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Population-level consequences of seismic surveys on fishes: An interdisciplinary challenge

Hans Slabbekoorn[1] | John Dalen[2] | Dick de Haan[3] | Hendrik V. Winter[3] | Craig Radford[4] | Michael A. Ainslie[5] | Kevin D. Heaney[6] | Tobias van Kooten[3] | Len Thomas[7] | John Harwood[7]

[1]Institute of Biology (IBL), Leiden University, Leiden, The Netherlands

[2]Soundmare, Bergen, Norway

[3]Wageningen Marine Research (WMR), IJmuiden, The Netherlands

[4]University of Auckland, Leigh, New Zealand

[5]JASCO/TNO, Safety & Defence, The Hague, The Netherlands

[6]OASIS Inc., Fairfax Station, Virginia

[7]Centre for Research into Ecological and Environmental Modelling (CREEM), University of St. Andrews, St. Andrews, UK

Correspondence
Hans Slabbekoorn, Institute of Biology (IBL), Leiden University, Leiden, The Netherlands.
Email: h.w.slabbekoorn@biology.leidenuniv.nl

Abstract

Offshore activities elevate ambient sound levels at sea, which may affect marine fauna. We reviewed the literature about impact of airgun acoustic exposure on fish in terms of damage, disturbance and detection and explored the nature of impact assessment at population level. We provided a conceptual framework for how to address this interdisciplinary challenge, and we listed potential tools for investigation. We focused on limitations in data currently available, and we stressed the potential benefits from cross-species comparisons. Well-replicated and controlled studies do not exist for hearing thresholds and dose–response curves for airgun acoustic exposure. We especially lack insight into behavioural changes for free-ranging fish to actual seismic surveys and on lasting effects of behavioural changes in terms of time and energy budgets, missed feeding or mating opportunities, decreased performance in predator-prey interactions, and chronic stress effects on growth, development and reproduction. We also lack insight into whether any of these effects could have population-level consequences. General "population consequences of acoustic disturbance" (PCAD) models have been developed for marine mammals, but there has been little progress so far in other taxa. The acoustic world of fishes is quite different from human perception and imagination as fish perceive particle motion and sound pressure. Progress is therefore also required in understanding the nature and extent to which fishes extract acoustic information from their environment. We addressed the challenges and opportunities for upscaling individual impact to the population, community and ecosystem level and provided a guide to critical gaps in our knowledge.

KEYWORDS

airgun, behavioural response, dynamic energy budget, fish hearing, population consequences of acoustic disturbance, stress physiology

1 | INTRODUCTION

Human activities at sea add sound to the world of fishes and hence elevate natural levels of ambient noise (Frisk, 2012; Hildebrand, 2009; McDonald, Hildebrand, & Wiggins, 2006). This has potential consequences for aquatic animals that live in a dark or low-visibility world and heavily rely on sound for many aspects of their life that affect survival and reproduction (Carroll, Przeslawski, Gunning, Bruce, & Duncan, 2017; Cox, Brennan, Gerwing, Dudas, & Juanes, 2018; Hawkins, Pembroke, & Popper, 2015; Peng, Zhao, & Liu, 2015). All fishes are likely to be sensitive to sound to some extent. Many species also use acoustic signals for communication among conspecifics and acoustic cues for detection of predators or prey: all of which may be affected by the presence of anthropogenic noise (Ladich, 2008; Popper & Hastings, 2009; Radford, Kerridge, & Simpson, 2014; Slabbekoorn et al., 2010). Furthermore, the whole variety of sounds in their surroundings creates a soundscape that is used for orientation and navigation (Fay, 2009; Slabbekoorn & Bouton, 2008). Consequently, their auditory sensitivity makes them vulnerable to damage in case of over-exposure and disturbance in case of any sound in the audible range that is perceived as a threat or causing distraction (Chan, Giraldo-Perez, Smith, & Blumstein, 2010; Kight & Swaddle, 2011; Shannon et al., 2016). Man-made sounds that overlap in time and frequency can also mask biologically relevant sounds, making them less audible and undermining detection and recognition (Brumm & Slabbekoorn, 2005; Dooling & Leek, 2018).

Noise pollution can affect well-being and fitness of individual fish through damage, disturbance and masking (Carroll et al., 2017; Cox et al., 2018). However, the impact of sound is not often very direct or obvious, except for rare cases of over-exposure, where dead or stunned fish come float to the surface during or soon after an acoustic event such as underwater pile driving or explosions (Halvorsen, Casper, Matthews, Carlson, & Popper, 2012; Popper et al., 2014). Sound levels underwater typically go unnoticed by humans that are on or near the water, and observing fish behaviour is even challenging to marine investigators that apply special tools (e.g. Bruce et al., 2018; Cooke et al., 2014; Metcalfe, Wright, Tudorache, & Wilson, 2016). Furthermore, it is challenging to determine the long-term impact on welfare or fitness from short-term behavioural changes in response to anthropogenic noise; the challenge is even greater if there is a physiological response but no apparent change in behaviour (Kight & Swaddle, 2011; Kunc, McLaughlin, & Schmidt, 2016). Nevertheless, scientific and public awareness has increased over the last decades, across taxa, and concerns from fisheries, conservationists and policymakers have resulted in noise pollution to be integrated in environmental legislation in a growing part of the world (Farcas, Thompson, & Merchant, 2016; Popper et al., 2014; Southall et al., 2007; Weilgart, 2007; Willsteed, Gill, Birchenough, & Jude, 2017).

The concerns about potentially detrimental effects of man-made sounds on marine life has led to regulation in the United States via the Marine Mammal Protection Act (MMPA), the Endangered Species Act (ESA) and the Magnuson–Stevens Fishery Conservation and Management Act (MSA), by which individual animals of specific species are protected against harm and harassment (Dolman & Jasny, 2015; Gordon et al., 2003; Merchant, 2019; Williams et al., 2015). The Marine Strategy Framework Directive (MSFD) of the European Union is different and requires member states to achieve or maintain Good Environmental Status (GES) by 2020. Descriptor 11 of the GES requires that "Introduction of energy, including underwater noise, is at levels that do not adversely affect the marine environment," for which two indicators are specified: distribution in time and space of loud, low- and mid-frequency impulsive sound (Indicator 11.1.1) and continuous low-frequency sound around 125 Hz (Indicator 11.2.1).

For the United States and the EU, regulators require insights that are currently limited or missing (Hawkins et al., 2015; Nowacek et al., 2015; Popper et al., 2014; Southall et al., 2007). Threshold sound conditions for physical damage of individual animals or behavioural or physiological effects that likely affect survival or probability of reproduction are only available for very few species (independent of whether they fall under the MMPA or ESA). Furthermore, data on sound impact or individual welfare and fitness are not only rare or non-existing for free-ranging animals (Nedelec et al., 2017; Simpson et al., 2016), but there is also still a large gap in knowledge when it comes to translating such data to "*adverse effects on the environment*," which is required to assess whether "*Good Environmental Status*" has been achieved (Kunc et al., 2016; New et al., 2014; NRC

2005; Shannon et al., 2016). Sufficient understanding of whether measures of mitigation are necessary or adequate consequently remains elusive.

Airguns used for seismic surveys are one of several prominent sources of noise pollution (Dragoset, 2005; Gisiner, 2016; Landrø & Amundsen, 2018; Laws & Hedgeland, 2008). Seismic surveys involve long series of intense sound pulses, reflections of which from the seabed provide information on the shape and composition of ocean bottom layers. They are used, for example, to obtain insight into the size and location of oil and gas resources. The airgun sound pulses can make a significant contribution to the underwater ambient sound profile over large areas as they can be audible over thousands of kilometres (Hildebrand, 2009; Nieukirk et al., 2012). Global trends in acoustic presence, since historical explorations with dynamite in the 1920s, have seen changes in source type and survey scale, while spreading of seismic exploration activity largely followed economic developments (Landrø & Amundsen, 2018), similar to the rising patterns in vessel noise since the 1950s (Frisk, 2012; McDonald et al., 2006).

The aim of this paper is to review the current state of knowledge on whether and how seismic surveys can have a detrimental effect on fishes. Our explicit target was to evaluate the evidence for impact from airgun acoustic exposure on fish in terms of damage, disturbance and detection of biologically relevant sounds and to address the potential for extrapolation of data and insights to population-level consequences. We therefore explored the interdisciplinary nature of impact assessment (cf. Rosa & Koper, 2018), focused on the abundant limitations in the data currently available, and provided an overview of relevant information and potential tools suitable for investigation once data become available. Critical for the evaluation is to understand (a) that effects on individual animals should be translated to consequences for stocks, populations, species, communities or whole ecosystems; and (b) that choices for spatial (local, regional, global) and temporal resolution (now, coming years or decades, forever) are likely to have a large impact on the outcome, while these choices can be regarded as political or strategic decisions.

The order in which we address topics and subdisciplines is as follows. We start with a brief description of general and more specific risk evaluation methods for environmental hazards. Special attention is allocated to so-called productivity susceptibility assessment (PSA; Milton, 2001; Patrick et al., 2009, 2010), as applied to fish stocks, and population consequences of disturbance (PCoD) models (Farmer et al., 2018; National Research Council, 2005; New et al., 2014), as applied mainly to marine mammals. We address the potential relevance for fishes exposed to sound in general and seismic surveys in particular. As marine biologists and policymakers typically have little knowledge about seismic operations, we further address the nature of seismic surveys to provide insights into the sound source of investigation and the potential exposure characteristics of marine fish.

Also critical for the evaluation is insight into what we know (and often do not know) about what and how fishes hear. We therefore provide a brief review on fundamentals of fish hearing, followed by a primer on sound propagation models that relate characteristics of the sound source to the spread and nature of the man-made sound field. We subsequently review published studies on behavioural and physiological response data related to airgun exposure and other experimental sound exposure studies relevant to potential effects of seismic surveys. We also address how to integrate such available and new data into a PCoD-type framework, using dynamic energy budgets (DEBs), individual-based models (IBMs), and multitrophic stock models (MSMs). Finally, we evaluate the feasibility of ecosystem-based assessments for sound impact assessment, which is an approach that can benefit from experience and modelling in fisheries, again provided that sufficient data become available about impact of acoustic disturbance on fishes.

2 | IMPACT ASSESSMENT

2.1 | Risk evaluation methods

Risk assessment is used to quantify the risk (i.e. expected adverse change to the environment due to one or more hazards) associated with different alternative actions (e.g. Halpern et al., 2008; Hammar, Wikström, & Molander, 2014; Hobday et al., 2007; New et al., 2014; Weed, 2005). There are many ways to categorize risk assessment methods, for example (a) rapid vs. in-depth; (b) top-down vs. bottom-up; (c) data-rich vs. data-poor; (d) qualitative, semi-quantitative or quantitative; and (e) empirical (i.e. based on data with little underlying theory) vs. mechanistic (based on theoretical models, possibly parameterized with data).

Qualitative methods typically categorize different risks into ordinal (i.e. ordered) classes such as “low,” “medium” and “high” along two axes: frequency (likelihood of occurrence) and severity (Figure 1a). The assignment of risk level to each element of the classification (e.g. something that is high frequency but low severity as not being of concern but something that is low frequency but high severity as being of moderate concern) is essentially based on an unstated algorithm.

Semi-quantitative methods, such as so-called productivity and susceptibility assessment (PSA), may have multiple axes and assign numerical values to each axis. These values are ordinal, but not nominal (i.e. the difference between 1 and 2 is not necessarily the same as the difference between 2 and 3—nor do numbers on different axes necessarily have the same scale). Overall risk is obtained by summing or averaging the numerical scores—something that is of dubious utility given the ordinal nature of the scores. Implicit or explicit weighting and rescaling is sometimes used. Aside from PSA, another example of such arbitrary summation is the cumulative impact analysis of Halpern et al. (2008).

Both qualitative and semi-quantitative methods suffer from the same fundamental problem: comparison or combination of different ordinal variables is essentially arbitrary. Potential solutions include groundtruthing, where possible, and simulation testing, for example through management strategy evaluation (Altenback, 1995). An example of simulation testing is that applied to the “catch limit algorithm” of the International Whaling Commission Revised

Management Procedure. Note that such tests are inherently quantitative. Possibly the best solution is to use a quantitative method in the first place.

Quantitative methods range from in-depth, bottom-up, data-rich, mechanistic methods, such as a full PCoD model (Costa et al., 2015; New et al., 2014), to semi-rapid, top-down, data-poor, semi-empirical methods, such as the "interim PCoD" approach of King et al. (2015), which used expert elicitation (described later) to parameterize a simplified full PCoD model. We are currently aware of one qualitative and one more quantitative analysis of population consequences of acoustic disturbance on fishes. Hammar et al. (2014) conducted an ecological risk assessment (ERA) on a threatened population of Atlantic cod (*Gadus morhua*, Gadidae) in the context of a wind farm project. They explored the potential impact of six stressors, three of which were sound related: moderate-level noise from working vessels and operating turbines and extreme over-exposure due to pile-driving noise in the construction phase. The analysis suggested that pile driving was the most hazardous stressor that could pose a serious risk to the cod population under study. A significant reduction of this risk was achieved in the model by avoiding pile-driving activity in the months of cod recruitment. Studies like this provide useful insights for urgent decisions and when data are lacking. However, they do not provide sufficient quantification and do not exploit the detailed insight physiological models may yield.

Sivle, Kvadsheim, and Ainslie (2014) modelled population consequences of sonar exposure for herring (*Clupea harengus*, Clupeidae) based on maximum reported sound levels of no behavioural response. Their predictions for the potential risk to the population of when these maximum levels were exceeded varied with season depending on the density of fish. The risk of any population consequence was lowest during spread-out feeding, but increased in periods of population aggregation. However, in general, the response estimates were low, and Sivle et al. (2014) concluded that it is unlikely that today's naval sonar activity will lead to any population-level effect for this species.

More sophisticated risk analyses take an exposure assessment and a dose–response assessment into account (see Boyd et al., 2008) to characterize and evaluate whether the level of environmental hazard is above some specified threshold for mitigation (Figure 1b), but these rely on available data and are quantitative in nature. The main issue with quantitative approaches is determining where the input comes from. The input comes either from data, which are often in short supply, or from expert elicitation, which can be unreliable if the analysis is not performed well and in very data-poor situations. The obvious remedy here is to collect sufficient and adequate input data or use appropriate methodology for expert elicitation in concert with the risk evaluation effort. Robustness to model misspecification can be evaluated through simulation testing. As we believe that semi-quantitative PSA could (with development) be a useful approach in some cases and that PCoD models have potential for marine mammals but also for fishes, we here give a brief description of the state of the art in both.

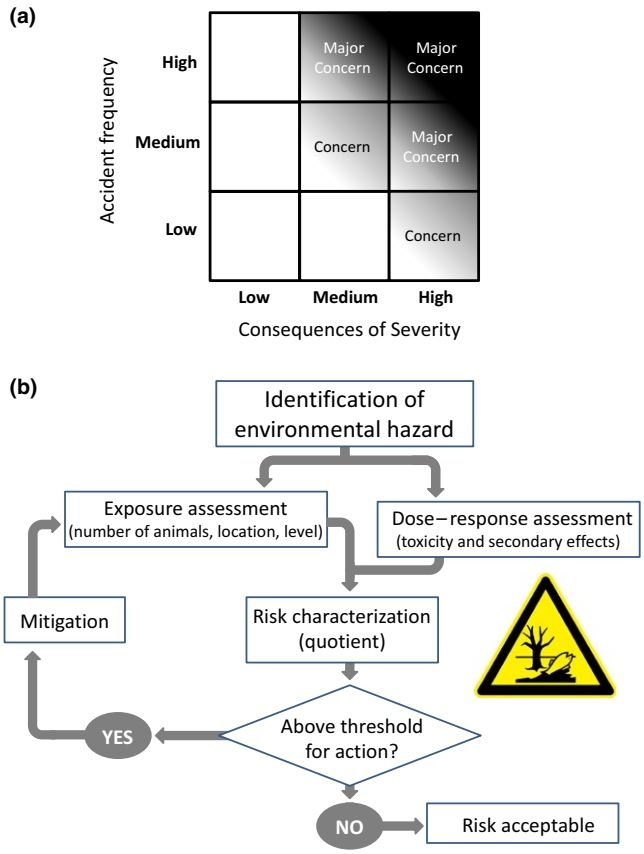

FIGURE 1 (a) Qualitative method of risk categorization into the qualitative classes: "low," "medium" and "high," based on evaluation along two axes: consequence severity and accident frequency (or probability). The combinations identify situations of concern or major concern (redrawn from Altenback, 1995). (b) General management framework for hazard identification and risk assessment to quantify the risk and evaluate alternative actions (mitigate or accept risk) (from Boyd et al., 2008)

2.2 | Productivity susceptibility assessment

Productivity susceptibility assessment (PSA; Milton, 2001) can be characterized as being rapid, top-down, data-poor, semi-quantitative and empirical and was originally developed to evaluate the risk that fisheries pose to specific target species in data-poor situations (Milton, 2001; Stobutzki, Miller, & Brewer, 2001). It has subsequently been expanded to cover a wide range of fisheries management effects on fish stocks (habitat impact, ecosystem considerations, management efficacy—e.g. Hobday, Smith, & Stobutzki, 2004; Hobday et al., 2007; Rosenberg et al., 2007). It involves scoring the productivity of a susceptible species in terms of a number of demographic parameters that affect population growth rate (survival, birth rate, etc.), and its susceptibility in terms of exposure to risk from fisheries (areal and vertical distribution, aggregation, etc.) and current status (current management strategy, etc.) (Patrick et al., 2009, 2010). The productivity scores are then averaged and the susceptibility scores multiplied together. Species that have a low productivity score and a high susceptibility score are considered to be particularly vulnerable.

The main productivity attributes of the PSA approach may be useful in any evaluation of detrimental impact and concern factors for fish stocks. The main attributes include maximum population growth, maximum individual size and age, the "von Bertalanffy" growth coefficient for how rapidly a fish reaches this maximum size and the age at maturity, natural mortality and fecundity, breeding strategy, recruitment pattern and mean trophic level (a high score for piscivores, intermediate for omnivores and a low score for planktivores). The main susceptibility attributes of the PSA approach in the context of fisheries concern catchability as determined by geographic area overlap and vertical distribution overlap between stock and fishing efforts, geographic concentration, seasonal migrations, schooling, aggregations and other behavioural and morphological traits in addition to desirability and market value (Patrick et al., 2009, 2010). Factors such as the effectiveness of management to control catch rates and the effects of fishing gear on habitat quality have also been added to these original attributes in order to determine susceptibility to fisheries (Hobday et al., 2007).

Additional susceptibility attributes that should be considered, if PSA were to be applied to seismic acoustic exposure, include the geographic and vertical distribution overlap of a particular fish species with the acoustic range of sound sources to determine exposure probability and level in terms of both sound pressure and particle motion. Any impact of acoustic exposure should be considered on top of and in the context of seasonal variation and specific life stage, size and reproductive conditions and the fisheries impact if the target species is also harvested. However, we believe that PSA cannot be used yet for evaluating the potential vulnerability of fish stocks to anthropogenic noise. Many of the susceptibility scoring categories currently used in PSA are not particularly appropriate for assessing the potential effects of anthropogenic noise. In addition, the appropriateness of the essentially arbitrary way in which the individual productivity and susceptibility scores are combined to provide a single metric needs to be evaluated. A new set of susceptibility scoring categories could be developed, for example using an expert elicitation process (Sutherland & Burgman, 2015) to identify fish species and stocks that are likely to be particularly vulnerable to the effects.

2.3 | Population consequences of disturbance models

The population consequences of disturbance (PCoD) and population consequences of acoustic disturbance (PCAD) models (NRC, 2005; New et al., 2014) consist of a series of transfer functions that describe how exposure to stressors (such as anthropogenic noise) affects individual behaviour; how the resulting changes in behaviour can affect health (defined as all internal factors that affect body condition or homoeostasis); and how variations in health may affect vital rates (survival, reproduction and growth/age at first breeding). Furthermore, the transfer function at the highest level of organization in the model addresses how the accumulation of data about the way in which different individuals are exposed to and affected by a stressor can be used to scale up the anticipated changes in vital rates to predict population-level effects.

PCAD models have now been applied to a number of marine mammal species, for example northern and southern elephant seals (*Mirounga angustirostris* and *M. leonina*, Phocidae; New et al., 2014; Costa et al., 2015), North Atlantic right whales (*Eubalaena glacialis*, Balaenidae; Schick, Kraus, et al., 2013), beaked whales (Ziphiidae; New, Moretti, Hooker, Costa, & Simmons, 2013), harbour porpoise (*Phocoena phocoena*, Phocoenidae; Harwood, King, Schick, & Donovan, 2014) and minke whale (*Balaenoptera acutorostrata*, Balaenopteridae; Christiansen & Lusseau, 2015), but there are hardly any examples so far for fish (but see Sivle et al., 2014).

Ideally, the predictions of PCAD models should be fitted to appropriate time series of empirical data obtained over a range of levels of disturbance. The results of such a fitting process can then be used to improve the parameter estimates and quantify the uncertainty associated with the model predictions, using approaches such as Bayesian hidden-process modelling (Newman, Buckland, Lindley, Thomas, & Fernandez, 2006). However, so far in no case has this been possible, and therefore, all models applied should still be considered as "exploratory." Exploratory models are particularly useful for comparing the possible consequences of different scenarios and for identifying priority areas for research. However, it is important that the uncertainties associated with their underlying parameter values are documented and that the effects of these uncertainties on their predictions are quantified.

It is useful to explore some of the details of the model applications in marine mammals to evaluate some of the problems and solutions that may also apply in some way to fishes. New et al. (2014), for example, used the PCoD model structure to investigate the potential effects of lost foraging dives on the health (measured by total lipid mass—see Schick, New, et al., 2013) of adult female southern elephant seals, and the implications of variation in health for pup survival and population dynamics. They used information obtained from data loggers that were attached to animals immediately before they embarked on their post-moult foraging trips. The data loggers allowed a reconstruction of their surface transit time and their foraging dive time. During portions of some foraging dives, elephant seals drift, and the rate of vertical movement during the drift is related to the ratio of lipid to lean body mass. The data logger information was calibrated against actual lipid gain during the foraging trip using measurements of body composition collected before and after the foraging trip, to enable estimation of daily lipid gain.

Furthermore, New et al. (2014) linked maternal mass at breeding to pup mass at weaning (Arnbom, Fedak, Boyd, & McConnell, 1993) and pup mass at weaning to pup survival (McMahon, Burton, & Bester, 2000, 2003). The model was then used to determine the effect of foraging dive disturbance on pup survival. It was assumed that there were no foraging dives for the duration of the disturbance and surface transit time was set to the observed maximum for that individual. If animals were disturbed for 50% of their time at sea in 1 year, the predicted decline in population size was small (<1%). However, if that disturbance would continue indefinitely (e.g. as a

result of variations in the extent of the Antarctic ice sheet caused by climate change), the predicted effects would be much greater (a 10% decline in abundance over 30 years).

The analyses in New et al. (2014) were only possible because detailed longitudinal data were available on the movements, health and reproductive success of a large number of adult female seals. Such extensive data sets require decades of intensive research and are only available for a few marine mammal populations. Researchers have adopted a range of techniques to build PCoD models in situations where empirical data are more limited. Nabe-Nielsen, Sibly, Tougaard, Teilmann, and Sveegaard (2014) used an individual-based model of the movements of harbour porpoises to estimate the potential effects of responses to the sound associated with wind turbine operation and shipping on their energy and reserves. They used a hypothetical relationship between energy reserves and survival to calculate population-level consequences. Villegas-Amtmann, Schwarz, Sumich, and Costa (2015) used a similar approach to predict the potential effects of reduced energy intake on reproductive success and survival for western grey whales (*Eschrichtius robustus*, Eschrichtiidae).

If empirical data are sufficient to estimate a relation between behavioural change and health, but not between health and vital rates, it may be possible to use a surrogate measure for the relevant vital rate. Christiansen and Lusseau (2015) used a bioenergetic model and empirical information on the behavioural response of adult female minke whales to whale-watching boats on their summer feeding grounds in Iceland to estimate the effects of these responses on the whales' health (as measured by their blubber volume). They calculated how different rates of encounter with whale-watching boats would affect an individual whale's health at the end of the summer, and then used an empirically derived relation between female blubber volume and foetal length (Christiansen, Rasmussen, & Lusseau, 2014) as a surrogate for the relationship between health and the probability of giving birth. Although interactions with whale-watching boats resulted in a 40% reduction in feeding activity, the predicted effect on a female's body condition over the course of the summer was very small (0.049% reduction), because boat encounters were actually rare. This reduction in body condition was not predicted to affect foetal survival. However, even if Christiansen and Lusseau (2015) had detected a significant effect on foetal survival, they would have been unable to forecast the population-level effects of exposure to whale-watching boats because the proportion of the North Atlantic minke whale population that feeds in Icelandic waters is not known.

In situations where even surrogate measures are unavailable, expert elicitation (Runge, Converse, & Lyons, 2011; Sutherland & Burgman, 2015) can be used to parameterize some of the transfer functions of the PCoD model. Expert elicitation is a formal process in which a number of experts on a particular topic are asked to predict what may happen in a particular situation. These predictions are combined into calibrated, quantitative statements, with associated uncertainty, which can be incorporated into mathematical models (Martin et al., 2012). King et al. (2015) used this approach to parameterize relationships between the number of days on which harbour porpoises were disturbed by noise associated with the construction of offshore wind farms and their survival and reproductive success. These relationships were then used to predict the potential population consequences of different scenarios for the construction of multiple wind farms.

There are several studies on different marine mammal species that have filled data gaps by asking experts. Lusseau et al. (2011) used an expert elicitation approach to predict the potential aggregate effect of noise associated with wind farm construction, tour boat operation and harbour expansion on a bottlenose dolphin (*Tursiops truncatus*, Delphinidae) population. Thompson et al. (2013) used it to assess population-level impacts of disturbance from pile driving on harbour seals (*Phoca vitulina*, Phocidae). Spatial distribution patterns and received noise levels were integrated with data on the potential for displacement and hearing damage. In general, uncertainties in ecological models are not unusual (see, e.g., Clark et al., 2001; Harwood & Stokes, 2003) and expert elicitation is one way to deal with them. A complementary approach is ecological risk assessment (ERA), possibly combined with weight of evidence (WOE) (see, e.g., Hammar et al., 2014; Hobday et al., 2007; Weed, 2005).

Based on the experience and examples of PCAD models for marine mammals, a flow chart is developed in Figure 2, which applies the same model components, transfer functions (Box 1) and vital rates in a model for population consequences of airgun disturbance to fishes. Before addressing the literature in more detail, the flow chart provides an overview of how exposure to the sounds of a seismic survey may change behaviour in such a way that it reduces individual foraging efficiency (Purser & Radford, 2011; Shafiei Sabet, Neo, & Slabbekoorn, 2015) and increases vulnerability to predation (Chan et al., 2010; Simpson, Purser, & Radford, 2015). Furthermore, swimming more or less efficient may also detrimentally affect individual energetics (Metcalfe et al., 2016; Villegas-Amtmann et al., 2015), while swimming less or in the wrong direction may result in missed mating or spawning opportunities (Boussard, 1981; Rossington, Benson, Lepper, & Jones, 2013). These changes in behaviour, together with acute or chronic stress physiological changes, may undermine individual body condition, immunocompetence and physiological investment in growth and reproduction (Barton, 2002; Sierra-Flores, Atack, Migaud, & Davie, 2015; Wendelaar-Bonga, 1997). The spectral and temporal structure of sounds will also affect physiological stress levels, as stronger responses have been reported to boat noise and intermittent noise than to more homogenous white noise (Nichols, Anderson, & Sirovic, 2015; Wysocki, Dittami, & Ladich, 2006, respectively).

The translation from individual-level effects to the population level in the PCAD model for fishes (Figure 2) is reflected in the consequences of these behavioural and physiological changes for the vital rates in terms of growth, survival and reproduction (cf. Costa et al., 2015; Harwood et al., 2014; New et al., 2014). The vital rates do not only determine individual fitness, important to understand selection pressures and evolutionary potential (Christiansen & Lusseau, 2015; Heino, Pauli, & Dieckmann, 2015), but also determine population or

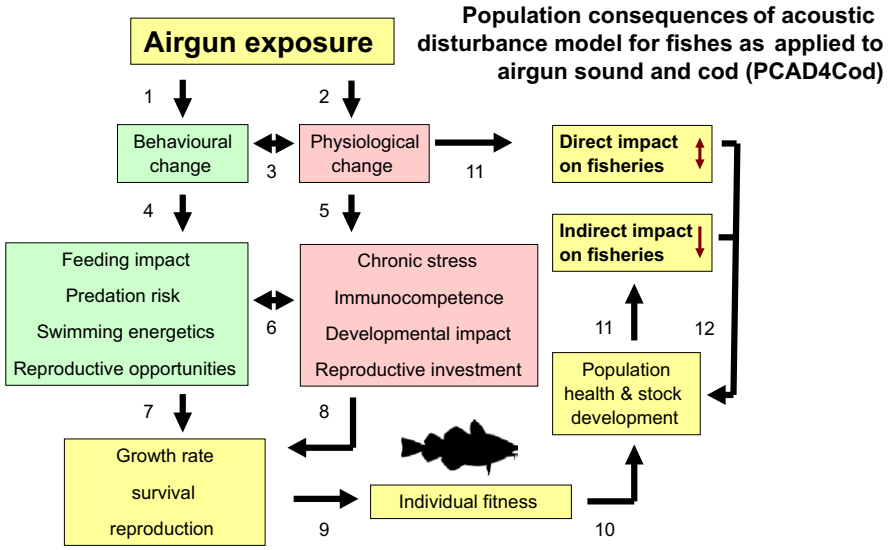

FIGURE 2 A flow chart of the population consequences of acoustic disturbance model tailored to fishes (as developed in the context of airgun sound and cod as a model species, hence the acronym PCAD4Cod). Direct impact on fisheries, indicated in the top right, is determined by positive or negative changes in catch rate due to fish movements during and after a seismic survey. Indirect impact on fisheries underneath is affected by behavioural (green) and physiological (pink) changes and their potentially negative effects for individual fitness, population health and stock development. Transfer functions that require critical evaluation are numbered 1–12 and are explained in detail in Box 1. Note that individual fitness concerns lifetime reproductive success which is the accumulation of vital rates at the individual level (growth, survival and reproduction). Furthermore, although transfer functions are depicted unidirectionally, the reversed pathway can also be relevant and important as population-level metrics such as abundance and shifts in predator-prey or competitor relationships may feed back from population to individual level (i.e. warranting bidirectional arrows)

Box 1 Transfer functions of the PCAD model for fishes (linked to Figure 2)

1. Behavioural changes following exposure to real airgun noise under natural conditions (larvae, juveniles and adults)
2. Physiological changes following exposure to real airgun noise under natural conditions (larvae, juveniles and adults)
3. Interactions between behavioural responsiveness and physiological state
4. Consequences of behavioural change (acute and chronic) for vital rates
   a. Impact on foraging efficiency and opportunities
   b. Impact on vulnerability to predation (especially juveniles)
   c. Energetic consequences of altered swimming patterns
   d. Reproductive consequences through missed breeding opportunities (adults)
5. Consequences of physiological change (acute and chronic) for vital rates
   a. Impact on chronic stress beyond regulatory fluctuations
   b. Impact on vulnerability to infections and disease
   c. Developmental consequences of physiological imbalance
   d. Reproductive consequences through follicle maturation (adults only)
6. Effects on vital rates of interactions between behavioural and physiological responses
7. Impact of behavioural effects on growth rate, survival and reproduction
8. Impact of physiological effects on growth rate, survival and reproduction
9. Impact of behavioural and physiological effects on individual fitness (lifetime reproductive success)
10. Consequences of changes in individual fitness at the population and stock level
11. Evaluation of direct and indirect effects of seismic surveys on fisheries
12. Evaluation of impact from seismic surveys in the context of (sustainable) harvesting by fisheries

stock developments (Hammar et al., 2014; New et al., 2014; Patrick et al., 2009). Direct impacts of seismic survey activities on fisheries are incorporated through increasing or reducing catch rates, while indirect impacts of seismic survey activities on fisheries are represented through potential impact on stock developments (McCully Phillips, Scott, & Ellis, 2015; Patrick et al., 2009). Behavioural and

physiological stress responses may affect fisheries directly by effects on catch rate (e.g. Løkkeborg, Ona, Vold, & Salthaug, 2012; Parry & Gason, 2006; Skalski, Pearson, & Malme, 1992; Streever, Raborn, Kim, Hawkins, & Popper, 2016) and through the suggested route of stock impact. The nature and intensity of fisheries itself will obviously also feed back to population health and stock development (Lilly et al., 2008; Savenkoff et al., 2006). It should also be realized that size and composition of fish stocks may also cause feedback effects, against the direction of arrows, on the vital rate level of growth rate, survival and reproduction (Claessen, De Roos, & Persson, 2000; Persson, Leonardsson, de Roos, Gyllenberg, & Christensen, 1998).

3 | ACOUSTIC EXPLORATION OF THE SEAFLOOR

3.1 | The nature of seismic surveys

It is important to know the nature of seismic surveys (Dragoset, 2005; Gisiner, 2016; Landrø & Amundsen, 2018; Laws & Hedgeland, 2008) to understand what the impact on fishes could be. We therefore review aspects of operational procedures, mostly based on survey strategies in the North Atlantic (see, e.g., Parkes & Hatton, 1986; Evans, 1997; and also Malme, Smith, & Miles, 1986; Dalen & Knudsen, 1987; Løkkeborg, 1991; Løkkeborg & Soldal, 1993; Engås, Løkkeborg, Ona, & Soldal, 1996; Løkkeborg et al., 2012), which will affect exposure conditions through shooting rate and variation in distance between fishes and sound source (Figure 3a). It is important to realize that there are several different types of seismic surveys, which vary in shooting density; that is, there are two-dimensional (2D) and three-dimensional (3D) surveys, both with towed hydrophone streamers. 3D surveys can also have hydrophones at the ocean floor, including so-called four-dimensional (4D) and multicomponent (4C) surveys, and site surveys. These type differences relate to variation in the ways of operation, for example distances between vessel course lines within the survey area and thereby time between visiting and revisiting locations in the survey area. They may also vary in quality requirements with respect to the seismic data, which may lead to restrictions on acceptable wind and sea surface conditions. When the weather is too rough, the seismic vessel often moves slowly at steerageway with no other sound energy emissions than from the vessel itself.

2D surveys are often used in large regional surveys in early exploration phases for oil and gas in an area. The vessel follows single course lines or lines in a grid where neighbouring lines may be relatively far apart (1 km and more) and lines may cross each other. Typically, a single sound source is used, composed of several airguns to form an airgun array, towed at 4–10 m under the water surface. Airguns generate sound by releasing a bubble of compressed air, generating a high-pressure spherical pulse that travels away from the source, with a complex interference patterns due to surface reflection and bathymetry-dependent propagation. The airgun array usually generates a sound pulse ("shot") every 10 s which yields a shot every 25 m when the vessel speed is about 5 knots (2.6 m/s). However, seismic pulse rate may also vary. Usually one hydrophone cable of 3,000–12,000 m length, called a streamer, is towed at 6–8 m depth.

3D surveys are carried out within parts of the previously 2D-surveyed area that the oil and seismic companies evaluate as interesting and "promising." From the mid-1980s, 3D surveys have been increasingly used by the oil industry because they provide much more information about the seabed and potential hydrocarbon reservoirs than 2D surveys. 3D surveys typically use one or two sound sources (in so-called flip-flop operation), each composed of many airguns in a large airgun array towed 250–400 m behind the

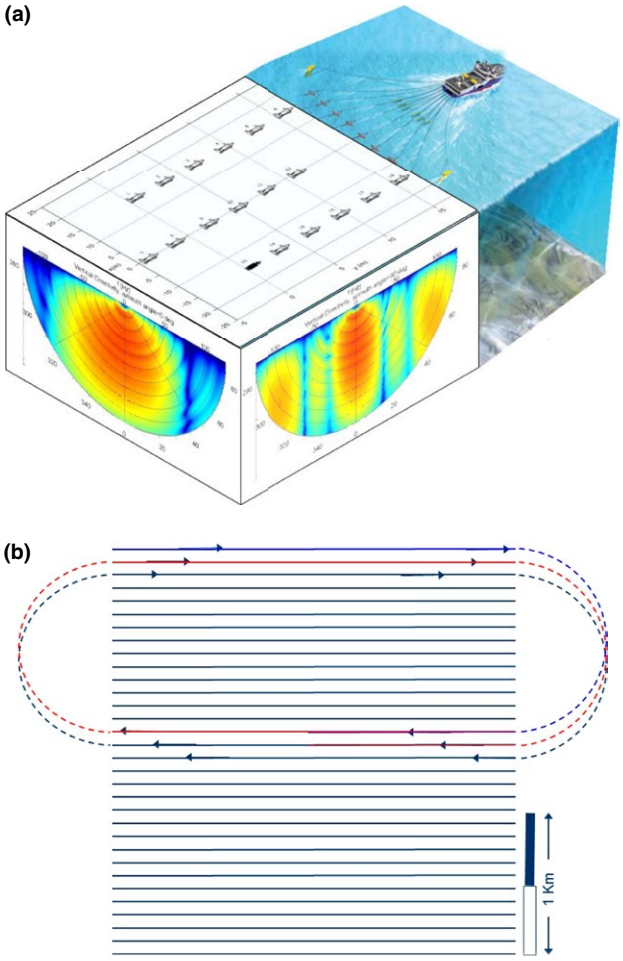

FIGURE 3 (a) Artistic impression of a seismic survey presented with the vertical directivity pattern of the energy source spectral density level (dB re 1μPa^2 m^2 s/Hz) for the airgun array at different azimuth angles (courtesy: Őzkan Sertlek). We developed an algorithm for the calculation of airgun signatures (AGORA) based on various branches of physics such as bubble motion, gas pressure laws, thermodynamics and mass transfer (Sertlek & Ainslie, 2015), which is now freely available from Leiden University at http://oalib.hlsresearch.com/. (b) Schematic representation of a 3D survey vessel course pattern. Each line represents a vessel sail-line. The arrows indicate vessel direction and pathway, starting in blue, changing to red and grey-blue with time in subsequent tracking courses (courtesy: J. Caldwell, OYO Geospace; and C. Walker, Seabed Geosolutions)

vessel at about 6 m depth (similar to 2D surveys). In contrast to the 2D survey, there are several hydrophone cables (6–16) with an inter-cable distance of 25–150 m. The distance between the course lines covering the 3D seismic area may vary between 50 and 200 m. The weather requirements are stricter for 3D than for 2D surveys: the Beaufort wind force must be equal to or <5, corresponding to wind speeds up to 21 knots (11 m/s), and the significant wave height must be equal to or <2.0 m.

The airgun pulse rate does not need to differ between 2D or 3D surveys, but besides pulse rate, it is also relevant to realize that the seismic survey often stops. When the vessel has finished one sail-line, the generation of seismic pulses typically stops, up to 2–4 hr, while the vessel turns to start on the next sail-line. Figure 3b shows how a 3D survey typically may be performed. The vessel takes one line, then turns with all the streamers on drag into the next selected line and sails back into the opposite direction. The more streamers, the larger the radius of the turn will have to be. More cables also means that the ship has to run fewer course lines to cover the same area. However, although this may reduce emission time at the vessel, during many 3D surveys the fish within the survey area may hear the emitted sound during the whole active period of survey, while they are likely to experience periods of relative silence during 2D surveys that cover larger areas.

4D surveys are used for reservoir monitoring, and they are equivalent to repeated 3D surveys over time; that is, the 4th dimension is time. It has several names as permanent reservoir monitoring (PRM), life-of-field surveys (LoFS) or time-lapse surveys (TLS) (Caldwell, Koudelka, Nesteroff, Price, & Zhang, 2015; Walker, 2014). The time interval between surveys may be variable and depends on the specifics of the reservoir being monitored. 4D surveys are precise repetitions of 3D surveys as described above in terms of course lines, source capacity and hydrophone streamers. One alternative operation strategy can be that the hydrophone cables are not towed close to the surface, but placed at the bottom. For the latter case, the survey is named ocean bottom seismic (4D OBS) or ocean bottom cable seismic (4D OBC). Cables are either placed at the bottom prior to the surveys and brought up again after the surveys, or buried at the seabed prior to the first 4D OBC survey until the exploitation end of the oil/gas field.

A variant of the 4D OBC, with the same shooting procedure but different sensor types, is the multicomponent OBC which is called 4C OBC. In this case, the bottom mounted cables, or sensors without connecting cables, contain several orthogonally oriented geophones (or equivalent particle motion sensors) in addition to pressure hydrophones yielding the possibility of measuring acoustic shear waves as well as pressure waves (Caldwell et al., 1999). This technique allows determination of both the type of wave and its direction of propagation. The distances between course lines of 4D and 4C surveys are rather small and the time between visiting and revisiting a particular position is rather short (1 hr to a few hours) depending on the size of the seismic area. Consequently, during the 4D and 4C surveys the fish are again likely to be exposed to airgun sound during the active periods of the whole survey.

Finally, so-called well site surveys are a thorough investigation of the seabed and sub-seabed features with sufficient penetration and resolution to gather data that are essential for the emplacement or anchoring of structures dedicated to hydrocarbon exploitation. The data acquisition mainly aims at improving the information quality of the bathy-morphological seabed features, of the upper layers of the bottom, for example providing higher resolution data than the seismic data acquired for exploration purposes. This is usually for mapping stratigraphy of shallow formations and to detect potential gas pockets in shallow layers to prevent blowouts or other dangerous events during drilling. These activities are performed prior to deciding on where to place a rig in the desired position for test drilling, and they are an integral part of the Health, Environment and Safety (HES) procedures. The acquired information shall ensure safe anchoring and handling of the rig.

For the well site surveys, typically 1–4 small airguns, on one or two airgun strings towed at 2–3 m depth, and sparkers (seismic sound sources based on high voltage discharge) are used with a single hydrophone cable of usually 600–1,200 m long. Furthermore, geotechnical sediment samples may be gathered by means of piston–gravity or vibrocore systems in order to determine mechanical characteristics of the seabed. The topographical mapping of the seafloor is typically done with a multibeam echosounder, side-scan sonar and sub-bottom profiler (the latter in case of very shallow subsurface layers), while a single-beam echosounder is used for navigation purposes. The survey areas are always relatively small (15–25 km^2 or 4–7 nmi^2). There are even further restrictions for a site survey than for the 3D surveys. The wind force must be equal to or less than Beaufort force 3 (up to 10 knots, 5 m/s), and the significant wave height must be equal to or less than 0.2 m. The distances between vessel course lines are small for site surveys and the time of line-change is short (half an hour to a couple of hours) depending on the size and water depth of the seismic area. Consequently, similarly to the 3D, 4D and 4C surveys the fish are again likely to be exposed to airgun sound during the active periods of the whole survey.

3.2 | Airgun array size and seasonality

The size of the airgun array is another critical parameter for the potential impact of seismic surveys on fishes. Although vessel movement prevents peak sound levels at the same spot for long periods, the contribution of seismic surveys to the overall ambient noise levels, averaged over time, can be considerable compared to other sound sources (see Figure 4a). The acoustic energy output from an airgun array is determined by the number of airguns and their chamber volumes, the supply pressure to the airguns, and the airgun configuration within the arrays (Anonymous, 2006, 2014a,b). We present a selection of technical and operational features of different types of seismic surveys in Table 1. For the geometric dimensions of airgun arrays, we have seen a reduction of the size (length (in-line) by width (cross-line)) of the arrays for 2D and 3D surveys from the beginning of the 1980s until today. Typically, dimension ranges

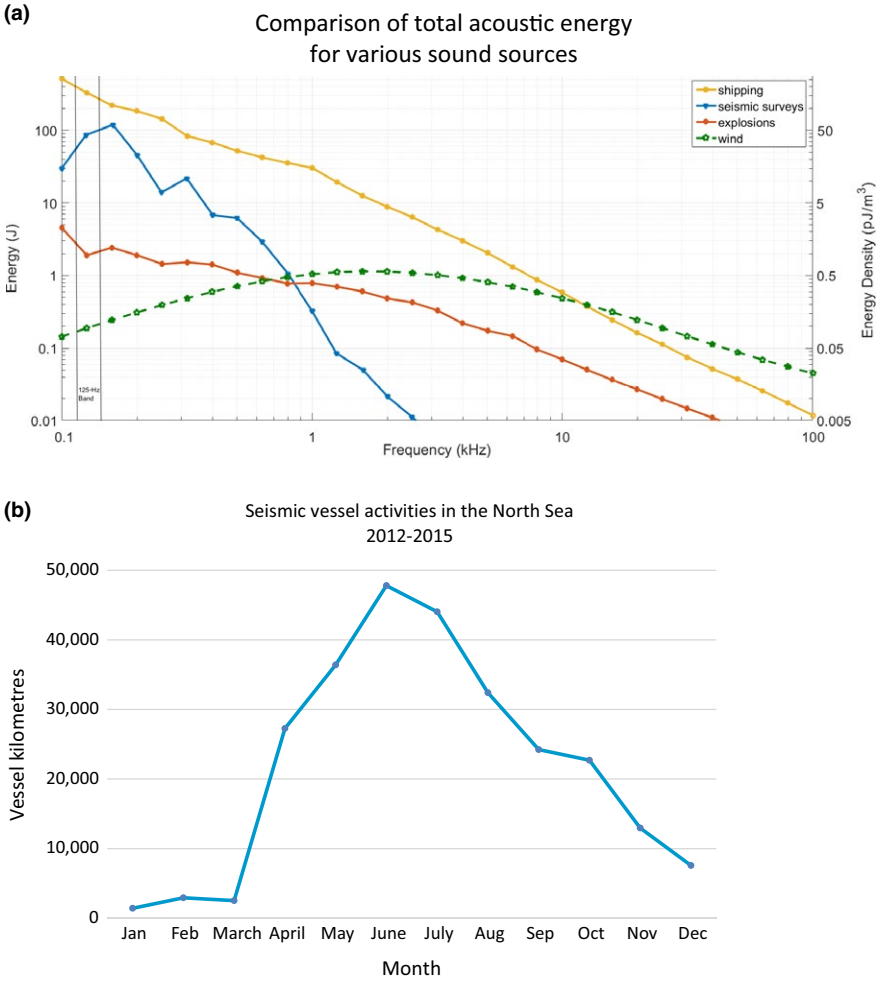

FIGURE 4 (a) Contribution of seismic surveys (solid blue line) to the total acoustic energy (2 year average) in the Dutch part of the North Sea (DEEZ), in decidecade bands, relative to two other anthropogenic noise sources (shipping and explosions) and natural wind noise (Sertlek, 2016; Sertlek et al., 2019). Shipping is making the largest contribution up to 10 kHz. Wind is a prominent contributor above 5 kHz. Seismic surveys are prominent at the low frequencies (between 0.1 and 1.0 kHz). The 125-Hz band is explicitly mentioned in the Marine Strategy Framework Directive of the European legislation. (b) Seismic vessel activities during 2012–2015, expressed by total vessel kilometres in the Norwegian part of the North Sea. Most surveys take place from April until October with peak activities in June and July (courtesy: The Norwegian Petroleum Directorate/J. Stenløkk)

today are 15–30 m (in-line) by 15–20 m (cross-line). Mean values and variations of the length and width of most used airgun arrays during 2010–2015 are 15 (± 1) m by 19 (± 2) m for 2D, 3D and 4D set-ups (Gisiner, 2016; Landrø & Amundsen, 2018).

A simple but reasonably precise indirect measure for the generated sound pressure, p, is the total chamber volume, V_c, of the airgun array(s) as a proxy for the emitted energy as the majority of the airgun set-ups work with the same supply pressure. This is based on the fact that there is a correlation between chamber volume and generated sound pressure (although chamber and opening design also affect pressure level) in the acoustic far field (ISO, 2017). For a single airgun, the peak sound pressure $p_{0\text{-}pk} \sim V_c^{0.33}$ (Vaage, Haugland, & Utheim, 1983), and for an airgun array, the pressure $p_{0\text{-}pk} \sim V_c^{0.385}$ (Malme et al., 1986). When the airguns are configured in an array, the array will act as an acoustic transducer with its vibrating surface amplifying the vertically down-going wave field in the central volume beneath the array, thus producing a directional sound field (Caldwell & Dragoset, 2000; Khodabandeloo, Landrø, & Hanssen, 2017; Parkes, Hatton, & Haugland, 1984; Tashmukhambetov, Ioup, Ioup, Sidorovskaia, & Newcomb, 2008). The acoustic energy from airguns is more biased to lower frequencies than for other anthropogenic sound sources such as vessels and explosives, and also contrasting with the wider and higher frequency range covered by wind.

The total number of days reported for a survey of any type is often not equal to the number of days in which there is actual seismic sound pulse emission. The reason for this is that part of the overall survey period almost always concerns operational downtime due to bad weather conditions or technical problems. Especially large weather impact is reported for site surveys, as these surveys are very sensitive to wind and rough sea surface conditions. For instance, a survey that requires 5 days of seismic data acquisition may take 1–2 months. A more precise measure of the effective time of seismic pulse exposure for a survey is therefore the vessel kilometres during which there is seismic survey activity. Estimates of effective survey duration in days (as in Table 1) can be calculated by assuming a realistic average vessel speed of 5 knots (2.6 m/s).

As the quality requirements for the airgun recording data are fairly strong, seismic surveys are typically restricted to seasonal periods with beneficial wind and sea surface conditions (and seasonal windows of legal permission). The weather conditions may, for example, be rather rough in the North Atlantic and adjacent waters during late autumn and winter which results in rather low activity for seismic data acquisition during this period. This leaves the period from mid-April to mid-October to be the high season for seismic surveys in these waters. While relatively calm seas may still allow some activities in the winter months until December in the North Sea (see

TABLE 1 Technical and operational characteristics of different types of seismic surveys during 2005–2014. We indicated the range by providing the minimum and maximum for the total chamber volume (in cubic inches; 1 cubic inch equals 0.0164 L) and the length of hydrophone cables and mean as well as range for the survey area size and duration. Descriptions of seismic survey types can be found in the text. 3D PDS refers to "3D Proprietary Data Surveys," which are 3D surveys of which the seismic data are proprietary to the licensee company, and 3D ADS refers to "3D Available Data Surveys," which are 3D surveys of which the seismic data are available to other companies (sharing a production licence of an oil/gas field, or available to other oil industry actors for a certain cost). NA: not applicable. Data are mainly based on surveys in the Norwegian Exclusive Economic Zone (NEEZ: the North Sea, the Norwegian Sea, the Barents Sea) and the British Exclusive Economic Zone (the North Sea)

Survey type	Number of airguns in arrays	Total chamber volume in litres (cubic inches)	Number of cables and length range [m]	Survey area size [km^2]—mean and range	Survey duration [days]—mean and range
2D surveys					
	18–48	21.3 (1,300) 100.3 (6,300)	1 3,000–12,000	NA	NA
3D surveys					
3D PDS	12–48	32.8 (2,000) 86.6 (5,280)	6–16 2,400–10,000	480 132–681	49 11–105
3D ADS	12–38	32.8 (2,000) 67.7 (4,130)	6–14 2,400–6,000	1,238 436–2,355	157 58–326
4D OBS surveys					
	12–38	32.8 (2,000) 83.4 (5,085)	6–12 2,400–5,000	229 47–438	47 18–124
4D/4C OBC surveys					
	12–38	32.8 (2,000) 65.4 (3,990)	Cables at/buried into the seabed	229 47–438	47 18–124
Site surveys					
	1–4	0.7 (40) 3.4 (210)	1–2 600–1,200	22	NA

Figure 4b), other rough seas further north may remain largely unexplored by seismic surveys between October and March. The seasonality of surveys can also be important relative to fish ecology as they may be differently sensitive and vulnerable to acoustic stressors over the year. Disturbance and deterrence patterns may, for example, vary among periods of pre-spawning migration, pre-mating at the spawning fields, and during spawning (Carroll et al., 2017; Cox et al., 2018; Hawkins et al., 2015; Peng et al., 2015).

4 | THE AUDITORY WORLD OF FISHES

4.1 | Fundamentals of fish hearing

There are more than 30,000 fish species, which have evolved substantial variation in the physical structures associated with hearing (Figure 5a). However, all fishes detect particle motion (PM) and share an accelerometer-like system for hearing (Ladich, 2014; Popper & Fay, 2011; Radford, Montgomery, Caiger, & Higgs, 2012). PM is detected by three pairs of otolith organs, which consist of a mass (the otolith itself) and the sensory hair cells. The hair cells act as transducers converting the mechanical stimulus of PM into an electrical signal that can be processed by the central nervous system. Fish and the sensory epithelia have approximately the same density as water and move in conjunction with the sound field at low frequency. The calcareous otolith is approximately 3–4 times denser and moves with a differential amplitude and phase to that of the fish body. As a consequence, the hair cells that are in contact with the otolith undergo a shearing displacement, which they "translate" into the neurological responses that feed auditory perception.

Many fish species can also detect sound pressure (SP), in addition to their motion sensitivity, via the gas-filled swim bladder (a hydrostatic organ) or other gas bubble (Fay, 1969; Sand & Enger, 1973). The swim bladder can be connected to the intestine by the pneumatic duct (physostome fishes, e.g. salmon) or can be closed (physoclist species, e.g. cod). In physostome fishes, the quantity of gas in the swim bladder can be regulated via gulps of air at the surface, while in physoclist fishes, this goes via gas absorption or release from the blood. The latter may be more susceptible to damage at extreme acoustic exposures, but both detect sound pressure through volume oscillations which are transferred to the inner ear. This is often facilitated by a physical connection, for example through paired bladder extensions, additional air cavities or a series of bones (Weberian ossicles) (reviewed in Popper & Fay, 2011).

The lateral line system can also detect sound, but this is typically not labelled as hearing (Bleckmann & Zelick, 2009; Braun, Coombs, & Fay, 2002; Higgs & Radford, 2013). The underlying mechanism of sensitivity, however, is similar between the lateral line and the inner ear: they are both based on sensitivity to particle motion via triggering of hair cells (Cofin et al., 2014; Popper & Fay, 2011). An indirect

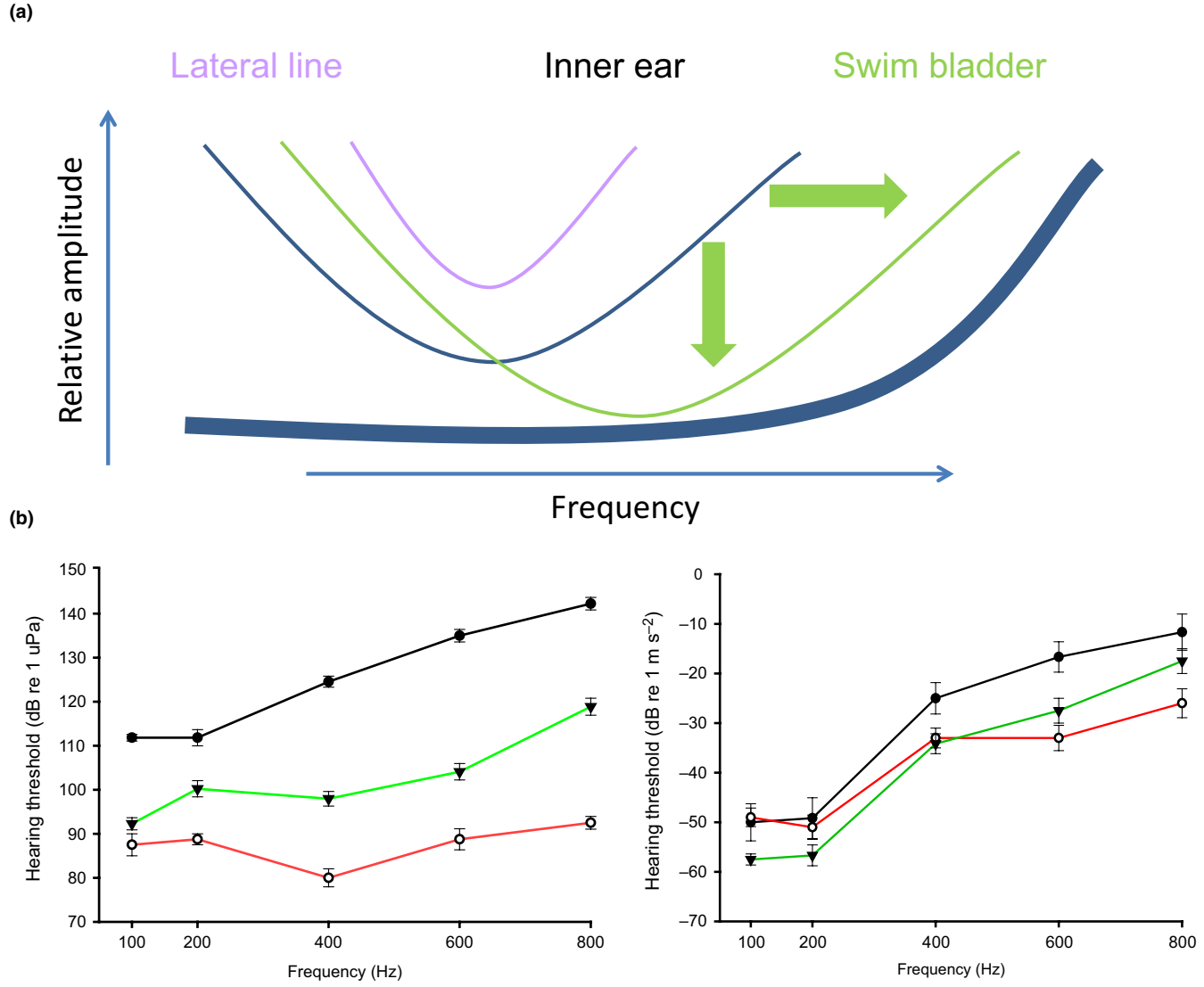

FIGURE 5 (a) Schematic overview of the capability of fish to perceive sounds in terms of relative amplitude and spectrum. The three thin lines reflect the following three auditory pathways: (1) the general sensitivity of all fishes to particle motion through innervation of hair cells close to the otoliths of the inner ear (in dark blue); (2) the sensitivity to particle motion originating from sound pressure through pressure-to-motion transduction for fish species with a swim bladder (in green), which typically results in a lower overall threshold and an extension of sensitivity towards higher frequencies (green arrows); and (3) the sensitivity to particle motion via the lateral line (in lilac). This concerns relatively low frequencies in the flow of water directly surrounding the fish (through movements of the fish itself, water flow currents, or turbulence by other fish or objects) and which is not likely to outcompete the inner ear in sensitivity. The bold blue line represents the cumulative shape of the audiogram: the sensitivity to sound across frequencies, attributable to a variable and unquantified combination of sensitivity through the three pathways. (b) Hearing thresholds of three different species for independent assessments of sound pressure level (left) and sound particle acceleration level (right). The common triplefin (*Forsterygion lapillum*, Tripterygiidae) has no swim bladder (black lines). The New Zealand bigeye (*Pempheris adspersus*, Pempheridae) has a swim bladder but no Weberian ossicles (green lines). The goldfish (*Carassius auratus*, Cyprinidae) has a swim bladder and specialized conduction to the inner ear via Weberian ossicles (red lines). In terms of particle motion, all three fish species have similar hearing thresholds, but when expressed as pressure thresholds, the goldfish is the most sensitive, followed by the bigeye and the triplefin being the least sensitive (Radford et al., 2012)

contribution of sound pressure via the swim bladder is also possible. The most likely function of the sensitivity of the lateral line system is fine-tuning responses to stimuli at close distance as it mostly provides sensitivity to motion in the water flow directly around the fish body. As this nearby water flow is affected by swimming activity, current and flow disturbance by other fish or objects in the water, sensory monitoring via the lateral line system is likely playing a critical role in schooling, rheotaxis and detection of both predators and prey (Dijkgraaf, 1962; Schwalbe, Bassett, & Webb, 2012). It is unclear to what extent interference or masking by low-frequency sound could undermine the sensory function of the lateral line, nor is it clear to what extent the lateral line plays a role in sensitivity

to disturbance by or coping with anthropogenic noise (Braun et al., 2002; Higgs & Radford, 2013).

Fish hearing depends on both how intense the sound is and its frequency and is typically depicted in species-specific hearing curves or audiograms, hearing thresholds across frequencies (Kenyon, Ladich, & Yan, 1998; Ladich & Fay, 2013). Within the audible range, fish exhibit auditory capabilities that go beyond mere detection, such as discrimination ability among sounds of different frequency and amplitude (auditory scene segregation), or among sounds from different directions (directional hearing, azimuth detection) or distances (ranging). Furthermore, fish also exhibit relevant perceptual phenomena, such as habituation and sensitization (Neo, Hubert, Bolle, Winter, & Slabbekoorn, 2018; Radford, Lefèbre, Lecaillon, Nedelec, & Simpson, 2016; Rankin et al., 2009), which may play a critical role in impact assessment (Bejder, Samuels, Whitehead, Finn, & Allen, 2009; Harding et al., 2018) and which apply across marine taxa (e.g. Götz & Janik, 2011; Samson, Mooney, Gussekloo, & Hanlon, 2014). However, we still know very little about the separate or integrated roles of sound pressure and particle motion sensitivity in these perceptual abilities of fish and most studies have just focused on hearing thresholds and frequency ranges.

There are two different approaches to obtaining hearing thresholds: behavioural methods and electrophysiological methods (Ladich & Fay, 2013). Behavioural methods provoke an active response of the fish to a sound after some form of conditioning (either reward or shock avoidance). Once a response has been established, the sound level is then progressively lowered until the fish no longer responds. This method provides the best evidence that a fish is not only able to hear, but also able to process and respond to the specific type and intensity level of sound. Electrophysiological methods register auditory evoked potentials (AEP) or auditory brainstem responses (ABR) (Kenyon et al., 1998). To apply the method, the fish is typically mildly anaesthetized and held in a tank either at the surface or mid-water and cutaneous electrodes are placed above the brainstem to record electrical signals from the auditory system. Thresholds are determined through decreasing the sound level until the experimenter can no longer detect the AEP or ABR signal (Ladich & Fay, 2013). However, very few studies provide adequate insights for understanding fish hearing under natural circumstances and are therefore limited for evaluating potential effects of sound exposure from anthropogenic sources. Behavioural studies in captivity and electrophysiological measures are both useful for determining crude spectral range limits and damage after exposure to loud sounds (e.g. Halvorsen, Casper, Woodley, Carlson, & Popper, 2012; Popper et al., 2005). They are much less useful for determining absolute hearing sensitivity, and one should be especially cautious in comparing audiograms of different species generated by different laboratories.

There are very few studies that provide insight into both sensitivity to PM and SP (Figure 5b). It is difficult to present PM and SP signals independently and usually requires specialized equipment, such as shaker tables or diametrically opposed speaker systems. For example, the cod has been shown to detect PM signals at frequencies below 100 Hz, but detect SP at higher frequencies (Chapman & Hawkins, 1973; Sand & Hawkins, 1973). They are also reported to be sensitive to infrasound (sound at frequencies below the lower limit of the human hearing range at 20 Hz) through linear accelerations (Sand & Karlsen, 1986, 2000), and it has been suggested that this particular component of the sound field may trigger the avoidance response to anthropogenic sounds (Sand, Enger, Karlsen, Knudsen, & Kvernstuen, 2000). For the large majority of literature, only sound pressure levels (expressed in dB re 1 μPa^2) are presented, while all fish are also prominently sensitive to particle acceleration level (dB re 1 $(\mu m/s^2)^2$).

Furthermore, the majority of studies have been performed in small tanks in noisy laboratories, where the sound fields are highly complex as a result of pressure-release surfaces (Hawkins et al., 2015; Parvulescu, 1964, 1967). The low-frequency cut-off at 30–100 Hz shown in many audiograms often represents the low-frequency limitations of the equipment or may reflect background noise that is masking the test stimuli. Consequently, audiograms provide a basic means for comparing the sensitivity and frequency range of different fishes, but the absolute thresholds should generally be considered unreliable. For example, reviews by Ladich and Fay (2013) and Maruska and Sisneros (2016) point out differences of 40–60 dB in reported hearing thresholds for the same species, largely attributed to differences in measurement methodology rather than hearing ability. Harmonization in measurement methodology is essential if progress is to be made towards improved quantitative understanding of comparative hearing sensitivity in fishes.

4.2 | Sound fields, hearing and potential for impact

Only an audible sound can trigger a behavioural or physiological response and have potentially detrimental impact. An auditory dose–response curve to a broadband sound could be used to assess the number of fishes hearing human activities. However, there is a considerable gap in our understanding of the natural variation in sound pressure and particle motion in the sound field around the fish, just before and during the seismic survey. The following information would be required for a plausible estimate: (a) density and distribution of fishes (geographically and within the water column); (b) level and spectral energy distribution of the sound source in sound pressure and particle motion; (c) propagation conditions between the sound source and the fish for both sound components; (d) ambient noise levels at the fish for both sound components; and (e) auditory sensitivity across the spectrum of potentially exposed fishes.

An important source of confusion in the implication of auditory sensitivity is the hearing curve or audiogram. This curve reflects the thresholds for single-frequency tone pulses across the spectrum above which sound is perceived by the ear. However, the threshold at each frequency is determined by detection of either the particle motion or sound pressure component of the sound or a combination of both. Another reason for why the current insights into hearing abilities of fishes are limited for applications to impact assessments is that most natural (conspecific, predator-prey, habitat signatures)

and anthropogenic sounds (transient or long-lasting), including airgun sounds, are broadband. This means that hearing thresholds and masking will depend on the accumulation of energy over frequency-dependent filter bandwidths. Critical bandwidths are known for hardly any species but cod: they have symmetrical filter functions that increase with frequency (e.g. 59 Hz at 40 Hz and 165 Hz at 380 Hz) (Hawkins & Chapman, 1975). Actual field data with behavioural response tendencies for free-ranging fish combined with adequate assessments of the sound field are required to get any further in terms of impact assessments.

As mentioned above, acoustic exposure probability and extent depend not only on auditory capacities of the fish, but also on sound source properties, the distance between the fish and the source, and the propagation through the water. Acoustic propagation in the ocean depends on the local environment, including physical oceanography (temperature and salinity), bathymetry, sea surface roughness, bubbles and sediment features (Brekhovskikh, Lysanov, & Lysanov, 2003; Jensen, Kuperman, Porter, & Schmidt, 2011). Significant advancements have been made in the past 20 years in computational ocean acoustics (e.g. Harrison, 2013; Khodabandeloo et al., 2017; Sertlek, 2016). Five main branches of numerical models are routinely applied to compute the acoustic field in ocean acoustics: parabolic equation (PE) models (Collins, 1993; Tappert & Nghiem-Phu, 1985), ray-based models (Weinburg & Burridge, 1974), wave number integration theory models (DiNapoli & Deavenport, 1980; Schmidt, 1987), mode theory-based models (Porter, 1995) and flux models (Weston, 1959). Hybrid models are also used, applying combinations of the above (e.g. Harrison, 2015; Hovem, Tronstad, Karlsen, & Løkkeborg, 2012; Sertlek, 2016; Sertlek, Slabbekoorn, ten Cate, & Ainslie, 2019).

A majority of effort in ocean acoustics has been focused on acoustic pressure (driven by the desire to quantify the performance of man-made sonar systems) and not on particle motion. Particle motion, the kinetic components of sound, can be characterized in terms of sound particle displacement, sound particle velocity, sound particle acceleration or any higher derivative. Once the velocity field is known in the frequency domain, it is straightforward to convert to displacement or acceleration. Given a reasonable understanding of bathymetry, sediment type and local oceanography, the numerical computation of the acoustic field (sound pressure and sound particle velocity) is a solved problem for a point source. Computation in the frequency domain is effected using:

$$P(f) = S(f) \cdot H(f) \quad (1)$$

where $S(f)$ is the source spectrum (ISO, 2017) and $H(f)$ is the transfer function (Green's function) (Jensen et al., 2011). The PE method has been applied to the wave equation for velocity potential (Smith, 2010), but this is not necessary if the acoustic pressure field is available on the computational grid. In this case, the particle motion can be computed using the range and depth discretized finite difference derivative to compute the particle acceleration vector from the sound pressure field (in the far field).

The prediction of the sound pressure or particle velocity field associated with a seismic survey transmission is a complex problem involving an understanding of acoustic propagation, source physics and local oceanography. Approaches to date have applied simplified models to each part of the problem and used them in series to predict the acoustic field. The parameters that describe the environment are often supplied from local or world databases of oceanography (Baranova, 2010), bathymetry (Amante & Eakins, 2009) and sediment type.

Source models exist for single airguns and for arrays of airguns, which typically provide the source waveform (time domain source signature, $s(t)$ (ISO, 2017)) and source spectrum (frequency domain source signature, $S(f)$) (ISO, 2017). Acoustic propagation models are well developed (Jensen et al., 2011) and can be used to handle broadband signals in arbitrary range-dependent environments. To predict the received sound field, a model is run at a subset of frequencies and the coherent transfer function $H(f)$ calculated at each frequency. The sound pressure in the time domain, $p(t)$, is the inverse Fourier transform of the frequency domain quantity $P(f)$:

$$p(t) = \int_{-\infty}^{+\infty} P(f)\, exp\,(+2\pi i f t)\, df$$

The use of acoustic cues for making decisions often requires the fish not only to detect a sound but also to be able to localize the sound source (Schuijf 1975; Schuijf & Hawkins, 1983). Perceptual localization mechanisms for fish remain poorly known, largely because of the difficulty in resolving the 180° ambiguity associated with the dominant axis of particle motion which points towards and away from a sound source (Rogers & Zeddies, 2009). Although several models have been proposed to address this issue (Kalmijn, 1997; Rogers, Popper, Hastings, & Saidel, 1988; Schellart & Munck, 1987; Schuijf & Buwalda, 1975), it is still not completely clear how fish localize sound. Nevertheless, there is good behavioural evidence that they can. Zeddies et al. (2012) studied the plainfin midshipman (*Porichthys notatus*, Batrachoididae) and showed that female fish directed their swimming towards male advertisement calls. Using a dipole source in a concrete tank, they showed that when females were released along the dipole vibratory axis, they took straight paths to the sound source, while when released approximately 90° to the vibratory axis, they took much more curved paths instead. This indicates that the fish localized the sound source by following the direction of prominent axes of PM in the local sound field (Zeddies et al., 2012). A follow-up experiment showed that sound pressure detection is likely to aid in the localization task and that the lateral line is probably not contributing significantly (Cofin et al., 2014).

Following from the above, a full understanding of potential impact of anthropogenic noise pollution, like in case of a seismic survey, will require more insight into the ambient sound pressure levels in combination with the local directionality of the particle motion sound field. Furthermore, we need to know whether, when and how the acoustic information is extracted by fishes for decision-making

and whether, when and how this is negatively affected by the presence of anthropogenic noise. The nature of anthropogenic sound features, such as rise time, reverberative temporal patterns, and spectral composition and fluctuation are likely critical and need further investigation from a fish perspective. Modification by sound propagation through the water has to be taken into account, as well as propagation through the seabed, including shear waves. At low frequency, in shallow water some of the energy from an airgun pulse might propagate along the water–seabed boundary in the form of so-called Scholte waves, which could increase the risk of disturbance to benthic fauna, but very little is known.

Filling the gaps of knowledge addressed above is required for a better understanding of potential disturbance and masking in fishes, but will likely also reveal potential for perceptual resistance, for example due to signal redundancy or the possibility that more noisy conditions make surroundings better audible through "acoustic illumination." A better understanding of the natural and human-altered acoustic world would also allow future studies on the inherently multimodal nature of the perceptual world of animals (Halfwerk & Slabbekoorn, 2015; Munoz & Blumstein, 2012; Van der Sluijs et al., 2011). Studies on perception and pollution taking a combination of sound, light, chemical or temperature conditions into account to study responsiveness (e.g. Heuschele, Mannerla, Gienapp, & Candolin, 2009; Kunc, Lyons, Sigwart, McLaughlin, & Houghton, 2014; Shafiei Sabet, van Dooren, & Slabbekoorn, 2016) or exposure to a combinations of stressors of different modality are critical for a proper understanding of acoustic ecology and noise pollution in the real world (Carroll et al., 2017; Hawkins et al., 2015; Nowacek et al., 2015).

5 | OVERVIEW OF AIRGUN IMPACT STUDIES

5.1 | Historical perspective and methodological considerations

Studies on impact from airgun exposure on fishes started in the beginning of the 1970s, after the development and testing in the late 1960s of the first commercial airgun assembly by Bolt Associates, Inc., USA. The first two studies were on caged coho salmon smolts (*Oncorhynchus kisutch*, Salmonidae; Weinhold & Weaver, 1972) and eggs and larvae of a variety of fish species (Kostyuchenko, 1973), while the third one was on free-swimming herring (Dalen, 1973). Most follow-up studies have been on confined and caged fish, and only some studies focused on behavioural impact on free-swimming fish (Bruce et al., 2018; Carroll et al., 2017; Cox et al., 2018). Sometimes, consequences of altered fish behaviour for different types of fisheries were target of the investigations (e.g. Dalen & Knudsen, 1987; Skalski et al., 1992; Streever et al., 2016).

Although the variety in methodology and approaches has yielded considerable insight, most fish studies were either limited in biological relevance or suffered from limited replication or lacking controls (which should also be replicated). Note that we do not argue that all studies with limited replication or controls are useless or wrong, we just call for caution in evaluating the state of the art, and wrong often only applies to the interpretation of such studies, being too broad or conclusive. Beyond fishes, there are several reports, typically also of anecdotal nature and investigating a single seismic survey event, in various other marine taxa (André et al., 2011; Andriguetto-Filho, Ostrensky, Pie, Silva, & Boeger, 2005; Day, McCauley, Fitzgibbon, Hartmann, & Semmens, 2017; Gordon et al., 2003; Guerra, González, & Rocha, 2004; McCauley et al., 2017; Parry & Gason, 2006; Przeslawski et al. 2018), with currently the most advanced experimental studies on marine mammals in their natural environment (Cato et al., 2013; Dunlop et al., 2016).

Despite methodological challenges, it has become clear that airgun sounds can potentially affect fishes in multiple ways (reviews, e.g., in Dalen & Knudsen, 1987; Hirst & Rodhouse, 2000; Handegard, Tronstad, & Hovem, 2013). At close range, extreme over-exposure may induce physical injury, potentially leading to death (e.g. McCauley, Fewtrell, & Popper, 2003) for the very few, nearby individuals (Popper et al., 2005). Beyond this close range, but within the audible range, there may be behavioural and physiological effects that are more subtle, but that apply to many more individual fish (general reviews in Slabbekoorn et al., 2010; Normandeau, 2012; Radford et al., 2014; Popper et al., 2014; Hawkins et al., 2015). Consequently, the effects that may occur beyond the range of physical damage, but within the audible range, are the main focus of the following review of behavioural and physiological responses.

5.2 | Behavioural response to airgun exposure

There are few good case-studies in the peer-reviewed literature that report on the impact of a seismic survey on the behavioural response of free-ranging fish or the direct impact on local fisheries (Bruce et al., 2018; Engås et al., 1996; Hassel et al., 2004; Løkkeborg et al., 2012; Skalski et al., 1992; Streever et al., 2016). There are also studies that just focused on the fish behaviour of more or less resident (e.g. Jorgensen & Gyselman, 2009; Miller & Cripps, 2013; Wardle et al., 2001) and exclusively pelagic fish populations (e.g. Peña, Handegard, & Ona, 2013; Slotte, Kansen, Dalen, & Ona, 2004). These studies do not yield completely coherent results but suggest that fishes exposed to airgun sound could stop foraging and start swimming down the water column. The impact on catch rates can be positive or negative depending on the type of fisheries: catch rates can go up for gill nets, which depend on swimming activity, or can go down for longlines, which depend on active foraging.

However, these studies provide little insight into the fish perspective (beyond the seismic survey-related changes in probability to be caught immediately by fisheries). Several studies on temporal or tropical reef systems (Boeger, Pie, Ostrensky, & Cardoso, 2006; Miller & Cripps, 2013; Wardle et al., 2001) have shown that airgun sound bursts can cause startle responses in relatively stationary fish, while they also suggest that startles do not necessarily lead to long-term

changes in behavioural patterns or spatial deterrence. However, this is rather premature as a general conclusion and we need more well-designed studies (cf. Slabbekoorn & Bouton, 2008) for the impact assessment on natural patterns that can already be quite variable by themselves. A recent temperate reef study by Paxton et al. (2017), still limited in replication and duration of the observations, and not taking other nearby vessel traffic into account, indicated that quite substantial spatial effects are also possible. Multispecies presence showed a 78% decline during evenings with seismic sound exposure, compared to the same time period on three previous observation days.

Bruce et al. (2018) conducted a large telemetry study on three fish species, in the western Gippsland Basin, between the coast of Southern Australia and Tasmania, before a 2D seismic survey was undertaken in April 2015. The M.V. Duke vessel towed a single 41-L (2530-cubic inch) airgun array (BOLT Long Life Array) with 16 airguns towed at 6 ± 1 m depth for a 10-day survey period. This study is first of all an illustration of how challenging it is to observe free-ranging fish in open water at sea. For the two elasmobranch species, 76 individuals were tagged and released, at the anticipated treatment site and a 10-km-away control site, but none of these yielded a presence in the target areas during the survey. The third species with telemetric data was a ray-finned teleost and concerned 11 tiger flatheads (*Neoplatycephalus richardsoni*, Platycephalidae), which were all released at the treatment site (so, without spatial control). Nine individuals (81%) were reported by the receivers beyond the first 2 days after tagging, of which eight were detected in the target area during the seismic survey.

The large tagging effort of Bruce et al. (2018) ended up with useful data on eight tiger flathead fish, which do not allow statistics, but do tell something about displacement and movement patterns before, during and after a seismic survey (each individual being its own temporal control). Four of the eight informative fish were present during the entire survey period, and four left the area during the survey. Of these latter four individuals, one had been present on 5 days prior and 6 days into the survey period and another had been present 4 days prior and 4 days into the survey. The other two fish that left during the seismic survey arrived on the first day of the survey to stay for 5 days or arrived on the second day to leave again before the next day. These four were not recorded to return in the following 4 months of continued monitoring. The analyses of displacement and movement revealed that the time of day at which the fish were most active varied before, during and after the survey. There were generally two peaks in activity over the day, which turned out to be later during the seismic survey than before the seismic survey. The fish also moved more frequently after than before or during the survey period and had a higher average speed during than before or after. The latter was attributed to possible disturbance effects in startle responses or events of erratic swimming.

The study on the tiger flatheads (Bruce et al., 2018) concerns a single survey event at one location at one moment in time, but is consistent with a possible response to the seismic survey operations. The response is not one of large spatial displacement (four even remaining in the target area for the full seismic survey period), but one of moderate changes in local activity as evident from variation in diurnal patterns and swimming speed. Such changes in activity patterns could have detrimental energetic consequences, due to increased investment in movement or decreased opportunity to feed, and warrant further quantification. Physiological stress was not investigated, but any potential impact cannot be excluded. In addition to the telemetric data on three fish species, fisheries catch data on 15 species were extracted from a database of the Australian Fisheries Management Authority for two gear types (Danish seine and gill nets). A variable and inconsistent pattern of increased and decreased catch rates per species came out of this analysis (Bruce et al., 2018).

We are aware of only a single study that followed individual free-ranging fish in the context of experimental airgun exposure, combining video with an individual tagging effort (Wardle et al., 2001). The study was conducted around an underwater reef ("fish rock") off the coast of western Scotland (<20 m depth) in 1997. They conducted 8 sessions, during which they generated 8–74 shots (one per minute) on five consecutive days. Video images revealed typical c-start startle responses (stereotypic reflex in which the whole fish body is curved into a c-shape, followed by rapid acceleration) at the sound burst without any obvious directionality and rapid recovery of pre-exposure behavioural patterns. No sound-induced changes in fish abundance and swimming patterns were observed to the repeated series of single airgun shots. Two out of five tagged fish yielded some interesting data.

One individual pollack (*Pollachius pollachius*, Gadidae) showed nice and consistent diurnal travels for 10 days before the arrival of the research vessel, between the reef and a spot about 250 m to the north-east, up to the day that the research vessel arrived at the east side of the rock and the fish swam to the west side of it to stay there relatively inactive for the duration of the exposure. So, this individual revealed a sudden shift in behaviour, but before the first airgun exposure. The coincidence with the arrival of the research vessel may indicate that the fish associated that moderate sound with the previous experience with the vessel on the event of being caught. A second individual showed a bit more variable swimming pattern and stayed closer to the rock before, during and after the 5 days with eight airgun exposures. Only during one of the exposures, movement path tracing revealed a clear increase in swimming speed and a track from the exposure on the east side to the sheltered side on the west. Other clear behavioural switches for this individual could be related to the arrival of a grey seal (*Halichoerus grypus*, Phocidae) and the presence of an active boat.

Together, these data provide anecdotal results (Wardle et al., 2001) indicating that tagging can work but that individuals can vary significantly in their behaviour. Furthermore, they also clearly show that there are other factors than the airgun exposure during such an experiment, which can lead to confounded results (tagging impact, presence of vessel, coincidence with arrival of predator). Any conclusive statements await new experimental studies with adequate replication and controls.

5.3 | Airgun exposure studies with caged fish

The studies on airgun responses from free-ranging fish reviewed above were suitable to obtain a general qualitative idea of what

natural response behaviours may look like and to analyse direct impact on fisheries, but not for the assessment of specific threshold values or understanding underlying mechanisms. Alternative research strategies have resulted in complementary insights. There are, for example, some studies that have aimed at obtaining some sort of behavioural threshold level for acoustic exposure to airgun to caged fish in outside conditions (Fewtrell & McCauley, 2012; Hassel et al., 2004; Pearson, Skalski, & Malme, 1992). These studies provide insight into the occurrence and nature of behavioural responses, although fish behaviour may be affected by the enclosure and by the animals' recent experience of being caught, or by their background in aquaculture. These studies do not yield sufficient quantitative data yet for any dose–response curve, but suggest at least that seismic surveys typically do not lead to immediate mortality, but can induce behavioural changes (i.e. startle and erratic flight responses, diving down, speeding up and forming tight schools, which may all vary with species) and, at extreme levels, can lead to hearing damage (McCauley et al., 2000, 2003).

Sadly, this is all that can be concluded from these often expensive experiments with ethically difficult exposure conditions for the fish. The studies report on behavioural thresholds for responses to airgun exposure involving sound pressure level (SPL) between 130 and 180 dB re 1 μPa^2 (see Box 2), but all suffer dramatically from lack of replication (typically: n = 1–3), lack of adequate controls (none or confounded) and use of variable mixtures of fish species of variable background (variable refers here to trial variability within studies). Future studies should aim at experimental designs with proper periods of observation before, during and after the seismic exposure (see Smith, 2002; Underwood, 1991; Smokorowski & Randall, 2017), with treatment and control sites in nearby, ecologically similar sites (control beyond acoustic and behavioural impact of the treatment). To gain the most robust insights, it is required to obtain replication of pairs of treatment–control sites over a range of ecologically diverse habitats and with diverse species communities.

As full-scale seismic surveys are quite expensive and labour-intensive, alternative methods have been used to study experimentally how behavioural response tendencies depend on sound levels and acoustic features (Figure 6). Hawkins, Roberts, and Cheesman (2014) used, for example, an approach with underwater playback of impulsive sounds, simulating the strikes from a pile driver (which

Box 2 Sound terminology

Basic concepts and physical quantities

The effects of seismic surveys considered are those of underwater sound. Effective communication about underwater sound requires a clear and concise language of underwater acoustics. Unlike for airborne acoustics, the terminology of which has been standardized for decades, underwater acoustical terminology is in its infancy. When reporting sound pressure and particle motion, it is of prime importance to use clear and consistent metrics. In order to minimize confusion caused by poorly defined terminology, throughout this paper we follow ISO 18405:2017 Underwater Acoustics—Terminology (ISO, 2017). ISO (2017) defines various quantities that are used to quantify the sound pressure field, including mean-square sound pressure ($\overline{p^2}$), time-integrated squared sound pressure (also known as sound pressure exposure, $E_{p,T}$) and zero-to-peak sound pressure (p_{0-pk}). Also defined are mean-square sound particle velocity ($\overline{u^2}$), time-integrated squared sound pressure (also known as sound particle velocity exposure, $E_{u,T}$) and corresponding statistics of the sound particle acceleration.

Levels in decibels

A level is a logarithmic measure of a power quantity P (e.g. sound exposure or mean-square sound pressure) and in acoustics is usually expressed in decibels (Ainslie, 2015). Specifically, the level of a power quantity P, in decibels, is ten times the base 10 logarithm of P/P_0, where P_0 is the reference value of P. For example, sound pressure level (abbreviated SPL) is the level of the mean-square sound pressure (symbol $L_{p,rms}$), sound pressure exposure level (abbreviated SEL, or SELp) is the level of the time-integrated squared sound pressure ($L_{E,p}$), and zero-to-peak sound pressure level ($L_{p,0-pk}$) is the level of the zero-to-peak sound pressure. Counterparts of the first two levels for the particle velocity field are the mean-square sound particle velocity level ($L_{u,rms}$) and time-integrated squared sound particle velocity level (or sound particle velocity exposure level (abbreviated SELu), symbol $L_{E,u}$), and corresponding levels are defined for sound particle acceleration.

Reference values

Levels in decibels are meaningless unless accompanied by the corresponding reference value. International standard reference values of sound pressure, sound particle velocity and sound particle acceleration are 1 μPa, 1 nm/s and 1 $\mu m/s^2$, respectively. These reference values may be squared to reflect the definition of level as a property of a power quantity (e.g. the reference values of mean-square sound pressure, mean-square sound particle velocity, and mean-square sound particle acceleration, all proportional to sound power, are 1 μPa^2, 1 $(nm/s)^2$ and 1 $(\mu m/s^2)^2$, and the reference values of the corresponding time-integrated quantities (exposures) are 1 μPa^2 s, 1 $(nm/s)^2$ s and 1 $(\mu m/s^2)^2$ s).

typically occur at a higher rate than airgun sound bursts, e.g. 30 strikes instead of 6 per minute) in a lough (lake) at the south-eastern coast of Ireland. The behaviour of pelagic fish in response to the sound playback was observed with an echosounder, and replication was achieved by repeated trials aiming presumably at different schools of relatively small sprat (*Sprattus sprattus*, Clupeidae) and larger mackerel (*Scomber scombrus*, Scombridae) by changing locations at the surface of the lough for different runs (but all within a few hundred metres).

Response patterns were shown to be dependent on sound level but also varied qualitatively for the different species (Hawkins et al., 2014). Sprat schools reacted to 50% of the presentations at sound pressure exposure level (SELp) of $L_{E,p,ss}$ = 135 dB re 1 μPa^{2}s and were more likely to spread laterally, while mackerel schools reacted at $L_{E,p,ss}$ = 142 dB re 1 μPa^{2}s, but were more likely to go down the water column ($L_{E,p}$ is the symbol for SELp, and the subscript "ss" is an abbreviation for "single strike" (pulse)). The echosounder was also able to trace a third trophic level of zooplankton, which revealed exposure-related downward movements. This is adding credibility to the study by McCauley et al. (2017), reporting zooplankton mortality up to 1200 m from an airgun array. However, inferring a causal relationship from a single observation is at best premature, especially without a mechanistic explanation for a possible "death by sound" for creatures of plankton size. Nevertheless, the study by Hawkins et al. (2014) showed that each of the three trophic groups may respond directly to the sound or indirectly by responding to movements of the other group. Importantly, this study showed that pulsed acoustic exposure can have effects that go beyond a single species and may cause changes in food web interactions (Francis, Ortega, & Cruz, 2009; Hubert et al., 2018; Slabbekoorn & Halfwerk, 2009).

Another approach that has been taken to assess behavioural response tendencies concerns playback of anthropogenic sounds to fishes in captivity. Thomsen et al. (2012), for example, exposed a mixture of fish species in a floating pen to playback of impulsive sounds (recordings of pile-driving strikes) and reported threshold sound levels at which fish moved (e.g. 140–161 dB re 1 μPa^2 zero-to-peak sound pressure level for cod). In another study, Kastelein, Jennings, Kommeren, Helder-Hoek, and Schop (2017) used a single pile-driving recording to assess response tendencies of hatchery-raised seabass, *Dicentrarchus labrax*, Moronidae, to intermittent sound pulses. Groups of four fish in a 1.75 × 4 m (2 m deep) basin were scored for behavioural response thresholds (defined in this study as 2 or more of the 4 individuals showing a startle or sudden swimming burst response). Two independent test series (with 8 and 9 groups of four fish, respectively) showed response thresholds at $L_{E,p,ss}$ = 131 dB and 141 dB re 1 μPa^{2}s and $L_{E,u,ss}$ = 67 and 77 dB re 1 (nm/s)^{2}s, respectively ($L_{E,u}$ is the symbol for sound particle velocity exposure level (SELu)). The difference between the two test series could be due to size-dependent response tendencies, variation in test or weather conditions between 2 years, or variation in captive history and acoustic experience. The short-term swimming response (up to few seconds) was not reflected in longer-term changes in group cohesion, which was only in one of the two test series significantly affected by sound level.

It is stressed that studies in captivity, on a specific mixture or a selected subset of fish raised in a hatchery, are of limited or no value for predicting absolute response levels for wild fishes responding in free-ranging conditions (Slabbekoorn, 2016). This kind of study, with proper replication, is most suitable to gain fundamental insight into response triggering potential of stimulus variation and exposure conditions. Behavioural observations in floating pens have, for example, confirmed that vessel noise should be taken into account when investigating impact of airgun exposure (De Robertis & Handegard, 2013; Doksæter, Handegard, Godø, Kvadsheim, & Nordlund, 2012). Neo et al. (2014, 2015, 2016, 2018) determined the impact of temporal variation in sound exposure with replicate sets of 16 groups of 4 seabass and reported consistent (in a basin and floating pen set-up) relatively long-term (~10–30 min) sound-induced behavioural responses, such as diving down the water column and increased group cohesion. Some important insights gained were that intermittent sound may lead to lower sound exposure levels (SEL) than continuous sound, but still can yield longer-lasting behavioural effects (Neo et al., 2014); that amplitude fluctuations and pulse rate interval may have subtle effects on the kind and intensity of a response (Neo et al., 2014, 2015); and that ramp-up procedures do not necessarily lead to mitigation targets (Neo et al., 2016). In the most recent study in this series, Neo et al. (2018) reported stronger responsiveness at night than during daytime and habituation in fading response patterns over eight repeated exposures during 2 days.

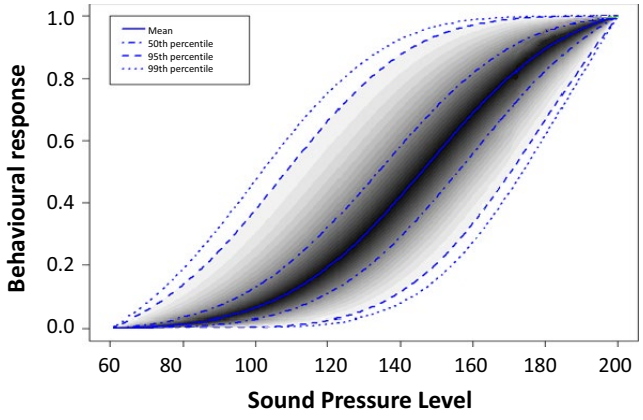

FIGURE 6 Example of how exposure to an acoustic stressor (of particular Sound Pressure Level) can affect the tendency to modify baseline behaviour (Behavioural Response) in a typical dose–response curve (based on killer whale (*Orcinus orca*, Delphinidae) data from a behavioural response study into acoustic exposure with naval sonar (Miller et al., 2014; also see Harris et al., 2018))

5.4 | Physiological stress responses to loud sounds

Physiological changes may or may not occur in parallel with the behavioural changes, but are typically investigated separately. The stress response in fish can be divided into a primary, secondary and tertiary response (Sapolsky, Romero, & Munck, 2000; Schreck, 1990). The primary response concerns the detection of the environmental

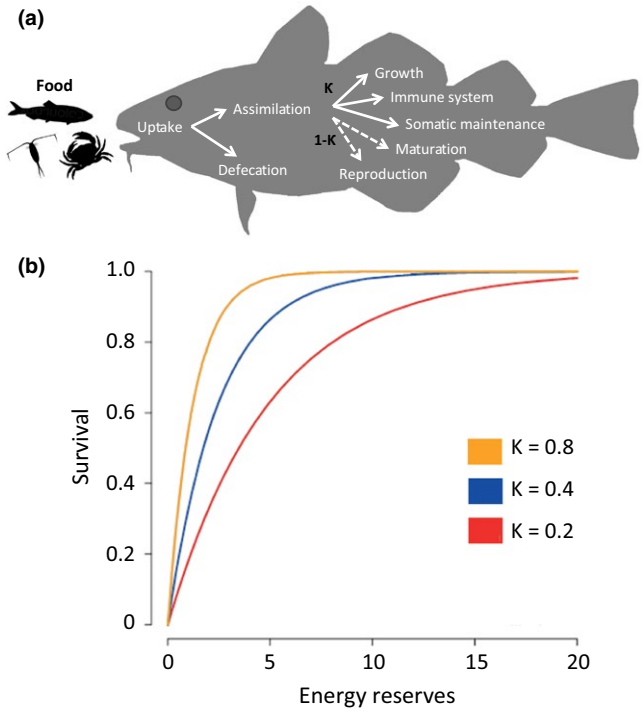

FIGURE 7 (a) Structure of the dynamic energy budget (DEB) framework. Food is assimilated into an energy reserve pool, from which a fixed proportion (K) is spent on growth, immune system and somatic maintenance, and deducted from the total (1- K) to get the energy available for maturation and reproduction (modified from Martin et al., 2013). (b) Example of how variation in body condition (Energy reserves, which may relate to anthropogenic noise-dependent behavioural decisions, reduced performance or physiological stress) can affect vital rates (Survival in this case, based on harbour porpoise data on impact from operational noise from wind farms; Nabe-Nielsen et al., 2014). More energy reserves yield higher survival rates. More investment in maturation or reproduction (lower K) requires more energy to keep survival up and leads to a shift in the curves to the right

stressor by the central nervous system and the associated neuroendocrine response. The secondary response is a consequence of the primary and concerns alteration of metabolic pathways. The tertiary response concerns changes in whole-body activity and performance. The primary response is a precondition for a potentially detrimental effect, but is also just a part of the natural fluctuations in a healthy fish to regulate daily activities. The secondary and tertiary responses may imply chronic stress and can be detrimental to growth, survival and reproductive success. Importantly, individual fish may not only show variation in behavioural response to environmental stressors, but also vary considerably and consistently in physiological response patterns associated with individual coping styles, which may play a critical role in the translation of any stress into fitness consequences (Conrad, Weinersmith, Brodin, Saltz, & Sih, 2011; Koolhaas et al., 1999; Øverli et al., 2007; MacKenzie et al., 2009).

Cortisol concentrations in circulating blood plasma are regarded as a valuable indicator of acute stress as part of the primary response as well as chronic stress of the secondary response that affects the energy regulation in the body and may undermine digestive and reproductive activity, immunocompetence and general homoeostasis of the body (Barton, 2002; Wendelaar-Bonga, 1997). Several recent studies (Midwood et al., 2014; O'Connor et al., 2010, 2011) have also addressed the tertiary response directly using exogenous cortisol implants (which is not a complete but elegant experimental mimic of the stressor-induced activation of the hypothalamic–pituitary–interrenal axis). The elevated cortisol levels (for 3–5 days) were typically associated with an expected increase in metabolic rate and overall activity but also caused growth rate depression and earlier winter mortality (compared to controls and sham-treated fish). Population models confirm that such consequences for the individual of single short-term stressors can translate to detrimental effects at the population level (Edeline et al., 2009; O'Connor et al., 2011).

Currently, there is still very little insight into physiological response patterns with respect to airgun exposure or any other loud sound. Artificial and loud sounds can induce a rise in cortisol in fish (and surrounding water), as has been shown in highly artificial conditions in a bucket in a laboratory (Wysocki et al., 2006). A slightly more natural experiment, but still in captive conditions of an aquarium, reported also stronger cortisol rises in giant kelpfish (*Heterostichus rostratus*, Clinidae) in response to randomly fluctuating presence of boat noise compared to continuous absence or presence of the same noise (Nichols et al., 2015). However, the current state of the art on sound-induced, physiological stress responses is by no means such that qualitative or quantitative translations can be made to population-level consequences. We are also only aware of one study directly investigating the physiological response in fish exposed to airguns. Santulli et al. (1999) conducted a study on biochemical responses to airgun exposure in seabass along the east coast of Italy in the Adriatic Sea. Although this study suffered from methodological issues such as pseudoreplication of multiple individuals per exposure cage and exposure conditions being confounded by time in the water, their data still suggest that several biochemical parameters were upregulated from 6 hr before to 6 hr after exposure and that the elevated levels were mostly gone after 72 hr.

Another recent aquacultural study confirmed the potential impact of acoustic exposure on the acute physiological stress response in cod (Sierra-Flores et al., 2015). In this study, cod were exposed to linear frequency sweeps (100–1,000 Hz) of 10 s for a period of 10 min in round fish tanks of 2 m diameter and 1 m depth (3.14 m^3) at moderately high levels that were aimed at common sound levels in aquacultural facilities (caused, e.g., by talking, feeding, netting or knocking). They were able to show a brief but significant increase in plasma cortisol concentrations, peaked 20 min after the onset of the acoustic exposure. Behavioural observations were limited, but freezing and "typical swimming responses" were reported. The physiological response in cortisol elevation returned back to baseline levels in about 20 min.

Sierra-Flores et al. (2015) also conducted a second experiment in which they explored the potentially negative effect of long-term acoustic exposure on spawning through chronic stress. They used two larger tanks of 5.3 m diameter and 2 m depth (44 m^3) and

exposed the fish in one tank, six times 1 hr at random times, to the same frequency sweep as mentioned above, and kept the other tank at ambient levels. The broodstock consisted of 10 females and six males in each tank (which were ready for spawning at about 60 cm length and about 3.4 kg mass). The two tanks differed in the period length in which eggs were produced with the noisy tank stopping 3 weeks earlier than the quiet tank, but overall egg production was not different. However, there were significantly higher cortisol levels measured in eggs from the noisy tank compared to the quiet tank, which were correlated with significantly lower fertilization rate and lower viability.

Although these patterns of apparent reproductive consequences of acoustic exposure correspond to reported effects on egg cortisol concentrations, fertilization rate and viability from cod stressed by confinement (Morgan, Wilson, & Crim, 1999), the experimental design is unreplicated. Any two batches of broodstock may show variation in stress levels and egg production; hence, testing the causal relationship with acoustic exposure requires appropriate replication. Extrapolation to outdoor conditions is further restricted by the use of specific and artificial sound stimuli, sound field conditions in the fish tanks that are different from natural water bodies, the behavioural space available for response patterns, and the hatchery-raised background of the test fish (Neo et al., 2016; Slabbekoorn, 2016). We should, therefore, be very careful with drawing conclusions from studies like Santulli et al. (1999) and Sierra-Flores et al. (2015). They should be considered as pilots for future studies of proper design (Cato et al., 2013; Slabbekoorn & Bouton, 2008; Underwood, 1991), with natural sound fields in open water and sound stimuli that resemble airgun sound features (taking distance-dependent modification with propagation into account).

6 | MODELLING CONSEQUENCES

6.1 | Modelling population-level effects

Two general strategies can be distinguished for gaining understanding in the population-level effects of seismic surveys on fish through modelling. One could be described as "bottom-up," where one builds a fully detailed, mechanistic, species-specific model, including all effects of underwater acoustic exposure on individuals and a realistic acoustic exposure scenario. This is then used to assess what the effects are of such a realistic exposure scenario at the population level. This strategy is probably the most direct way to find out whether and to what extent there is a problem with airgun acoustic exposure conditions of current seismic surveying procedures.

The opposite route is also possible and starts by asking the question "what would we consider a problematic population-level effect?" This allows for an "upfront" discussion about what is an acceptable effect (e.g. a certain percentage decrease in the number of adult individuals). The modelling approach now works "top-down" in that first an assessment is done to what extent the relevant model parameters can be changed before the threshold effect is reached. This result can be compared to the known pathways of sound effects on individuals, which reveals the most likely pathways that can yield population-level effects above the threshold. Ideally, this also eliminates one or more pathways, for which the model shows that the population dynamics are relatively insensitive.

The advantage of the second approach is that potential effects can be prioritized in terms of their likelihood to generate population-level effects. This way, resources for expensive field and laboratory studies can be directed towards the "most promising" individual-level effects of exposure. On the other hand, the prioritization is based on the assumptions underlying the models, and if these are inappropriate, the approach could miss the most crucial effects. Consequently, it appears logical to always include the cost-effective second strategy and invest wisely in collection of specific and potentially crucial field data to enter as parameters to confirm findings with the first strategy. The types of models are the same for both bottom-up and top-down strategies (e.g. De Roos & Persson, 2013; Martin, Jager, Nisbet, Preuss, & Grimm, 2013).

One suitable modelling framework for the individual level is that of dynamic energy budget models (DEB; Kooijman, 2000, 2010; Nisbet, Muller, Lika, & Kooijman, 2010). In this framework, individuals are described in terms of their size and energetic state, and the model specifies how ingested energy is used for growth, maturation and reproduction, given the state of the individual (Figure 7a). The DEB framework includes highly mechanistic descriptions of how energy flows through an organism (Teal, van Hal, van Kooten, Ruardij, & Rijnsdorp, 2012; Metcalfe et al., 2016). It can therefore readily incorporate the various individual-level effects of underwater sound, which affect individual energetics (e.g. higher stress levels leading to higher metabolic rates) and/or time budgets (e.g. more time spent on avoidance behaviour yielding less time left for feeding).

It is straightforward to use the DEB model as a basis for simulating population dynamics by assuming that individuals share a common source of food, and keeping track of births and deaths (Figure 7b). The population-level model simply consists of a bookkeeping system to account for all individuals (Martin et al., 2013), all cohorts (De Roos, Diekmann, & Metz, 1992) or a distribution over individual states (Andersen & Beyer, 2006). Because all assumptions in this framework are made at the individual level, all population-level effects are emergent properties of the individual-level effects on the model population. This strict separation between assumptions, which are made on one level of organization (individual), and results, which are on another level of organization (population), is a major advantage of this type of modelling framework.

An example DEB study on anchovy (*Engraulis encrasicolus*, Engraulidae) reliably predicted temperature and age-class-specific growth and reproductive performance (Pecquerie, Petitgasa, & Kooijman, 2009). Alternative modelling approaches use slightly different conversion routes, with, for example, available energy allocated to three structure pools: soma, lipids and eggs. The alternative approaches allow sensitivity analyses for variation in external environmental conditions and internal allocation strategies (e.g. Frisk et al., 2015; Megrey et al., 2007). It is arbitrary whether one uses DEB or any other similar framework, as they should all give results

pointing in the same direction (Andersen & Beyer, 2006; De Roos et al., 1992; Martin et al., 2013).

Because DEB is highly mechanistic, it does require considerable knowledge about the species to be modelled, in particular about the individual-level parameters that specify energy expenditure. This can be a problem if the aim is to study species for which such in-depth knowledge is unavailable. Furthermore, some of the parameters to DEB are difficult to obtain from experiments. For this last problem, a set of statistical routines have been developed which can estimate DEB parameters from common experimental outputs such as growth curves and population time series (Lika, Kearney, & Kooijman, 2011). Still, this procedure requires experimental results, which are not always available, in which case estimates can be based on related species with known parameters (e.g. Van der Veer, Kooijman, & van der Meer, 2001). Physiological models also allow impact analyses for deviating parameters that enter the model, and apparently subtle variation may accumulate to significant changes in individual fitness that may alter population forecasts. Toxic effects on individuals have been translated in this way to population-level effects (Jager & Klok, 2010), which should therefore also be possible for sound impact.

What is needed is accurate field data for sound-exposure-induced changes in behavioural and physiological parameters that can enter the models. These data should be collected under a variety of ecological conditions to also allow these to play a role in the model and enable further exploration of the potential for interactions and consequences across the feasible parameter range. For example, growth rate, time of metamorphosis and mortality of cod larvae are all affected by temperature and food availability (e.g. Cook, Kunzlik, Hislop, & Poulding, 1999; Hawkins, Soofiani, & Smith, 1985; Morgan, Rideout, & Colbourne, 2010; Olsen et al., 2011). Increasing temperatures have therefore a strong effect on recruitment and available habitat in general (Kell, Pilling, & O'Brien, 2005; Rindorf & Lewy, 2006). Consequently, impact analysis of anthropogenic factors is likely to gain biological relevance by taking the climatic and macro-ecological context into account that may be critical by themselves for collapse, recovery or outburst (Beaugrand, Brander, Lindley, Souissi, & Reid, 2003; Cook, Sinclair, & Stefansson, 1997; Cushing, 1984). For example, the North Sea cod stock is close to the southern edge of the species distribution and climate change may affect stock developments directly through temperature and indirectly through the abundance of zooplankton (Beaugrand & Kirby, 2010; Pörtner et al., 2001).

Vulnerability to disturbance by sound will also vary with age and size. Although sound impact on larval stages may be limited in a physical sense, we have little knowledge of behavioural effects. Even though experimental exposure to pile-driving sounds did not affect mortality in captivity (see Bolle et al., 2012 for sole larvae, *Solea solea*, Soleidae), fish larvae may still be physically injured (De Soto et al., 2013; Loes Bolle, personal communication) and may not survive or perform well in their natural environment. We do know that larval stages of fishes and other marine taxa are sensitive to sound (Montgomery, Jeffs, Simpson, Meekan, & Tindle, 2006), and anecdotal case-studies on seismic survey effects on similarly small marine animals have reported mixed results (and need replication): no effect on three shrimp species (small decapod crustaceans) targeted by fisheries (Andriguetto-Filho et al., 2005); detrimental effects on mortality, behaviour and physiology for scallops (*Pecten fumatus*, Pectinidae; Day et al., 2017); and potentially fatal effect on zooplankton (cf. McCauley et al., 2017, but see Fields et al., 2019).

Acoustic exposure may also affect larval feeding rates, for which consequences could be modelled in a similar way as the effects of light-dependent detectability and turbulence-dependent efficiency (see Fiksen et al., 1998 for herring and cod larvae). When juveniles get older and larger, they move to another position in the marine food web. Size composition of stocks and their main prey species are critical for understanding recruitment and stock development (Hjermann et al., 2007), and age-specific harvesting has considerable impact on stock depletion and recruitment (Diekert, 2013). Similarly, the potential impact of acoustic disturbance on local predator-prey interactions will likely heavily depend on size-classes.

We can start thinking about fitness consequences once we have assessed behavioural and physiological effects. Changes in food uptake or swimming activity can be converted to gains and losses in energy (e.g. Daan, 1973; Dutil & Lambert, 2000). Changes in predation risk (e.g. Hammill & Stenson, 2002; Köster & Möllmann, 2000; Savenkoff et al., 2006) or reproductive opportunity (Folkvord et al., 2014) may yield more discrete events that may have strong effects on individual fitness. It should be realized here that not only the target species may be affected by the acoustic exposure, but also predator and prey species may be affected (cf. Hawkins et al., 2014). Consequently, detailed knowledge about the ecology of the target species and stock-specific conditions is required to get a full picture on factors that may contribute to the potential impact of acoustic over-exposure in a particular area for a particular time.

6.2 | Individual-based models

Individual-based models (IBMs) may also be a useful tool to explore the effects of environmental stressors on fish behaviour and vital rates (Grimm et al., 2005; Willis, 2011; and see, e.g., Sibert, Hampton, Fournier, & Bills, 1999; Daewel et al., 2008). IBMs are a class of computational models for simulating the actions and interactions of autonomous agents, the individual animals, to explore consequences for the local population as a whole. They may also include energy budget features, but in contrast to the DEB models, they include spatial realism. IBMs can include the impact of physical properties of fish habitat, such as currents, temperature, tides or turbulence on migration or spatial distribution. If these models are coupled with 3D hydrodynamic models, they can include subroutines for energy budgets (gain through foraging and loss through metabolism) and provide insight into environmental impact on vital rates dependent on, for example, age class and specific food abundance. IBMs often use Lagrangian modelling of individual fish linked to spatially resolved hydrodynamic models by which they can account for factors such as the variability in exposure to environmental

stressors and thereby for individual variability in dispersal through a patchy environment (Heath & Gallego, 1997; Hernandez et al., 2013; Lough, Buckley, Werner, Quinlan, & Edwards, 2005).

IBMs can be applied in combination with sound propagation models, using species-specific data on typical swimming depths, hearing sensitivity and spectral range to assess exposure probability and consequences for over-exposure and behavioural responses of fish for any particular sound event (Erbe & King, 2009; Hovem et al., 2012; Southall et al., 2007). An example of this approach can be found in harbour porpoises and their exposure to the loud sounds of underwater detonations of explosives (Aarts et al., 2016; Von Benda-Beckmann et al., 2015). In this work, the authors estimated that detonations in the Dutch part of the North Sea (WWII explosives) cause permanent hearing damage for 800–8,000 porpoises per year and many more animals with some temporary impact on their hearing.

Rossington et al. (2013) used an IBM approach in which they combined a hydrodynamic model and an underwater sound propagation model to assess the behavioural impact of an explicit pile-driving event for an offshore wind farm on movement patterns of cod off the coast from Liverpool and the Dee Estuary. Rossington et al. (2013) used realistic mean swimming speed for cod and locally observed size distributions and tested the impact of being sensitive to sound disturbance (adjusting swimming direction and speed: freezing or doubling) or not (continuation on the same trajectory determined by correlated random walk). They found out that sensitive fish experienced significant delays compared to simulated counterparts that were insensitive ("deaf") on their migration from the feeding grounds to their coastal target, which concerns a known spawning and nursing ground for cod. In the context of sound pollution as an environmental stressor, it may also be possible to apply a combination of energy flow models and individual-based models.

6.3 | Multitrophic stock models

Insights into multitrophic relationships and the human impact of fisheries are also likely to play an important role in the evaluation of potential for sound impact on fishes. Trophic layers of predator and prey fish and various groups of zooplankton and zoobenthos play a significant role in natural food webs, and fisheries at any trophic layer inherently affect interactions (Lindegren, Möllmann, Nielsen, & Stenseth, 2009; Lindegren et al., 2010; Neuenfeldt & Köster, 2000; Persson et al., 1998; Van Leeuwen, De Roos, & Persson, 2008). Large piscivorous fish are typically the most profitable for fisheries, but also forage fish compose 30% of global fisheries landings. Similarly, sound impact will not be restricted to single species at a single life stage. Sound may affect every species in a different way, thereby affecting interactions indirectly, while sound may also affect interactions directly by an impact on predator-prey relationships (e.g. Purser & Radford, 2011; Shafiei Sabet et al., 2015).

Modelling the interactions between trophic layers is also important for the understanding of the effect of stressors on dynamical feedbacks between trophic layers (Claessen et al., 2000; Persson et al., 1998). Feeding interactions among groups are size-specific and have consequences for both groups: predation results in food for predators and mortality for prey. Due to dynamical feedbacks between trophic layers, an impact of fisheries or additional stressors may have counter-intuitive effects. For example, fishing on clupeids, which are dominant prey species for cod in the Baltic, may prevent a fisheries-induced collapse of the cod population. The fishermen may appear to compete with cod, but instead, their activities can reduce competition for food within the prey population and thereby cause a shift in the size distribution of clupeids that actually improves the food availability for cod (De Roos & Persson, 2013; Van Leeuwen et al., 2008).

Mortality through fisheries is recognized as a major factor that has to be taken into account for any type of population model as it is the confirmed cause of historical declines (Frank, Petrie, Choi, & Leggett, 2005; Hutchings, Bishop, & McGregor-Shaw, 1999). Acoustic impact analyses of seismic surveys on specific populations should therefore integrate not only expected projections of climate change but also current harvesting regimes (Drinkwater, 2005; MacKenzie, Gislason, Möllmann, & Köster, 2007). Modelling efforts to assess impact of anthropogenic sound will also benefit from the

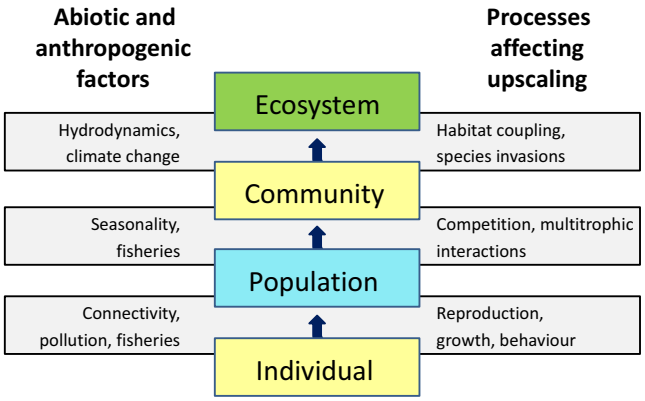

FIGURE 8 Many biological organization levels play a role in understanding the mechanisms underlying the potential impact of a pollutant such as airgun sound on fish populations. It is the individual that is in contact with its local environment and environmental stressors. Upscaling to populations, communities and ecosystems requires investigating processes at various levels and taking different kinds of abiotic and anthropogenic factors into account (modified from Cooke et al., 2014). Anthropogenic noise can affect upscaling from the individual to the population level (Cox et al., 2018; Kunc et al., 2016; Slabbekoorn et al., 2010) through a direct impact on vital rates, such as survival and reproduction, but also through an indirect impact via growth (e.g. altering cohort body condition and size at maturation) or behaviour (e.g. displacement from an area or lowered feeding efficiency). Upscaling from population to community level occurs through disturbing effects on predator-prey interactions (Shafiei Sabet et al., 2015) and other inter-specific effects such as competitive release (Hubert et al., 2018; Slabbekoorn & Halfwerk, 2009) or through noise-induced habitat alterations (Solan et al., 2016). Habitat-related stressors and cumulative effects from other factors than sound pollution are the link between communities and ecosystems (Carroll et al., 2017; Hawkins et al., 2015; Jones, 2016)

lessons learned with modelling efforts in fisheries (Fogarty, 2014; Hilborn & Liermann, 1998; Mace, 2001). For example, as mentioned before, including environmental influences would make a model significantly more dynamic and realistic, which is also true and implemented for predicting impact from fisheries (Köster et al., 2005). Another aspect of similarity concerns connectivity among populations or stocks and variation in impact. Acoustic exposure on fish populations through seismic surveys will inherently vary spatially. Also fisheries impact is never homogenous across large areas, related to the typical heterogeneity in fishing pressure determined by socioeconomic and regulatory factors. Council and Die (2015) applied a hybrid type of model to investigate this spatial variety in fishing pressure and revealed relevant effects on the age distribution of mortality, which had in turn again effects on the stock spawning attributes.

Finally, although matters become increasingly complex with scaling up to population, community and even ecosystem level (Figure 8), we believe these steps are essential. Not only has it become clear that the evaluation of sound impact should look beyond single-species effects (Francis et al., 2009), but there are also already terrestrial and marine reports on noise-induced habitat modification through the effects on the local animal community (Francis, Kleist, Ortega, & Cruz, 2012; Solan et al., 2016). The Marine Strategy Framework Directive of the EU already talks about "Good Environmental Status," which obviously concerns ecosystem level. Also in fisheries management strategies, lessons were learned with single-species or single-stock approaches, before more complex integrated or ecosystem-based models became more popular (Mace, 2001; Pauly, 1996). Maximum sustainable yield (MSY) was formerly a common management target, which meant that it was a target to fish as much as possible without causing a reduction that would involve a serious risk of stock extinction. However, it has become clear that individual management plans for separate species inevitably yield conflicts and ignore interactions among harvested species. The MSY has therefore become more of an upper limit, and management strategies are being upgraded with ecological complexity.

Current management strategies move towards ecosystem-based fisheries management (EBFM) (Fogarty, 2014). EBFM aims at sustainable harvesting of fishes to retain the important ecosystem services of the marine environment. EBFM is therefore a relevant concept for future developments in modelling sound impact beyond the single-species level as it concerns a more location-based rather than a species-based approach and takes ecological regions as the management target (see, e.g., Fogarty & Murawski, 1998; Liu, Liang, Chen, Chen, & Shen, 2012; Liu et al., 2012). EBFM solves the challenge of incorporating too many factors and players into a model for a complex ecosystem as the marine environment by not using specific species but size-classes or guilds, while taking both environmental influences and human impact as integral part of the ecosystem (Arkema, Abramson, & Dewsbury, 2006; Ashley et al., 2003; De Jonge, Pinto, & Turner, 2012; Dolan, Patrick, & Link, 2016; Fogarty, 2014; Tamis et al., 2016).

7 | CONCLUSIONS

Our review reflects the interdisciplinary challenge of assessing population-level consequences of seismic surveys on fishes. The information, data and insights treated crossed many different disciplines and subdisciplines. The overview yields a few key insights for the current state of the art and main gaps in our knowledge (see Box 3). Data on the behavioural and physiological responses of fish to seismic surveys are currently limited; there are no species for which there are well-replicated and adequately controlled data sets

Box 3 Summary overview of current insights

- The most effective way to make progress in impact assessment is through complementary efforts in data collection (behaviour, physiology, acoustics) and modelling (individual based and energy budget) with feedback to one another at each stage and with every new insight.
- We currently lack (a) dose–response data for any behavioural or stress physiological effect; (b) translation into vital rates for potential behavioural or physiological responses, given fluctuating ecological conditions with season, life stage and locality; and (c) insight into population-level consequences of any potential effects on vital rates.
- Behavioural and stress physiological effects are likely to be most relevant for population-level consequences and should be prioritized over injury and death for further exploration, since the potential for behavioural effects, in terms of animals involved, is orders of magnitude larger.
- Data collected during a single seismic survey can provide statistical evidence for sound-related fish activity or distribution at this event, but cannot serve as evidence for such a pattern in general. Replication at the level of the question is critical for the validity of any practical data collection effort.
- Accurate assessments of the sound field at the fish, in terms of both pressure and particle motion, are critical for any behavioural or physiological effect study. In general, there is a strong need for data on natural patterns of variation in particle motion in fish habitat.
- Harmonization in audiogram measurement methodology is a prerequisite for advances in quantitative understanding of hearing sensitivity in fishes.

to start quantifying the population consequences of airgun exposure. However, unlike for marine mammals, there exists a wealth of data on physiology and energetics for many fish species that could be useful in translating changes in behaviour into changes in energy budgets, and which could subsequently be used to infer impact on growth, maturation, reproduction and survival.

With respect to potential for modelling impact, the most suitable candidate approach for risk assessment depends on the objectives of management, the amount of available data and level of expert knowledge and resources. However, there is, perhaps, better potential for data-intensive approaches for fish than for the relatively harder-to-study marine mammals, for which PCAD models were developed in the first place. Proper use of qualitative and semi-quantitative methods becomes inherently quantitative, and we therefore believe that it is better to focus on quantitative methods. Expert elicitation is a useful method to synthesize knowledge, potentially extending the reach of explicitly quantitative methods to data-poor situations. Whatever method is chosen, it is unlikely to be correct in every case. This provides a motivation for monitoring outcomes in a sensitive way, and for adaptive management strategies (see, e.g., Nichols & Williams, 2006). Furthermore, there are many stock monitoring studies and predictive models for fish stock that take biotic, abiotic and anthropogenic influences into account (e.g. Cardinale & Svedäng, 2004; Heath et al., 2013).

Consequently, fish seem an excellent taxonomic group to further explore the validity of PCAD-type models and to potentially expand the application. It will be impossible to develop a single model that applies to all fish species. However, the same problem applies to fisheries impact for which advanced theories and methodology have been developed (e.g. McCully Phillips et al., 2015; review in Patrick et al., 2009). Seismic survey sound pulses are just one anthropogenic pollutant, which is not likely to become less abundant in the future. Many impulsive sound sources caused by human activities likely have similar potential for impact, such as pile driving for wind farm construction and explosions related to detonation of warfare ammunition. We therefore believe that marine conservation concerns are likely to grow and more studies are warranted that integrate different disciplines and also consider the accumulation of different sound sources.

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ORCID


Hans Slabbekoorn https://orcid.org/0000-0003-2309-0048

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