

Review

A critical review of the potential impacts of marine seismic surveys on fish & invertebrates



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ABSTRACT

Marine seismic surveys produce high intensity, low-frequency impulsive sounds at regular intervals, with most sound produced between 10 and 300 Hz. Offshore seismic surveys have long been considered to be disruptive to fisheries, but there are few ecological studies that target commercially important species, particularly invertebrates. This review aims to summarise scientific studies investigating the impacts of low-frequency sound on marine fish and invertebrates, as well as to critically evaluate how such studies may apply to field populations exposed to seismic operations. We focus on marine seismic surveys due to their associated unique sound properties (i.e. acute, low-frequency, mobile source locations), as well as fish and invertebrates due to the commercial value of many species in these groups. The main challenges of seismic impact research are the translation of laboratory results to field populations over a range of sound exposure scenarios and the lack of sound exposure standardisation which hinders the identification of response thresholds. An integrated multidisciplinary approach to manipulative and *in situ* studies is the most effective way to establish impact thresholds in the context of realistic exposure levels, but if that is not practical the limitations of each approach must be carefully considered.

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1. Introduction

The extent to which anthropogenic noise in the world's oceans impacts marine fauna is a subject of growing concern (Slabbekoorn et al., 2010; Azzellino et al., 2011; Williams et al., 2015). Sources of marine anthropogenic noise include high-intensity acute sounds produced by activities such as military exercises (Dolman et al., 2009), oil and gas exploration (McCauley et al., 2000) and pile driving (Bailey et al., 2010), as well as lower-level chronic noise generated by commercial shipping and recreational and commercial fishing vessels (Codarin et al., 2009; Malakoff, 2010). Many marine animals, from small invertebrates to large cetaceans, make extensive use of underwater sounds for important biological activities such as intraspecific communication, predator avoidance, navigation, larval orientation, foraging and reproduction (Montgomery et al., 2006; Vermeij et al., 2010; Mooney et al., 2012b). The ability to detect low-frequency sound in particular may have evolved in fish, cephalopods, and other mobile marine invertebrates to avoid predators (Mooney et al., 2010). Anthropogenic noise can interfere with the ability of an animal to detect and/or use its 'acoustic' or 'auditory' scene and potentially decrease its fitness and chance of survival (Popper and Hastings, 2009). Potential effects of anthropogenic sound sources on marine animals range from disturbance that may lead to displacement from feeding or breeding areas, to auditory damage, tissue trauma and mortality (Popper and Hawkins, 2012). Alternatively, some marine species may experience no effect of exposure to intense sources, particularly if the received frequency does not exceed hearing thresholds (Popper and Hastings, 2009). The area over which anthropogenic noise may adversely impact marine species depends upon multiple factors including the extent of sound propagation underwater, its frequency characteristics and duration, its distribution relative to the location of organisms, and the absolute sensitivity and range of spectral hearing among species (Slabbekoorn et al., 2010; Popper and Hawkins, 2012).

Marine seismic surveys typically involve the use of airgun arrays that are towed behind vessels and produce high intensity, low-frequency impulsive sounds at regular intervals. There are two common seismic survey configurations: 2-D seismic surveys involve a ship towing a single airgun array and a single streamer of hydrophones to provide a two-dimensional image of the subsea geology, and 3-D seismic surveys involve a ship towing two airgun arrays with ten or more parallel streamers to provide data which are processed to create a complete three-dimensional image of the subsea geology. Optimum frequency range for a particular array is a trade-off between resolution and depth of penetration. These sounds are directed down towards the substrate and are used to generate detailed images of the seafloor and its underlying geological formations (McCauley et al., 2000; Gausland, 2003). The predominant frequency range of seismic airgun emissions is within the detectable hearing range of most fishes and elasmobranchs (Popper et al., 2003b; Popper and Fay, 2011; Ladich and Fay, 2013) and can also elicit a neurological response in cephalopods (Mooney et al., 2010) and decapods (Lovell et al., 2005).

Although offshore seismic surveys have long been considered to be disruptive to fisheries (McCauley et al., 2000; Engås and Løkkeborg, 2002), most studies on the effects of noise focus on cetaceans (reviewed by Gordon et al. (2003)), while comparatively few studies target commercially important species (Williams et al., 2015), particularly invertebrates. Furthermore, much information on the effects of seismic operations on marine life is derived from 'gray' literature or anecdotal

reports which may lack appropriate experimental design or fail to adequately describe it (Hawkins et al., 2015). There have been concerns from various fishing industry groups that seismic operations negatively affect catch rates within a given area (e.g. snow crabs in northwestern Canada (Christian et al., 2004), rock lobsters and commercial scallops in southeastern Australia (Parry and Gason, 2006; Harrington et al., 2010)). Efforts are being made to improve relationships between fisheries and petroleum industries regarding improved regulation of seismic surveys (Knuckey et al., 2016), as well as to develop a coordinated global plan to address noise impacts (Nowacek et al., 2015), but the lack of robust studies and clear interpretations may hinder such efforts. Several countries have adopted precautionary principles in their approvals process for seismic survey activities based on potential impacts to fish and invertebrates (e.g. St Lawrence Seaway in Brêthes et al., 2004; Canada in Department of Fisheries and Oceans (DFO), 2004; Norway in Dalen et al., 2007). These policies restrict the timing, location, and duration of seismic exploration and can often be a source of conflict between various stakeholders (Lewandowski, 2015). As such, there is an urgent need to conduct a critical review of the associated science and identify knowledge gaps so that such precautionary policies can be developed or further refined according to the best information on species-specific responses to known exposure levels of low-frequency sound (Parsons et al., 2009; Prideaux and Prideaux, 2016).

Previous reviews on aquatic noise impacts have focussed on particular taxa, including cetaceans (Gordon et al., 2003; Erbe et al., 2016), turtles (Nelms et al., 2016) and fish (Popper and Hastings, 2009; Radford et al., 2014), or often in the context of general noise pollution (Popper and Hastings, 2009; Slabbekoorn et al., 2010). Hawkins et al. (2015) identified knowledge gaps in our understanding of noise effects on fish and invertebrates and provided valuable recommendations for priority research, but a comprehensive review of existing studies was outside their scope. Only McCauley et al. (2000) has critically reviewed a broad range of taxa specifically related to seismic sound impacts. The number of experimental studies has considerably increased since that review, and we therefore provide an updated, critical synthesis of the effects of seismic surveys on marine fish and invertebrates.

This review aims to summarise scientific studies which investigate the impacts of low-frequency sound on marine fish and invertebrates, as well as to critically evaluate how such studies may apply to field populations exposed to noise from seismic surveys. We also provide recommendations for future research investigating the potential impacts of seismic surveys on marine biota. For the purposes of this study, we define seismic operations as those using airguns, and we target peer-reviewed studies that focus on impulsive low-frequency sound (<300 Hz), which is distinct to marine seismic surveys and a few other activities (e.g. pile driving). Due to the limited number of marine environmental impact studies involving airguns (particularly for invertebrates), we occasionally draw on studies using other sound sources such as laboratory playback, pile driving or ship noise (continuous low frequency), as well as studies that examine the impacts of low-frequency sound on some freshwater and estuarine fish species, to highlight potential responses and areas of future research.

This paper is organised into five additional sections: Sections 2 and 3 briefly summarise the acoustic properties of marine seismic sound and sound detection in fish and invertebrates, respectively. Section 4 reviews the impacts of seismic surveys on marine invertebrates and fish, including a knowledge gap analysis. When quantifying the impact of any anthropogenic activity, an understanding of the

magnitude and type of response is critical to developing associated management or mitigation plans. We have therefore grouped impacts in this section based on physical (e.g. barotrauma, survival), physiological (e.g. metabolic rate, biochemical stress indicators) and behavioural (e.g. alarm movement, anti-predator behaviour) responses, as well as impacts on local abundance and catch which may manifest as a result of any of the above responses. Section 5 critically evaluates the limitations and challenges of quantifying marine seismic impacts in relation to existing studies. Finally, Section 6 provides general conclusions and a list of recommendations for future research on marine seismic impacts. We address characteristics and limitations of individual studies, and provide a complete list of studies and their key features (e.g. lab, field, or caged) in Supplementary Materials B (fish) and C (invertebrates).

2. Acoustic properties of marine seismic sound

Although their greatest acoustic output is vertically downward, seismic arrays radiate significant amounts of energy at elevation angles close to the horizontal, and that energy can propagate long distances in the ocean under some circumstances (Laws and Hedgeland, 2008). This radiation is highly directional in the horizontal plane with a pattern that depends on both direction and frequency. As a result of their rectangular layout, most arrays have their highest horizontal plane output in either the in-line direction (i.e. in the direction the survey vessel is travelling) or the cross-line direction (i.e. perpendicular to the direction in which the survey vessel is travelling). The output of most arrays is symmetric fore and aft and left-right (see Supplementary Material 1). Quantification of a sound wave can be relative to a number of the wave's

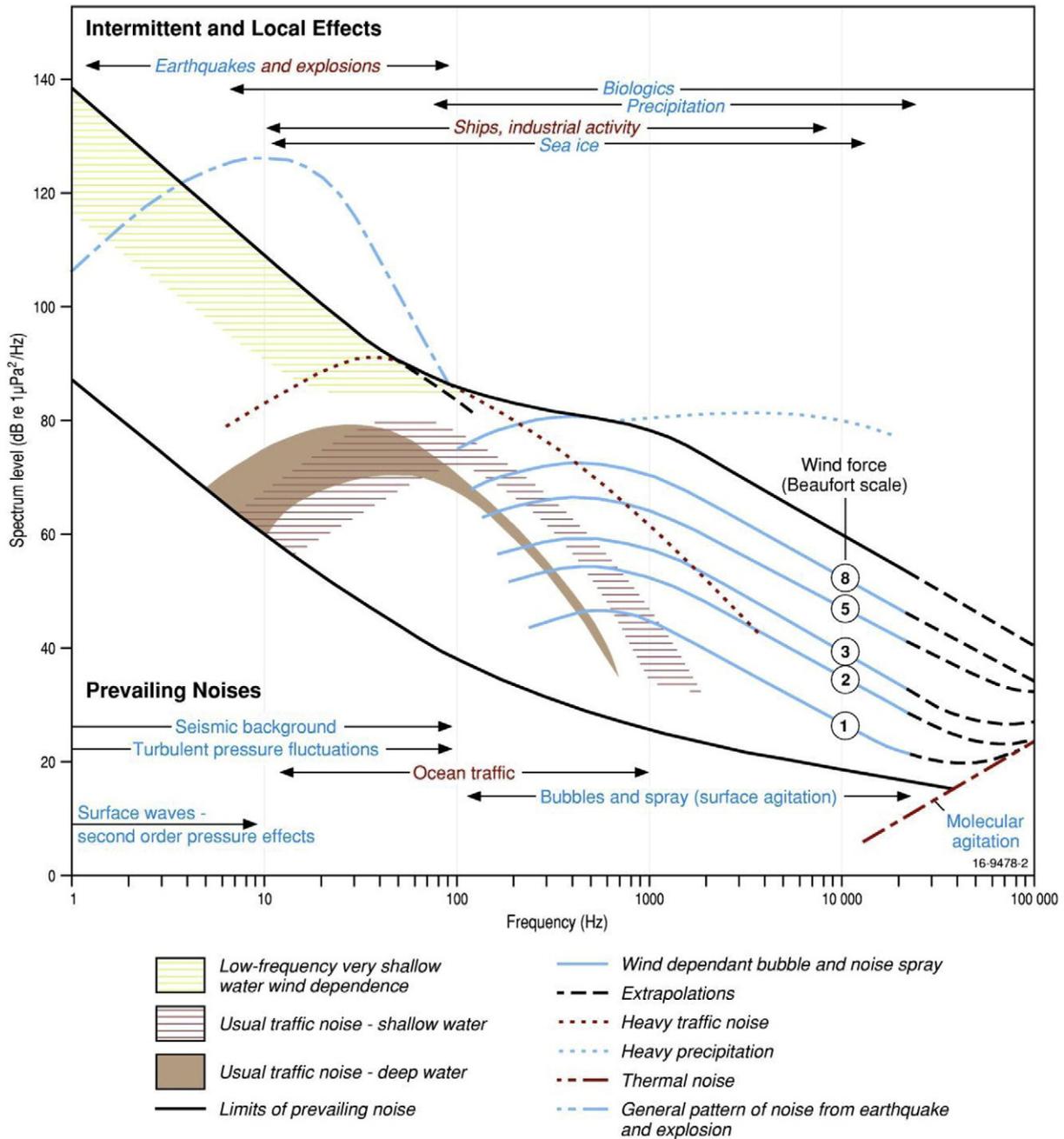


Fig. 1. Diagram of ambient noise spectra levels (commonly referred to as the Wenz curves) in a marine environment showing pressure spectral density levels of marine ambient noise from precipitation, wind, geological activity, and anthropogenic activity (commercial shipping and seismic activity). Horizontal arrows show the approximate frequency band of influence of the various sources. Adapted from figure shown in Wenz (1962).

properties, and four of these need to be considered with respect to the impact of seismic sound on marine life: relative pressure, frequency, particle motion, and duration (i.e. impulse). The frequency and pressure ranges of many sources of ambient ocean noise are outlined in Fig. 1. Further technical details on underwater sound propagation are included in Supplementary Material A and can be found elsewhere (McCauley et al., 2003a; Duncan and McCauley, 2008; McCauley et al., 2008; Duncan et al., 2013).

As a sound wave travels through water, the pressure will fluctuate as the alternating compression and decompression of the fluid occurs; these changes in pressure can be detected by a receiver such as a hydrophone or a marine animal. The amplitude of the pressure change is often expressed as decibels (dB). The decibel is proportional to the logarithm of the ratio of a measured quantity to a reference value and is not in itself an absolute measure, so it is important that the reference value is stated. When sound pressure is expressed in decibels the resulting quantity is called a sound pressure level (SPL), and for underwater sound the standard reference value is 1 μPa . Note that the standard reference value for sound in air is 20 μPa , so a SPL in water is not directly comparable to one in air.

It is conventional to quantify the output from a sound source by its source level, which is the sound pressure level at a specified distance (usually 1 m) from an equivalent point source in the direction of interest. An equivalent point source is a hypothetical point source of sound that would produce the same sound pressure levels as the real source at distances much greater than the dimensions of the real source (Kinsler et al., 1999). The actual SPL at a distance of 1 m from a large source such as an airgun array that may have a length and width of >10 m, will vary depending on the exact location of the measurement, but will be lower than the source level. Airgun arrays are highly directional, and have different source levels and source spectra in different directions.

The number of pressure waves that pass a point per second is known as the frequency, expressed in hertz (Hz). Sound sources transmit across discrete frequency ranges (spectra), and receivers, including ears and other auditory systems, are only sensitive to specific frequency ranges. Most of the energy from airgun arrays occurs in the frequency range of 10–100 Hz, although the source spectrum typically extends to over 2200 Hz (Goold and Fish, 1998).

Particle motion is a vector quantity with both magnitude and direction, and represents the oscillatory displacement (m), velocity (m/s), or acceleration (m/s^2) of fluid particles in a sound field (Popper et al., 2014). Sufficiently far from any sound source the pressure and particle velocity will be in phase and, in the absence of boundaries, both will be inversely proportional to the distance from the source. This region is known as the acoustic far-field of the source. The region closer to the source, where these simple relationships do not hold, is known as the acoustic near-field. The distance at which the transition between the near-field and far-field occurs depends on the acoustic frequency and the physical dimensions of the source and is discussed more fully in Supplementary Material 1.

As a sound wave propagates from its source, various factors, including its frequency, direction and the ocean and seabed environment through which it travels, have a strong bearing on how quickly the wave attenuates (Fig. 2a) (Supplementary Material 1). Differences can be extreme, with signals fading at a range of tens of kilometres due to upslope propagation from a seismic source in shallow water over a low reflectivity seabed, whereas other signals may be detectable at ranges thousands of kilometres from the source when sound travels down the continental slope (McCauley et al., 2008; Duncan et al., 2013). The primary reason for using low frequency sources in seismic acquisition is that there is less (Popper et al., 2014) attenuation as the signal travels through the earth and therefore lower frequencies are better able to image deeper geology. When the sound wave produced by the source reaches an interface, it will be partly reflected and partly transmitted through that interface (Fig. 2a). The incident angle of the

wave combined with the relative physical properties of the interface will determine the transmission and reflection behaviour of the wave (Fig. 2a).

3. Sound detection

The structure and function of the auditory system in fishes has been extensively reviewed (Fay and Popper, 2000; Popper et al., 2003a; Popper and Schilt, 2008; Popper and Fay, 2011; Popper et al., 2014), and all fishes studied to date are able to detect sound and show sensitivity to gravity and acceleration (Popper et al., 2014). The main auditory organs associated with sound detection in teleost (bony) fish are the otolithic organs (sacculae, lagena, and utricle) of the inner ear (see Supplementary Material 1 for morphological details) each containing hardened, calcareous otoliths overlying epithelia with sensory cilia. These otoliths are fully developed within a day or two after hatching (Leis et al., 2011), with well-developed swimming, orientation and sensory abilities developing early in the larval stage (Fisher et al., 2005; Montgomery et al., 2006; Leis, 2007; Siebeck et al., 2015). The inner ears of cartilaginous fish (sharks, rays and their relatives) possess essentially similar auditory structures to teleost fishes, with the addition of a fourth structure, the macula neglecta, which is a non-otolithic detector composed of two large patches of sensory epithelium (Myrberg Jr, 2001; Casper, 2011). However, unlike the hardened otoliths found in teleosts, the sensory epithelia (maculae) of the sacculae, lagena, and utricle in elasmobranchs are covered by otoconia, a gelatinous matrix of calcium carbonate granules, while the macula neglecta is covered by a gelatinous cupula that is similar to the cupula found in the lateral line organs and ampullae of the semicircular canals (Casper et al., 2012a).

Hearing in fish primarily involves the ability to sense acoustic particle motion via direct inertial stimulation of the otolithic organs or their equivalent (Casper, 2011; Popper and Fay, 2011). When a fish is exposed to sound, the greater rigidity or density of otoliths and otoconia causes them to move at a lower amplitude and different phase than the surrounding tissue (Popper et al., 2014). Their relative motion to the epithelium results in a deflection of the cilia, thereby activating the hair cells (Popper et al., 2014). While the otolithic organs of all fishes respond to particle motion of the surrounding fluid in this way, there is substantial interspecific variability in the structure of the inner ear anatomy (including the orientation of hair cell patterns on the sensory epithelia), resulting in a wide range of variation in hearing capabilities and/or mechanisms among fishes (Popper and Fay, 2011; Popper et al., 2014).

Many species also have the ability to detect sound pressure using an indirect path of sound stimulation involving gas-filled chambers such as the swim bladder, suprabranchial chambers, otic gas bladders or otic bullae (Braun and Grande, 2008). In these species, fluctuations in sound pressure generate particle motion, causing the gas-holding chambers to oscillate in volume, which in turn stimulates the inner ear by moving the otolith relative to the sensory epithelium. The proximity of gas-holding chambers and/or their direct mechanical connection to the inner ear enable fish to detect sound pressure and improve their hearing ability by enhancing their detectable frequency range and lowering their sound pressure threshold (Lechner and Ladich, 2008; Popper et al., 2014). Gas bladders, and their anatomical location within the body, also make fish more susceptible to pressure-mediated injury to the ears and general body tissues than species lacking gas bladders (Popper et al., 2014) (see Section 4).

Popper and Fay (2011) discussed the designation of fishes based on sound detection capabilities and proposed a 'continuum' of fish hearing and pressure detection mechanisms to replace the previous hearing 'specialist' vs. 'generalist' concept. Popper et al. (2014) more recently proposed three main categories for analysing the effects of sounds in fishes, based on the presence or absence of gas-filled structures and the potential of those structures to improve hearing range and sensitivity. The first category includes fishes that only detect particle motion.

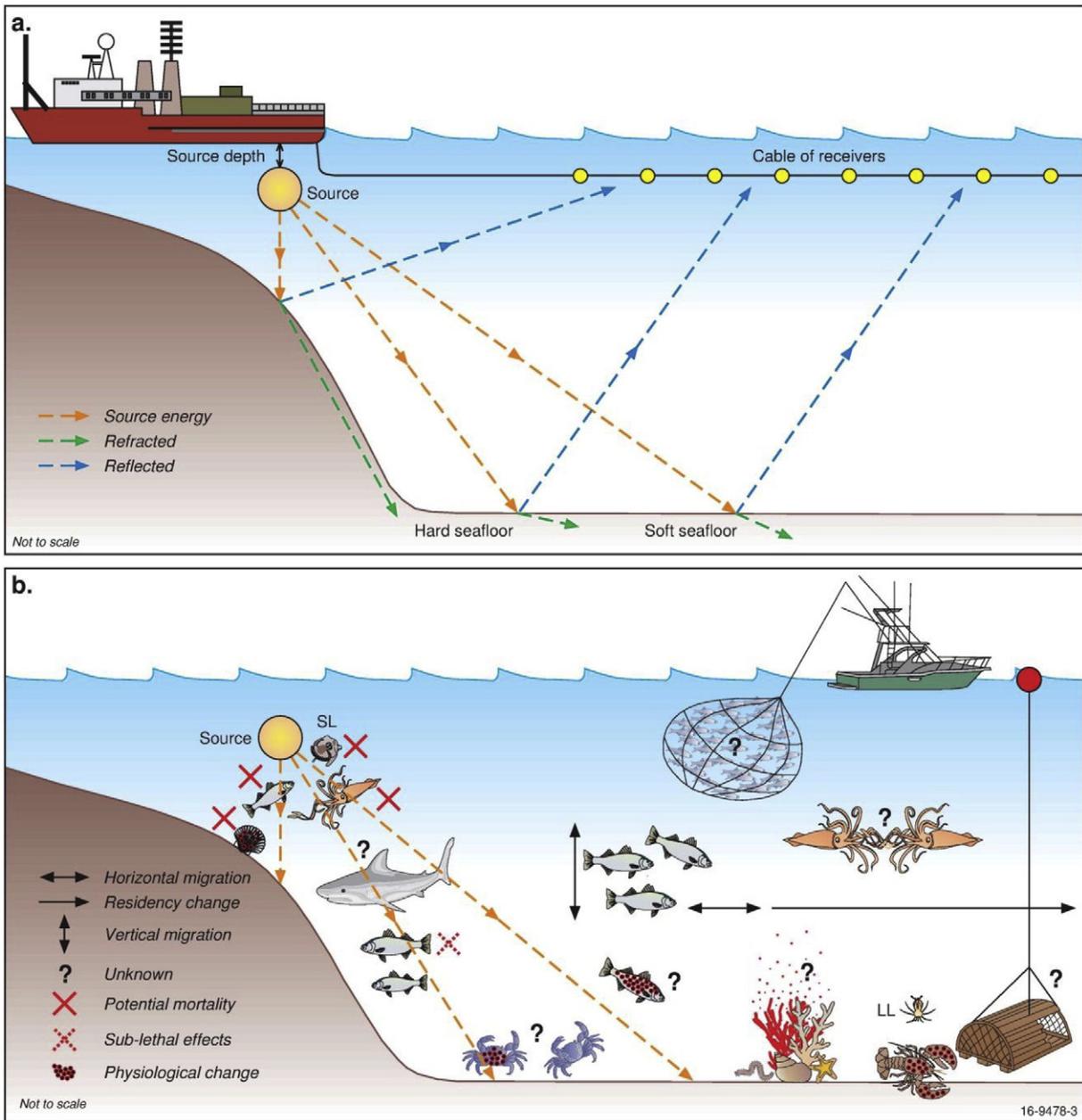


Fig. 2. Conceptual models showing a) physical characteristics and variation regarding sound propagation through the water column and seabed, and b) potential biological impacts of low frequency sound exposure as described in main text. SL = Scallop larvae; LL = Lobster larvae. References can be found in Figs. 3 (fish) and 4 (invertebrates). Figure not to scale.

The cartilaginous fishes (i.e. elasmobranchs) have the highest sensitivity to low frequency sound (~20 Hz to ~1500 Hz) (Myrberg, 2001; Casper, 2011). This group's lack of a swim bladder or other gas-filled chambers restricts their detection capabilities to the particle motion component of sound (Myrberg, 2001; Casper et al., 2012a). Evidence suggests that pelagic species have more sensitive hearing (thresholds at lower frequencies) than demersal species. However, studies have been conducted on only a small number of the 1200+ extant species to date, and the hearing sensitivities of most elasmobranchs are generally very poorly understood (Casper, 2011). Most studies have examined either the acoustic thresholds of species or the attracting power of low-frequency sound (Myrberg et al., 1972; Nelson and Johnson, 1972; Casper and Mann, 2007). The second category includes fishes with swim bladders in which hearing does not involve the swim bladder or other gas volume (e.g. Atlantic salmon in Hawkins and Johnstone, 1978). These species are susceptible to physical injury such as barotrauma, although hearing only involves particle motion, not

sound pressure (Popper et al., 2014). The third category includes squirrel fish, mormyrids, herrings and a diverse range of other species that are not only sensitive to particle motion but are also highly sensitive to sound pressure due to specialised otophysical connections between pressure receptive organs and the inner ear (see Supplementary Material 1) (Popper and Fay, 2011; Popper et al., 2014). This ability serves to increase hearing sensitivity and broaden the hearing bandwidth (Popper et al., 2014).

Like elasmobranchs, marine invertebrates lack a gas-filled bladder and are thus unable to detect the pressure changes associated with sound waves. However, all cephalopods as well as some bivalves, echinoderms, and crustaceans have a sac-like structure called a statocyst which includes a mineralised mass (statolith) and associated sensory hairs (e.g. crustaceans in Edmonds et al., 2016). Statocysts develop during the larval stage (Young et al., 2006) and may allow an organism to detect the particle motion associated with sound waves in water to orient itself (Sekiguchi and Terazawa, 1997; Kaifu et al., 2008). In addition

to statocysts, cephalopods have epidermal hair cells which help them to detect particle motion in their immediate vicinity (Kaifu et al., 2008), comparable to lateral lines in fish. Similarly, decapods have sensory setae on their body (Popper et al., 2001), including on their antennae which may be used to detect low-frequency vibrations (Montgomery et al., 2006). Whole body vibrations due to particle motion have been detected in cuttlefish and scallops, although species names and details of associated behavioural responses are not specified (André et al., 2016)

Hearing thresholds in both marine fish and invertebrates have been studied using behavioural and neurological responses to auditory stimuli called auditory evoked potentials (AEPs) (Ladich and Fay, 2013). Generally, fish species with specialisations for sound pressure detection (e.g. swim bladder) have lower sound pressure AEP thresholds (55–83 dB re 1 μ Pa) and respond at higher frequencies (200 Hz–3 kHz) than fishes lacking these morphological adaptations, which have thresholds between 78 and 150 dB re 1 μ Pa and best frequencies of below 100 to 1 kHz (Ladich and Fay, 2013). Fishes examined by measuring AEP particle acceleration threshold levels have thresholds between 30 and 70 dB re: 1 μ m s⁻² (Ladich and Fay, 2013). For invertebrates, AEPs have revealed responses in cephalopods at 400 Hz (Hu et al., 2009; Mooney et al., 2010), with sensitivity steeply dropping below 10 Hz (Packard et al., 1990). Similarly, a behavioural study on squid (*Doryteuthis pealeii*) revealed their optimal hearing range of 200–400 Hz, with the capacity to respond down to at least 80 Hz (Mooney et al., 2016). Prawns showed an AEP response at 500 Hz (Lovell et al., 2006), while the lobster *Homarus americanus* showed ontogenic variation in AEP response to up to 5000 Hz as adults (Pye and Watson, 2004). Despite their prevalence in establishing hearing thresholds through neurological responses, AEPs often do not accurately reflect behavioural responses (Hawkins et al., 2015; Sisneros et al., 2016), incorporate natural soundscapes (Ladich and Fay, 2013), or differentiate between pressure and particle motion (Popper et al., 2014), thereby making their application to the prediction of field responses questionable. Threshold determination using AEPs is also problematic due to tank interference and animal holding which can lead to suspect thresholds such as 1500 Hz for cephalopods (Hu et al., 2009) and 3000 Hz for shrimp (Lovell et al., 2005) (see Section 4). See Supplementary Material 1 for further details on AEPs and hearing thresholds. One of the few studies to investigate thresholds of particle motion on invertebrates found that hermit crabs behaviourally respond to 0.09–0.44 m s⁻² (RMS) (Roberts et al., 2016), but unfortunately most threshold studies on invertebrates report sound pressure rather than particle motion.

4. Responses to low-frequency sound

4.1. Knowledge gap analysis

A total of 70 studies were compiled which address the impacts of low-frequency seismic sound (<300 Hz) on fish (Supplementary Material 2) or invertebrates (Supplementary Material 3) (excluding AEPs discussed in Section 2). In Sections 4 and 5, we review and critically evaluate these studies. For invertebrates, several studies with broad ranges of treatment frequencies (e.g. 200–20 kHz in (Jeffs et al., 2003)) (Supplementary Material 3) are included due to the lack of information otherwise available on sound impacts. A total of 68 species of fish and 35 species of invertebrates were included, as well as several studies in which species were not differentiated (e.g. bivalve larvae in Parry et al., 2002; demersal and small pelagic fish in Dalen and Knutsen, 1987). Of these, commercial species represented 81% of fish (55 of 68) and 66% (23 of 35) of invertebrates. Laboratory experiments accounted for 35% of all studies (24 of 70); caged field studies for 25% (17 of 70), and uncaged field studies for 40% (28 of 70), with one study theoretical (Lee-Dadswell, 2009) and another incorporating both field and lab experiments (Payne et al., 2007). A total of 39% (27 of 70) of studies did not include a control, although several field studies

included a before and after component. Of the laboratory studies, sound exposure widely varied in amplitude, pulse duration and experimental duration (Supplementary Material 2, 3). Few studies reported values for particle motion (e.g. Aguilar de Soto et al., 2013; Samson et al., 2014; Roberts et al., 2015; Day et al., 2016a; Mooney et al., 2016; Przeslawski et al., in press), even though most invertebrates and many fish are sensitive only to the particle motion, not pressure, associated with sound waves.

For fish, there are few data on the physical effects of seismic airguns (e.g. mortality, barotrauma), and of these none have shown mortality (Fig. 3). Behavioural effects are the most studied aspect, although most studies are confined to the laboratory or cages (Supplementary Material 2). A number of studies have shown both negative and no impacts of seismic airguns on fish catch and abundance (Fig. 3), presumably due to changes in fish behaviour and distribution. There are no data on masking of natural sound cues by seismic airgun sources, and there remain significant gaps in our knowledge of the effects of seismic sounds on important physiological and biological processes such as metabolic rate, reproduction, larval development, foraging and intraspecific communication.

For invertebrates, crustaceans are the most studied group with respect to the broad range of metrics that have been investigated including catch rates and physical, behavioural, and physiological effects (Fig. 4) (Edmonds et al., 2016). There have been a few studies on molluscan and crustacean larvae, but information on early life stages for other invertebrate taxa is lacking (Fig. 4). Catch or local abundance are the most common variables studied in assessments of low-frequency sound on invertebrates, although no effects of low-frequency sound have been identified (Fig. 4).

4.2. Physical responses due to low-frequency sound

Prolonged or extreme exposure to high-intensity, low-frequency sound, may lead to physical damage such as threshold shifts in hearing (likely caused by the particle motion component) or barotraumatic ruptures (likely caused by the pressure component of sound) (Fig. 2b). Physical trauma may be detected through morphological or histological studies, and in extreme cases this physical trauma may result in mortality.

There is little information available on permanent hearing loss in fish (often referred to as permanent threshold shift, PTS) resulting from exposure to high-intensity sounds, although this type of physical response may be considered less likely to occur given the ability of fish to regenerate lost or damaged sensory cells of the ear (Smith, 2016). There is a growing body of literature however, which shows that anthropogenic sounds exceeding normal ambient noise may result in a temporary change in hearing sensitivity from which the animal will recover over time (Popper et al., 2005; Popper and Hastings, 2009; Popper et al., 2014). This impairment of hearing, referred to as temporary threshold shift (TTS), is a temporary reduction in hearing sensitivity caused by exposure to intense sound. While experiencing TTS, fish may experience a decrease in fitness in terms of communication, detecting predators or prey, and/or assessing their environment (Popper et al., 2014). The level and duration of exposure that causes TTS varies widely and can be affected by factors such as repetition rate, frequency and duration of the sound, SPL, as well as the health of the exposed organisms (Popper and Hastings, 2009) and unknown developmental and/or genetic impacts (Popper et al., 2007).

For fish, the high-intensity of airgun emissions may damage hair cells and cause changes in associated hearing capabilities. McCauley et al. (2003b) demonstrated that exposure to repeated emissions of a single airgun (1 m of 222.6 dB re 1 μ Pa peak-to-peak) from 5 to 300 m caused extensive damage to the sensory hair cells in the inner ear of caged pink snapper (*Pagrus auratus*). Although no mortality was observed, the damage was severe with no evidence of repair or replacement of damaged sensory cells up to 58 days post-exposure. However,

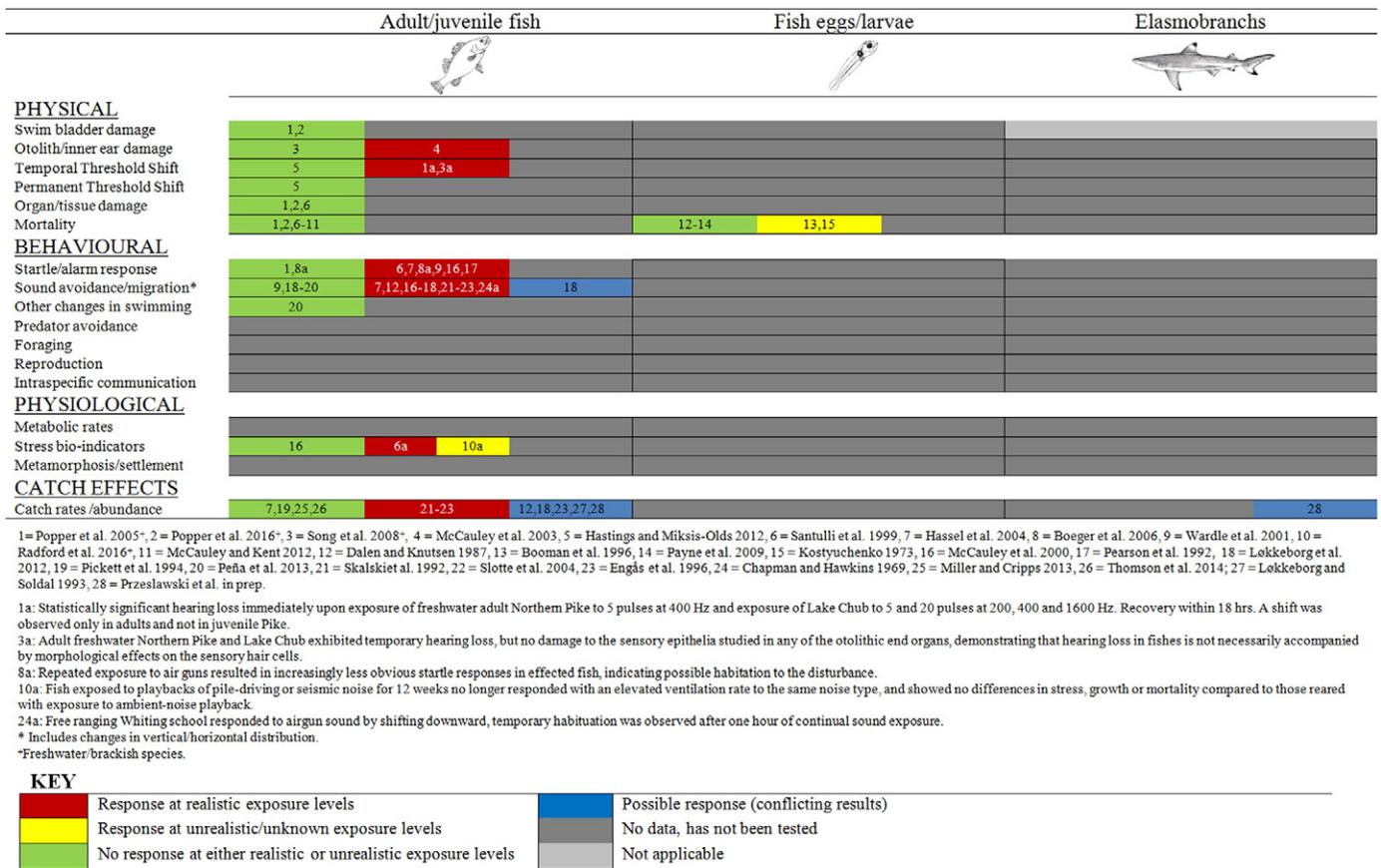


Fig. 3. A summary of potential impacts of low-frequency seismic sound on fish. Impacts are classified according to the sound exposure treatments as realistic (i.e. short bursts of low-frequency sound at a distance of >1–2 m) or unknown/unrealistic (i.e. long duration and/or short distance of <2 m to sound source, nearfield sound exposure in aquaria). There are significant differences between seismic studies regarding sound exposure and the environment in which studies were conducted. See Supplementary Material 2 for characteristics of each study (e.g. lab, field, caged).

in the absence of neurophysiological experimentation, the functional hearing of the snapper was unknown (McCauley et al., 2003b). In contrast, other studies have found no or limited evidence of hearing damage in fish following exposure to seismic airguns (despite some fish showing temporary hearing loss) (Popper et al., 2005; Song et al., 2008; McCauley and Kent, 2012), or exposure to higher sound intensity and duration (193 dB re 1 µPa for over 10 min) (Popper et al., 2007) (but see Section 5 for limitations associated with caged experiments).

Caged freshwater pallid sturgeon (*Scaphirhynchus albus*) and paddlefish (*Polyodon spathula*) exposed to a single pulse from a small seismic airgun array (10,160 cm³) showed no significant lethal injury (i.e. no mortality or mortal injury) either immediately or within seven days of exposure (Popper et al., 2016). However, extrapolation of these findings to other species and other environments (i.e. marine) requires caution, and further work is needed to understand fully the specific physical effects of seismic airguns on fishes (Popper et al., 2014; Hawkins et al., 2015; Popper et al., 2016). With the exception of Popper et al. (2016), much of the research on fish barotrauma due to low-frequency sound has focused on pile driving which generates similar acute, high-intensity, low-frequency sound as seismic operations. Exposure of freshwater fishes to pile driving has been shown to result in substantial damage to internal organs including the swim bladder, liver, kidney and gonads (Casper et al., 2012b; Halvorsen et al., 2012; Casper et al., 2013a, b; Halvorsen et al., 2013). Fishes with physoclistous swim bladders (closed from the gut) appear more susceptible to barotrauma from pile driving than fishes with physostomous swim bladders (connected to the gut). Larger fish are more likely to be injured than smaller fish, presumably due to the difference in swim bladder resonance, although smaller fish may show delayed onset of injuries and

take longer to recover (Casper et al., 2013a). Elasmobranchs may be similarly susceptible to some forms of barotrauma (e.g. to the liver, kidney and intestines) displayed by teleosts exposed to high intensity noise (Casper et al., 2012a), but the lack of studies on elasmobranchs makes it difficult to evaluate potential physical effects that could be associated with their exposure to seismic noise.

For marine invertebrates, exposure to near-field low-frequency sound may cause anatomical damage, although research is limited. Anecdotal evidence shows pronounced statocyst and organ damage in seven stranded giant squid after nearby seismic surveys (Guerra et al., 2004). After two hours of continuous sound treatment (1-second sweeps, 50–400 Hz) in 200-litre glass tanks, four species of cephalopod exhibited acoustic trauma in their statocysts, including lesions, hair cell loss and damage, and neuron swelling (André et al., 2011; Solé et al., 2013) (see Section 5 for limitations associated with artificial tanks). Day et al. (2016a) found airgun exposure caused damaged statocysts in rock lobsters up to a year later. However, no such effects were detected in snow crabs after exposure to 200 shots at 10 s intervals and 17–31 Hz) (Christian et al., 2003). A theoretical study similarly found that particle displacements produced in crabs due to seismic sound would be too small to damage tissue (Lee-Dadswell, 2009). The disparate results between these studies therefore seem to be due to differences in sound exposure levels and duration, in some cases due to tank interference, although taxa-specific differences in physical vulnerability to acoustic stress cannot be discounted.

In the absence of more subtle anatomical studies on most marine invertebrates after exposure to acute low-frequency sound, mortality may be the most useful indicator of barotrauma in marine invertebrates. Previous field-based studies on adult populations revealed no evidence of

	Molluscs				Crustaceans		Echinoderms	
								
	Cephalopod	Gastropod	Bivalve	Larvae	Decapod ^a	Stomatopod	Larvae	Ophiuroid
PHYSICAL								
Air bladder damage					4,5	5		
Otolith/statocyst damage	1-3				4,5	5		
Organ/tissue damage	6		7,8		9			
Mortality/abnormality	6		7,8,10 ^c	5	11	5,9,12		4,13,14
BEHAVIOURAL								
Startle response	15-19		5,20		4,21			
Sound avoidance	18				22			
Predator avoidance			5		5,12,23			
Foraging					23			
Reproduction					24			
Bioturbation			25		25			25
PHYSIOLOGICAL								
Metabolic rates ^b	26			11	4,12,27,28		13	
Stress bio-indicators	25		25,29	5	4,5,12,22,25,27,30			25
Immune response					5			
Energy stores			10					
Metamorphosis/settlement							31	13
CATCH EFFECTS								
Catch rates / abundance	29	29	7,10,29	8	4,9,27,29,32,33	29		

1 = André et al., 2011, 2 = Solé et al. 2013a, 3 = Solé et al. 2013b, 4 = Christian et al. 2003, 5 = Day et al. 2016a, 6 = Guerra et al. 2004, 7 = Harrington et al. 2010, 8 = Parry et al. 2002, 9 = Courtenay et al. 2009, 10 = current study, 11 = Aguilar de Soto et al. 2013, 12 = Payne et al. 2007, 13 = Pearson et al. 1994, 14 = Day et al. 2016, 15 = Fevtrrell and McCauley 2012, 16 = McCauley et al. 2000, 17 = Samson et al. 2014, 18 = Komak et al. 2005, 19 = Mooney et al. 2016, 20 = Roberts et al. 2015, 21 = Roberts et al. 2016, 22 = Celi et al. 2013, 23 = Wale et al. 2013a, 24 = Lagardere 1982, 25 = Solan et al. 2016, 26 = Kaifu et al. 2007, 27 = Christian et al. 2004, 28 = Wale et al. 2013b, 29 = La Bella et al. 30 = Filicetto et al. 2014, 31 = Branscomb and Rittschof 1984, 32 = Andriquetto-Filho et al. 2005, 33 = Parry and Gason 2006

^a DFOC 2004 also examined the effects of various physical and physiological effects of seismic signals on snow crabs but is not included here because no baseline data acquired before seismic survey, and refined experiments in Courtenay et al. 2009 supersede these results.

^b Includes proxies for metabolic rate such as food consumption, growth, respiration, developmental rate

^c Also includes Chalmer (1986), Kosheleva (1992) and Matishov (1992) as cited in Parry et al. (2002)

KEY

	Response at realistic exposure levels		Possible response / conflicting or anecdotal results
	Response at unrealistic/unknown exposure levels		No data, has not been tested
	No response		Not applicable

Fig. 4. A summary of potential impacts of low-frequency sound on various responses of marine invertebrates. Impacts are classified according to the sound exposure treatments as realistic for seismic surveys (i.e. few short bursts of low-frequency sound at >1–2 m) or unknown/unrealistic (i.e. continuous sound exposure, >100 bursts of nearfield sound exposure, in aquaria). There are significant differences between seismic studies regarding sound exposure and the environment in which studies were conducted. See Supplementary Material 3 for characteristics of each study (e.g. lab, field, caged).

increased mortality due to airgun exposure in scallops up to ten months after exposure (Parry et al., 2002; Harrington et al., 2010; Przeslawski et al., in press), clams two days after exposure (La Bella et al., 1996), or lobsters up to eight months after exposure (Payne et al., 2007; Day et al., 2016a). Similarly, there was no evidence of mortality-associated population effects such as reduced abundance or catch rates in plankton a few hours after exposure (Parry et al., 2002), reef-associated invertebrates four days after exposure (Wardle et al., 2001), snow crabs up to 12 days after exposure (Christian et al., 2003), shrimp two days after exposure (Andriquetto-Filho et al., 2005), or lobsters weeks or years after exposure (Parry and Gason, 2006). However, Day et al. (2016a) found dose-dependent increased mortality in transplanted scallops reared in suspended lantern nets four months after exposure to an airgun.

Larval stages are often considered more sensitive to stressors than adult stages (Byrne and Przeslawski, 2013), but exposure to seismic sound reveals no differences in larval mortality or abundance for fish (Dalen et al., 2007; Payne et al., 2009), crabs (Pearson et al., 1994), or scallops (Parry et al., 2002). There were similarly no effects on the mortality, abnormality, competency, or energy content of lobster larvae (*Jasus edwardsii*) after exposure of early embryonic stages to airgun shots with sound exposure levels >185 dB re μPa 2 s (Day et al., 2016b). However, intense and lengthy periods of exposure to low-frequency sound such as those adopted for scallops in Aguilar de Soto et al., 2013 (3 s shot intervals for 90 h, 1 m distance from sound source in lab) or fish in Booman et al., 1996 (unknown number of shots, 220–242 dB re 1 μPa SPL, 0.75–6 m from sound source in caged experiments) can increase abnormality and mortality rates, indicating that larvae exposed to near-field airgun shots may be vulnerable (see Section 5 for

limitations on caging and laboratory studies). Research on the effects of boat noise on sea hare development has also shown reduced survivorship of embryos exposed to boat noise playback (10–3000 Hz) in controlled field conditions, although due to the large frequency range used, it is difficult to extrapolate results here to potential impacts of seismic surveys.

4.3. Behavioural responses due to low-frequency sound

High levels of sound can elicit various types of behavioural responses in marine fish and invertebrates, some of which may negatively affect a population (e.g. reduced rate of foraging or predator avoidance), and others which may pose no overall risk (e.g. brief startle response) (Fig. 2b). Behavioural effects are more likely than physical and physiological effects at lower sound levels (Hawkins et al., 2015) and may thus be a more useful indicator of effects of seismic noise over a large spatial scale. However, behavioural effects are more difficult to monitor *in situ* than physical and physiological effects, and many studies on the effects of seismic operations on behaviour are therefore conducted in laboratories or using caged individuals (detailed in Supplementary Material 1). Results of these studies must be cautiously interpreted as they relate to effects in field populations (see 'Limitations and Challenges' below).

Airgun discharges have been reported to elicit varying degrees of startle and alarm responses in caged teleost fish, including C-starts (see Supplementary Material A) and changes in schooling patterns, water column positions, and swimming speeds (Pearson et al., 1992; Santulli et al., 1999; Wardle et al., 2001; Hassel et al., 2004; Boeger et

al., 2006; Fewtrell and McCauley, 2012) (Fig. 2b). There is some indication that a sudden onset of sound can also cause a startle response in sharks (Myrberg et al., 1978), although research on the behavioural response of elasmobranchs to low-frequency sounds is lacking. Thresholds at which airgun sounds elicit behavioural responses in captive marine fish have been shown to vary among species; for example the threshold for startle responses of caged olive and black rockfish (*Sebastes serranoids* and *S. melanops*) lay between 200 and 205 dB re 1 μ Pa whereas no response was observed vermilion (*S. miniatus*) or brown (*S. auriculatus*) rockfish up to the maximum exposure of 207 re 1 μ Pa dB (Pearson et al., 1992). Startle and alarm responses have been observed in captive fish several kilometres from the sound source, with European sea bass and the lesser sandeel responding at distances up to 2.5 and 5 km from a seismic source, respectively (Santulli et al., 1999; Hassel et al., 2004). Collectively, these caged studies provide an indication of acoustic and environmental conditions in which fish may show behavioural responses to seismic noise, but startle responses of captive fish may have little or no resemblance to responses in open conditions (e.g. Jorgenson and Gyselman, 2009).

Behavioural studies on unrestrained fish exposed to airgun sound are scarce, but while logistically challenging, they provide the most ecologically realistic evidence of seismic survey impacts. Chapman and Hawkins (1969) observed that the depth distribution of free-ranging whiting (*Merluccius bilinearis*) changed in response to an intermittently discharging stationary airgun, which resulted in fish exposed to an estimated SPL of 178 dB re 1 μ Pa. The fish school responded to the airgun sound by shifting downward, forming a more compact layer at greater depth although temporary habituation was observed after one hour of continual sound exposure (Chapman and Hawkins, 1969). Minor effects were also observed in tagged tiger flathead which increased their swimming speed during the seismic survey period and changed diel movement patterns after the survey but showed no significant displacement (Przeslawski et al., in press). Investigation of the possible influence of seismic sound on the distribution and abundance of pelagic fish (herring, blue whiting and mesopelagic species) revealed insignificant short-term horizontal distribution effects (Slotte et al., 2004). However, blue whiting and mesopelagic species were found in deeper waters during seismic exposure compared to their pre-exposure distribution (Slotte et al., 2004). These studies indicate that vertical movement rather than horizontal movement could be a short-term reaction to seismic sound. Wardle et al. (2001) exposed free-ranging marine fish (juvenile saithe and cod, and adult pollock and mackerel) and invertebrates (crustaceans, echinoderms and molluscs) inhabiting a small inshore reef system to sound from three 2.5 L (150 cu.in) airguns (195–218 dB re 1 μ Pa peak pressure). Fish exhibited startle responses to all received levels, but no avoidance behaviours were observed in either fish or invertebrates. Exposure to airgun emissions did not interrupt the diurnal rhythm of fish, and only slight changes to the long-term day-to-night movements of two tagged pollock were recorded (Wardle et al., 2001).

Potential habituation to repeated airgun exposure has been demonstrated for some fish. During airgun activity, some captive rockfish returned to pre-exposure behavioural patterns late in the exposure period, suggesting habituation to the airgun sounds (Pearson et al., 1992). Similarly, behavioural observations of three coral reef fish species (*Lutjanus synagris*, *L. apodus*, *Chaetodipterus faber*) in field enclosures before, during and after exposure to airguns showed that repeated exposure resulted in increasingly less obvious startle responses (Boeger et al., 2006). Temporary habituation to airgun discharges was observed in schooling whiting when they returned to pre-exposure depth range following continual exposure to airgun sound over one hour, but again ascended to greater depths when airgun discharges recommenced after a period of non-shooting (Boeger et al., 2006). Fewtrell and McCauley (2012) also reported a gradual weakening of startle responses in *Pelates* sp. (Terapontidae) over a continuous exposure to airgun signals.

Behavioural studies on the response of marine invertebrates to seismic sound are also dominated by those using startle responses. Jetting and inking in squid have been observed during airgun operations, with startle responses occurring more frequently as sound levels increase (Fewtrell and McCauley, 2012), and scallops have shown a distinctive flinching response although no energetically costly responses such as swimming (Day et al., 2016a). Laboratory studies have also found inking and jetting of cuttlefish at frequencies of 80–300 Hz, sound levels above 140 dB re 1 μ Pa rms and $0.01 \text{ m} \cdot \text{s}^{-2}$; although these responses disappeared at higher frequencies and lower sound levels (Samson et al., 2014). Unlike cephalopods, decapods only exhibited alarm behaviour when they were <10 cm away from the sound source (Goodall et al., 1990) and showed no such behaviour in response to seismic sound at distances of 1 m or more (Goodall et al., 1990; Christian et al., 2003). Sound avoidance behaviours have a more lasting impact on populations than startle responses, particularly if animals migrate out of an area in which seismic surveys are conducted. Previous studies have found that neither squid (McCauley et al., 2000), snow crabs (Christian et al., 2003), nor shrimp (Celi et al., 2013) move to avoid low-frequency sounds, although the latter study was conducted in a tank in which shrimp may have been unable to detect the direction of the sound (see Section 5). Further research is warranted, particularly in light of potential interactions between seismic sound and shipping noise, the latter of which has been shown to increase mobility in decapods (Filiciotto et al., 2013) and elicit avoidance behaviour effects in some fish (e.g. Handegard et al., 2003; Codarin et al., 2009).

Behaviour not necessarily associated with startle responses has been observed in invertebrates (e.g. mussel valve closure, hermit crab antennae movement in Roberts et al., 2015, 2016), but the biological relevance of these minor responses extends only to establishing thresholds of sound detection or intraspecific differences. For example, based on valve closure, sensitivity to particle motion was higher in smaller than larger mussels (Roberts et al., 2015). On the other hand, changes in predator avoidance behaviours may have population-level implications if predation rates increase due to sound-induced behavioural changes in prey. Scallops were faster to recess into sediments after exposure to airguns, but they were slower to right themselves after overturning (Day et al., 2016a). Similarly, the rock lobster (*Jasus edwardsii*) showed delayed time to right itself after exposure to airguns (Day et al., 2016a). In contrast, no differences in righting time were detected in the American lobster (*Homarus americanus*) 9, 65, or 142 days after exposure to airgun noise, indicating no immediate or long-term effects on predator avoidance behaviour of this species (Payne et al., 2007). Other invertebrate behaviours may also be affected by low-frequency sound associated with seismic surveys, although available information is not specific to sound produced from airgun arrays. Shrimp displayed less agonistic behaviour during a broad range of sound frequencies (100–25,000 Hz) compared to control conditions (Celi et al., 2013), and crabs showed feeding disruptions during exposure to shipping noise but no effect on the ability to find food sources (Wale et al., 2013a). There is also evidence that bioturbation may be affected due to intra- and inter-specific variation in the behaviour of clams (*Ruditapes philippinarum*), lobster (*Nephrops norvegicus*), or ophiuroids (*Amphiura filiformis*) after exposure to continuous or impulsive low-frequency noise (Solan et al., 2016). Further studies on bioturbation, feeding and defensive behaviour in field conditions are warranted to provide more realistic sound exposure scenarios. Seismic activities may also impact larval behaviour of invertebrates (Branscomb and Rittschof, 1984; Jeffs et al., 2003; Vermeij et al., 2010); this is covered in more detail below.

As with fish, some invertebrates may become habituated to sound, with squid showing fewer alarm responses with subsequent exposure to noise from airguns (Fewtrell and McCauley, 2012), cuttlefish habituating to repeated 200 Hz tone pips (Samson et al., 2014), and squid showing decreased responses over sound exposure trials (Mooney et al., 2016). There is also some indication of habituation in crabs to

vibrations, with greatest sensitivity to particle motion in crabs held in captivity for the shortest period (Roberts et al., 2016). Cephalopods may also be able to adapt their behaviour to particular sounds types. In a series of caged trials in which turtles, fish, and squid were exposed to airguns, the squid were the only animals to shelter in the sound shadow at the ocean surface (McCauley et al., 2000).

4.4. Physiological responses due to low-frequency sound

Physiological response indicators include stress bioindicators such as hormones, immune responses, and heat shock proteins. Metabolic rate is the most direct indication of potential physiological stress and can be measured via respiration, oxygen consumption, excretion, or food consumption rates. Physiological responses to airgun sound may not be as immediately obvious as physical and behavioural responses, but they are equally important to provide early indications of negative effects, as well as to explain the underlying mechanisms behind physical and behavioural responses. Despite this, the physiological consequences of acoustic stimulation on fish and invertebrates remain poorly understood.

For fish, there is some evidence to suggest that seismic sounds may elicit endocrinological stress. Experimental seismic noise (underwater explosions in laboratory conditions) has been shown to affect primary stress hormones (adrenaline and cortisol) in Atlantic salmon (*Salmo salar*) (Sverdrup et al., 1994), and European seabass (*Dicentrarchus labrax*) have shown elevated ventilation rates, indicating heightened stress, in response to impulsive additional noise (playbacks of recordings of pile-driving and seismic surveys), but not to a more continuous additional noise source (playbacks of recordings of ship passes) (Radford et al., 2016). In the latter study, fish exposed to playbacks of pile-driving or seismic noise for 12 weeks no longer responded with an elevated ventilation rate to the same noise type, and showed no differences in stress, growth or mortality compared to those reared with exposure to ambient-noise playback. However, it is important to note that there are both behavioural and acoustic limitations to tank-based playback experiments (see Section 5 for limitations associated with caged and artificial tank experiments); hence, the relevance of these findings to actual airgun exposure in open-water conditions remains uncertain. Santulli et al. (1999) reported significant changes in cortisol, glucose, lactate, AMP, ADP, ATP and cAMP levels in different tissues of caged sea bass (*Dicentrarchus labrax*) after exposure to airgun emissions, indicating a primary and secondary stress response. No mortality or physical trauma were observed, and the variations of biochemical parameters returned within normal physiological values within 72 h indicating a rapid recovery of homeostasis following the acoustic stress (Santulli et al., 1999). Conversely, found no significant change in cortisol, glucose or white blood cells in caged pink snapper (*Chrysophrys auratus*) that could be directly attributed to airgun exposure.

For marine invertebrates, there are a very limited number of studies examining the effect of seismic noise on metabolic rates. The respiration rate of cephalopods may be affected by low-frequency sound, with *Octopus ocellatus* suppressing their respiration at 50–150 Hz (120 rms dB re 1 μ Pa) (Kaifu et al., 2007). Payne et al. (2007) found no clear evidence of seismic effects on the food consumption rate of lobsters. Another study, however, showed size-dependent effects of low-frequency sound on oxygen consumption rate of crabs; only large crabs showed higher oxygen consumption rates after sound exposure (Wale et al., 2013b).

There are a suite of stress bio-indicators that can be extracted from invertebrate haemolymph to detect sub-lethal effects of low-frequency sound. Shipping noise has been shown to significantly increase glucose, total protein, heat-shock proteins, and total haemocyte count in lobster (Filiciotto et al., 2014), but neither shipping noise nor impulsive noise was found to have any effect on tissue levels of glucose or lactate in lobsters, clams, or ophiuroids (Solan et al., 2016). Studies focussed explicitly on low-frequency sound found no such stress bioindicators in lobster (Payne et al., 2007) or snow crab (Christian et al., 2003;

Christian et al., 2004), but the clam *Paphia aurea* had increased levels of glucose, hydrocortisone, and lactate in its muscle and hepatopancreas immediately after exposure to seismic airgun pulses (La Bella et al., 1996). Day et al. (2016a) provide evidence that exposure to airguns may interfere with the long-term capability of scallops to maintain homeostasis, as revealed by reduced haemocyte counts and altered haemolymph biochemistry up to 120 days post-exposure. Importantly, it remains unknown if observed biomolecular indicators of stress actually cause physical or behavioural responses which could negatively affect populations and therefore an associated fishery. In addition, stress tests can be employed as a general indication of overall physiological quality, in which an organism is subjected to a stressor until a designated response is observed. There has been only one study using a stress test response to gauge impacts of seismic surveys, and this found no effect of seismic sound exposure on time to death after ice baths for snow crabs (Christian et al., 2004). More subjective indications of stress may also be examined using the condition of meat or gonads. For example, scallop meat and roe quality were assessed between control and impact sites before and after two different seismic surveys with no adverse effects detected (Harrington et al., 2010; Przeslawski et al., in press). Low-frequency sound may also affect the physiology of developing embryos and larvae (Christian et al., 2003; Aguilar de Soto et al., 2013); this is covered further below.

4.5. Catch and abundance effects due to low-frequency sound

If an animal is affected by seismic sound, associated catch may also be affected, regardless of whether the response is physical, behavioural or physiological. Lethal (physical), and sub-lethal effects including avoidance (behavioural), and reduced fitness (physiological) may all result in a reduced population within a given area, thereby reducing fisheries catch. Analysis of catch effects do not reveal the underlying mechanisms that may cause declines in catch rates and are thus less useful than other response types from a biological perspective. However, catch and abundance effects are the response type most directly of interest to the fisheries industry and they are relatively simple to measure *in situ*.

The potential effects of seismic operations on fish distribution, local abundance or catch have been examined for some teleost species (reviewed by Hirst and Rodhouse, 2000, McCauley et al., 2000, Popper and Hastings, 2009), with varying results (Fig. 3), possibly due to gear- and species-specific effects (Løkkeborg et al., 2012). Commercial trawl and longline catches of Atlantic cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) have been shown to fall by 45% and 70%, respectively, five days after seismic surveys in the Barents Sea (Engås et al., 1996). Based on the local decline in fish density across the central study area, Engås et al. (1996) hypothesised that the reduction in catch rates was most likely the result of fish moving away from the seismic area due to an avoidance behaviour, but this was not quantified. Similar reductions in catch rates (52% decrease in Catch Per Unit Effort (CPUE) relative to controls) have been demonstrated in the hook-and-line fishery for rockfish (*Sebastes* spp.) during controlled discharges of a single airgun (186 to 191 dB) at the base of rockfish aggregations off the central Californian coast (Skalski et al., 1992). The authors suggested that the mechanism underlying the pronounced CPUE decline was not dispersal but rather decreased responsiveness to baited hooks associated with an alarm behavioural response. Based on a companion behavioural study which showed that alarm and startle responses were not sustained following the removal of the sound source (Pearson et al., 1992), Skalski et al. (1992) suggested that the effects on fishing may be transitory, primarily occurring during the sound exposure itself.

In contrast, other studies on fish have found positive, inconsistent, or no effects of seismic surveys on catch rates or abundance (Fig. 3). A desktop study of four species (gummy shark, tiger flathead, silver warehou, school whiting) in Bass Strait, Australia, found no consistent

relationships between catch rates and seismic survey activity in the area, although the large historical window of the seismic data may have masked immediate or short-term effects which cannot therefore be excluded (Thomson et al., 2014). A subsequent desktop study targeting a single seismic survey in 2015 found that of the fifteen commercial species examined, six species showed higher catch following the survey, three species showed reduced catch, and five species showed no change (Przeslawski et al., in press). Following exposure to airgun noise in a Norwegian fishing ground, gillnet catches increased substantially for redfish (*Sebastes norvegicus*) and Greenland halibut (*Reinhardtius hippoglossoides*) (by 86% and 132%, respectively), while longline catches of Greenland halibut and haddock decreased (by 16% and 25%, respectively, compared to pre-shooting levels) (Løkkeborg et al., 2012). A study investigating the effects of a 3-D seismic survey at Scott Reef, Northern Australia found no significant effect of the seismic survey on the abundance or species richness of pomacentrid fish (a family that exhibits a high degree of site fidelity) or non-pomacentrid fish (larger more mobile roaming demersal species that have a greater ability to “flee” from the affected area and return once the disturbance had passed) (Miller and Cripps, 2013). Another study used an omnidirectional fisheries sonar to investigate the real-time behaviour of herring schools exposed to a 3-D seismic survey in the same area and found no changes were observed in school sizes, swimming speed or direction that could be attributed to the transmitting seismic vessel as it approached from a distance of 27 to 2 km over a 6 h period (Peña et al., 2013). The lack of a response to the seismic survey was interpreted by the authors as a combination of a strong motivation for feeding, a lack of suddenness of the airgun stimulus, and an increased level of tolerance to the seismic shooting (Peña et al., 2013). Further studies employing sonar to monitor fish schools during the approach of an operating seismic vessel are highly recommended, as they allow *in situ* observations of behaviour of schooling species that can then be used to predict potential effects on catch rates. However, such studies can only monitor the fish when the seismic vessel is > 1 km away, as other vessels must clear the area on a seismic vessel's approach.

For marine invertebrates, the potential effects of seismic signals on catch rates or abundances have been tested on cephalopods, bivalves, gastropods, decapods, stomatopods, and ophiuroids with no significant differences detected in any of these studies between sites exposed to seismic operations and those not exposed (Wardle et al., 2001; Parry et al., 2002; Christian et al., 2003; Parry and Gason, 2006; Courtenay et al., 2009; Przeslawski et al., in press) (Fig. 4).

4.6. Responses to low-frequency sound of early life stages

Although seismic activity has been implicated in larval recruitment declines (e.g. <http://www.abc.net.au/site-archive/rural/tas/content/2012/08/s3576796.htm>), there are few scientific experiments which have directly investigated the effects of low-frequency sound on larvae and other early life stages of fish and invertebrates (Figs. 3 and 4). Due to differences in the physiology and life history requirements between adults and larvae, larval responses to seismic activity may vary quite dramatically from adults. The larvae of some groups (e.g. flounders/soles/flatfishes, gobies) have swim-bladders that are subsequently lost on settlement as juveniles. These early life stages may therefore be more susceptible to underwater sound than older life stages.

For fish, there is some indication of possible mortality immediately adjacent to a seismic sound source, but results are conflicting (Fig. 3) and may reflect inter- or intra-specific variation or differences in sound characteristics. Kostyuchenko (1973) studied the effects of energy released from a single large airgun (300 in.³) discharge on the survival and injury to the eggs of several commercial fish species. Survival in the fish eggs was over 75% at 0.5 m from the airgun, over 87% at 5 m and over 90% when placed 10 m from the sound source. Although this may reflect increasing mortality with proximity to sound source, the low samples sizes and different cohorts used in this study mean results

should be cautiously interpreted. Conversely, Dalen and Knutsen (1987) found no significant change in the survival of cod (*Gadus morhua*) eggs following close-range exposure (1–10 m) to airgun emissions. Similarly, Payne et al. (2009) found no statistical differences between controls and exposed larvae of monkfish (*Lophius americanus*) or capelin (*Mallotus villosus*) eggs in relation to survival (24–72 h post exposure). Experimental exposure of common sole (*Solea solea*) larvae to piledriving sound levels (up to 210 dB re 1 μPa^2 0-peak) did not result in increased larval mortality (Bolte et al., 2012).

Many benthic invertebrates have a free-swimming larval stage which means that the magnitude of seismic sound exposure also depends on ontogeny. Repeated exposure to near-field seismic sound caused slower developmental rates and higher mortality or abnormality rates in larvae of crabs exposed to peak sound levels of 216 dB re 1 μPa every 10 s for 33 min (Christian et al., 2003), and scallops exposed to sound exposure levels of 161–165 dB RMS re 1 μPa every 3 s for 90 h (Aguilar de Soto et al., 2013). However, these studies were conducted in the laboratory with associated limitations (Section 5), and experimental conditions would not be experienced by larvae during routine seismic operations. Field-based studies using more realistic sound exposures revealed no evidence of delayed development, increased mortality, or reduced abundance in bivalve or decapod larvae (Pearson et al., 1994; Parry et al., 2002). Although the studies detailed here found no effect or used experimental conditions unlikely to be encountered by larvae, effects of seismic sound on marine invertebrate larvae cannot be excluded.

For both fish and invertebrate larvae, sound plays an important role in orientation and settlement (Jeffs et al., 2003; Montgomery et al., 2006; Vermeij et al., 2010; Leis et al., 2011). Sound associated with wind and tidal turbines (125–245 dB re 1 μPa , up to 10 kHz) can delay metamorphosis of two species of estuarine crabs, likely due to interference with natural sound associated with mudflats which has been shown to mediate crab metamorphosis (Pine et al., 2012); however, the large frequency range and continuous sound exposure makes it difficult to relate these findings specifically to seismic airguns. Further hypothesis-driven testing is needed to determine potential impacts of low-frequency, high intensity sound on larval behaviour, including settlement site selection and potential flow-on population effects.

5. Limitations and challenges

Despite the importance of quantifying the potential environmental impacts of marine seismic surveys on commercially important species, we still have fundamental knowledge gaps which hamper our understanding of the field. The knowledge we do have is often limited due to experimental conditions or design (unrealistic or unknown sound exposures, artificial tanks, absence of controls) or those focused on a single species which preclude generalisation and extrapolation to other regions, seismic surveys, species, or biological responses. Elasmobranchs in particular remain a very poorly understood group (Fig. 3), and Casper et al. (2012a) noted the lack of experiments examining the impact of anthropogenic sound sources on any elasmobranch species. In addition, the responses of most marine invertebrates remain unknown, with field studies to date focused on a few species of crab, lobster, and scallops and little to no information on other groups (Fig. 4, Supplementary Material 3). The absence of anatomy related to sound reception such as ears, otoliths, or statocysts does not necessarily mean an animal is unable to detect or react to sound (Montgomery et al., 2006). As such, there is still much debate as to whether and how many marine invertebrates detect sound, even among the relatively well-studied taxa such as cephalopods and crustaceans (Mooney et al., 2012a). Due to this lack of information regarding basic neurological and physiological responses for most species at realistic exposure levels, inferences about the effects of seismic activity on marine invertebrates can be challenging and fraught with uncertainty.

5.1. Standards for assessing sound exposure

It is now recognised that the lack of standardisation in terminology and measurements related to sound exposure is one of the main limitations in providing a broadscale assessment of potential impacts of underwater noise (Hawkins et al., 2015; Ainslie and De Jong, 2016; Prideaux and Prideaux, 2016). Variation in metrics and methods used to quantify sound exposure makes comparisons among studies challenging if not impossible. Until such standardisation is achieved, the findings of research on the effects of airguns and other sound sources in the marine environment will only apply to individual studies, and the general applicability of these studies to other marine seismic surveys, regions or taxa will remain questionable. Particle motion, in particular, needs to be more widely considered in sound impact research on fish and invertebrates (Hawkins et al., 2015).

5.2. Short and long-term impact assessment

Although several studies have shown that low-frequency sounds negatively affect certain species of fish and invertebrates (Figs. 3 and 4), the duration of effects and potential cascades are rarely considered. In order to predict any potential impact to populations (such as what may affect fisheries catch rates), recoverability must also be tested. For example, riverine fish that show temporary threshold shifts (TTS) following exposure to seismic sounds recover within relatively short timeframes (e.g. 18–24 h in Popper et al., 2005). This is also the case with some physiological impacts, with biochemical parameters in sea bass returning to physiological values within 72 h post-seismic exposure, indicating a rapid recovery of homeostasis following the acoustic stress (Santulli et al., 1999). In contrast, Day et al. (2016a) found that transplanted scallops failed to recover from disruption to homeostasis even four months after airgun exposure; however, the relevance of these findings to natural populations remains uncertain (Przeslawski et al., in press). Examination of the short and long-term effects of low-frequency sound on marine fish and invertebrates is critical for understanding the broad range of impacts, especially on important biological processes such as reproduction, larval development and recruitment.

5.3. Experimental tanks

The ability to accurately measure responses to noise hinges on an appropriate experimental set-up. Holding tanks can lead to misinterpretation of results, particularly related to behaviour, for several reasons, all of which have been well-documented in other studies (Parvulescu, 1964; Gray et al., 2016; Rogers et al., 2016): 1) Sound reflects off tank walls causing interference, 2) organisms are unable to escape, and 3) real sound sources usually cannot be used. For example, avoidance behaviour can be difficult to detect in a laboratory if the sound source is not obvious to the test organism (e.g. due to reverberation) (Celi et al., 2013). Pressure measurements taken in enclosed spaces cannot be compared to open marine conditions due to reflections off surfaces and their interference with wave propagation as well as the invalidation of the particle motion relationship to pressure due to being in the near-field (Gray et al., 2016), a situation that occurs when the receiver is close enough to the source such that the ratio of particle velocity amplitude to pressure amplitude is no longer constant (see Supplementary Material 1).

It is incorrect to assume that larger or thicker tanks are more realistic surrogates for field conditions than smaller tanks. For example, an analysis of acoustic pressure and particle velocity maps at 325 and 800 Hz in cylindrical tanks 4–9 m diameter revealed that what may be considered a large experimental tank in relation to the studied animal may in fact be subject to unpredictable boundary interactions that transform acoustic fields (Gray et al., 2016) (see Supplementary Material A). Such interactions would be further exacerbated with the longer wavelengths of the low-frequency sound of airguns (10–300 Hz). If the specific

properties of sound generated in the experiment are not adequately considered in the experimental design, results may actually reflect this rather than the desired treatment. For examples, Hu et al. (2009) found two species of cephalopod had 'hearing' ranges up to 1500 Hz, but this conflicts with other studies showing cephalopods are not sensitive to higher frequencies (Packard et al., 1990; Mooney et al., 2010). These results have been criticised due to the potential response of squid instead to the unmeasured pressure release at the water surface where animals were held (Mooney et al., 2010). According to Montgomery et al. (2006), "the wavelengths of sound in water and the practical restrictions of the size of laboratory tanks make it essentially impossible to do meaningful behavioural studies involving the broadcast of sound in a tank," a sentiment shared by other researchers (Goodall et al., 1990; Popper et al., 2001; Gray et al., 2016).

5.4. Interpretation and extrapolation

Laboratory experiments can provide valuable insight to the potential physical or physiological effects of low-frequency sound on marine organisms due to the high level of experimental control associated with such studies (Slabbekoorn, 2016). Nevertheless, it may be tempting to overstate or simplify results to show effect or no effect, whereas results should instead be interpreted in the context of realistic exposure scenarios, experimental limitations, and field conditions. There can be pressure to accentuate significant effects (i.e. impacts), but null responses are equally important and must be considered in any interpretation (e.g. Solan et al., 2016). The noise levels and durations used in experiments are just as important as the actual biological responses because they determine the transferability of results from lab to field, as well as informing effective mitigation strategies if required (Fewtrell and McCauley, 2012). Most benthic organisms would be exposed to few if any near-field (maximum) shots of a 2-D seismic airgun array if the vessel follows a typical seismic exploration pattern (e.g. Pearson et al., 1994), while 3-D seismic surveys could result in exposure to more shots (e.g. 200 shots in Christian et al., 2003), although very few of these would be near-field. Laboratory experiments should attempt to mimic similar exposure durations. Many of the laboratory studies that found impacts of seismic sound on invertebrates and fish have done so at unrealistic exposure levels or durations (Fig. 3), mimicking sound exposure at 1–2 m, a distance that is ecologically unrealistic for benthic animals and unlikely for all but a few larvae, or for durations that do not occur with routine seismic operations. For example, Aguilar de Soto et al. (2013) conducted widely-cited research in which seismic sound increased the abnormality rates of scallop larvae, but the exposure time to low-frequency sound included continuous shots at 3-second intervals for up to 96 h in an experimental tank. Increasing levels of potential stressors will eventually elicit a biological response, and such experiments must be tempered with knowledge (or at least acknowledgement) of conditions actually experienced by the organism in their natural environment.

Caged studies provide an intermediate experimental option that allow for realistic sound sources (i.e. a passing airgun array) while also ensuring organisms are able to be appropriately monitored and retrieved for data acquisition (e.g. McCauley et al., 2003b, Day et al., 2016b). However, the ecological realism of caged experiments is questionable, and this requires careful consideration when interpreting results. The main issues with caged studies are whether sound exposure is realistic (e.g. if the organism would normally move away from the sound source) and whether the response observed is natural (e.g. potential confounding responses of captivity stress or intraspecific interactions at high stocking densities). The studies themselves are not flawed and can provide valuable information about potential responses and possible thresholds; however the interpretation of them must not be simplified to imply effect or no effect without acknowledging limitations.

One of the main challenges in underwater sound impact studies is the meaningful translation of laboratory results to the field. Underwater sound properties are affected by the sound source and duration, as well as characteristics of the water column, substrate, and biological communities. For example, sound propagation in shallow waters is affected by several factors, which may either increase or decrease an organism's overall exposure to sound. If the range between airgun and animal is greater than the water depth, cylindrical spreading results in an increase in the effective range of sound (Montgomery et al., 2006). However, shallow water also limits the propagation of low-frequency sound, with relatively strong attenuation due to the interaction with the sea bottom (Hamilton and Bachman, 1982; Montgomery et al., 2006). Variations in sound propagation due to seafloor characteristics, water conditions, and seismic system specifications (McCauley et al., 2003a) therefore mean that it is not ideal to adopt an *ad hoc* approach and investigate potential impacts by compiling seismic data from multiple historical surveys (Thomson et al., 2014). Instead, potential effects should be examined by focusing on individual surveys in a given location, preferably with sound exposure at the seafloor modelled or measured (e.g. Przeslawski et al., in press).

While it is evident that both gear- and species-specific effects may occur (e.g. Løkkeborg et al., 2012), it remains difficult to compare results among studies primarily due to differences in experimental designs (e.g. differences in sound pressure levels, frequency of exposure to airgun emissions and many other factors) (Bolte et al., 2012). Extrapolation of the effects of high-intensity acoustic sources to different species and seismic surveys must therefore be done with caution.

5.5. Experimental design of field studies

Compared to laboratory studies, field studies on the effects of seismic operations on marine organisms are more likely to measure natural responses at realistic sound exposures (Slabbekoorn, 2016). The simplest yet most scientifically robust way to determine if seismic operations are negatively affecting fisheries in an area is to conduct BACI (before/after, control/impact) or beyond-BACI sampling (Underwood, 1992). However, many field studies use less rigorous experimental designs, with many either lacking control sites so that potential seismic effects are confounded with unrelated temporal effects (La Bella et al., 1996; Christian et al., 2003; Andriquetto-Filho et al., 2005) or failing to include 'before' sites so that potential seismic effects cannot be separated from spatial environmental variability (Parry et al., 2002; DFOC, 2004). Even if controls are incorporated, without sound monitoring or modelling it is difficult to determine if a given control is appropriate (e.g. control zones in Harrington et al. (2010) were 3.5 km from seismic operations). Very few field studies concurrently monitor sound, thus restricting the ability to establish appropriate controls, identify potential thresholds and predict impacts in other regions with other seismic array configurations. These issues may reflect the opportunistic nature of *in situ* studies on the effects of seismic airguns on marine life, as such projects may develop in response to stakeholder concerns (e.g. Parry et al., 2002; Harrington et al., 2010), which often require quick planning and implementation, even after seismic operations have ceased. Improved communication between stakeholders, scientists, and industry will facilitate the design of robust experiments on marine seismic impacts.

5.6. Confounding effects and multiple stressors

The effects of multiple abiotic and biotic stressors and associated interactions must also be considered in any impact assessment of sound effects (Hawkins et al., 2015). To date there has been no research targeting potential interactions between low-frequency impulsive sound and other potential stressors, although this has been identified as a priority focus for future research (Nowacek et al., 2015). Single stressors related to sound exposure may show no effects in isolation

but when combined with other stressors (e.g. temperature, food competition) effects may become pronounced (Przeslawski et al., 2015). If such interactions are not considered, potential effects may be underestimated or overestimated based on whether the interaction is synergistic, additive, or antagonistic (Crain et al., 2008). Two concurrent but independent studies on scallops have suggested multiple stressors as a reason for differential responses to airguns: Day et al. (2016a) suggested that stress associated with dredging may have synergistically interacted with airgun exposure to depress haemocytes, while (Przeslawski et al., in press) showed that both high sea surface temperatures and a seismic survey preceded a scallop mortality event in 2010. Both studies speculated that seismic surveys may act as a tipping point at which other stressors may cause adverse effects on some marine invertebrates; future research using multifactorial experiments can test such a hypothesis.

One of the main confounding factors of interest is ship noise which is almost always concurrent with seismic airguns in real-world scenarios. Shipping noise can have significant effects on marine fish and invertebrates (Slabbekoorn et al., 2010; Hawkins and Popper, 2014), but it can be very difficult to separate such effects from those due to seismic airguns in field conditions. For example, interactions between seismic noise and shipping noise may affect fish response if fish avoidance behaviour is triggered by general shipping noise, thereby potentially ameliorating negative effects due to seismic airgun noise. Controlled field experiments offer a way for separating such effects by using single airguns able to be towed by small vessels with minimal ship noise (e.g. Day et al., 2016a, b).

6. Conclusions and recommendations

There is currently a disparity between results obtained in the field, in which biological responses can be difficult to detect in combination with natural environmental variability, and results obtained from the laboratory, in which exposure treatments or behavioural responses may be unrealistic. It is difficult to separate whether the lack of impacts from seismic sounds in field populations are true or simply a result of low power due to high variability and interactions with other environmental factors. Conversely, it is difficult to determine if most of the impacts of low-frequency sound observed in the laboratory may also apply to field populations.

Mitigation strategies may be developed to factor in biological information to minimise sound effects, such as conducting seismic surveys outside spawning periods. Similarly, changes to the sound source can minimise effects (Hawkins et al., 2015), but it is challenging to develop an effective mitigation strategy without accurately knowing the sound exposure threshold that results in a given response. Based on the current review, we recommend the following considerations for future research, interpretation of results, and development of mitigation strategies:

- The development and refinement of standards for quantifying sound exposure is crucial to allow comparisons among field and laboratory studies (Hawkins et al., 2015). Such standards are already being developed and followed by researchers, allowing sound exposure guidelines to be developed for fishes and sea turtles (Popper et al., 2014). Similar standards and guidelines related to marine invertebrates should not be long to follow and will further assist industry in compliance and monitoring.
- The physics of sound propagation must be taken into account in any seismic impact assessment, particularly when interpreting impacts based on experiments conducted in laboratory tanks.
- Particle motion should be considered in noise impacts studies on fish and invertebrates, particularly those species lacking a gas-filled bladder (all elasmobranchs and marine invertebrates). Threshold studies reporting only sound pressure may be of limited use for these species, as they do not detect the pressure component of sound.

- An integrated multidisciplinary approach to laboratory and field (both manipulative and *in situ*) studies is the most effective way to establish impact thresholds in the context of realistic exposure levels, and the limitations of each approach must be considered. In general, laboratory studies on the direct effect of acoustic waves on organisms offer much more experimental control than field studies, while field studies incorporate more realistic sound exposure and propagation scenarios, as well as associated behavioural responses (Slabbekoorn, 2016).
- Additional research examining the effects of masking by seismic airgun sources and the short and long-term intraspecific effects of seismic sounds on important biological processes such as reproduction, larval development, post-settlement survival and recruitment, and foraging and communication, is clearly needed to enable further refinement of sound exposure guidelines developed for fish (Popper et al., 2014) and the establishment of guidelines for invertebrates.
- Specific information on the impacts of seismic surveys on elasmobranch fishes are lacking and such studies are required to adequately address and advise on fishing industry concerns.
- Improved communication between stakeholders (to identify the need for the study), scientists (to appropriately design the study), and industry (to provide information about timing and location of seismic surveys) are crucial in order to appropriately, and cost-effectively, conduct rigorous *in situ* studies on the effects of marine seismic operations on fish and invertebrates. Research on the impacts of seismic surveys on marine organisms is of great interest to fisheries and petroleum industries, as well as marine managers.
- Scientists must make their data accessible and clearly communicate research results to these stakeholders, while also avoiding oversimplification and clearly identifying limitations and uncertainty associated with the methods or interpretations. Rather than negating the importance of such results, such an approach should foster a more collaborative relationship between regulators, scientists, fisheries, petroleum industry, and marine managers.

Our review has identified scientific evidence for high-intensity and low-frequency sound-induced physical trauma and other negative effects on some fish and invertebrates; however, the sound exposure scenarios in some cases are not realistic to those encountered by marine organisms during routine seismic operations. Indeed, there has been no evidence of reduced catch or abundance following seismic activities for invertebrates, and there is conflicting evidence for fish with catch observed to increase, decrease or remain the same. While catch or local abundance may be the most relevant responses for fisheries species, they provide no information about the underlying biological cause of catch rate reduction. Rather, studies on physical trauma, behavioural changes, or physiological indicators of stress provide a more mechanistic and valuable understanding of potential impacts. There remains a vast gap in our knowledge about sound thresholds and recovery from impact in most fish and almost all invertebrates. Without this information, generalisations about impacts among taxa, airgun arrays, and regions are not scientifically valid.

Author contribution

Conceived idea and scope: RP, AGC. Compiled literature and gap analysis: AGC, RP. Wrote the paper: AGC, RP, AD, M-EG, BB.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.marpolbul.2016.11.038>.

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