view, imply that the onset for concern for injuries should be placed at the sound exposure that leads to TTS (for example using the 6 dB hearing threshold shift definition of Southall et al., 2007) in a given species and not PTS. Injury has not been documented in marine mammals at those levels, but one obvious reason is that we have not looked for it when just testing detection thresholds. It seems very clear from studies on mice and humans that PTS is certainly not a conservative proxy for the onset of injury. We therefore advocate that the SEL or peak pressure required to generate statistically significant TTS, as established for a group of animals for a given noise type, is used to define the limit below which there is little risk of direct sound induced injuries.

3 Exposure criteria for behavioural responses

Exposure criteria for behavioural responses to underwater sound are discussed at length by Southall et al. (2007), but they conclude that it is still premature to establish general limits for safe exposure. This conclusion is reached in realisation that the experimental results upon which such criteria should rest are too scattered across taxonomic groups, types of sounds/noises assessed and contexts under

which observations or experiments were conducted. Nevertheless, in discussing the available results and in particular the obvious research needs, a number of assumptions are made. Of these, two are considered by us as key assumptions and will be discussed in the following. First is the assumption that impact scales with severity of the behavioural reaction and second is the assumption that absence of a detectable reaction can be equalled with an absence of impact.

3.1 Scaling of impact with severity of response

The discussion of behavioural criteria by Southall et al. (2007) takes off from a thorough review of the diverse literature and a filtering of reports to include only studies and observations that contained sufficient information with regards to the specifics of the exposure and observed reactions to allow inclusion in a meta-analysis. For each study Southall et al. (2007) then assign severity scores to the reported reactions per weighted individual at the given exposure level. These are intended to infer the importance of these behaviours in terms of their potential to induce non-lethal consequences for marine mammals that will compromise their ability to survive and reproduce successfully (i.e., that are detrimental to the animals' fitness). Southall et al. (2007) then created a frequency distribution table for each combination of functional hearing group and sound exposure type accordingly.

Ellison et al. (2011) later revisited the severity scale behind the behavioural criteria. Most importantly, they discussed the need for behavioural responses to be considered in terms of their audibility to the receiving animals. Furthermore, they indicate that contextual factors such as prior experience and current state and activity of the receiving animal, as well as its spatial relation to the sound source will be highly influential, especially at the lower end (categories 0-4, ranging from no observable response to moderate changes in locomotion or vocal behaviour) of the severity spectrum. However, they maintain that a dose-response relationship (as per Southall et al., 2007) is more likely to be acting at the higher severities (5-9, ranging from more prolonged changes in locomotion or vocal behaviour to anti-predator behaviours and outright panic), although there is likely to be some overlap in the middle (4-5). Although not explicitly stated, the severity scoring system (along with similar efforts presented in other notable reports on this topic, e.g., NRC, 2005) is based on the assumption that a greater behavioural response is indicative of a greater impact to the animal.

In this, the fundamental assumption is that behavioural reactions provide a reasonable proxy for the size of 'impact'. Impact can be defined in several ways. In the following we use a definition of impact as 'a negative change in the ability of an exposed animal to survive and reproduce successfully': i.e., something that is detrimental to the animals' fitness. Noise exposure can result in reduced communication, stress responses, reduced energy intake or increased energy expenditure and attention diversion, as well as other mental states and conditions (such as induced fear, learning difficulties and altered cognitive bias), all of which can have fitness implications (e.g., Bateson, 2007; Clarke & Stansfeld, 2007; Wright et al., 2007a,b; Götz & Janik, 2011). Likewise, they can all influence the subsequent behaviour of the animal, included responses to later exposures to noise events. However, as these indirect or long-term consequences in most cases are beyond our present capability to study in wild animals (with notable exception such as Lusseau et al., 2006), which is why immediate behavioural responses is the primary choice for researchers and subsequently used by legislators and managers. On closer inspection it is clear however, that a general scaling of impact (fitness consequences) with severity of the immediate behavioural reaction is not present. For example, it has been argued that behaviours induced immediately in response to some acoustic exposure (e.g., alarm or defensive responses; approach; aggression) are

merely short-term reactions and that these are insignificant in terms of long-term fitness consequences (e.g., Finneran & Jenkins, 2012). However, there are now indications that fear conditioning can arise through acoustic startle reflexes observed in grey seals (Götz & Janik, 2011). Accordingly, these seeming insignificant brief behavioural reactions may in fact lead to a more prolonged disruption of, for example, sleeping and resting behaviour.

Similarly, avoidance as an active process is often considered to be a useful reaction, reducing the exposure of the animal, and as such is incorporated into mitigation plans through soft-starts and ramp-ups. However, when avoidance, or some other response, is mal-adaptive the consequences for the animal may exceed the apparent severity of the reaction (e.g., Beale & Monaghan, 2004; Beale, 2007). For example, this would occur if the interruption of beaked whale diving behaviour leads to decompression sickness-like results (as may be the case: Cox et al., 2006; Rommel et al., 2006; Tyack et al., 2006) or if moving near to the surface in response to novel sounds increases the risk of ship strikes (as described for right whales, *Eubalaena glacialis*, Nowacek et al., 2004). More problems arise regarding observations of a general lack of response in a population, as this may result from the previous unseen abandonment of the area by a sensitive subset of that population (Bejder et al. 2006a,b). Similarly, it has been argued that a reduction in behavioural reaction over time may indicate an end of impacts as the animals have become 'habituated' to the disturbance (e.g., MMS, 2007). However, this may in fact simply be tolerance of exposure due to necessity of access to a habitat, learning that the noise does not represent an immediate threat to life, or acceptance that avoidance may not be possible. Such eventualities have been discussed in detail elsewhere, along with the details of the concepts of tolerance and habituation (see Wright et al., 2007a,b; Bejder et al., 2009).

3.2 Absence of reaction equals absence of impact

A logical consequence of the severity index scoring is that no reaction implies no impact. This assumption implicitly carries a prerequisite: that all reactions to the sound are observable. There are, however, several reasons why this might not be the case. For example, a study may simply not be set up appropriately to detect the actual response. This may be due to the experimental design, (such as undertaking a visual study when the response is acoustic, or more subtly looking for periods of silence while actual vocal responses involve altered signal characteristics), an inadequate baseline or control for comparison, or perhaps the resolution or unit of the statistical analysis (for example, considering responses over the first hour, when the first day would be a more appropriate unit, or vice versa). Behavioural responses may also go unnoticed if they are simply changes in behavioural state that might otherwise be considered normal (e.g., a change from foraging to travelling) or if they are manifested in terms of behaviours that do not occur that would otherwise have done so. The latter could result from either some suppressive effect perhaps mediated by a fearful response, or a missed opportunity as could occur through disruption of foraging behaviour (e.g., Williams et al., 2006) or if the presence of a prey item was obscured by noise or simply distraction. For example, in one study of bottlenose dolphin (*Tursiops* spp.) responses to whale-watching in Doubtful Sound, New Zealand, females responded linearly to increased disturbance intensity while males almost immediately adopted an avoidance strategy by substantially increasing their dive duration, without further increases with intrusiveness (Lusseau, 2003). Had the sex of the animals been unknown and all individuals pooled, a single statistical test may thus have resulting in non-significant results for either type of response.

Another problem is that various responses that carry fitness consequences can occur with no obvious external reaction at all, including acute, prolonged or repeated stress responses (see Fair & Becker, 2000; Wright et al., 2007a,b), diversion of attention that may lead to increased susceptibility to predators (or other human interactions; Todd et al., 1996; Wright et al., In review; and also suggested by Nielsen et al., 2012) or failure to take advantage of foraging opportunities, and annoyance. Fitness consequences of disturbance may also be more direct, as in the case of an observed increase in perinatal deaths of bottlenose dolphin in Doubtful Sound in association with an escalation in whale-watching activities (Lusseau et al., 2006).

One of the most commonly discussed mechanisms for noise to produce effects without behavioural responses is through masking (Møhl, 1980, 1981; Clark et al., 2009). Masking is the concealing or obfuscation of one sound as a consequence of the presence of another sound. In addition to interfering with the detection of signals from prey, predators or conspecifics, human-introduced noise can interfere with detecting signals of interest, including sounds for auditory scene analysis. Auditory scene analysis is the means by which animals can extract general information about their environment from the various sounds that reach them (Bregman, 1994). For example, we determine that there is a road nearby from traffic noise, while marine mammals might be able to recognise that they are approaching a coastline if they hear increasing surf noise. As a consequence of this, it is likely that masking of important acoustic cues represents a considerable challenge to marine mammals and other marine fauna.

Although masking can be studied in captivity (e.g. Johnson, 1968b; Au & Moore, 1990; Erbe et al., 1998; Kastelein et al., 2009; Popov et al., 2006) it is difficult to assess and quantify in wild animals. The main reason for this is that (by definition) masking effects represent an elevation of detection thresholds and outwardly detectable consequences are typically the absence of behaviours: failure to detect a conspecific, a potential prey or a potential predator, one way or the other leading to a smaller or larger decrease in fitness. For masking to occur the signal must be audible to the animal in the absence of the masker and the masking sound must be long enough in duration, as well as close enough in time and frequency to the signal (e.g., Jesteadt et al. 1982; Kastelein et al., 2010). Total masking also requires that the masker has an intensity comparable to, or louder than, the signal of interest at the receiver, although masking at lower levels can reduce the availability of information contained within a signal, which can in turn influence the response of the receiver to that signal (see Bateson, 2007).

We believe that we have demonstrated, through the above examples, that there are no behavioural responses that can reliably ensure that only a negligible reduction in fitness has occurred. Furthermore, we have shown that small changes in behaviour do not by necessity equate to small fitness consequences, and larger changes do not necessarily reflect larger fitness consequences. Accordingly, it is problematic to use behavioural responses as indicators of fitness consequences, despite their relative ease of study, without a great deal of consideration on not only the context within which exposure occurred.

3.3 Assessing non-injurious impacts

Given that a lack of behavioural response does not necessarily represent a lack of impact (and vice versa) and that the severity of a behavioural response is not necessarily meaningful without contextual and ecological information, it is reasonable to ask if non-injurious impacts can be assessed through behaviour at all. However, if assessments are limited to behaviours where context is known, at least

in general, as are the basic consequences for their interruption, then some indication of impact in terms of fitness cost can be determined. Let us consider, for example, avoidance of noise. In this case, avoidance represents a 'decision'¹ by an animal to maintain a distance from a sound source that will be balanced between: (1) the perceived unfavourable nature of the source (presumably in terms of the perception of the source as a possible threat, annoyance and ultimately discomfort); and (2) the value of the resources in the area avoided (such as food, potential mates, resting sites, etc.) in addition to the cost, if any, of transport away from the source (see discussion in e.g., Beale & Monaghan, 2004; Beale, 2007). Accordingly, transient habitats, such as routes of migration (i.e., context), may have little cost to the animal in terms of additional distance covered or resource value (i.e., consequence).

Conversely, foraging and breeding sites contain resources with a value to fitness. Therefore, in the absence of other information, avoidance of noise in transit is unlikely to reflect the true extent of possible impact, while avoidance of breeding or foraging sites is likely to represent an exposure beyond the level where the animal 'decides' it is better to accept a certain loss of fitness. Thus, avoidance of breeding or foraging sites not only represents a certain level of fitness impact, but also an associated level of disruption by the sound exposure. In turn, this can be interpreted as a point beyond which non-injurious fitness impacts have begun, although, it should be noted that the extent of these impacts cannot be fully assessed without additional information, such as relating to the general availability of good-quality prey or mates. Similarly, it should also be noted that avoidance can occur on a relatively small scale, representing switches in activity to avoid immediate disturbance, and still generate sizable fitness impacts (see Williams et al., 2006). In addition to avoidance of foraging or breeding sites, non-lethal, non-injurious fitness impacts can occur if anthropogenic noise increases to levels where it functionally interferes with sound production and hearing. This interference could occur if the noise either causes animals to stop producing sounds or masks sounds of importance to them. If severe enough, i.e. occurring over extended periods of time this could lead to fitness consequences, such as calf-offspring separation, loss of foraging or breeding opportunities, or increased risk of predation. In contrast, the fitness consequences of many other behavioural responses (such as aggressive displays, vocal responses, and startle reactions) may be unclear without additional information, which may be harder to obtain (e.g., Götz & Janik, 2011).

The way forward is to consider the actual impact on fitness by changes in behaviour, as for example captured in the PCAD model (NRC, 2005). However, although the PCAD model is a very useful conceptual model for the mechanisms involved in impact from noise on fitness, it is less useful when it comes to actual assessments (see discussion in Wright, 2006). This realisation has led to new initiatives, based on agent based models, such as the PCoD model (Lusseau et al., 2012) and models for noise impact on harbour porpoises (Nabe-Nielsen et al., In prep). Such models simulate natural and avoidance behaviour by virtual animals (agents) moving and behaving in a virtual environment and as the agents reproduce and can be followed over many generations, it becomes possible to detect long term effects of even small, but cumulative effects on fitness. These models are still in their infancy, but they carry promises for the ability to assess not only immediate effects of isolated disturbances, but also effects of long term exposure and cumulative exposure to several types of impact, not necessarily all being acoustic.

¹ By 'decision' we mean an ecological choice by the animal, rather than a conscience decision. See Beale & Monaghan, 2004; Beale, 2007 for more details.

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