

Chronic ocean noise and cetacean population models

ROB WILLIAMS¹, DANIELLE CHOLEWIAK², CHRISTOPHER W. CLARK³, CHRISTINE ERBE⁴, J.C. ‘CRAIG’ GEORGE⁵, ROBERT C. LACY⁶, RUSSELL LEAPER⁷, SUE E. MOORE⁸, LESLIE NEW⁹, E.C.M. PARSONS¹⁰, HOWARD C. ROSENBAUM¹¹, TERI K. ROWLES¹², MARK P. SIMMONDS¹³, RAPHAELA STIMMELMAYR⁵, ROBERT S. SUYDAM⁵ AND ANDREW J. WRIGHT¹⁴

Contact e-mail: rob@oceansinitiative.org

ABSTRACT

Recent years have seen the rapid development of tools and approaches to model the population consequences of disturbance in several marine mammal populations from high-amplitude, acute sound sources. Ocean noise from shipping and other maritime activities is now recognised as a chronic, habitat-level stressor. Advances are needed in several key areas in order to understand the population consequences of chronic ocean noise to cetaceans and their populations. One promising approach is to predict population-level consequences of noise-mediated disruption of feeding, which can include both behavioural responses and foraging opportunities lost due to acoustic masking. Masking may be defined as both the process and the amount by which the threshold of hearing of one sound is raised by the presence of another. Parameterising any model of population consequences of the masking caused by chronic ocean noise requires information on sensitivity and vulnerability of large whales to ocean noise, in which sensitivity is the degree to which marine organisms respond to a stressor (e.g. behavioural responses to noise or proportional reduction in foraging efficiency due to masking), and vulnerability is the probability that whales are exposed to noise to which they are sensitive. Our review draws from case studies inspired by the Population Consequences of Disturbance framework, as well as those that use Population Viability Analysis approaches. Much of the work completed to date focuses on odontocetes, particularly coastal odontocetes. Efforts are underway to provide much-needed information on hearing sensitivity in baleen whales, the role of acoustic cues in foraging, and deriving links between long-term variability in prey availability and whale demography. As new information becomes available, we expect rapid advancement on modelling population consequences of acoustic masking in baleen whales, because those efforts can leverage substantial investments in statistical methodological approaches to model population consequences of disturbance. Although the models presented explore population consequences of noise via a tractable approach that considers noise-mediated impacts on foraging, other pathways of effects (e.g. stress hormones affecting reproduction or disease) are possible. By considering only one pathway of effects, the modelling approaches discussed may underestimate the magnitude of effects of noise on cetacean populations. Case studies of local, national, international, and inter-governmental efforts were highlighted to monitor and reduce the contribution of global shipping to ocean ambient noise, and outline approaches that can be used to assess the risk to cetacean population recovery of existing levels of ocean noise, and consequently, predict the benefits likely to arise from reducing chronic ocean noise.

KEYWORDS: CONSERVATION; HABITAT; MODELLING; NOISE

INTRODUCTION

Marine mammals produce and use sound in all of their major life functions (e.g. mating, feeding, predator avoidance, and resting). Of all the possible impacts of anthropogenic noise, masking is perhaps the most pervasive, yet least understood. We define masking as both the process and the amount by which the threshold of hearing of one sound is raised by the presence of another (Erbe *et al.*, 2016). Masking is caused by the interference of sound, often in the form of aggregate noise levels, with acoustically mediated activities, such as listening and communicating. The term ‘acoustic environment’ refers to the acoustic characteristics of a place or region (e.g. spectrum levels) independent of an organism, whereas the term ‘acoustic habitat’ refers to the acoustic characteristics of a place or region from the perspective of a

listener – that is, the same acoustic environment may represent different acoustic habitats to different species, based on their auditory perception capabilities and acoustic cue production (Clark *et al.*, 2009; Moore *et al.*, 2012). From the perspective of marine acoustic habitats and cetaceans, higher levels of acoustic interference reduce the space over which individuals and populations can listen and be heard. Consequently, they lose opportunities to effectively engage in acoustically mediated activities such as communicating, foraging, and navigating. Additionally, from the acoustic habitat perspective, the impacts of increased ocean noise tend to be chronic rather than acute, large-scale rather than small-scale, and occur across multiple species, with some populations likely losing large portions (> 50%) of their acoustic habitats for many months of the year over many

¹ Oceans Initiative, 117 E Louisa St, #135, Seattle WA 98102, USA.

² Northeast Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, 166 Water Street, Woods Hole, MA 02543, USA

³ Bioacoustics Research Program, Cornell Laboratory of Ornithology, Cornell University, 159 Sapsucker Woods Road, Ithaca, NY 14850, USA

⁴ Centre for Marine Science & Technology, Curtin University, PO Box U1987, Perth, WA 6845, Australia

⁵ Department of Wildlife Management, North Slope Borough, Box 69, Utqiagvik (Barrow), AK 99723, USA

⁶ Species Conservation Toolkit Initiative, Chicago Zoological Society, 3300 Golf Road, Brookfield, IL 60513 USA

⁷ International Fund for Animal Welfare, London, UK

⁸ Center for Ecosystem Sentinels, Department of Biology, University of Washington, Seattle WA USA

⁹ Department of Mathematics and Statistics, Washington State University, Vancouver, Washington 98686 USA

¹⁰ Centre for Ecology and Conservation, Daphne du Maurier Building, Penryn Campus University of Exeter, Cornwall, UK

¹¹ Wildlife Conservation Society, Ocean Giants Program, 2300 Southern Blvd., Bronx, NY 10460 USA

¹² National Marine Fisheries Service, 1315 East West Highway, Silver Spring, 20910, Maryland, USA

¹³ School of Veterinary Sciences, University of Bristol, Langford House, Langford, Bristol, BS40 5DU, UK

¹⁴ Fisheries and Oceans Canada Maritimes Region, Bedford Institute of Oceanography, 1 Challenger Drive, Dartmouth, NS B2Y 4A2, Canada

years (Cholewiak *et al.*, 2018; Gabriele *et al.*, 2018; Hatch *et al.*, 2012; Williams *et al.*, 2014).

Although the population consequences from such broad-scale acoustic habitat loss are difficult to estimate, there is increasingly broad agreement that existing levels of chronic ocean noise and associated masking effects are likely to result in population-level consequences to whales (IWC, 2016). In recent years, there has been considerable effort to scope the problem of masking from anthropogenic noise (Cholewiak *et al.*, 2018; Clark *et al.*, 2009; Erbe *et al.*, 2016; Gabriele *et al.*, 2018). Similarly, over the last decade several statistical approaches have been developed to assess the population-level impacts of disturbance on marine mammals (King *et al.*, 2015; New *et al.*, 2013a; New *et al.*, 2013b). We review briefly the progress made on both themes (i.e. acoustic masking, and modelling population consequences of disturbance), and outline methods that could be used to integrate these two research areas to help model population consequences of acoustic masking in cetaceans. The review also places the science in the context of a policy arena in which there is increasing attention paid to measuring, monitoring, and mitigating chronic ocean noise.

ACOUSTIC MASKING

Progress on understanding population-level effects of masking in cetaceans includes advances in modelling, measurement and visualisation tools; increased understanding of uncertainties in model input; recognition of the role of behavioural context (e.g. foraging, mating, migrating) for estimating impact on cetaceans (Ellison *et al.*, 2012; Gomez *et al.*, 2016); and examples of population-level consequences (Lacy *et al.*, 2017). Given cetacean dependence on listening to and producing sounds for survival, it is important to expand the specific issue of acoustic masking impact from a focus on individual whales to the broader topics of acoustic habitat quality and population-level effects.

Key developments in international policy

Much of the scientific advancement in this field has been driven by a policy push to address ocean noise around the world. For example, discussion of noise at the International Whaling Commission's Scientific Committee (IWC-SC) began in earnest in 2004, following the use of the term 'noise pollution' by the International Whaling Commission (IWC) itself in the year prior (IWC, 2005; Wright *et al.*, 2017). These discussions led the IWC-SC to agree in 2014 that increased efforts should be made to avoid, minimise and mitigate the adverse effects of anthropogenic noise on cetaceans. In particular, the IWC-SC recommended that IWC Contracting Governments should promote and facilitate the adoption, by industry, of noise-reducing technologies, including quieting technologies for ships.

The IWC-SC specifically began considering noise from shipping in 2008 (IWC, 2009), following a workshop held in Hamburg in 2008 (Wright and Okeanos Foundation for the Sea, 2008), which had wide participation including shipping operators, designers and builders. That workshop agreed on a simple target for reducing shipping noise by half within ten years. This target was endorsed by the IWC-SC which further strongly recommended in 2010 that:

- (1) the goal of noise reduction from shipping set in 2008 (i.e. 3dB in 10 years; 10dB in 30 years in the 10–300Hz band) be actively pursued;
- (2) new and retro-fit designs to reduce noise from ship propulsion be advanced within the goals of the International Maritime Organization (IMO), when and wherever practicable; and
- (3) the IWC and IMO continue to work collaboratively to advance the goal of worldwide reduction of noise from commercial shipping when and wherever practicable including reporting progress on noise measurements and implementing noise reduction measures.

The IMO has recognised the problem of underwater noise pollution from shipping and agreed in 2009 that scientific uncertainty as to the effects of noise should not preclude efforts towards developing quieting technologies for commercial ships. Through a process within the IMO Marine Environment Protection Committee (MEPC), non-mandatory technical guidelines for reducing ship noise were adopted in 2014 (MEPC.1/Circ.833). During that process, member states were encouraged to review their merchant fleets to identify the vessels that would benefit most from efficiency-improving technologies, as the quieting of a relative few of the loudest ships had been identified as a potential way to efficiently reduce the overall contribution of shipping noise to the global ocean noise budget (IMO, 2013).

The IWC and IMO have been developing stronger links, including observer status for the IWC with the IMO. At a meeting between the Secretariats in January 2016, underwater noise, amongst other issues, was discussed. IWC submitted a paper to the IMO MEPC 72 meeting in April 2018 providing an update on noise impacts (IWC, 2018).

The IMO is the competent UN body to regulate shipping, but the UN also included a strong commitment to the world's oceans under Goal 14 of the 17 Sustainable Development Goals agreed in August 2015 by the 193 member nations¹⁵. Addressing ocean noise is undoubtedly essential to meet at least two of the targets under Goal 14. These are 14.1 'By 2025, prevent and significantly reduce marine pollution of all kinds, in particular from land-based activities, including marine debris and nutrient pollution' and 14.5 'By 2020, conserve at least 10% of coastal and marine areas, consistent with national and international law and based on the best available scientific information'.

During the preparatory meeting for the June 2017 United Nations Ocean Conference (UNOC) to discuss implementation of Sustainable Development Goal 14, the IUCN, the Wildlife Conservation Society (WCS) and the Government of France hosted a side event to raise awareness among United Nations member states and other stakeholders about global shipping and impacts of noise on whales and other marine mammals. A complete recording of the meeting and all documents related to outcomes and recommendations related to anthropogenic underwater noise is available¹⁶. Specific mention was subsequently made by member states about ocean noise in the final UNOC Call for Action. This event also initiated a collaborative effort that led to the formulation and

¹⁵<http://www.un.org/sustainabledevelopment/oceans/>.

¹⁶<https://sdg14.wcs.org/Events/Global-Shipping-and-Whale-Conservation>.

Table 1

Recommendations, examples, and associated efforts required, combined from the Leiden workshop in 2014 and this review.

Recommendation	Examples	Efforts required
1. Noise generation		
1.1. Compile a log/registry of what noise sources operate where and when	Ship Automatic Identification System data, licensed activities generating intense sounds such as seismic surveys, and offshore pile driving.	Book-keeping, no research need but has proven challenging. Within Europe, states are developing registries of noise-generating activities to meet requirements of the Marine Strategy Framework Directive.
1.2.a Compile inventory of sound source signatures, and	(a) Source levels and spectra and spectrograms, beam patterns; (b) as a function of vessel speed, draught, etc.	Some data collection left to do, in particular on parameters affecting signatures. Some desktop work/data compilation, some research.
1.2.b parameters that affect signatures		
1.3. Identify noisiest sources/vessels	What are the noisiest ships that could most benefit from application of noise quieting?	Data collection, data mining.
1.4. Create an inventory of ambient noise	Statistical distribution of noise levels, on various time scales.	Some data collection necessary in specific areas, otherwise data mining.
2. Noise modelling and prediction		
2.1. Create inventory of parameters that affect sound propagation	Sound speed profile in the water and seafloor, absorption.	There are databases on bathymetry and ocean parameters with large-scale coverage and detailed information in specific areas; depending on area, might need to do additional data mining or collection.
2.2. Model noise levels on a variety of time, space and spectral scales	Need high-resolution model for short-term, localised monitoring; low-resolution for ocean-basin scale.	Data mining, slow processing exercise.
2.3. Quantify uncertainty and accuracy; validation	Validate existing models (some available as shareware) with spot measurements, or model against model.	Data mining and processing exercise.

Note: 1.1, 1.2, 1.4, 2.1, 2.2, 2.3 were recommendations made by the Leiden 2014 workshop; 1.3 are new recommendations from the authors.

registration of United Nations voluntary commitment¹⁷ OceanAction18553, entitled ‘A commitment to reduce Ocean Noise Pollution’.

Each year the UN General Assembly has a standing agenda item to review implementation of UNCLOS and then adopts a resolution entitled ‘Oceans and the Law of the Sea’ as the outcome of this review. The focus of the 2018 Informal Consultative process was anthropogenic underwater noise held at the UN between 18–22 June 2018. The full proceedings presentations of panelists (including IWC Secretariat and members of the IWC-SC), as well as the report of the Co-chairs of the ICP are available¹⁸. The conclusions from this process will be included in the next Oceans and the Law of the Sea resolution.

In addition to these developments at a global level, there have also been some notable regional and national developments. For example, the European Marine Strategy Framework Directive contains an acoustic indicator for Good Environmental Status. Although the specific indicators selected have been debated (van der Graaf *et al.*, 2012), and their implementation has made some trans-boundary work challenging (Authier *et al.*, 2017), they are now shaping the way that European nations approach noise-related issues (e.g. Merchant *et al.*, 2016). It also represents a shift from the consideration of noise impacts on individuals specifically, to consideration at an ecosystem level. Furthermore, the US National Oceanic and Atmospheric Administration (NOAA) has recently released an Ocean Noise Strategy Roadmap (ONSR) that, among other things, also highlights the importance of acoustic habitats (Hatch *et al.*, 2016).

Efforts to characterise and reduce ship noise

Recognising that the IMO has already asked its Member States to review their merchant fleets, it is possible to

identify a number of recent extensive data sets with source characteristics of individual vessels (e.g. source level, spectral characteristics, sound radiation characteristics) that could be used to identify the noisiest vessels. For instance, vessel approaches to Boston off the east coast of the US have been monitored through the Stellwagen Bank right whale alert system. Off the west coast of the US and Canada, ships were recorded at several points on their approach into the Port of Vancouver, before and during a voluntary slow-down trial of piloted ships transiting that region¹⁹. We thus recommend that such ship source characteristic data be evaluated to identify the noisiest ships and quantify their relative contribution to overall ocean noise. A recent study near the Port of Vancouver identified that the noisiest 15% of ships generated 50% of the underwater noise power in the region (Veirs *et al.*, 2018). We further recommend that ships that contribute disproportionately to ocean noise be considered a priority for replacement, or at least retrofit with available ship-quieting technologies (reviewed in Williams *et al.*, 2019).

Advances in the measurement and mapping of ship and ambient noise

The IWC, International Quiet Ocean Experiment (IQOE), National Oceanic and Atmospheric Administration (NOAA), Office of Naval Research Global (ONRG), Netherlands Organization for Applied Scientific Research (TNO) and Netherlands Ministry of Infrastructure and the Environment hosted a 2-day workshop in April 2014 in Leiden, Netherlands, on ‘Predicting sound fields: Global soundscape modelling to inform management of cetaceans and anthropogenic noise’ (IWC, 2015). The motivation for this workshop was a need by decision makers to characterise, monitor, and manage chronic anthropogenic noise for which

¹⁷<https://oceanconference.un.org/commitments/?id=18553>.

¹⁸http://www.un.org/depts/los/consultative_process/consultative_process.htm.

¹⁹<https://www.portvancouver.com/environment/water-land-wildlife/echo-program/vessel-slowdown-trial-in-haro-strait/>

soundscape modelling and mapping tools would be useful. Twenty-six participants from 11 countries evaluated existing sound mapping approaches and identified data gaps and research needs. Targets of a 2-year workplan, possibly focussing on a couple of case studies, include: a registry of anthropogenic operations by geographic region, an inventory of sound signatures of anthropogenic activities, a growing database of ambient noise recordings, standardised recording and data analysis paradigms, agreed modelling parameters, model validation, and visualisation tools that could predict noise footprints and cumulative noise maps, as well as quickly compare alternative operational scenarios. The workplan did not discuss exactly how the recommendations could be achieved. Accordingly, we provide examples of how the recommendations (as well as our own measurement-related recommendation made above) might be implemented (Table 1).

In a complementary effort, the International Organization for Standardization (ISO) released ISO 17208-1:2016 for measuring noise characteristics of individual vessels in deep water with precision for comparison purposes. Although the standard cannot be applied to historic data, some existing data sets match the prescribed procedures, and the standard does offer scientists a standard metric for comparing noise from ships in future work. That said, the prescribed methodology is applicable only in deep water, yet port approach channels where measurements are easily taken exhibit shallow water. The development of a shallow-water standard is in progress.

There is thus still a need for a simple metric for the overall contribution of individual vessels. This can be considered as the ‘acoustic footprint’ of that vessel. Such a metric could be used to address questions about the relative contribution of different vessels. For example, what is the relative effect of replacing several smaller vessels with one larger, potentially louder, one? Two studies (Leaper *et al.*, 2009; Leaper *et al.*, 2014) used the simple two-dimensional area estimated to be ensonified to a certain received level to represent the acoustic footprint. This allowed an estimate of the relative contribution of different vessels to the overall acoustic footprint of the fleet and an evaluation of the change as a result of slow steaming practices. This definition of footprint is a simple generalisation that does allow comparisons to be made taking into account that shipping is truly global, with individual vessels transiting through many different whale habitats and propagation environments. The results were sensitive to different assumptions about propagation but indicated that the noisiest 10% of vessels may contribute between around 48% and 88% of the total acoustic footprint. The more recent study by Veirs *et al.* (2018) using a much larger data set found similar results with 15% of vessels contributing 50% of the sound energy. Based on a review of the general relationship between source level and speed, the results suggested substantial noise reduction associated with slow steaming. For example, for a typical container ship travelling at 25 knots, the total acoustic footprint would be reduced to 21% for slower steaming at 20 knots. Although the relationship between source level and speed is not the same for all vessels, requiring future study, such work may support replacement or retrofit prioritisation efforts.

Extending estimates of the acoustic footprints of individual vessels to the total pressure on an acoustic habitat or ecosystem will require some modelling efforts. For example, individual ship signatures will need to be integrated with ship density data, probably originating from Automatic Identification System (AIS) information, together with propagation models before the loss of acoustic habitat from shipping noise can be estimated. Soundfield predictions from AIS data can also be applied in regions where acoustic impacts may be particularly severe but empirical measurements of noise levels are not available.

Understanding and measuring masking and its consequences

A recent review summarised understanding of masking in marine mammals and identified major data gaps on marine mammal hearing as they relate to masking (Erbe *et al.*, 2016). The ‘Power Spectrum Model of Masking’ assumes the auditory system consists of a series of overlapping bandpass filters; a listener attends to (i.e. focuses on) the filter that encompasses the signal, or has the highest signal-to-noise ratio (SNR); and there exists a critical SNR (the critical ratio), below which the signal is masked. Studies with captive animals indicate that the Power Spectrum Model often effectively predicts masking, in particular when the signal is of tonal character and the noise is broadband and continuous. However, it is more difficult to assess and model masking in more natural scenarios, such as when the noise has temporal gaps (e.g. pulsed noise from pile driving and seismic airgun arrays, and strongly amplitude-modulated ship noise), or when signal and noise are spatially separated, arriving at the listener from different directions. The spectro-temporal characteristics of noise can change as noise propagates through the ocean (e.g. the brief broadband pulses from seismic airguns can turn into extended frequency-modulated sounds), meaning that masking potential can also change with range from the source. Additionally, while we can predict if a (tonal) signal is detectable in many types of noise, there are no data on signal discrimination, recognition, or comfortable communication in any marine mammal. Based on information from terrestrial animals and humans, it is known that SNRs significantly higher than the critical ratio are needed for successful communication. In fact, there are many marine mammal species for which even the most basic information on hearing capabilities is non-existent. Masking studies with realistic signals (e.g. communication or echolocation sounds) and realistic noise are needed, and studies are needed to investigate natural masking release phenomena. For a full review of the current state of knowledge on masking see Erbe *et al.* (2016) and references therein.

Following from early work by Møhl (1980; 1981) and Clark *et al.* (2009), many current efforts to assess and manage masking focus on acoustic habitat loss related to the ability of cetaceans to detect the calls of conspecifics (i.e. ‘communication space’), environmental signals, and echolocation (i.e. ‘foraging space’, Williams *et al.*, 2014). An acoustic space can be defined by the dimensions of the frequency band in which the sound occurs, the distance over which it operates (e.g. communication range for cetaceans,

echolocation distance, or range over which noise propagates), and the duration of the sound.

Vessel noise should be considered over a broad frequency range and not just at low frequencies, where the emission might be strongest. Reyes Reyes *et al.* (2016) documented that several types of vessels increase ambient noise levels not only at low frequencies but also at medium and high frequencies, where toothed whale hearing seems to be most sensitive. Accordingly, having access to sufficient audiometric data is critical to assess masking. There are indications that auditory thresholds for low-frequency specialists such as baleen whales, for which experimental audiometric data are lacking, are driven by historical, natural ambient noise levels that can be used to estimate how vessel noise reduces communication space (i.e. masking).

Tools and approaches for calculating the dynamics of lost acoustic environment are now well established (Clark *et al.*, 2009). Although there are uncertainties in the mechanisms (e.g. environmental factors for computing transmission loss), the limiting factors in estimating lost acoustic space, masking, or acoustic habitat loss are primarily driven by biological uncertainties (e.g. animal distribution, density, behavioural context, auditory sensitivity), rather than in the domain of physical acoustics. However, while these studies and approaches are useful, some of the remaining biological uncertainties are considerable. For example, simple detection of an acoustic signal does not mean an individual will be able to recognise the content of the signal and little information exists on this in marine mammals. Furthermore, received levels at the listener are influenced by noise levels at the producer in cases where animals may change their behaviour in response to perceived increases in noise. Such changes include increasing the signal level (Lombard effect; Lombard, 1911), repeating the signal, ceasing signal production, and shifting the signal frequencies away from the noise band. While the Lombard response has been documented in animals, it is unknown to what extent it improves communication or whether there are unknown consequences for recognition and information transfer (Holt *et al.*, 2011; Hotchkyn and Parks, 2013).

Added complications arise from the possibility that aggregated impacts of repeated short-term exposures may

produce long-term effects such as reducing fitness of the animals due to, for example, disruption of foraging, even though any given acoustic masking event may be a short-term consequence of a single exposure. Furthermore, received levels do not necessarily predict an individual’s response to sound, but may be dependent on the individual’s behavioural context. For example, an individual faced with multiple ‘small’ stressors, such as whale-watching vessels, may not react to what might normally be considered the larger disturbance (e.g. a nearby container ship) because of the more proximate source of disturbance. This may also lead to other indirect effects, such as an increased risk of ship strikes or entanglement due to the individual’s distraction (see Wright, 2017) and highlights the need to consider the different impacts of various vessel types and the relationships among disturbance, distance, and duration. Finally, the context of exposure has been found to be more important than received level for behavioural responses (Gomez *et al.*, 2016), although how context might influence masking has yet to be determined.

In terms of masking, we are currently unable to answer the question of ‘how much is too much?’ and given the various remaining questions, further studies will be needed before masking can effectively be incorporated into the management of specific anthropogenic operations (Table 2). Despite this, there also remains a need to address masking in current management.

Quantifying how changes in the acoustic environment from anthropogenic sound sources translate into effective acoustic habitat loss for particular species, and then onto reduced opportunities for essential life functions, and possible impacts at population levels is challenging. Studying the differences between thresholds of detection and recognition is thus important, but will also prove challenging, as it is not possible to reproduce the sound field of many sound sources of interest (e.g. seismic airguns) in a captive setting. Some possibilities may exist to compare dynamics of populations exposed to various levels of anthropogenic sound through comparison of closely related species in different regions, such as the North and South Atlantic, although this raises the question of appropriate scales from a biological and management perspective.

Table 2
Recommendations for further research on masking parameters.

Recommendation	Examples	Efforts required
1. Compile inventory of parameters relevant to masking	Audiograms, critical ratios, critical bandwidths, temporal integration, etc.	Experiments, data collection, research. Parameters can be measured from animals in captivity, using behavioural paradigms or auditory evoked potentials. Some parameters (e.g. audiograms) can also be estimated from behavioural response studies with wild animals.
2. Need better understanding of masking release mechanisms	Spatial release from masking, co-modulation masking release, Lombard effect	The Lombard effect has successfully been demonstrated with some animals in the wild, but data are needed from other species and other situations (i.e., other call types, other noise types and levels). Studies on spatial release from masking require control over the directions from which signal and noise are received and hence more feasible in captivity. Studies on co-modulation masking release require controlled exposure to different noise types and more feasible in captivity as well.
3. Undertake research on signal-to-noise ratio required for signal detection, discrimination, recognition, comfortable communication	A higher signal excess is required to ‘make sense’ of a signal	This requires training animals that can not only indicate when a signal is detected in noise, but also discriminate between two signals in noise, recognise specific signals amongst others in noise, and derive meaning from signals in noise.

Integrating masking into statistical models of whale population dynamics

Population Consequences of Acoustic Disturbance Framework

In 2005, a US National Research Council (NRC) working group attempted to address the issue of the population-level impacts of individual responses to noise exposure, by outlining a conceptual framework, known as the ‘Population Consequences of Acoustic Disturbance’ (PCAD), which linked changes in behaviour to population effects via ‘life functions’ (NRC, 2005). Developments in statistical research and increases in computational power made it possible to begin implementing the PCAD framework in 2009, well ahead of the 10-year prediction offered by the NRC (2005). Initial application of the PCAD framework to elephant seals (*Mirounga sp.*; New *et al.*, 2014; Schick *et al.*, 2013b) led researchers to expand the framework to include additional sources of anthropogenic and environmental disturbance, as opposed to focusing solely upon noise. Additional developments included acknowledging that there may be physiological as well as behavioural responses to disturbance, and that the effect of these responses on individual vital rates is mediated through individual health (defined as internal factors that impact an individual’s fitness) for chronic effects, but may impact vital rates directly for more acute effects. These generalisations resulted in the framework being renamed the ‘Population Consequences of Disturbance’ (PCoD; New *et al.*, 2014)). In addition to elephant seals, the PCoD framework has now been applied to studies of coastal bottlenose dolphins (*Tursiops sp.*; New *et al.*, 2013b; Pirodda *et al.*, 2014), North Atlantic right whales (*Eubalaena glacialis*; Schick *et al.*, 2013a), beaked whales (family Ziphiidae; New *et al.*, 2013a), and gray whales (*Eschrichtius robustus*; Villegas-Amtmann *et al.*, 2015).

Masking, however, has not been included in PCoD models to date. This is because masking is not a behavioural or physiological response in and of itself. Instead, the ensonification of the oceans can lead to masking, which can influence how an animal interacts with their environment to produce subsequent behavioural or physical changes that, in turn, result from interruption to foraging or call behaviour. It is these potential changes that may then result in an effect on individual health, vital rates and then population dynamics.

While the application of the PCoD framework has been successful, it has its limitations. Primary among these is that there are few other marine mammal populations that have been as intensively studied as those listed above, resulting in a lack of appropriate datasets for many species of conservation and management concern. This has led to the development of two alternative approaches to the PCoD

framework (Table 3). The first approach, known as ‘PCoD-lite’, draws on estimated relationships between behaviour and vital rates to fill data gaps. For example, with killer whales (*Orcinus orca*), disturbance from boats is known to alter behavioural budgets, reducing the time spent foraging (Williams *et al.*, 2006). Additionally, killer whale survival is correlated to Chinook salmon (*Oncorhynchus tshawytscha*) abundance (e.g. Ford *et al.*, 2009). Thus, the interruption of foraging can be linked to a vital rate, through an effective reduction in the availability of Chinook salmon, which could then be used to determine the effects on the population dynamics (e.g. Williams *et al.*, 2016).

The second approach to addressing data limitations in the PCoD framework is the use of expert elicitation and is known as interim PCoD. In this case, knowledge is elicited from experts regarding parameter values that might otherwise be obtained through field research and analysis (King *et al.*, 2015). Expert elicitation is a structured and formalised process for obtaining required information (e.g. Estévez *et al.*, 2013; Hayes *et al.*, 2007), to reduce the biases in estimates obtained through less-structured expert judgement (Elith *et al.*, 2013) that is dominated by cognitive biases and heuristics (e.g. McBride and Burgman, 2011). The interim PCoD approach has been used to assess the effect of offshore wind farm construction on harbour porpoise (*Phocoena phocoena*) in the North Sea (King *et al.*, 2015), as well as the exposure of bottlenose dolphin populations to anthropogenic disturbances in the Moray Firth, Scotland (Lusseau *et al.*, 2011). The use of the term ‘interim’ is important, because the approach is not meant to replace scientific research, but rather to be used as a temporary measure, allowing management and conservation decisions to be made while empirical data are collected. However, the results of expert elicitation can be influenced through the way questions are phrased or depending on which experts are included or excluded. These issues are important when such processes form the basis for decisions may have high costs, such as those related to the survival of endangered species.

While the PCoD framework shows promise, it does currently have some notable limitations. For example, PCoD models developed to date have explored the consequences of varying levels of a single disturbance, often assuming that the animals’ observed baseline behaviour and/or physiology incorporates the effects of existing background levels of disturbance. Even were multiple stressors included, there is a lack of information on how cumulative effects interact (e.g. additive, multiplicative). An emerging framework offers promise in modelling population consequences of multiple stressors in marine mammals (PCoMS; National Academies

Table 3

Definitions for the various PCAD/PCoD modeling frameworks.

PCAD	The original 2005 NRC framework (NRC, 2005).
PCoD	Data are available to parameterise all the transfer functions (e.g. the equations describing the link between disturbance and behavioural change, vital rates and population dynamics) in the framework (New <i>et al.</i> , 2014).
PCoD-lite	Data are not available to parameterise the transfer functions between behavioural and physiological changes and an individual’s health. Instead, the transfer functions between these changes and vital rates are informed from the scientific literature.
Interim PCoD	Data are not available and there is no information in the scientific literature for some of the transfer functions in the framework (e.g. the amount of disturbance an individual can tolerate before there is a change in behaviour). Expert elicitation is used to inform these transfer functions, but only until empirical data are available (King <i>et al.</i> , 2015).

of Sciences Engineering and Medicine, 2017). Efforts to include masking in population models should be prioritised, as should field research and modelling efforts to help quantify the relationship between reduction in acoustic space and prey intake.

Population Viability Analyses Models

Population Viability Analysis (PVA) is a class of scientific techniques that uses demographic modelling to assess risks to wildlife populations and evaluate the likely efficacy of protection, recovery, or restoration options (Beissinger and McCullough, 2002; Shaffer, 1990; Sjögren-Gulve and Ebenhard, 2000), and can be incorporated into a PCoD framework. PVA can extend standard demographic projections (Caswell, 2001) by incorporating the impacts of forces external to the population (e.g. harvest, changing habitat quality, etc.) on the demographic rates, which allows for the cumulative impacts and potential synergies of multiple threats to a population to be examined. Additionally, uncertainty in the population trajectory arising from intrinsic (e.g. demographic stochasticity, inbreeding impacts, etc.) and extrinsic (e.g. environmental variation, occasional catastrophes, etc.) factors can be explicitly modeled, usually using simulations (e.g. see Lacy, 2000; Lacy and Pollak, 2014).

PVAs have been used to assess threats to hundreds of species, including cetaceans such as killer whales (Lacy *et al.*, 2017; Taylor and Plater, 2001) and bottlenose dolphins (Lacy and Wells, 2009; Manlik *et al.*, 2016), with some simulations being confirmed to produce population trajectories that are consistent with monitored wildlife populations (Brook *et al.*, 2000).

The impacts of noise on one or more demographic rate(s) must be specified to model the impacts of noise (or any stress) on populations. Ideally, these functional relationships would be obtained from studies on the populations of interest, but otherwise they might be assumed to be similar to relationships measured on related species, elicited from expert opinions based on understanding of the ecology of the species, or specified as hypotheses to be explored in terms of the possible impacts and the concordance of population trajectories generated by the model with survey trends. Inevitably, there will be considerable uncertainty around the values of many of the parameters entered into a PVA. Therefore, sensitivity testing of the impacts of alternative values on the population trends is an important part of PVA. Such tests involve running scenarios with different parameter values or by sampling, in each iteration of the simulation, each parameter value from a distribution describing its uncertainty. The variability in the population fates generated by the simulation can then be partitioned into that caused by the uncertainty in the basic demography of the species, uncertainty in the levels of threatening processes impacting the populations, and uncertainty in the demographic responses to those threats.

The above PVA approach was used to examine the likely impacts of the three main threats limiting recovery of endangered southern resident killer whales (SRKWs), namely limitation of the whales' preferred prey (Chinook salmon), masking and disturbance from vessel noise, and

chemical pollution. The modelling focused on assessing impacts of current levels of noise and disturbance from vessel traffic, as well as predicted increases in noise arising from increased oil tanker traffic (Lacy *et al.*, 2017). These threats were assessed individually and as cumulative impacts in addition to a currently depleted base of the whales' preferred prey (Chinook salmon), with expected changes in Chinook abundance. These analyses examined what would be required for SRKWs to reach one stated recovery goal of 2.3% annual growth sustained over 28 years. The importance of considering multiple factors is demonstrated here as it was found that the recovery target could not be reached through mitigation of any one factor alone (a 50% reduction in noise disturbance and a 25% increase in the Chinook abundance would be sufficient).

The above analyses focused on a population that is very well studied, with 40 years of detailed demographic data, assessments of demographic consequences of changing prey availability over time, and measurements of the reduction in feeding behaviour caused by boat noise. Such long-term ecological data are rare. However, the same approach might be used to explore possible noise (and other) impacts on population projections, with the understanding that the results will indicate relative impacts of threats only to the extent that the sparse data, proxy species, or expert opinion provide plausible estimates of key demographic parameters, magnitude of threats, and relationships between threats and demographic consequences. Even with such limitations, sensitivity testing can help to clarify what is known and is not known, document what assumptions and hypotheses are made with respect to the threats, quantify the sensitivity of outcomes to the uncertainty in parameter values, identify research priorities to reduce the more influential uncertainties, identify species characteristics that increase vulnerability, and test the relative benefits of management actions. For example, through a series of four PVA models on oceanic dolphin species with different life-histories, higher estimated population growth rates (due to longest potential longevity and highest birth rates) were associated with a higher tolerance of noise (and other) threats, but were still reduced to about zero population growth at the highest levels tested for any one threat (Ashe *et al.*, In review).

In common with the PCoD framework, PVAs are limited by available data and the best scientific efforts to fill these data gaps take time. In some cases, by the time the research is completed, the populations under study may already be suffering irreversible decline. Despite this, PVAs can be used to identify populations that may be most resilient to external stressors, and therefore prioritise population protection (and research) where it would be most effective.

Moving models forward

The PCoD framework and PVA provide approaches for understanding the influence of environmental stressors on population dynamics. Despite the lack of data to support all of the links in any given model, the approaches are still extremely useful for organising the way scientists think about threats, identifying data gaps, and prioritising species and threats for allocation of future research funding. They are also promising tools for consideration of masking

impacts of populations and provide an opportunity for researchers to work with policy makers and managers to document ways of reducing the effects of noise. However, some stressors may act through multiple pathways, which have not been incorporated into any of the PCoD or PVA models presented to date. For example, masking may lead to a reduction in foraging efficiency as well as loss of mating opportunities. Furthermore, it is crucial to recognise and emphasise that unknown threats cannot be quantified in models. Accordingly, the importance of identifying all relevant threats that may affect population dynamics cannot be overstated.

In order to integrate changes in acoustic habitat into statistical models of whale population dynamics, we highlight the importance of interdisciplinary efforts to:

- (1) provide and incorporate the best estimates of all aspects of a model (e.g. functional links, parameters, sound field maps) along with associated measures of uncertainty;
- (2) develop model structures and outputs to address pertinent management questions about impacts of anthropogenic noise and the effectiveness of mitigation to reduce ocean noise; and
- (3) use these models as a heuristic tool to help researchers define their thinking, construct hypotheses and explore uncertainty in ways that may not be possible through field studies alone.

Given current knowledge, one way to model the population consequences of loss of acoustic habitat is through reduction in foraging opportunities or caloric intake. This approach hinges on two critical links: one between noise and prey intake; and another between prey intake and demography. Prey-demography links are available (or could be derived) for several well-studied marine mammal populations (summarised in Williams *et al.*, 2016), but fewer data exist to quantify effects of acoustic habitat changes on prey intake. In particular, data to quantify the link between acoustic habitat and prey intake do not yet exist for most baleen whale species. We are not suggesting that effects of noise on foraging represent the largest pathway of effects (e.g. see effects of noise on physiological stress (Münzel *et al.*, 2014), but we do believe this to be a tractable way forward, given available information. To prioritise future work, it is necessary to identify two sets of priority cetacean case study species or populations. One set could be selected based on urgent conservation needs (e.g. central Baltic harbour porpoise). Another set of data-rich case studies could be selected to form ‘archetype’ populations that would be useful to refine and improve population models. For example, prey-demography links are available for many baleen whale populations: North Atlantic fin whales (Williams *et al.*, 2013); right whales (Meyer-Gutbrod *et al.*, 2015; Miller *et al.*, 2011) and humpback whales (Robbins, 2007). Results from future studies on these tractable populations may then have to be extrapolated to those populations of high conservation priority for which we lack sufficient data for direct application of these models. Accordingly, fully parameterised models from archetype case studies should be evaluated for their potential for extrapolation to other species and habitats.

Regardless, it must be acknowledged that the scientific development of PCoD, PVAs and other modelling tools has been hindered by a lack of guidance from policy makers on the level of risk that might be considered acceptable (Williams *et al.*, 2016). A key strength of both PCoD and PVA frameworks is the ability to model the likely outcome of both continued habitat degradation and habitat restoration that would result from management actions. By communicating the population consequences of alternative management actions (including no action), PVA is an effective tool for communicating the risk and benefit of alternative management options to stakeholders, managers and policy makers.

SUMMARY

Noise is one of many stressors in the environment in which cetaceans live. Therefore, noise should be explicitly considered as part of a suite of cumulative effects in models being developed for cetacean conservation and efforts to manage anthropogenic impacts. We thus recommend that noise impact models should consider single noise stressor, aggregate noise stressors, and the combination with other non-acoustic stressors.

While efforts are already being undertaken to evaluate the impacts of loss of acoustic habitat on foraging, similar research must be initiated to look at other impacts of noise on other life functions (e.g. breeding). Specifically, research is needed that explores the linkages between masking of sounds/loss of acoustic habitat and the effect on other life functions, similar to what has been done with the examples presented on foraging.

Despite the remaining data gaps, the IWC-SC has recognised emerging evidence that compromised acoustic habitat can affect some cetacean populations adversely (IWC, 2006; King *et al.*, 2015). The IWC-SC has noted that there is now compelling evidence that chronic anthropogenic noise is having an effect on the marine acoustic environment in many regions (Clark *et al.*, 2009; Hatch *et al.*, 2016; Moore *et al.*, 2012), and may be a significant factor in governing population dynamics of some cetacean species (Lacy *et al.*, 2017). Given cetacean dependence on listening to and producing sounds for their survival, we recommend that a focus on acoustic habitat quality become a routine part of research and management activities designed to guide cetacean conservation efforts.

While we acknowledge the inherent difficulty of drawing causal linkages between loss of acoustic habitat and adverse effects on cetacean populations, we believe that the lack of scientific certainty should not hinder management actions to reduce ocean noise. We thus recommend that management efforts be undertaken to keep quiet areas quiet and make noisy areas quieter (Williams *et al.*, 2015). Ships that contribute disproportionately to ocean noise levels should be considered a priority for replacement or application of ship quieting technologies (Veirs *et al.*, 2018). Some approaches to reducing ship noise (e.g. re-routing) may involve displacement of efforts, or tradeoffs (e.g. between noise amplitude and duration of exposure inherent in any speed limit Veirs *et al.*, 2018). Addressing these tradeoffs will involve decisions to be made on a case-by-case basis.

Finally, in any research or management effort, climate change is a major potential confounding variable that will likely be introducing a complex array of multiple new stressors into any given system. The IWC-SC has recommended that reducing the most tractable stressors, such as anthropogenic noise, will offer managers a means to increase populations' resilience to climate change and improve future prospects for cetaceans (IWC, 2016).

ACKNOWLEDGEMENTS

This manuscript originated from discussions undertaken at the IWC-SC Workshop on Acoustic Masking and Whale Population Dynamics held in Bled, Slovenia, 4–5 June 2016. The authors thank the Secretariat for help with planning and implementation of the workshop, and NOAA for funding the workshop. The authors thank all participants (Frank Cipriano, Samba Diallo, Caterina Fortuna, Pierre Gallego, Hyun Woo Kim, Dave Lundquist, Fabian Ritter, Vanesa Reyes, Naomi Rose, Hawsun Sohn) for helpful suggestions during the workshop. RW thanks the Pew Fellows in Marine Conservation program and Fisheries and Oceans Canada for financial support during the writing and McLean and Marisla Foundations for long-term general support for Oceans Initiative's acoustic ecology program. The authors thank two anonymous reviewers for careful, constructive reviews of a previous version of this manuscript.

REFERENCES

- Ashe, E., Williams, R., Clark, C.W., Erbe, C., Gerber, L., Hall, A., Hammond, P.S., Lacy, R., Reeves, R.R. and Vollmer, N. In review. Averting the data-gap trap: predicting sensitivity of abundant species to threats in the face of uncertainty. [Available from the author]
- Authier, M., Commanducci, F.D., Genov, T., Holcer, D., Ridoux, V., Salivas, M., Santos, M.B. and Spitz, J. 2017. Cetacean conservation in the Mediterranean and Black Seas: fostering transboundary collaboration through the European marine strategy framework directive. *Mar. Policy* 82: 98–103.
- Beissinger, S.R. and McCullough, D.R. 2002. *Population Viability Analysis*. Chicago University Press, Chicago. 577pp.
- Brook, B.W., O'Grady, J.J., Chapman, A.P., Burgman, M.A., Akcakaya, H.R. and Frankham, R. 2000. Predictive accuracy of population viability analysis in conservation biology. *Nature* 404: 385–87.
- Caswell, H. 2001. *Matrix Population Models. Construction, Analysis and Interpretation*. 2nd ed. Sinauer Associates, Inc, Sunderland, Massachusetts, USA. i–xxii+722pp.
- Cholewiak, D., Clark, C.W., Ponirakis, D., Frankel, A., Hatch, L., Risch, D., Stanistreet, J.E., Thompson, M.A., Vu, E.T. and Van Parijs, S.M. 2018. Communicating amidst the noise: modeling the aggregate influence of ambient and vessel noise on baleen whale communication space in a national marine sanctuary. *Endanger. Species Res.* 36: 59–75.
- Clark, C.W., Ellison, W.T., Southall, B.L., Hatch, L., Van Parijs, S.M., Frankel, A. and Ponirakis, D. 2009. Acoustic masking in marine ecosystems: intuitions, analysis, and implication. *Endanger. Species Res.* 39(5): 201–22.
- Elith, J., Simpson, J., Hirsch, M. and Burgman, M.A. 2013. Taxonomic uncertainty and decision making for biosecurity: spatial models for myrtle/guava rust. *Austral. Plant Path.* 42: 43–51.
- Ellison, W.T., Southall, B.L., Clark, C.W. and Frankel, A. 2012. A new context-based paradigm to assess behavioral responses of marine mammals to sound. *Conserv. Biol.* 26: 21–28.
- Erbe, C., Reichmuth, C., Cunningham, K., Lucke, K. and Dooling, R.J. 2016. Communication masking in marine mammals: a review and research strategy. *Mar. Pollut. Bull.* 103: 15–38. [<http://doi.org/10.1016/j.marpolbul.2015.12.007>].
- Estévez, R.A., Walshe, T. and Burgman, M.A. 2013. Capturing social impacts for decision-making: a Multicriteria Decision Analysis perspective. *Divers. Distrib.* 19: 608–16.
- Ford, J.K.B., Ellis, G.M., Olesiuk, P.F. and Balcomb, K.C. 2009. Linking killer whale survival and prey abundance: food limitation in the oceans' apex predator? *Biol. Lett.* 6: 139–42. [Available at: <http://rsbl.royalsocietypublishing.org/content/early/2009/09/14/rsbl.2009.0468.full.pdf+html>].
- Gabriele, C.M., Ponirakis, D.W., Clark, C.W., Womble, J.N. and Vanselow, P. 2018. Underwater acoustic ecology metrics in an Alaska Marine Protected Area reveal marine mammal communication masking and management alternatives. *Front. Mar. Sci.* 5: 270.
- Gomez, C., Lawson, J.W., Wright, A.J., Buren, A.D., Tollit, D. and Lesage, V. 2016. A systematic review on the behavioural responses of wild marine mammals to noise: the disparity between science and policy. *Can. J. Zool.* 94(12): 801–19.
- Hatch, L., Wahle, C.M., Gedamke, J., Harrison, J., Laws, B., Moore, S.E., Stadler, J.H. and Van Parijs, S.M. 2016. Can you hear me here? Managing acoustic habitat in US waters. *Endang. Species Res.* 30: 171–86.
- Hatch, L.T., Clark, C.W., Van Parijs, S.M., Frankel, A.S. and Ponirakis, D.W. 2012. Quantifying loss of acoustic communication space for right whales in and around a US National Marine Sanctuary. *Cons. Biol.* 26: 983–94.
- Hayes, K.R., Regan, H.M. and Burgman, M.A. 2007. Introduction to the concepts and methods of uncertainty analysis. pp.188–208. In: A.R. Kapuscinski, K.R. Hayes, S. Li, and G. Dana (eds). *Environmental Risk Assessment of Genetically Modified Organisms, Volume 3: Methodologies for Transgenic Fish*. CABI Publishing, Oxfordshire, UK.
- Holt, M., Noren, D. and Emmons, C. 2011. Effects of noise levels and call types on the source levels of killer whale calls. *J. Acoust. Soc. Am.* 130(5): 3100–06.
- Hotchkiss, C. and Parks, S. 2013. The Lombard effect and other noise-induced vocal modifications: insight from mammalian communication systems. *Biol. Rev.* 88(4): 809–24.
- International Maritime Organization. 2013. Provisions for reduction of noise from commercial shipping and its adverse impacts on marine life. Paper DE 57/WP 8 presented to IMO Subcommittee on Ship Design and Equipment.
- International Whaling Commission. 2005. Report of the Scientific Committee. Annex K. Report of the Standing Working Group on Environmental Concerns. *J. Cetacean Res. Manage. (Suppl.)* 7:267–81.
- International Whaling Commission. 2006. Report of the Scientific Committee. Annex K. Report of the Standing Working Group on Environmental Concerns. *J. Cetacean Res. Manage. (Suppl.)* 8:185–220.
- International Whaling Commission. 2009. Report of the Scientific Committee. Annex K. Report of the Standing Working Group on Environmental Concerns. *J. Cetacean Res. Manage. (Suppl.)* 11:266–302.
- International Whaling Commission. 2015. Report of the Scientific Committee. Annex K. Report of the Standing Working Group on Environmental Concerns. *J. Cetacean Res. Manage. (Suppl.)* 16:248–76.
- International Whaling Commission. 2016. Report of the Workshop on Acoustic Masking and Whale Population Dynamics, 4–5 June 2016, Bled, Slovenia. *J. Cetacean Res. Manage. (Suppl.)* 18:615–27.
- International Whaling Commission. 2018. Further information related to impacts of underwater noise on marine life. IMO document MEPC 72/INF9. 15pp.
- King, S.L., Schick, R.S., Donovan, C., Booth, C.G., Burgman, M., Thomas, L. and Harwood, J. 2015. An interim framework for assessing the population consequences of disturbance. *Methods Ecol. Evol.* 6(10): 1150–8.
- Lacy, R.C. 2000. Structure of the VORTEX simulation model for population viability analysis. *Ecol. Bull.* 48: 191–203.
- Lacy, R.C. and Pollak, J.P. 2014. VORTEX: A Stochastic Simulation of the Extinction Process. Version 10.0. Chicago Zoological Society, Brookfield, Illinois, USA.
- Lacy, R.C. and Wells, R. 2009. Population Viability Analysis (PVA). pp.25–29 In: R.R. Reeves and R.L. Brownell, Jr. (eds). *Indo-Pacific bottlenose dolphin assessment workshop report: Solomon Islands case study of Tursiops aduncus*. Occasional Paper of the Species Survival Commission, No. 40. IUCN, Gland, Switzerland. 53pp.
- Lacy, R.C., Williams, R., Ashe, E., Balcomb, K.C. III, Brent, L.J.N., Clark, C.W., Croft, D.P., Giles, D.A., MacDuffee, M. and Paquet, P.C. 2017. Evaluating anthropogenic threats to endangered killer whales to inform effective recovery plans. *Sci. Rep.* 7: 14119. [doi: 10.1038/s41598-017-14471-0].
- Leaper, R., Renilson, M., Frank, V. and Papastravrou, V. 2009. Possible steps towards reducing impacts of shipping noise. Paper SC/61/E19 presented to the IWC Scientific Committee, June 2009, Madeira, Portugal (unpublished). 5pp. [Paper available from the Office of this Journal].
- Leaper, R., Renilson, M. and Ryan, C. 2014. Reducing underwater noise from large commercial ships: current status and future directions. *J. Ocean Technol.* 9(1): 50–69.
- Lombard, É. 1911. Le signe de l'élévation de la voix. *Annales des Maladies de l'Oreille et du Larynx*. XXXVII(2), 101–109. [In French]
- Lusseau, D., New, L.F., Donovan, C., Cheney, B., Thompson, P.M., Hastie, G. and Harwood, J. 2011. The development of a framework to understand and predict the population consequences of disturbances for the Moray Firth bottlenose dolphin population. Scottish Natural Heritage Commissioned Report no. 468, Inverness, Scotland.

- Manlik, O., McDonald, J.A., Mann, J., Raudino, H.C., Bejder, L., Krützen, M., Connor, R.C., Heithaus, M.R., Lacy, R.C. and Sherwin, W.B. 2016. The relative importance of reproduction and survival for the conservation of two dolphin populations. *Ecol. Evol.* 6: 3496–512.
- McBride, M.F. and Burgman, M.A. 2011. What is expert knowledge, how is such knowledge gathered, and how do we use it to address questions in landscape ecology? pp.11–38. In: A. Perera, A. Drew and C. Johnson (eds). *Chapter 2. Expert Knowledge and its Applications in Landscape Ecology*. Springer, New York.
- Merchant, N.D., Brookes, K.L., Faulkner, R.C., Bicknell, A.W.J., Godley, B.J. and Witt, M.J. 2016. Underwater noise levels in UK waters. *Sci. Rep.* 6: 36942. [<https://doi.org/10.1038/srep36942>].
- Meyer-Gutbrod, E.L., Greene, C.H., Sullivan, P.J. and Pershing, A.J. 2015. Climate-associated changes in prey availability drive reproductive dynamics of the North Atlantic right whale population. *Mar. Ecol. Prog. Ser.* 535: 243–58. [<https://doi.org/10.3354/meps11372>].
- Miller, C.A., Reeb, D., Best, P.B., Knowlton, A.R., Brown, M.W. and Moore, M.J. 2011. Blubber thickness in right whales *Eubalaena glacialis* and *Eubalaena australis* related to reproduction, life history status and prey abundance *Mar. Ecol. Prog. Ser.* 438: 267–83.
- Möhl, B. 1980. Marine mammals and noise. *Arctic Seas Bull.* 2: 1–2.
- Möhl, B. 1981. Masking effects of noise; their distribution in time and space. The question of sound from icebreaker operations. pp.259–68. In: Peterson, N.M. (eds). *The Question of Sound from Icebreaker Operations. Proceedings of a Workshop, 23 and 24 February 1981*. Arctic Pilot Project, Toronto, Canada.
- Moore, S.E., Reeves, R.R., Southall, B.L., Ragen, T.J., Suydam, R.S. and Clark, C.W. 2012. A new framework for assessing the effects of anthropogenic sound on marine mammals in a rapidly changing Arctic. *Bioscience* 62: 289–95.
- Münzel, T., Gori, T., Babisch, W. and Basner, M. 2014. Cardiovascular effects of environmental noise exposure. *Eur. Heart J.* 35(13): 829–36.
- National Academies of Sciences Engineering and Medicine. 2017. *Approaches to Understanding the Cumulative Effects of Stressors on Marine Mammals*. Washington, DC: The National Academies Press. [<https://doi.org/10.17226/23479>].
- National Research Council. 2005. *Marine Mammal Populations and Ocean Noise: Determining When Noise Causes Biologically Significant Events*. National Academies Press, Washington, DC. 142pp.
- New, L., Moretti, D., Hooker, S., Costa, P. and Simmons, S. 2013a. An energetics model for the survival and reproduction of beaked whales (family Ziphiidae). *PLoS One* 8(e68725). [<https://doi.org/10.1371/journal.pone.0068725>].
- New, L.F., Clark, J.S., Costa, D.P., Fleishman, E., Hindell, M.A., Klanjscek, T., Lusseau, D., Kraus, S., McMahon, C.R., Robinson, P.W., Schick, R.S., Schwarz, L.K., Simmons, S.E., Thomas, L., Tyack, P. and Harwood, J. 2014. Estimating the long-term fitness of southern elephant seals on the basis of short-term measures of behaviour. *Mar. Ecol. Prog. Ser.* 496: 99–108.
- New, L.F., Harwood, J., Thomas, L., Donovan, C., Clark, J.S., Hastie, G., Thompson, P.M., Cheney, B., Scott-Hayward, L. and Lusseau, D. 2013b. Modelling the biological significance of behavioural change in coastal bottlenose dolphins in response to disturbance. *Funct. Ecol.* 27: 314–22.
- Pirotta, E., New, L., Harwood, J. and Lusseau, D. 2014. Activities, motivations and disturbance: An agent-based model of bottlenose dolphin behavioral dynamics and interactions with tourism in Doubtful Sound, New Zealand. *Ecol. Model.* 282: 44–58.
- Reyes Reyes, M.V., Tossenberger, V.P., Iñiguez, M.A., Hildebrand, J.A. and Melcón, M.L. 2016. Communication sounds of Commerson's dolphins (*Cephalorhynchus commersonii*) and contextual use of vocalizations. *Mar. Mamm. Sci.* 32(4): 1219–33. [<http://doi.org/10.1111/mms.12321>].
- Robbins, J. 2007. Structure and dynamics of the Gulf of Maine humpback whale population. PhD thesis, University of St Andrews, Scotland. [Available at: <http://hdl.handle.net/10023/328>].
- Schick, R.S., Kraus, S.D., Rolland, R.M., Knowlton, A.R., Hamilton, P.K., Pettis, H.M., Kenney, R.D. and Clark, J.S. 2013a. Using hierarchical Bayes to understand movement, health, and survival in the endangered North Atlantic right whale. *PLoS One* 8. e64166. [<http://doi.org/10.1371/journal.pone.0064166>].
- Schick, R.S., New, L.F., Thomas, L., Costa, D.P., Hindell, M.A., McMahon, C.R., Robinson, P.W., Simmons, S.E., Thums, M., Harwood, J. and Clark, J.S. 2013b. Estimating resource acquisition and at-sea body condition of a marine predator. *J. Anim. Ecol.* 82: 1300–15.
- Shaffer, M.L. 1990. Population viability analysis. *Biol. Conserv.* 4: 39–40.
- Sjögren-Gulve, P. and Ebenhard, T. 2000. *The Use of Population Viability Analyses in Conservation Planning*. Munksgaard, Copenhagen.
- Taylor, M. and Plater, B. 2001. Population viability analysis for the Southern Resident Population of the killer whale (*Orcinus orca*). Center for Biological Diversity, Tucson, Arizona. 30pp. [Available from: <https://www.biologicaldiversity.org/>]
- van der Graaf, A.J., Ainslie, M.A., Andre, M., Brensing, K., Dalen, J., Dekeling, R.P.A., Robinson, S.M., Tasker, M.L., Thomsen, F. and Werner, S. 2012. European Marine Strategy Framework Directive – Good Environmental Status (MSFD GES): Report of the Technical Subgroup on Underwater Noise and other forms of Energy. JRC Scientific and Technical Report, Brussels: Published by TSG Noise & Milieu Ltd. 75pp.
- Veirs, S., Veirs, V., Williams, R., Jasny, M. and Wood, J. 2018. A key to quieter seas: half of ship noise comes from 15% of the fleet. *Peer J PrePrints* [<https://doi.org/10.7287/peerj.preprints.26525v1>]
- Villegas-Amtmann, S., Schwartz, L.K., Sumich, J.L. and Costa, D.P. 2015. A bioenergetics model to evaluate demographic consequences of disturbance in marine mammals applied to gray whales. *Ecosphere* 6(10, art. 183): 1–19.
- Williams, R., Clark, C.W., Ponirakis, D. and Ashe, E. 2014. Acoustic quality of critical habitats for three threatened whale populations. *Anim. Conserv.* 17: 174–85.
- Williams, R., Erbe, C., Ashe, E. and Clark, C.W. 2015. Quiet(er) marine protected areas. *Mar. Pollut. Bull.* 100: 54–61.
- Williams, R., Lusseau, D. and Hammond, P.S. 2006. Estimating relative energetic costs of human disturbance to killer whales (*Orcinus orca*). *Biol. Conserv.* 133(3): 301–11.
- Williams, R., Thomas, L., Ashe, E., Clark, C.W. and Hammond, P.S. 2016. Gauging allowable harm limits to cumulative, sub-lethal effects of human activities on wildlife: A case-study approach using two whale populations. *Mar. Policy* 70: 58–64.
- Williams, R., Veirs, S., Veirs, V., Ashe, E. and Mastick, N. 2019. Approaches to reduce noise from ships operating in important killer whale habitats. *Mar. Pollut. Bull.* 139: 459–69.
- Williams, R., Vikingsson, G.A., Gislason, A., Lockyer, C., New, L., Thomas, L. and Hammond, P.S. 2013. Evidence for density-dependent changes in body condition and pregnancy rate of North Atlantic fin whales over four decades of varying environmental conditions. *ICES J. Mar. Sci.* 70(6): 1273–80.
- Wright, A. 2017. *Marine mammals and noise*. KOROS Press Limited, 2017. [ISBN 1785693565]. [Available from: <https://www.amazon.com/Marine-Mammals-Noise-Andrew-wright/dp/1785693565>].
- Wright, A.J. and Okeanos Foundation for the Sea. 2008. Report of the International Workshop on Shipping Noise and Marine Mammals, held by Okeanos – Foundation for the Sea, Hamburg, Germany, 21–24 April 2008. Okeanos – Foundation for the Sea, Auf der Marienhole 15, D-64297 Darmstadt. 34pp.