Contents lists available at ScienceDirect

Marine Environmental Research

journal homepage: www.elsevier.com/locate/marenvrev



How effectively do horizontal and vertical response strategies of longfinned pilot whales reduce sound exposure from naval sonar?



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ARTICLE INFO

Article history: Received 20 September 2014 Received in revised form 16 February 2015 Accepted 23 February 2015 Available online 24 February 2015

Keywords: Cetaceans Disturbance Behaviour Environmental impact Noise Risk assessment Individual-based models Sonar

ABSTRACT

The behaviour of a marine mammal near a noise source can modulate the sound exposure it receives. We demonstrate that two long-finned pilot whales both surfaced in synchrony with consecutive arrivals of multiple sonar pulses. We then assess the effect of surfacing and other behavioural response strategies on the received cumulative sound exposure levels and maximum sound pressure levels (SPLs) by modelling realistic spatiotemporal interactions of a pilot whale with an approaching source. Under the propagation conditions of our model, some response strategies observed in the wild were effective in reducing received levels (e.g. movement perpendicular to the source's line of approach), but others were not (e.g. switching from deep to shallow diving; synchronous surfacing after maximum SPLs). Our study exemplifies how simulations of source-whale interactions guided by detailed observational data can improve our understanding about motivations behind behaviour responses observed in the wild (e.g., reducing sound exposure, prey movement).

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1. Introduction

Human activities that introduce sound energy in the marine environment have the potential to affect marine mammals on the scales of individuals and populations (National Research Council, 2003, 2005; Tyack, 2008; Weilgart, 2007). Because of the difficulties in studying marine mammals in their natural habitat, the ultimate costs of man-made noise to individual fitness (e.g. survival and reproductive success) are generally inferred from proximate costs (McGregor et al., 2013). Among these proximate costs are masking of the sounds from conspecifics and predators (Clark et al., 2009; Erbe, 2002), stress responses (Rolland et al., 2012), temporary or permanent hearing loss (Finneran and Schlundt, 2013; Kastak and Schusterman, 1996), and changes in vocal behaviour (Alves et al., 2014; Miller et al., 2000; Parks et al., 2007) as well as other behavioural responses (Nowacek et al., 2007). For example,

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tonal sounds from powerful naval active sonars during multi-ship exercises can cause large-scale area avoidance by beaked whales (McCarthy et al., 2011; Tyack et al., 2011) and killer whales (Orcinus orca) (Kuningas et al., 2013; Miller et al., 2014); displacement of harbour porpoises (Phocoena phocoena) by tens of kilometres from the sound source has been observed following impulsive noise produced by pile driving during offshore wind farm construction (Brandt et al., 2011; Dähne et al., 2013; Tougaard et al., 2009); and continuous noise from vessel traffic may cause chronic stress in endangered North Atlantic right whales (Eubalaena glacialis) (Rolland et al., 2012) and reduce their acoustic communication space (Clark et al., 2009).

Recent research on man-made noise has focused mainly upon direct physiological effects such as hearing loss, but behavioural and stress responses that can translate into population consequences may be of greater concern (Bejder et al., 2006). National and international legislation recognise that man-made noise can affect marine mammals, and require that the environmental risks of noise are appropriately assessed and managed (e.g. US Marine Mammal Protection Act [50 CFR 216]; EU Marine Strategy Framework Directive [2008/56/EC]). However, considerable individual

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and species variation exists in short-term behavioural responses to man-made noise (e.g. Antunes et al., 2014; Goldbogen et al., 2013; Götz and Janik, 2011; Houser et al., 2013a, 2013b; Kastelein et al., 2011, 2006a; Miller et al., 2012, 2014; Moretti et al., 2014; Nowacek et al., 2004; Tyack et al., 2011; Williams et al., 2014), and a general lack of information about the biological significance of responses, efficacy of mitigation measures, and how to extrapolate from experimental data, for example, makes impact assessment and management challenging.

One approach that National Research Council (2005) recommended for the assessment of population-level effects of underwater noise, and the interactions between marine mammals and noise sources, is individual-based modelling (IBM). With this technique, the behaviour of individuals within a system and their interactions with the environment and other individuals are modelled to understand the properties and dynamics of the system (Grimm and Railsback, 2004). In the context of man-made noise and marine mammals, this generally means constructing the exposure histories of simulated animals that move through virtual sound fields and evaluating whether levels reach certain risk thresholds (Frankel et al., 2002). Sonar-related mass strandings of beaked whales (Balcomb and Claridge, 2001; Jepson et al., 2003) accelerated the development and use of IBM-based risk assessment models that are designed to investigate the impacts and associated uncertainties of naval sonar on marine mammals (Dolman et al., 2009; Donovan et al., 2012; Gisiner et al., 2006; Houser, 2006). Comparable methods are used in the Environmental Impact Statements of the US Navy to estimate the number of marine mammals that are affected behaviourally or physiologically by noise (Schecklman et al., 2011; U.S. Department of the Navy, 2014; Wartzok et al., 2012). Recently, individual-based methods have also been used to assess the efficacy of operational mitigation procedures for sonar (von Benda-Beckmann et al., 2014), to evaluate interactions between whales and whale-watch boats (Anwar et al., 2007), and to investigate potential impacts of noise on cetaceans from non-sonar sources such as pile driving, seismic surveys, wind turbines and/or vessel traffic (e.g. Gedamke et al., 2011; Nabe-Nielsen et al., 2014; New et al., 2013; NSF and USGS, 2011; Thompson et al., 2013). However, it is necessary to quantify observed behavioural response strategies of cetaceans in reaction to sound sources and to estimate the changes in acoustic exposures that result from these strategies, to increase confidence in the outcomes of quantitative risk assessment models that are based on hypothetical responses (Barlow and Gisiner, 2006).

The avoidance behaviour of a cetacean near a sonar source modulates the sound pressure level (SPL) at the position of the animal (henceforth 'received SPL'). At close range, movement away from a non-directional sound source will decrease the received SPL in most situations. Therefore, not including rules of repulsion/aversion in IBM will generally be conservative when risk thresholds are high (i.e. it will overestimate the number of times exposure thresholds are exceeded). Movement away from the source can also increase received SPL in case of a directional sound source, acoustic near field or a complex multipath propagation environment (DeRuiter et al., 2006; Madsen et al., 2006).

Intrinsically, the underlying motivation(s) of the animal will determine the shape of the movement response; for example, a marine mammal could be motivated to: 1) avoid the acoustic intensity and/or energy itself because it is painful or annoying (Culik et al., 2001; Kastelein et al., 2006a, 2006b, 2008; Kvadsheim et al., 2010; McCauley et al., 2000), 2) evade the source by keeping a safe distance without losing visual or acoustic contact with the threat (Lazzari and Varjú, 1990; Williams et al., 2002), or 3) flee or haul out as part of an anti-predator response template (Deecke et al., 2002; Ellison et al., 2012; Ford and Reeves, 2008). In addition, an animal

might not have the motivation or option to avoid if the perceived benefit of staying outweighs the cost of leaving (Frid and Dill, 2002). Although the underlying motivations of animals are generally not well understood, avoidance responses of wild and captive cetaceans to various sound sources have been described by a number of studies (see for review: Nowacek et al., 2007; Richardson et al., 1995; Southall et al., 2007) and some studies have measured avoidance movements with sufficient spatial and temporal resolution to be useful for the construction of geometrical models of avoidance (e.g. Curé et al., 2012, 2013; DeRuiter et al., 2013; Dunlop et al., 2013; Goldbogen et al., 2013; Miller et al., 2014; Tyack et al., 2011). Most studies have used stationary sources; however, many anthropogenic noise sources such as towed and hull-mounted active sonar systems, boats, and seismic airguns arrays are moving when they are used.

Many of the detailed observations of behavioural responses of cetaceans were made during field experiments in which the dose of the acoustic stimulus was controlled, called Controlled Exposure Experiments (CEEs; Tyack et al., 2003). Some of these CEEs were conducted with a moving sonar source in 2006-2009 on killer whales, long-finned pilot whales (Globicephala melas), and sperm whales (Physeter macrocephalus) (Miller et al., 2011, 2012). The three species exhibited behavioural responses of various duration and severity (Miller et al., 2012), with clear species differences in avoidance response thresholds (Antunes et al., 2014; Miller et al., 2014). There was a recurring pattern of killer whales moving perpendicular to the source ship's line of approach (Miller et al., 2012, 2014). Pilot whales often switched from deep foraging diving to shallow transit diving, or remained shallow diving throughout the exposure (Miller et al., 2012; Sivle et al., 2012). Pilot whales showed fewer horizontal displacement responses to the sonar than killer whales did, with pilot whales more often slowing down and/or changing orientation, similar to what has been reported for their responses to seismic surveys (Stone and Tasker, 2006; Weir, 2008). In two cases a pilot whale appeared to surface multiple times in near-perfect synchrony with the interval of arriving sonar pulses (Miller et al., 2012).

In the present study we combined an analysis of behavioural data recorded during CEEs with the modelling of threedimensional (3D) animal trajectories, in order to investigate avoidance responses of cetaceans to approaching sound sources. First, we conducted a quantitative analysis of DTAG (Johnson and Tyack, 2003) data to test the qualitative judgement by Miller et al. (2012) that two long-finned pilot whales responded by surfacing in near-perfect synchrony with the arrival of sonar pulses. Pinnipeds are known to increase their surface durations or haul out in response to underwater noise exposures (Götz and Janik, 2011; Houser et al., 2013a; Kastak et al., 1999; Kvadsheim et al., 2010; Mate and Harvey, 1987), so we hypothesized that the pilot whales' behaviour reported by Miller et al. (2012) could have represented similar attempts to reduce received SPL and/or sound exposure level (SEL) by exploiting lower sound pressures at the sea surface (Jensen, 1981; Weston, 1980). Second, we defined and quantified a number of theoretical response strategies that pilot whales and other cetaceans may use in response to an approaching sound source, and we used IBM to assess how the maximum SPL and cumulative SEL received by a simulated whale differs among these theoretical response strategies. Finally, we compared our simulation results with real-world avoidance responses of marine mammals to man-made noise.

2. Materials and methods

Data were collected from experiments in northern Norway in May/June 2008, 2009, and 2010, as part of an international project

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