Attachment A – Publications supporting Geoscience Australia's answers to questions on notice to the Environment and Communications Reference Committee Inquiry on the impact of seismic testing on fisheries and the marine environment

An integrated approach to assessing marine seismic impacts: Lessons learnt from the Gippsland Marine Environmental Monitoring project

Rachel Przeslawski*, Brendan Brooke, Andrew G. Carroll, Melissa Fellows

National Earth and Marine Observation Branch, Geoscience Australia, GPO Box 378, Canberra, ACT, 2601, Australia

A B S T R A C T

Marine seismic surveys are a fundamental tool for geological research, including the exploration of offshore oil and gas resources, but the sound generated during these surveys represents a source of noise pollution in the marine environment. Recent evidence has shown that seismic surveys may negatively affect some cetaceans, fish and invertebrates, although the magnitude of these impacts remains uncertain. This paper applies a case study on marine seismic impacts (the Gippsland Marine Environmental Monitoring (GMEM) project) to the critical assessment of the advantages and challenges of field-based methods in the context of future research and management priorities. We found that an interdisciplinary approach, using both conventional (e.g. dredging) and innovative (e.g. autonomous imagery) experimental components, make for more robust interpretations and also provide a failsafe in case of limited suitable data (e.g. equipment issues related to image acquisition). Field observational studies provide an unparalleled capability to undertake ecologically realistic research, although their practical challenges must be considered during research planning. We also note the need for appropriate environmental baselines and accessible time-series data to account for spatiotemporal variability of environmental and biological parameters that may mask effects, as well as the need for a standardised technique in sound monitoring and equipment calibration to ensure accuracy and comparability among studies.

1. Introduction

Environmental impacts are changes to an aspect of the environment (physical, biological, chemical) caused by a stressor. In the context of marine management, environmental impacts can be quantified by measuring biological responses (e.g. changes in abundance or diversity) or surrogate physical parameters (e.g. chlorophyll-*a* for phytoplankton). The methods to quantify environmental impacts vary according to bioindicators (Cooper et al., 2009), criteria of impact significance (Liu et al., 2012), and consideration of cumulative effects (Jones, 2016). There has been increasing attention directed towards the potential impacts of ocean noise on marine fauna (Williams et al., 2015), with low-frequency acute sound from activities such as marine seismic surveys being of particular concern (Gordon et al., 2003; Nowacek et al., 2015; Wright and Cosentino, 2015; Hawkins and Popper, 2016; Carroll et al., 2017; McCauley et al., 2017).

Marine seismic surveys are a fundamental tool for research on the structure, composition and dynamics of the Earth's crust. These data help reveal the deep-Earth processes that drive plate tectonics and associated seismic (earthquakes/faulting) and volcanic (eruptions) activity. The same tools are also essential for the exploration of oil and gas

resources that occur in offshore sedimentary basins. In such surveys, an array of airguns release compressed air into the water column as a bubble, thereby generating low-frequency sound waves that propagate through the seafloor to the subsurface. Hydrophones and accelerometers towed behind a vessel measure the reflections of the sound, allowing the imaging of geological formations deep below the seafloor. These images can be interpreted by geologists to identify potential oil and gas reservoirs. Seismic surveys are undertaken in two configuration types: 2-D seismic surveys in which a single airgun array and streamer of hydrophones are used to generate 2-dimensional images of the subsea geology, and 3-D seismic surveys in which multiple (usually ≥ 10 or more) parallel hydrophone streamers allow the creation of a 3-dimensional model of the subsea geology. In addition to seismic surveys, vertical seismic profiling (VSP) is used down the borehole in offshore drilling to correlate the stratigraphy with seismic data.

Alternative techniques to acquire comparable marine geophysical data are in their infancy (e.g. Summerfield et al., 2005; Pramik et al., 2015), and the use of airguns remains the most effective way to identify potential offshore oil and gas resources (Gisiner, 2016). The international economic significance of the offshore petroleum industry will
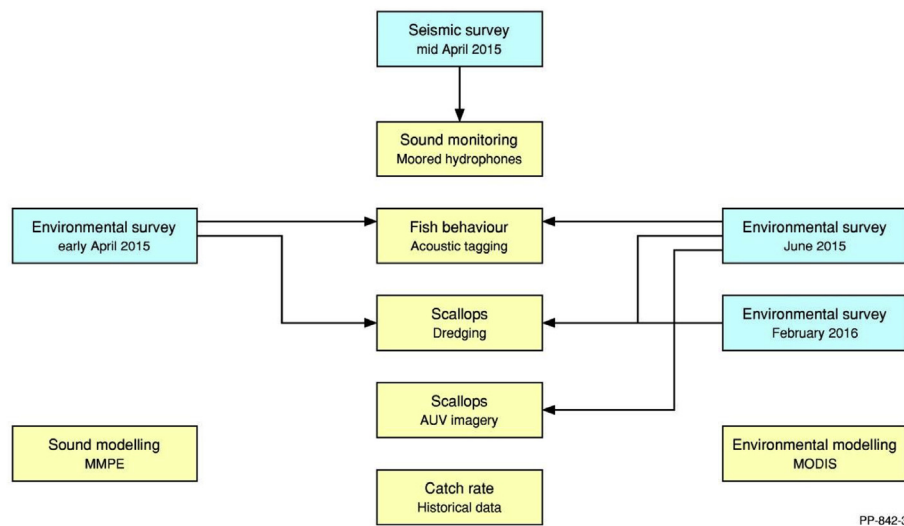

Fig. 1. Components of the Gippsland Marine Environmental Monitoring (GMEM) project, with field surveys (blue) connected to their respective experimental components (yellow). Large text describes the project component, and small text indicates the date (for surveys) or method (for experimental components). AUV = Autonomous Underwater Vehicle, MODIS = Moderate Resolution Imaging Spectroradiometer, MMPE = Monterey Miami Parabolic Equation. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

continue in the immediate future with oil demand still projected at over 103 million barrels per day in 2040 (IEA, 2016), until renewable energy sources are able to be adopted at a global scale (Kaivo-oja et al., 2016). Until such time as demand for petroleum resources is substantially diminished, or alternatives to seismic surveys are found, seismic surveys will remain a source of noise in the ocean. Consequently, there is a continued need to understand the environmental and biological impacts of sound sources on regions, habitats, and species. However, achieving this understanding is challenging, due to the technical issues associated with measuring the impacts of sound on organisms (e.g. lack of standards as reviewed in Carroll et al., 2017), as well as limited information on marine habitats and the distribution of species (e.g. National Marine Science Plan, 2015).

Once these impacts have been assessed, the next step is the translation of this assessment into effective policy and regulation, as well as the assurance that mitigation measures are indeed effective. Many countries have adapted legislation or advice incorporating precautionary principles to protect marine mammals from potential impacts of seismic surveys (e.g. *Statement of Canadian Practice with respect to the Mitigation of Seismic Sound in the Marine Environment* for Canada, *2013 Code for Minimising Acoustic Disturbance to Marine Mammals from Seismic Survey Operations* for New Zealand) and have a regulatory body in place to assess the risk of proposed activities (e.g. Bureau of Ocean Energy Management in United States, National Petroleum Safety and Environmental Management Authority in Australia). However, there are fewer legislative and regulatory directives that address potential impacts on other species. Australia is one exception to this, with proposed seismic surveys requiring an approved environment plan (EP) that includes a risk assessment of impacts and measures to reduce to a level deemed acceptable by the regulator. Importantly, the EP is not confined to marine mammals, but includes all species of stakeholder concern (e.g. commercial invertebrates and fish).

Investment in well-designed impact studies helps inform decisions around the regulation of seismic survey activities and mitigation strategies (e.g. Cato et al., 2013; Dunlop et al., 2016). Mitigation measures may include visual and acoustic observations, shutdown and low-power zones, soft-starts (i.e. ramp-ups), and avoidance of biologically important areas and times. However, many of these measures are only applied to a small group of animals, mirroring the legislative requirements underpinning them. For example, Australia's *Environmental Protection of Biodiversity and Conservation Act 1999* provides guidelines for seismic surveys to minimize impacts only on whales, excluding dolphins and porpoises. While elements of these, such as soft-starts, have been used to mitigate effects on marine vertebrates, there have been limited studies on the effectiveness of these procedures (Dunlop et al., 2016).

This paper applies a case study (the Gippsland Marine Environmental Monitoring (GMEM) project) to critically assess a multifaceted approach to investigate the potential impacts of marine seismic operations, particularly in the context of future research and management priorities for Australian marine resources. We do not intend to advocate the GMEM project as a global template; rather we use it as a case study to examine issues that should be universally considered in seismic impact studies. We focus on Australia due to the location of the case study, drawing on international examples where suitable. Similarly, this paper centres on the impacts on fish and invertebrates due to the target species of the case study, with some extensions to cetaceans when relevant to policy and management. The paper is divided into two main sections: a section devoted to the case study and its characteristics that can inform future studies, and a section focussing on application of the insights generated by such studies to marine environmental managers and policymakers.

2. Case study

The Gippsland Marine Environmental Monitoring (GMEM) project was developed in response to concerns from the fisheries industry about seismic survey activity in the Gippsland Basin (Bass Strait, Australia), as well as a broader need to acquire baseline data to quantify potential impacts of seismic operations on marine organisms. This project combined field and desktop studies (see yellow boxes in Fig. 1) in experimental (0–1 km from seismic survey lines) and control (≥10 km from seismic lines) zones to examine the potential impacts of a 2-D marine seismic survey in 2015 on fish and scallops, as well as environmental conditions associated with a known 2010 scallop mortality event in this region (Hall, 2010).

Results showed no evidence of consistent adverse effects on scallops, fish, or commercial catch rates due to the 2015 seismic survey. Specifically, commercial *(Pecten fumatus)* and doughboy *(Mimachlamys asperrima)* scallops from dredged samples and *in situ* images were found to have high variability in abundance and size among locations and time periods, but this was not linked to the seismic survey, nor was there observed scallop mortality attributable to the seismic survey (Przeslawski et al., 2018). Three fish species found in abundance (gummy shark *Mustelus antarcticus*, swell shark *Cephaloscylum laticeps*, tiger flathead *Neoplatycephalus richardsoni*) were acoustically tagged and released, with various tagged individuals returned sporadically over the monitoring period, including during the seismic survey operations. Behaviour consistent with a possible response to the seismic survey operations was restricted to flathead which increased their swimming speed during the seismic survey period and changed their

diel movement patterns after the survey. Fifteen commercially important species were analysed in a desktop study using Commonwealth fisheries logbook data. The catch rates in the six months following the seismic survey were significantly different than predicted in nine out of the 15 species examined, with six species (tiger flathead, goatfish, elephantfish, boarfish, broadnose shark and school shark) showing increases in catch following to the seismic survey, and three species (gummy shark, red gurnard, sawshark) showing reductions. Full details of the GMEM project methods and results can be found in Przeslawski et al. (2016). In this section, we use our experience with planning, implementing, and communicating the GMEM project to support particular aspects of this approach for inclusion in future studies on the potential impacts of marine seismic surveys.

2.1. Multiple experimental components

The GMEM project included multiple experimental components (Fig. 1), each of which represented a discrete study that contributed to the overall project aim of understanding seismic impacts on fish and invertebrates. The first advantage of a multi-component seismic impact project is that it provides an opportunity to concurrently identify impacts via BACI (before-after-control-impact, Smokorowski and Randall, 2017) or similar designs (e.g. Beyond BACI, Underwood, 1992), as well as the capacity to establish impact thresholds via sound monitoring and modelling. It is of limited use knowing there is an impact if the magnitude of the stressor cannot be determined, and this is particularly important in scenarios that don't use a commercial airgun array. The second advantage of having multiple integrated components for this type of scientific study is that several species with different habitats or biology can be targeted. Methods of impact assessment are often not transferable across species and habitats, thereby requiring separate experimental components. In the GMEM project, we used a commercial dredge and seafloor imagery to assess scallops due to their sedentary nature and concerns from fishermen about mortality. In contrast, reduced catch due to behavioural changes (e.g. displacement due to scaring effects) was the major concern related to demersal fish, and we therefore used acoustic tags to monitor fish movement during the seismic survey. Finally a multi-component study provides a failsafe if one of the other components is not successful. For example, we used two methods to assess impacts on scallops: an innovative use of autonomous underwater vehicle (AUV) to acquire seafloor imagery so that scallops could be assessed in situ, and a conventional sampling method using a commercial scallop dredge (Przeslawski et al., 2016). The AUV used on the first environmental survey did not obtain suitable images for analyses, and we therefore were unable to obtain data prior to the seismic survey for this component of the project. The dredging component, however, provided appropriate data from all environmental surveys, thereby supporting the experimental design.

A multi-component study requires a collaborative interdisciplinary approach. Understanding the effects of seismic surveys on marine organisms requires knowledge of physics, geology, and ecology (Fig. 2). Specifically, experts are needed in: acoustic measurements to understand how to accurately measure intense low-frequency sound; underwater sound physics to accurately model sound source and transmission; seabed composition to inform sound propagation modelling and habitat selection; marine biology to measure and interpret behavioural or physiological response; and statistics to identify significant impacts related to seismic airguns (Carroll et al., 2017). Within a given discipline, further expertise may also be required. For example, it is not enough to engage a marine biologist, and instead, a marine biologist with targeted knowledge relevant to the study objective is needed (e.g. specialist in fish behaviour, invertebrate larval development, cetacean hearing). Importantly, no single person or even group can meet all the required expertise, and interdisciplinary and cross-agency scientific collaboration is crucial. The GMEM project ultimately involved two government scientific agencies to manage the scallop and fish
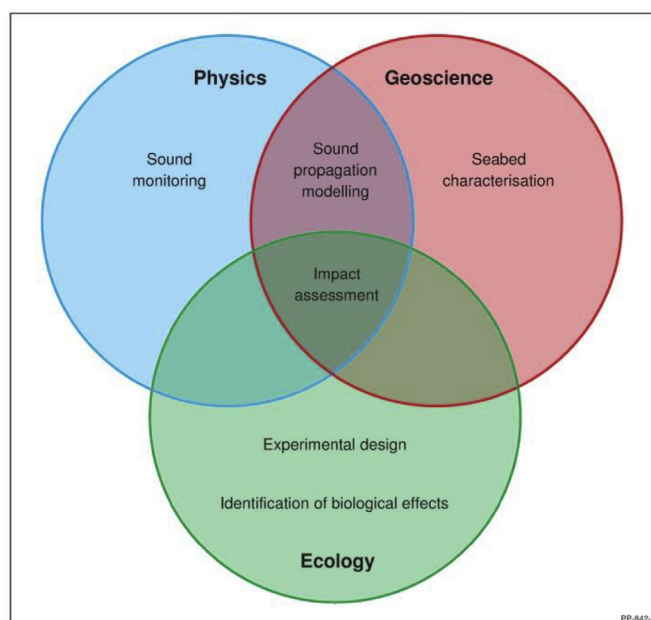

Fig. 2. Diagram showing discipline-specific tasks relevant to seismic impact research.

components of the project, a fishing company (to provide a suitable vessel and liaise with fishermen), two universities (to provide AUVs), and two private contractors (to monitor and model sound).

2.2. Ecological realism

One of the main strengths of the GMEM project was its ecological realism, specifically its use of an open water environment, a commercial air-gun array and in situ populations. In this way we were able to adopt appropriate survey conditions to provide insights into the likely responses of marine organisms to an actual marine seismic survey. By using the organisms' actual habitat, we observed natural responses to seismic airguns and avoided artefacts that can be introduced by aquaria or cages. Previous research on seismic impacts on scallops and fish has often been limited regarding application to real-world scenarios. The use of aquaria or cages can lead to misinterpretations of results, particularly as they relate to behaviour (Parvulescu, 1964; Gray et al., 2016; Rogers et al., 2016). Similarly, the responses of transplanted individuals may not reflect actual responses to seismic airguns owing to handling stress (Guderley et al., 2008) or local adaptation in which new environmental conditions are outside the optimal local conditions to which an organism has adapted (Sanford and Kelly, 2011). Even if appropriate controls are used to account for transplantation effects, the role of multiple stressors in which the effects of sound are exacerbated by other stressors cannot be discounted (Nowacek et al., 2013; Przeslawski et al., 2015).

Despite its benefits, the wholly field-based approach of the GMEM project was also the source of various challenges. As commonly occurs with field studies, inclement weather caused several days of planned fieldwork to be lost which reduced the amount of time available to collect data. Other challenges were more specific to the methods used to investigate seismic impacts. For example, the acoustic tagging component involved numerous sharks leaving the study area before the seismic survey even started, thereby precluding statistical tests on the effects of survey noise on these species' movement. In addition, the spatial variability of scallops and lack of associated distribution data meant that the first environmental survey was tasked with not only collecting appropriate baseline (i.e. 'before') data but also with identifying suitable study sites with scallop beds. Finally, and most broadly

applicable to future field studies on marine seismic impacts, there was uncertainty as to when the seismic survey would be passing overhead. This made sound monitoring observations difficult due to limited available recording time and also precluded plans to monitor scallops *in situ* during seismic operations. In light of the advantages and challenges associated with field-based studies on seismic impacts, we recommend adopting multiple experimental components as in the GMEM project. This provides built-in redundancy for any data loss due to the unpredictability of sound source location and timing, equipment malfunction, or inclement weather. These multiple experimental components should include either i) combined laboratory and field methods thereby incorporating the ecological realism of a field study with the controlled setting of the laboratory (Slabbekoorn, 2016) or ii) an airgun array and vessel under the jurisdiction of the research team to ensure control over the location and timing of airgun operations (e.g. the North West Shoals to Shore program, Australian Institute of Marine Science, www.aims.gov.au/nw-shoals-to-shore).

2.3. Innovative applications of technology

The GMEM project employed two methods rarely used to assess seismic impact, both of which allowed *in situ* observations to support ecological realism: acoustic telemetry and AUVs. Previous research on the impacts of marine seismic surveys on fish behaviour have relied on caged animals (see Carroll et al., 2017 for discussion of limitations), and few studies have employed acoustic technology to track animals in open water conditions (Wardle et al., 2001; Slotte et al., 2004). The reason for this may simply be related to logistics; it can be difficult to deploy acoustic receiver arrays and tag fish in a timeframe prior to a seismic survey that ensures animals stay within the study area. Indeed, 30–35% of the sharks tagged in the GMEM project left the acoustic receiver arrays within two days of release prior to the start of air-gun operations (Przeslawski et al., 2016). Nevertheless, the tagging yielded valuable information on the remaining individuals, as well as another species (flathead *Neoplatycephalus richardsoni*) that was also tagged but remained in the area. Overall, the use of acoustic telemetry, although challenging, allowed us to quantify natural responses to a marine seismic survey.

AUVs have been used in Australian waters to map and monitor seafloor habitats and animals in coastal and shelf environments (Barrett et al., 2010; Bridge et al., 2011; Smale et al., 2012; Ling et al., 2016). As related to the GMEM study, an AUV has previously been used to estimate size of epifaunal scallops (Singh et al., 2014), and it is fairly common to employ video to measure noise impacts on behaviour (e.g. Wardle et al., 2001; Filiciotto et al., 2014). The GMEM project was the first to use seafloor images acquired from an AUV to monitor *in situ* populations after a marine seismic survey. The acquired imagery provided important baseline environmental data at a fine-scale (centimetres) along the Gippsland Basin seafloor, and we were able to differentiate scallop species and also record abundance and distribution, while simultaneously characterising the physical environment. Nevertheless, the use of AUVs in the GMEM project was associated with some challenges. The limited time available during the planning phase of the project meant that appropriate equipment was not used during the first environmental survey, and images acquired before seismic operations were therefore unsuitable for analysis. To account for this, we added conventional dredging to the study, thereby providing a complementary dataset to assess scallop condition. Another issue was the inability to assess viability of partially buried animals on the images which meant that a large proportion of animals were classified as 'unknown'. Complementary dredging again resolved this issue and provided sufficient data on scallop viability (Przeslawski et al., 2018), thus highlighting the need to incorporate conventional contingency methods when employing new or technologically complex methods in seismic impact research. Notably, the rapid development of AUV technology means that its monitoring utility will continue to increase with improved image resolution, reduction in cost, and increased vehicle robustness (e.g. stronger propulsion systems).

2.4. Quantification of sound exposure

The GMEM project included field-based sound monitoring and sound propagation modelling (including both sound pressure and particle motion) so that results could be applied more generally to impact assessments. Without measuring or predicting the received sound exposure levels, our findings would only have been relevant for a single seismic survey. However, sound monitoring via the acoustic recording units may have suffered from error at low frequencies due to the fact that there is currently no standard for the calibration of hydrophones attached to a digital recording unit at low frequencies. Appropriate calibration of hydrophones is needed to obtain accurate measurements of sound, and this becomes particularly challenging at low frequencies where wavelengths are longer than available calibration tanks. In addition, the enclosure of hydrophones in acoustic recorders is now common but poses issues for calibration (Hayman et al., 2016). Sound propagation modelling was an alternative method to quantify sound, and indeed showed that sound exposure levels (SELs) more closely matching SELs from other commercial arrays (up to 170 dB re 1 μPa^2 s directly beneath and extending up to 250 m from the airgun array) (Przeslawski et al., 2016). This again highlights the importance of having multiple components in a project to provide a failsafe. Nevertheless, our engagement with two independent environmental contractors yielded different and incomparable sound metrics, requiring us to modify the scope of works during the project. The lack of industry standards for underwater sound measurements means that monitoring and modelling outputs can be difficult to compare among surveys.

2.5. Perceived bias

The perception of bias was a challenge that we addressed throughout the GMEM project. Perceived bias occurs when results from a scientific study are thought to be misrepresented, often due to an assumed conflict of interest related to funding in which scientists are encouraged to cater results and interpretations to a particular agenda (Slooten, 2011). Conflicts of interests are an issue for some studies (Wade et al., 2010), but even the perceptions of such bias can be damaging. For example one well-respected scientific journal has refused to publish papers based on any data from the Norwegian whale register due to perceived bias associated with the ethics of commercial whaling (Torrissen et al., 2012).

The key aspects to managing perceived bias are transparency and independence, and we implemented several actions related to these for the GMEM project. During the planning stages, we formed a Project Board that included members selected based on their knowledge and temperament, representing key stakeholders across diverse sectors (petroleum industry, fisheries, government, university) who were able to provide forthright but considered advice. During the implementation stage, we engaged qualified collaborators from independent sources (CSIRO, universities and private contractors). During the review process, we sought expert independent reviews from external experts. Finally, our data, analyses, and interpretations were publicly released (Przeslawski et al., 2016) and will be useful to both the fisheries and petroleum industries to increase their knowledge of the potential impacts of marine seismic surveys on commercially important species. Ultimately, the GMEM project made a concerted effort to contribute to public confidence in the scientific assessment of environmental impact by including the management of perceived bias from the planning stages through to data release (Richert et al., 2015).

3. Application to managers

To ensure the results of scientific research on seismic impacts are

applicable to marine managers and policymakers, it is important to i) identify useful metrics and species (during study design); ii) have the ability to generalise results among regions, species, or sound sources (during data analysis and interpretation); iii) manage perceptions of bias (see above); and iv) balance between restrictive regulations and loss of resource benefit (during management and policy decisions). This requires the involvement of an interdisciplinary team of scientists (Fig. 2), as well as industry and regulators, to frame scientific results and interpretations in a socioeconomic and legislative context and to identify the communication strategies to enable uptake (e.g. plain-English summaries).

An important consideration for managers of the marine environment and funders of marine research is to efficiently synthesise and harness existing information to inform decisions around acceptable levels of risk involved in marine resource use (National Marine Science Plan, 2015). Scientific literature reviews are one such way to do this (Carroll et al., 2017; Popper and Hawkins, 2018), as are information papers from regulators (e.g. NOPSEMA) and targeted scientific consortiums (e.g. Scientific Committee on Antarctic Research). Field-based seismic impact studies complement this approach by capturing both the complexity of the receiving environment across commonly encountered marine settings (e.g. inner to outer shelf; soft to bedrock seabed) as well as a wide range of ecological communities (e.g. coral reef to infaunal). These *in situ* studies can then be effective and efficient by measuring the response to a signal generated in an actual industry exploration survey that integrates the interaction of the seismic signal with the surrounding seabed environment and water column (depth, temperature, salinity, substrate, relief, slope, and ecosystem processes, Fig. 3). In this way, these environmental surveys capture the spatial variability in the influence of different marine environmental settings (e.g. deep, soft seabed; shallow, hard/rough) on the impact of the seismic signal on biota of interest (Duncan et al., 2013).

Marine environmental baselines are an important consideration in field-based impact assessments, particularly where there are significant spatiotemporal variations in environmental conditions. Variations in seabed type can occur over relatively fine spatial scales (Siwabessy et al., 2013) and should be assessed prior to a field survey. Significant spatiotemporal variability in oceanographic conditions (e.g. water temperature, turbidity, currents) occurs at various spatial scales due to natural fluctuations that occur seasonally or over cycles of several years (e.g. El Nino Southern Oscillation; Indian Ocean Dipole) (Foster et al., 2014). The identification of longer-term trends is also important in assessments of potential impact (e.g. shifts in species range due to changes in climate in Pecl et al., 2017).

The application of innovative technology in environmental impact

assessments can provide an alternative to conventional survey methods and may alleviate constraints that can impede scientific objectives (e.g. artefacts from caging experiments). For example, recent advancements in marine acoustic detection capabilities have made passive acoustic monitoring (PAM) an effective method to augment standard visual survey methods for the detection of whales (Cato et al., 2006; Soldevilla et al., 2014), particularly for beaked whales that are unsuited to visual detection due to time spent at depth, low profiles, and inconspicuous behaviour at the surface (Yack et al., 2013). In this instance, visual surveys may lead to misleading conclusions about the abundance and distribution of various beaked whale species, which translates to inaccurate information for policy makers and resource managers about conservation management (Yack et al., 2013). In contrast, PAM uses a fixed or towed hydrophone array to detect and track beaked whales and other acoustically active cetaceans (e.g. sperm whales Thode, 2004) throughout the water column. While the technique is inherently limited to animals that produce sound (e.g. not all cetaceans produce communication vocalisations or whistles, and the vocal activity of some whales is seasonally variable), PAM has become a fundamental tool, not only for researching the behaviour of whales, but for designing real-time mitigation protocols that may minimise the potential impacts of anthropogenic activities such as marine seismic surveys and ship-strikes on whales (Nowacek et al., 2013; Soldevilla et al., 2014).

Although alternative technologies to seismic surveys are being developed and trialled (Summerfield et al., 2005; Pramik et al., 2015), there is currently no feasible alternative to airgun-based systems (e.g. marine vibroseis in LGL and MAI, 2011). However, continued advances in airgun technology and seismic signal generation, acquisition and analysis methods could lead to a reduction in the lowest frequencies, number, line density and duration of seismic surveys, thereby reducing potential future impacts (Rassenfoss, 2016). Also, the further development of sound propagation models for the rapid prediction of the potential extent of biological impact (McCauley et al., 2016) may reduce excessive or insufficient restrictions of survey areas.

4. Conclusions & lessons learnt

In this paper we have summarised the lessons learnt from the GMEM project to provide recommendations for future research priorities and approaches, while still acknowledging the challenges associated with such field-based studies:

- Multiple experimental components make for more robust interpretations and also provide a failsafe in case of inability to acquire suitable data.
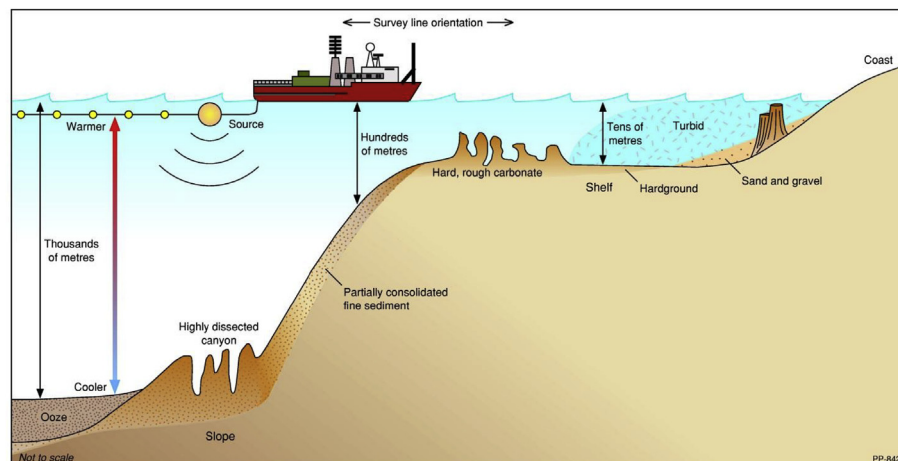

Fig. 3. Conceptual model showing some abiotic factors (depth, temperature, substrate, relief, slope) that can affect sound propagation and associated sound exposure levels.

- Some of these experimental components may include the innovative application of technology to help facilitate *in situ* observations; however, the limitations of such approaches must be considered. Coupling these approaches with conventional methods to investigate seismic impacts (e.g. direct sampling, lab-based behaviour studies) may provide useful complementary data.
- Without ecologically realistic studies (i.e. *in situ* observations, commercial seismic array), the translation of results to other environments, populations, and sound sources remains fraught with uncertainty.
- The challenges of field-based observational studies may be addressed by complementary laboratory or manipulative experimental studies.
- Spatiotemporal variability of field populations and environmental conditions may potentially mask any impacts. There is thus a need for appropriate environmental baselines and accessible time-series data (Lewis et al., 2017).
- 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), particularly as it relates to the calibration of hydrophones attached to autonomous recording devices. A standardised technique developed by an expert scientific community of practice will ensure that measurements are not only accurate but comparable among studies.

Results from research projects such as the GMEM can be used as a foundation for environmental assessments in which value is placed on a potential impact in relation to a proposed activity (Liu et al., 2012). Although there are several popular types of environmental assessment, including environmental impact assessments (Prideaux and Prideaux, 2016), cumulative effects assessments (Jones, 2016), and life cycle assessments (Woods et al., 2016), a unified approach such as that advocated in Tamis et al. (2016) may integrate fragmented frameworks to help managers and regulators standardise assessments among regions and jurisdictions. These ecological frameworks can then be combined with economic and social ones to usefully inform marine policy (de Jonge et al., 2012).

Acknowledgements

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Quantifying fish behaviour and commercial catch rates in relation to a marine seismic survey

Barry Bruce[a], Russ Bradford[a], Scott Foster[a], Kate Lee[b], Matt Lansdell[a], Scott Cooper[a], Rachel Przeslawski[c],*

[a] Commonwealth Scientific and Industrial Research Organisation (CSIRO), GPO Box 1538, Hobart, TAS, 7001, Australia
[b] Sydney Institute of Marine Science, 19 Chowder Bay Rd, Mosman, NSW, 2088, Australia
[c] National Earth and Marine Observations Branch, Geoscience Australia, GPO Box 378, Canberra, ACT, Australia

ABSTRACT

The impact of seismic surveys on the catchability of marine fish is a contentious issue, with some claims that seismic surveys may negatively affect catch rates. However little empirical evidence exists to quantify the impacts or identify the mechanisms of such impact. In this study, we used a 2-D seismic survey in the Gippsland Basin, Bass Strait, Australia in April 2015 as an opportunity to quantify fish behaviour (field-based) and commercial fisheries catch (desktop study) across the region before and after airgun operations. Three species found in abundance (gummy shark, swell shark, tiger flathead) were acoustically tagged and released within one of two acoustic arrays (experimental and control zone) and monitored before, during and after the seismic survey. In the field study, only 35% of the gummy sharks and 30% of the swell sharks were subsequently detected two days after release, suggesting movement outside the study area. Various tagged individuals returned sporadically over the monitoring period, including during the seismic survey operations. Behaviour consistent with a possible response to the seismic survey operations was observed for flathead which increased their swimming speed during the seismic survey period and changed their diel movement patterns after the survey. We also investigated the potential impacts of the seismic survey on catch rates using Commonwealth fisheries logbook data from Jan 2012–Oct 2015. Fifteen species and two gear types (Danish seine, gillnet) were modelled to examine differences in catch rates before and after the seismic survey. The catch rates in the six months following the seismic survey were significantly different than predicted in nine out of the 15 species examined, with six species (tiger flathead, goatfish, elephantfish, boarfish, broadnose shark and school shark) showing increases in catch following the seismic survey, and three species (gummy shark, red gurnard, and sawshark) showing reductions. With the exception of flathead movement, we found little evidence for consistent behavioural or catch rate changes induced by the seismic survey in the targeted species, although behavioural data were limited because many sharks left the acoustic receiver array prior to the commencement of the seismic survey.

1. Introduction

The impact of seismic surveys on the behaviour, distribution and catchability of fish has been a much debated issue both internationally as well as in Australian waters (Carroll et al., 2017), with claims from various commercial fisheries that seismic surveys have negatively affected catch rates (e.g. Hall, 2010; OceanCare, 2013). Despite the considerable interest in and potential impacts of seismic surveys on catch rates, there are few empirical field studies from which to determine the potential impacts of seismic operations on fish (Engås et al., 1996; Hassel et al., 2004; Løkkeborg et al., 2012). A change in catch rate may reflect a number of physical, behavioural, or physiological responses due to airgun operations, including mortality, sound avoidance, decreased bait attraction, or reduced fitness. However, there has been no direct association between these potential responses and a reduced catch rate following a seismic survey. Since there is no evidence of fish mortality and only limited evidence of a physiological response after airgun exposure despite several studies (reviewed by Carroll et al., 2017), any reductions in catch rates after a seismic survey seem most likely be due to behavioural changes.

Movement and displacement are two metrics that can be used to quantify behavioural responses to underwater noise. Movement can be defined as a change in behaviour that may be characterised by greater/lesser activity within a defined area. For example, a fish may move up
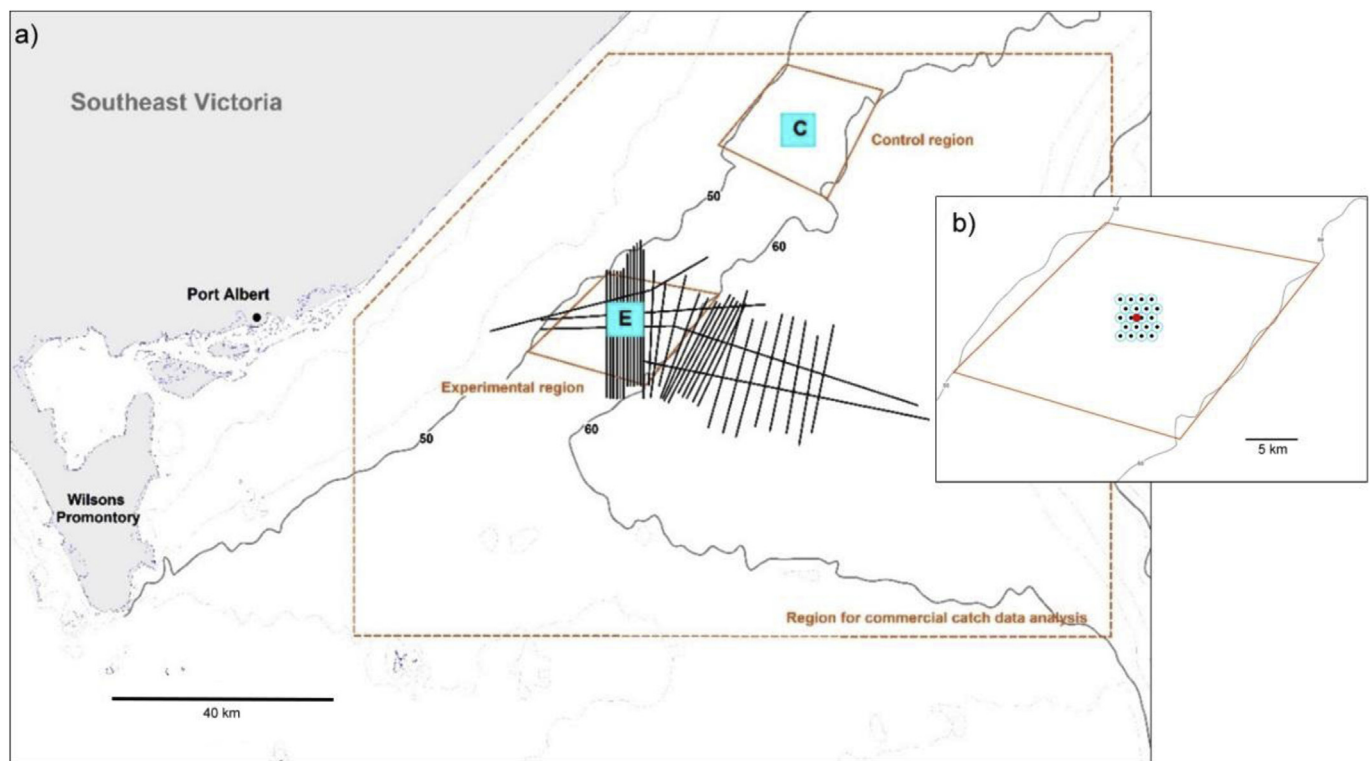
Fig. 1. Map of study area in the (a) Gippsland Basin with (b) inset showing detail of acoustic receiver arrays. Orange trapezoids mark areas where fish were collected for tagging. Blue squares mark acoustic receiver arrays (E = experimental array, C = control array). Orange dotted lines enclose the region over which commercial catch analyses were conducted. Black straight lines indicate seismic survey shot lines, while curved lines show 50, 60, and 200 m depth contours. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

or down in the water column in response to the sound wave from the seismic airgun discharge but remain in the same area (Chapman and Hawkins, 1969). Displacement, on the other hand, can be defined as a fish leaving or returning to an area exposed to airgun operations. Movement and displacement are not mutually exclusive. An increase in movement and displacement would be observed if a fish quickly departed (e.g. a flight response) the area exposed to airgun operations. A decrease in movement and displacement could occur if a fish rested on the seafloor after exposure to airgun operations.

Several previous studies have examined the impact of seismic airgun discharge on the behaviour and sensory capabilities of caged fish. These experiments have produced mixed results ranging from significant epithelial damage within auditory systems (McCauley et al., 2003), to a startle response (Boeger et al., 2006), to no observed damage or behavioural response (Peña et al., 2013). However, interpretations based on behavioural studies of caged animals are challenging because several factors may confound results (e.g. stress, inability to move away from source, realistic sound exposure), and it remains unknown how such effects may influence catch of commercial fishers.

There are very few field studies examining the direct effects of seismic airgun discharge on unrestrained fish, particularly elasmobranchs. Sonar has been successfully used to identify movement of pelagic fish schools during seismic surveys, in which no changes in abundance were attributed to airgun operations (Slotte et al., 2004; Peña et al., 2013). Visual assessments using video or diving observations have also been used to observe startle reflexes (Wardle et al., 2001) and abundance (Miller and Cripps 2013) of reef fish during seismic surveys. Acoustic telemetry has been used in relation to seismic impacts, with no evidence of sound avoidance by fish (Pickett et al., 1994; Wardle et al., 2001; Evans et al., 2017).

In contrast to active observation of behavioural responses, an analysis of catch rates can be used to indirectly identify potential effects of seismic surveys on unrestrained fish. For example, Skalski et al. (1992)

and Engås et al. (1996) found significant reductions in catch rates following a seismic survey. However, the effect of the seismic survey may be gear-specific (Løkkeborg et al., 2012) or an artefact due to decreased responsiveness to baited hooks (Skalski et al., 1992). Other studies have found increases or no changes in catch rates of commercial species after a seismic survey (La Bella et al., 1996; Christian et al., 2003; Andriguetto-Filho et al., 2005; Parry and Gason, 2006; Løkkeborg et al., 2012). Most catch rate analyses are based on field studies, but a few attempts have been made to compare fisheries logbook data to historical seismic data (Parry and Gason, 2006; Thomson et al., 2014). These attempts met with limited success due to the lack of data on precise timing and location of seismic operations. Rather than focussing on multiple seismic surveys over a large area, Thomson et al. (2014) recommended that future desktop studies should focus on a single seismic survey. In Australia, there have been no peer-reviewed publications documenting the effects of seismic surveys on fish behaviour or commercial catch rates capturing data from before, during and after the survey (Carroll et al., 2017).

In this study, we used a seismic survey of the Gippsland Basin in 2015 in which the seismic survey timing and line locations were known in advance, and navigation data from the vessel were made available. This provided an opportunity to quantify fish behaviour and commercial fisheries catch rates across the region before and after the survey in order to test for potential impacts. We hypothesized that such impacts may manifest as i) changes in displacement (distance moved within the area monitored, in this case, by the acoustic arrays), the extreme of which would be complete departure from the monitored area, ii) changes in movement as measured by accelerometer sensors, and iii) changes in commercial catch rates. We tested these hypotheses using both a field study (fish behaviour analysis) and a desktop study (catch rate analysis). Our findings will help disentangle potential impacts from normal variability and provide for better informed debate and policy development.

Table 1
Model selection table of compound Poisson GLMMs (CPG) for displacement of swell sharks. The unique fish identity code was used as the random effect and the model was fitted with a log-link function using a Tweedie distribution.

Model	df	AICc	ΔAICc	Model weight
null	3	214.92	0.00	0.41
hour	4	215.83	0.91	0.26
region	4	217.78	2.86	0.10
temperature	4	217.93	3.01	0.09
temperature + hour	5	218.80	3.87	0.06
region + hour	5	219.22	4.30	0.05
region + temperature	5	221.16	6.24	0.02
region + temperature + hour	6	222.44	7.52	0.01

2. Methods

2.1. Seismic survey

In April 2015, a 2-D marine seismic survey was undertaken over part of the western Gippsland Basin as part of the Australian Government's National CO_2 Infrastructure Program investigating targeted offshore basins as potential CO_2 geosequestration sites (Langford et al., 2016). The *M.V. Duke* was used to tow a single 2530 cubic inch airgun array (BOLT Long Life Array), comprised of 16 airguns towed at 6 ± 1 m depth. The array was operated at a working pressure of 2000 psi, with a lower acceptable limit of 1800 psi. The locations of seismic lines are shown in Fig. 1, and the seismic acquisition times can be found in Table 1 of Przeslawski et al. (2016b). Vessel location and time for each airgun shot were provided by Gardline data from the log of the *M.V. Duke* and amounted to 50972 shot points recorded from 9 April 2015 23:44:15 (GMT) to 18 April 2015 22:27:09 (GMT).

Four autonomous recording units (ARUs, Song Meter SM2M + Marine Recorders) were moored to the seabed (≥ 35 m below the surface) before the seismic survey and collected afterwards, thus measuring benthic sound exposure before, during and after airgun operations. The highest measured sound exposure level (SEL) was 146 dB re 1 μPa^2s at 51 m depth when the airguns were operating 1.4 km away, and sound propagation modelling estimated maximum SEL received one metre above the seafloor with airguns directly overhead to be 170 dB re 1 μPa^2s, extending 200–250 m from the ARU depending on sound directionality and water depth (Przeslawski et al., 2016a). SELs measured from similar environments (thin sand over limestone) from a larger airgun array (3090 cui) at 100–200 m water depth have been shown to be 165 dB re 1 μPa^2s at a distance of 1 km from the sound source (McCauley et al., 2016). We refer the reader to (Przeslawski et al., 2018) for a discussion of the challenges regarding monitoring of low-frequency sound and to (Wenz, 1962) for comparative sound levels of underwater sound sources.

In addition, the highest modelled peak particle velocity of sound was 171 dB re 1 nm/s at 40 Hz and 166.7 dB re 1 nm/s at 80 Hz, both values at 100 m from the sound source (Przeslawski et al., 2016a). Since elasmobranchs and invertebrates are sensitive only to particle motion, this aspect of sound is most applicable to impact assessments on these taxa (Hawkins and Popper, 2016).

2.2. Study area

The study area was defined by the planned location of the seismic survey, located in the Gippsland Basin region of eastern Bass Strait, Australia (Fig. 1). The highest density of survey lines (at 600 m intervals) defined the experimental (E) zone for the fish behaviour component of this study. The control (C) zone was chosen to be more than 10 km from airgun operations, based on a compromise between previous Bass Strait studies (control zone < 4 km away in Harrington et al., 2010), (20 km away in Parry et al., 2002), logistics (survey

duration precluded a further zone), and underwater sound modelling (Przeslawski et al., 2016a). Control and experimental zones (Fig. 1) were in 50–60 m water depth.

The commercial catch analysis was restricted to fishing operations within an area of 13,000 km^2, extending to distances of approximately 50 km from the geographical mid-point of the survey area and encompassing both the experimental and control acoustic receiver arrays (Fig. 1). We used the conclusion by Kenchington (2000) that effects on commercial catch rates from seismic surveys may extend to distances of up to 50 km as a guide in setting this area for catch analyses.

2.3. Study species

Due to concerns from stakeholders regarding the potential impacts of seismic surveys on fisheries, this study focused on commercial species, including tiger flathead (*Neoplatycephalus richardsoni*), gummy shark (*Mustelus antarcticus*), and several other species included in the catch analysis for which there were sufficient data (Table 5). For the field study, we also included the swellshark (*Cephaloscyllium laticeps*), a potential surrogate with similar habitat and life history to tagged species of commercial interest (gummy shark, tiger flathead). All three species collected and tagged for behavioural analysis are demersal.

The gummy shark is distributed throughout the temperate waters of Australia in depths from nearshore to approximately 80 m and is capable of long-distance migrations throughout this region (Last and Stevens, 2009). This species forms the major component of the Southern and Eastern Scalefish and Shark Fishery (SESSF) and is currently managed under an individual transferable quota system (Daley et al., 2002). The swell shark is distributed throughout southern Australian waters in depths from nearshore to approximately 650 m (Gomon et al., 1994). Tagging studies have indicated that this species does not move large distances, but instead remains in the area where they were tagged (Last and Stevens, 2009). This species has little commercial value but are a common bycatch species of the SESSF and southern rock lobster fishery (Daley et al., 2002; Last and Stevens, 2009). The tiger flathead is distributed throughout southeastern Australian waters in depths 10–400 m. There are no tagging studies to indicate the degree to which tiger flathead are capable of migrating; however, there is evidence that mature fish migrate to shallower waters prior to spawning (AFMA, 2016). The tiger flathead is an important commercial species throughout its range.

2.4. Fish behaviour

2.4.1. Acoustic receiver arrays

Acoustic receivers (VR2W and VR2AR, Vemco-Amirix), tuned to detect frequencies of 69 kHz, were deployed in an array configuration within the experimental and control zones and used to detect tagged animals. Each array comprised 20 acoustic receivers arranged in five rows of four receivers each, spaced at 1000 m intervals (Fig. 1b). Every second row was offset by 500 m, providing acoustic receiver coverage of an approximate 20 km^2 area of seafloor, assuming a nominal receiver detection range of 500 m. Two types of acoustic receivers (30 × VR2W and 10 × VR2AR) were deployed on three mooring styles. The receiver type determined the style of mooring used in each case (Supplementary Material A). The VR2AR acoustic receivers recorded temperature at hourly intervals; the sensor data were combined to calculate an overall average daily water temperature for both the Control and Experimental arrays.

2.4.2. Fish capture and tagging

Fish were collected in the experimental and control zones primarily with a bottom-set, baited longline, with opportunistic rod and reel fishing as weather and time permitted. The bottom-set longline consisted of 350–450 circle hooks (either 6-O or 8-O) attached via 1.5 m nylon snoods to an approximate 2500 m, weighted, main line that was

anchored at both ends. Long-line sets were deployed either at dusk or pre-dawn with soak times of approximately 2–3 h. Bait used was chopped mackerel (*Trachurus* sp.). Rod and reel fishing was conducted throughout the day and night as conditions and other workload permitted. Upon landing, all fish were carefully de-hooked; fish deemed unsuitable for tagging (unwanted species or those that were injured or showed a lack of vigour) were immediately returned to the water. Fish suitable for tagging were transferred to holding tanks (approximately 1000 L each) with flow-through seawater. Tanks were covered with heavy netting to prevent loss of fish during vessel movement. Fish were observed in the holding tanks and assessed for post-capture vigour. Any fish showing additional signs of distress or injury during the holding period were also released.

Upon arrival to the acoustic array, each fish was weighed and measured. Tagging followed the protocols outlined in Bradford et al. (2009), with each fish getting an internal acoustic tag incorporating an accelerometer sensor (Vemco V13A or V9A, depending on fish size) and external plastic streamer (Hallprint) tag. Fish were released in a central location over each acoustic array to maximise the probability of detection and residency in each monitored area.

In total, 87 fish were tagged and released between 30th March and 1st April 2015, comprising 33 gummy sharks (20 in the Experimental (E) array; 12 in the Control (C) array), 43 swell sharks (24 E; 19 C), and 11 tiger flathead (all E) (Supplementary Material B). Due to the low numbers of flathead collected, all were released into the experimental array precluding our ability to compare behavioural changes between a control and experimental site. However, we were able to quantify flathead movement and activity responses within the experimental array before, during, and after the seismic survey.

2.4.3. Quantification of fish behaviour

Acoustic telemetry data was used to examine whether tagged fish responded to the seismic survey by estimating displacement (the distance (metres) travelled 'between' receivers within each of the arrays) and movement (speed of movement in metres/second^2, determined by the accelerometer data). Data for the first two days after release were excluded to allow for a recovery period after the release of tagged fish.

For displacement, a centre of activity (COA) was estimated for each fish following the methods of Simpendorfer et al. (2002), and the resulting set of estimated positions used as input for analysis. The COA is a weighted average of a fish's position over a time interval (Δt) based on the locations of all receivers that detected it, and weighted by the number of detections registered by each receiver. An appropriate time interval (Δt) is chosen that ensures fish are detected on multiple receivers without allowing the fish to move too much (Simpendorfer et al., 2002). To determine the appropriate Δt, we tested six different values of Δt for each species: 10, 20, 30, 60, 90 and 120 min. Values of greater than 120 min were not tested as movement of fish was likely to be too great to provide meaningful position estimates. For each Δt, we calculated the mean number of receivers that detected each tag (NR) and the mean number of detections across all receivers for each tag (ND). Data from both acoustic arrays (Experimental and Control) were included in the analysis. The most suitable Δt was identified as being when the increase in NRs was ≤10% between two consecutive values of Δt and the NDs were > 10 (Villegas-Ríos et al., 2017). The most suitable Δts were 90 min for tiger flathead (NR = 1.1 ± 0.03, ND = 12.1 ± 2.3 [mean ± SE]) and 120 min for the gummy and swell sharks (gummy: NR = 1.8 ± 0.1, ND = 10.4 ± 1.1 [mean ± SE]); swell: NR = 1.7 ± 0.1, ND = 10.6 ± 1.0).

Displacement was then measured as the distance between COAs for each fish, over each consecutive Δt that it was detected. This was modelled against: 1) hour of the day, to determine any diel patterns, 2) average daily water temperature (as recorded by VR2AR receivers and averaged across each array), 3) zone (Experimental or Control) if sufficient data were available, 4) period (before, during or after the seismic survey) if sufficient data were available, and 5) a period-hour

interaction to test for changes in diel displacement due to the seismic survey. Data were modelled using linear mixed effects models (LMMs). If the data contained a high number of zeros and the residuals were not normally distributed, a Compound Poisson Generalised (CPG) LMM with a Tweedie distribution (Foster and Bravington, 2013; Qian et al., 2016) and a log-link function was applied. LMMs were performed using the *lmer* function in the *lme4* R package, and CPG LMMs were modelled using the *cpglmm* function from the *cplm* R package (Zhang, 2013). The tag code for each fish was used as a random effect for all the models. Correlation between variables was checked prior to modelling using the Pearson correlation coefficient. Correlated variables were not used in the same model structure.

Movement was measured using the accelerometer values transmitted by each tagged fish. One tagged fish died as a result of an observed seal predation event on release and the tag remained on the bottom within the range of one of the receivers for 81 days. This provided an opportunistic 'sentinel tag' that was used to provide a base-line measure for accelerometer data provided by a stationary tag. The median accelerometer value for this tag (0.057 m s^{-2}) was subtracted from all accelerometer data to standardise stationary readings to zero.

The movement of each fish was modelled using the same model structures as displacement. Fish movement was also modelled against distance to the seismic shot to determine if behaviour was impacted differently during survey periods when the vessel was operating close to the experimental area. As exact fish location at any point in time is unknown, distance to the seismic shot was measured between the calculated COA of each fish and the vessel location at the time of each shot. Hour and date were chosen to account for any diel changes in movement over the period of the study. Since only a few tag detections and seismic shots occurred at essentially the same time (i.e. within a second of each other), we combined the number of fish detections and seismic shots over different time periods so the two data sets could be compared. Four different time intervals (5, 10, 15 and 20 s) were tested to see which interval produced a large enough number of fish detections, while maintaining the temporal resolution of the seismic shots (i.e. median number of shots per time interval = 1). Ten seconds was chosen as it substantially increased the number of tag detections compared to a 5 s interval (5 s = 2366; 10 s = 3553).

Flathead movement combines numerous periods of inactivity (movement = zero) with periods of active swimming. Data were further investigated via a binomial generalised linear mixed model (GLMM) to examine if the number of active 'swims' and their magnitude (based on the accelerometer values) differed before, during and after the seismic survey.

Prior to modelling for both series of analyses (i.e. *Displacement* and *Movement*), data were examined to identify patterns and outliers using Cleveland dot plots, boxplots, and scatterplots of residuals. The most parsimonious model structure was found following a step-down protocol (Zuur et al., 2009). Support for each model was measured using the differences in Akaike Information Criterion with a correction for small sample size (AICc). Models were compared using delta AICc (ΔAIC) where in the 'best' model tested ΔAIC equals zero and ΔAICc of less than ten show models with reasonable support (Burnham and Anderson, 2002). If ΔAICc showed support for more than one model, model averaging across normalised Akaike's weights was conducted using the *MuMIn* R package (Barton, 2012).

2.5. Catch rate

Fisheries catch data (kg whole weight) were extracted from the Australian Fisheries Management Authority (AFMA) Commonwealth logbook database for two gear types (Danish seine and gill-net). Choice of gear type for analyses required that there be a minimum of 400 operations (shots) available after the seismic survey period, with similar spatial distribution of these operations to a period before the seismic survey; only Danish seine and gill-net gear types met these

requirements (Supplementary Material C). Analyses were further restricted to those species that made up more than 5% of total catch biomass in 'before' fishing operations. Catch per unit effort (CPUE) was calculated as 'per operation' for Danish seine and 'per 1000 m net-length' for gill-net. For each gear type and fishing operation, the key variables in the analysis were: 1) catch biomass for each species/species-group (herein referred to as 'species'), 2) the amount of effort (e.g. hours trawled; length of net, number of fishing operations), 3) the date, and 4) the vessel. Analyses compared the catch rates within each gear type before and after the seismic survey (Jan 2012–Oct 2015), incorporating data from three years previous to the seismic survey to take into account seasonal and interannual variation and six months after to examine potential impacts. Danish seine had a lower spatial coverage of fishing data compared to gillnet (Supplementary Material), but there were sufficient data to assess regional fluctuations in catch as would be detected with regional displacement due to seismic operations. Very few fishing operations were recorded during the seismic survey period (9–18 April), and these were removed from the analysis.

A Generalised Additive Model (GAM) was used to determine if the observed catch rates varied before and after the seismic survey for each gear type. Date, the day of the year (1–365), and period (before or after the seismic survey) were used as the explanatory variables.

The model is defined as follows: Let the catch in the *ith* trawl be denoted by y_i. It is taken at time t_i (specified by date and time), which is partway through a calendar year whose fraction is denoted by d_i. The shot is undertaken by a known vessel applying a known effort (e.g. net-length in the case of a gill-net vessel). For convenience (and completeness) the vessel information is arranged into a vector z_i whose elements indicate the vessel for the *ith* shot. Finally, we let s_i be 1 if the shot was performed prior to the seismic survey and 0 otherwise. The GAM is specified as:

$$\log(E(y_i)) = \alpha + \beta s_i + f_1(t_i) + f_2(d_i) + z_i^T b + \log(\eta_i)$$

where β is the enduring effect of the survey, $f_1(\ )$ is a smooth long-term trend of catch rates (i.e. are catches of a particular species increasing/decreasing in general over time), $f_2(\ )$ is a seasonal smooth (how much do catch rates go up and down during the course of a year), b is a random vessel effect to adjust for boats' varying in their ability to catch a given species, and $\log(\eta_i)$ is an offset term that standardises catches for different amounts of effort. The model is finished with distributional assumptions: the distribution of the data, around $E(y_i)$, is described by a Tweedie distribution and the random vessel effects are assumed to be normally distributed with zero mean and variance to be estimated from the data.

The model was fitted separately to each of the species and gear types using the *gam* function in the *mgcv* R package (Wood, 2006). To determine if the catch rate increased or decreased after the survey, the expected catch was predicted from each of the GAM models using the predict function in the *mgcv* R package. Estimates of model parameters were converted to multiplicative effects on the biomass scale from additive on the log-scale. This resulted in a multiplicative factor whereby values of less than one infer a lower catch than expected (and hence an inferred reduction in catch) after the seismic survey, whilst those greater than one inferred an increase in catch for a particular species after the seismic survey.

3. Results

3.1. Fish behaviour

3.1.1. Detection

All tags were detected in their respective arrays immediately after release, however, only 11 (35%) of the gummy sharks and 13 (30%) of the swell sharks were subsequently detected after the first two days (Fig. 2a and b). This was probably due to movement out of the

monitored area after tagging rather than post-release mortality; two tagged gummy sharks and one tagged swell shark were recaptured by commercial fishers after the completion of this study. Various individuals returned sporadically over the period of monitoring including during the seismic survey operations (Fig. 2a and b). The movement of tagged sharks out of the monitored area provided limited data from which to assess their behavioural characteristics in response to the seismic survey. In contrast to the sharks, nine tiger flathead (81%) were detected in the experimental array for extended periods after release (Fig. 2c). Eight of these were detected during the seismic survey, of which four were present during the entire seismic survey and four ceased detection during the seismic survey (Fig. 2c).

3.1.2. Displacement

For swell sharks, no tagged individuals were detected in the experimental array during the seismic survey period (Fig. 2b), which removes any ability for quantitative analysis. Instead, displacement was modelled against zone, hour of the day and water temperature. There were eight candidate models produced in the model selection (Table 1); however, none of the variables provided evidence of importance. Hour was the best predictor variable with a relative importance of 0.38, while temperature and region were included in fewer of the models (relative importance: 0.18 and 0.17 respectively) (Supplementary Material D). The distance the swell sharks moved decreased at higher water temperature (log-scale estimate = −0.23), and sharks tagged in the experimental array travelled smaller distances than those in the control array (log-scale estimate: Control = 7.45, Experimental = 6.95). Swell sharks moved larger distances during the night and early morning (Supplementary Material E). For gummy sharks, displacement was unable to be modelled due to insufficient data. Similarly, tiger flathead showed only a few displacement events registered at the scale of the receiver deployments which precluded meaningful analyses (Supplementary Material E).

3.1.3. Movement

For shark movement, there were sufficient data to model movement only against hour and temperature, not zone (experimental, control) or period (before, during, after seismic survey). There were four candidate models for gummy sharks and two models for swell sharks (Table 2). For gummy sharks, average daily temperature was the most important variable with a relative importance of 0.94. Hour of the day was a poor predictor with only a relative importance of 0.27, although gummy sharks tended to be more active at night (Fig. 3a). For swell sharks, hour was the best predictor variable (relative importance: 1.00), whereas temperature was a poor predictor (0.29). Swell sharks were slightly more active in the afternoon to early evening (Fig. 3b).

For flathead movement, two candidate models were produced (Table 3). Temperature, hour and period all had a relative importance of 1.00, and the period-hour interaction had an importance of 0.78. However, the differences between the periods were minimal (estimates: before = 0.532, during = 0.534 and after = 0.544 m s^{-2}); this was likely influenced by the dominance of records where flathead showed no movement (Supplementary Material E). To account for this, we analysed the number of times that flathead moved and the magnitude (speed) of this movement during each period.

A binomial GLMM of flathead movement vs no movement resulted in two candidate models (Table 4). Temperature and hour-period interaction provided the best model indicating that the times of day during which flathead moved the most differed between periods (before, during and after the seismic survey) and were influenced by temperature. The influence of temperature, however, was not linked to the period indicating that temperature variability was consistent over all time periods and did not overly influence movement in any one period.

Flathead showed a bimodal pattern of diel movement before and during the survey, although there were differences in their timing. Peak
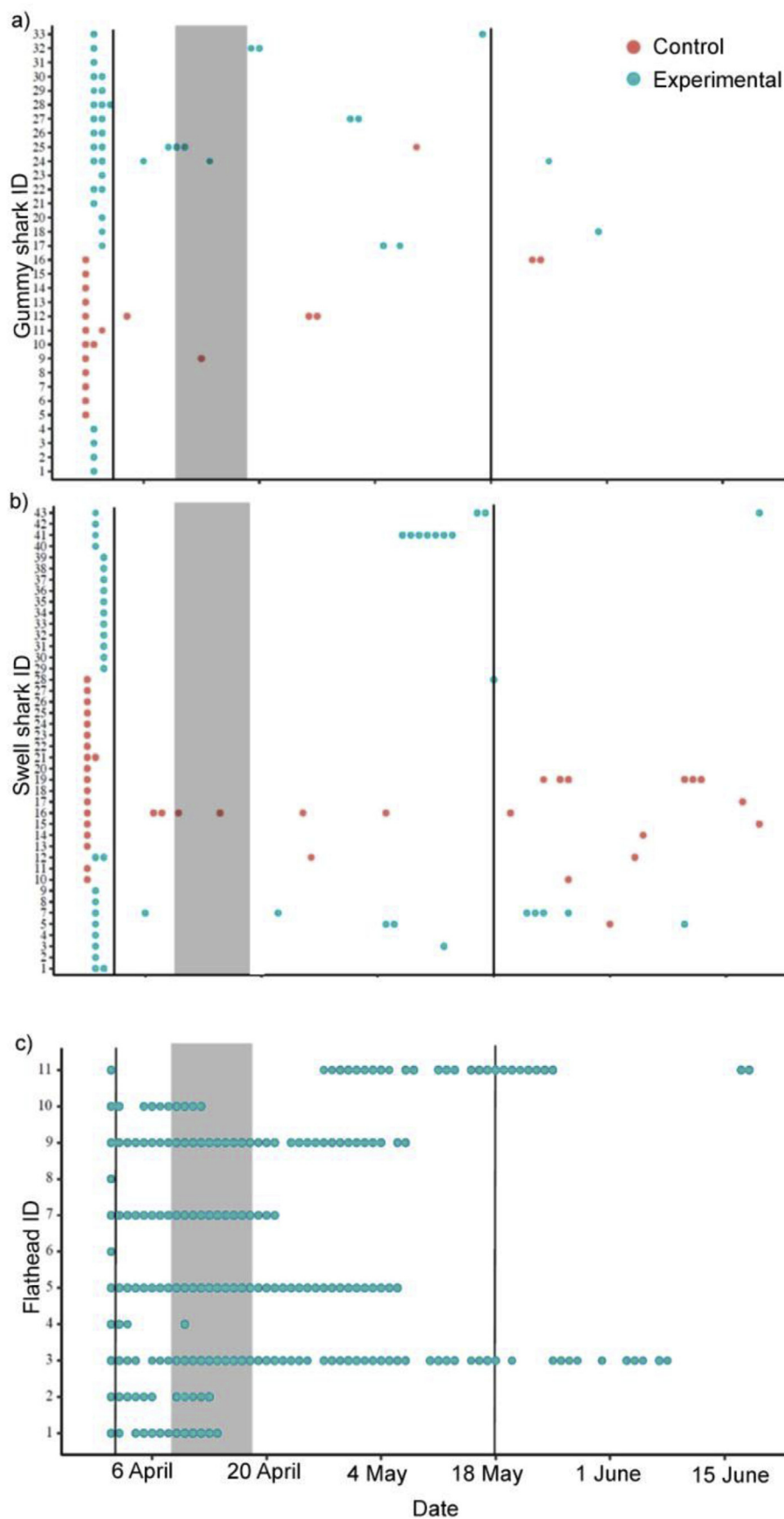
Fig. 2. Daily presence of tagged a) gummy sharks, b) swell sharks and c) flathead across the study period in both the Control (orange dots) and Experimental (blue dots) acoustic receiver arrays. The grey shaded area denotes the seismic survey period. Vertical bars define the period over which tag data were considered for fish behavioural analyses being from two days post-release to one month (18 May 2015) after the end of the seismic survey (see text for details). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Table 2
Model selection table of compound Poisson GLMMs for movement of a) gummy sharks and b) swell sharks. The unique fish identity code was used as the random effect and the model was fitted with a log-link function using a Tweedie distribution.

	Model	df	AICc	ΔAICc	Model weight
a)	null	3	35.41	5.46	0.04
	hour	4	37.29	7.34	0.02
	temperature	4	29.95	0	0.69
	temperature + hour	5	31.99	2.04	0.25
b)	null	3	214.92	0.00	0.41
	hour	4	215.83	0.91	0.26
	region	4	217.78	2.86	0.10
	temperature	4	217.93	3.01	0.09
	temperature + hour	5	218.80	3.87	0.06
	region + hour	5	219.22	4.30	0.05
	region + temperature	5	221.16	6.24	0.02
	region + temperature + hour	6	222.44	7.52	0.01

Table 3
Model selection table of LMMs for movement of tiger flathead. The unique fish identity code was used as the random effect.

Model	df	AICc	ΔAICc	Model weight
temperature + period × hour	9	11384.43	0	0.78
temperature + hour + period	7	11386.97	2.54	0.22

Table 4
Binomial GLMM model selection table for a) movement and no movement and b) movement speed of tiger flathead.

	Model	df	AICc	ΔAICc	Model weight
a)	temperature + period × hour	8	27069.04	0	0.97
	temperature + hour + period	6	27076.26	7.21	0.03
b)	temperature + hour + period	7	−6832.1	0	0.33
	temperature + hour × period	9	−6831.77	0.34	0.28
	hour + period	6	−6831.49	0.61	0.24
	hour × period	8	−6830.45	1.65	0.14

movement periods before the survey were at approximately 0800 and 1700–1800. During the survey, flathead movement peaked in frequency from 1000 to 1300 and again at 1800–1900 with a minor peak at 0100. After the survey, movement was more evenly distributed during a 24 h cycle (Fig. 4). Overall, flathead moved more frequently after the survey than before or during it (log-scaled estimates: before = −9.78, during = −9.57 and after = −9.36) (Supplementary Material E).

The GLMM of flathead movement speed produced four candidate models (Table 4b). Hour and period were the most important predictors of speed (relative importance = 1.00). The importance of temperature and the period-hour interaction were 0.61 and 0.42, respectively. However, temperature variation showed no pattern between periods, primarily being within the range of 16.75–17.75 °C with occasional drops to 15.50 °C. This indicated that although temperature influenced flathead movement, the effect of temperature was similar across regions
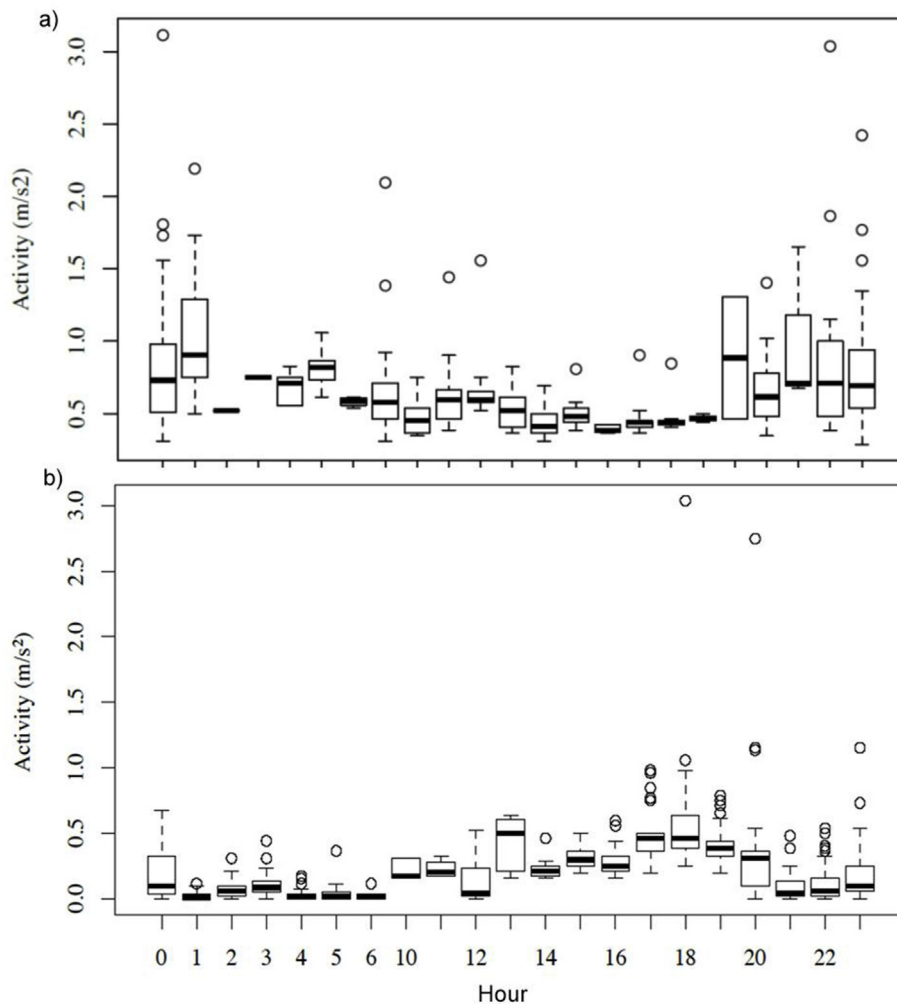

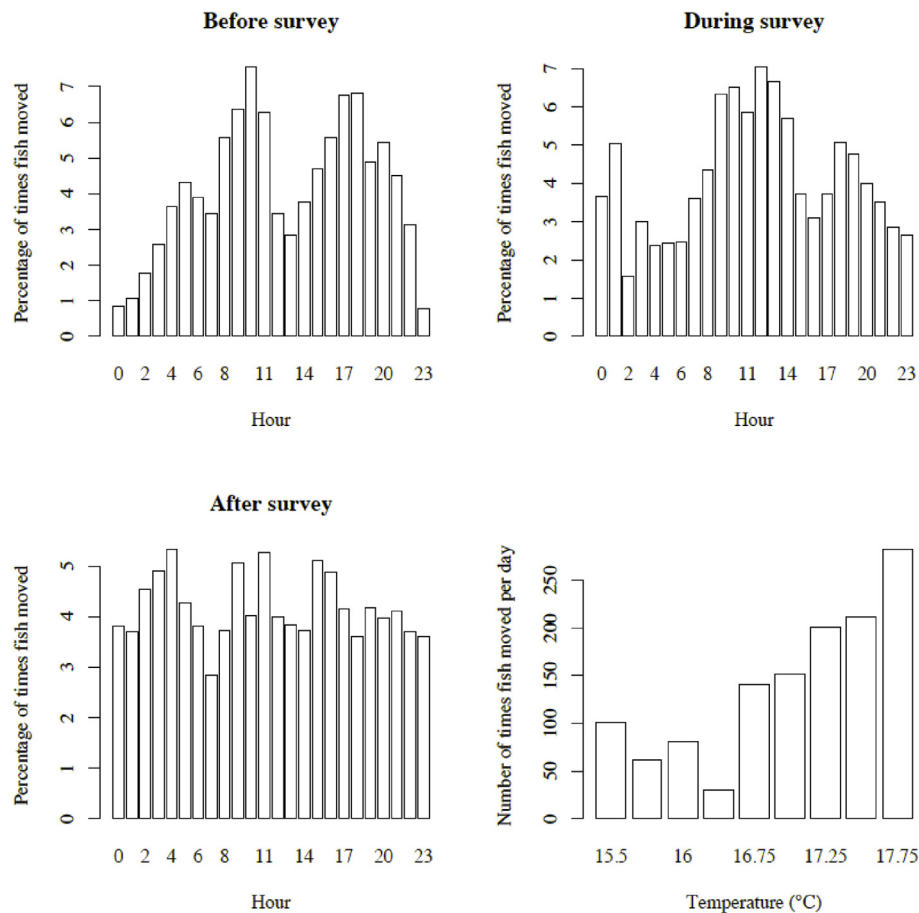**Fig. 3.** Diel movement pattern in a) gummy sharks and b) swell sharks.

Fig. 4. Percentage frequency of movement events for tiger flathead before during and after the seismic survey. Temperature range experienced is provided in the bottom right panel.
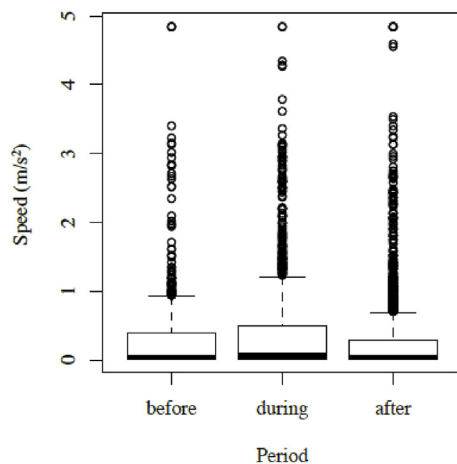

Fig. 5. Speed of movement by tiger flathead over the periods before, during and after the seismic survey.

during the study period. Overall the range of speed of movement recorded when flathead did move was greater during the survey than before or after (Fig. 5).

3.2. Catch rate analysis

The number of fishing days and number of vessels undertaking fishing operations varied by gear type, and the biomass of each of the species caught varied between seasons and years (Supplementary

Material F). A total of 15 species were taken in sufficient quantities by each gear type (Danish seine, demersal gill-net) to examine catch histories before and after the seismic survey. However, only three of those species (gummy shark (*M. antarcticus*), sawshark (*Pristiophorus* spp), and elephantfish (*Callorhynchus milii)*) were common to both Danish seine and demersal gill-net operations. Six additional species were examined from Danish seine catches: John dory (*Zeus faber*), tiger flathead (*N. richardsoni*), red gurnard (*Chelidonichthys kumu*), morwong (*Nemadactylus macropterus*), goatfish (*Upeneichthys* spp), and Gould's squid (*Nototodarus gouldi*). And an additional six species were examined from demersal gill-net catches: Boarfish (Pentacerotidae), swell shark (*Cephaloscyllium* spp), angel shark (*Squatina* spp), broadnose shark (*Notorynchus cepedianus*), school shark (*Galeorhinus galeus*), and snapper (*Pagrus auratus*).

Of the three species common to both gear types (Danish seine, demersal gill-net), significant deviations ($p \leq 0.05$) from the predicted catch rates for after the seismic survey were only detected in the Danish seine operations. Both gummy shark and sawshark had significant declines in catch rates, while elephantfish showed a significant increase in catch rate (Table 5, Figs. 6 and 7). Of the remaining nine species examined, six indicated a significant deviation from the predicted catch rate after the seismic survey (Table 5, Figs. 6 and 7). Danish seine operations showed an increase in catch rates for goatfish and tiger flathead, and a decrease in catch rate for red gurnard. For demersal gill-net operations there were post seismic survey increases in catch rates of boarfish, broadnose shark and school shark.

Table 5
Catch rate comparisons – multiplicative effect in recorded catch after the seismic survey for each species and gear type. The p-value refers to the null hypothesis that there is no effect. Multipliers less than 1 infer a reduction in catch, whilst those greater than one imply greater catch. Bold text and shaded cells denote a significant p-value (≤ 0.05); red indicating a significant decrease; green a significant increase.

Species*	Danish seine		Demersal gillnet	
	Multiplier	**p-value**	**Multiplier**	**p-value**
Angel shark	-	-	0.87	0.76
Goatfish	**30.66**	**<0.0001**	-	-
Boarfish	-	-	**1.93**	**0.001**
Broadnose shark	-	-	**3.76**	**< 0.0001**
Elephantfish	**16.27**	**< 0.0001**	1.20	0.43
Gould's squid	1.15	0.77	-	-
Gummy shark	**0.58**	**0.01**	1.15	0.11
Jackass morwong	0.61	0.07	-	-
John dory	0.77	0.20	-	-
Red gurnard	**0.34**	**0.008**	-	-
Sawshark	**0.09**	**< 0.0001**	1.33	0.08
School shark	-	-	**2.95**	**0.004**
Snapper			0.87	0.80
Swell shark	-	-	1.91	0.22
Tiger flathead	**1.46**	**< 0.0001**	-	-

4. Discussion

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. We incorporated both field-based and desktop research to show that the range of responses expressed by fish exposed to seismic survey noise is complex and species-specific. In hindsight, the spatial coverage of the acoustic receiver arrays used in this study did not allow for the degree of dispersal that should have been expected of more mobile species such as gummy sharks and swell sharks. Although our focus was on fine-scale movement patterns, deploying fringing arrays at lower density may have allowed for a more in-depth analysis of overall movement patterns.

4.1. Behaviour

Altered behaviour of marine fish can be measured through changes in displacement and 'normal' movement patterns. Changes in displacement and movement may manifest via a decrease in overall movement for species that lay still on the seabed when disturbed or an increase for species that show a startle response and flee. These aspects of behaviour have been detected or inferred in a variety of fish species in response to airgun shots under laboratory conditions or from field-based caged experiments (McCauley et al., 2003; Hassel et al., 2004; Popper et al., 2005; McCauley and Fewtrell, 2008). However, very few studies have been conducted that have examined changes in the behaviour of unrestrained fish that may be the result of seismic survey activities (Chapman and Hawkins, 1969; Wardle et al., 2001; Slotte

et al., 2004; Streever et al., 2016; Paxton et al., 2017).

In the current study, we examined displacement and movement of three species of unrestrained fish common to the region in which the seismic survey took place. Movement out of the monitored areas was observed for gummy sharks and swell sharks, but this was largely prior to the commencement of the seismic survey. Nevertheless, individuals of both shark species were observed to move in and out of the monitored areas throughout the study period, and two gummy sharks returned to the experimental zone during seismic survey operations. Observations of gummy shark movement in the current study support limited previous research in which gummy sharks showed similar movement patterns between night and day (Barnett et al., 2010).

Tiger flathead provided a more substantive data set, with extended periods of detections for most individuals. Of the flathead present in the experimental array during seismic operations, 50% remained in the area for the entire period of operations and 50% departed. None of the four flathead that departed the experimental array during the seismic survey were recorded to return. Flathead detected for extended periods during seismic survey operations were generally recorded for extended periods after the survey indicating a degree of residency, supporting similar findings of site attachment of blue-spotted flathead (*Platycephalus caeruleopunctatus*) in soft sediment habitats (Fetterplace et al., 2016). All but one tiger flathead had departed the monitored area by mid-June, suggesting a possible seasonal movement out of the area (Jordan, 1998). Tiger flathead were most commonly recorded in a stationary mode throughout each period (before, during and after the seismic survey). However, the percentage of recorded movement events was greater during the period after the survey, and movements during this latter period were more consistently spread throughout a diel cycle.
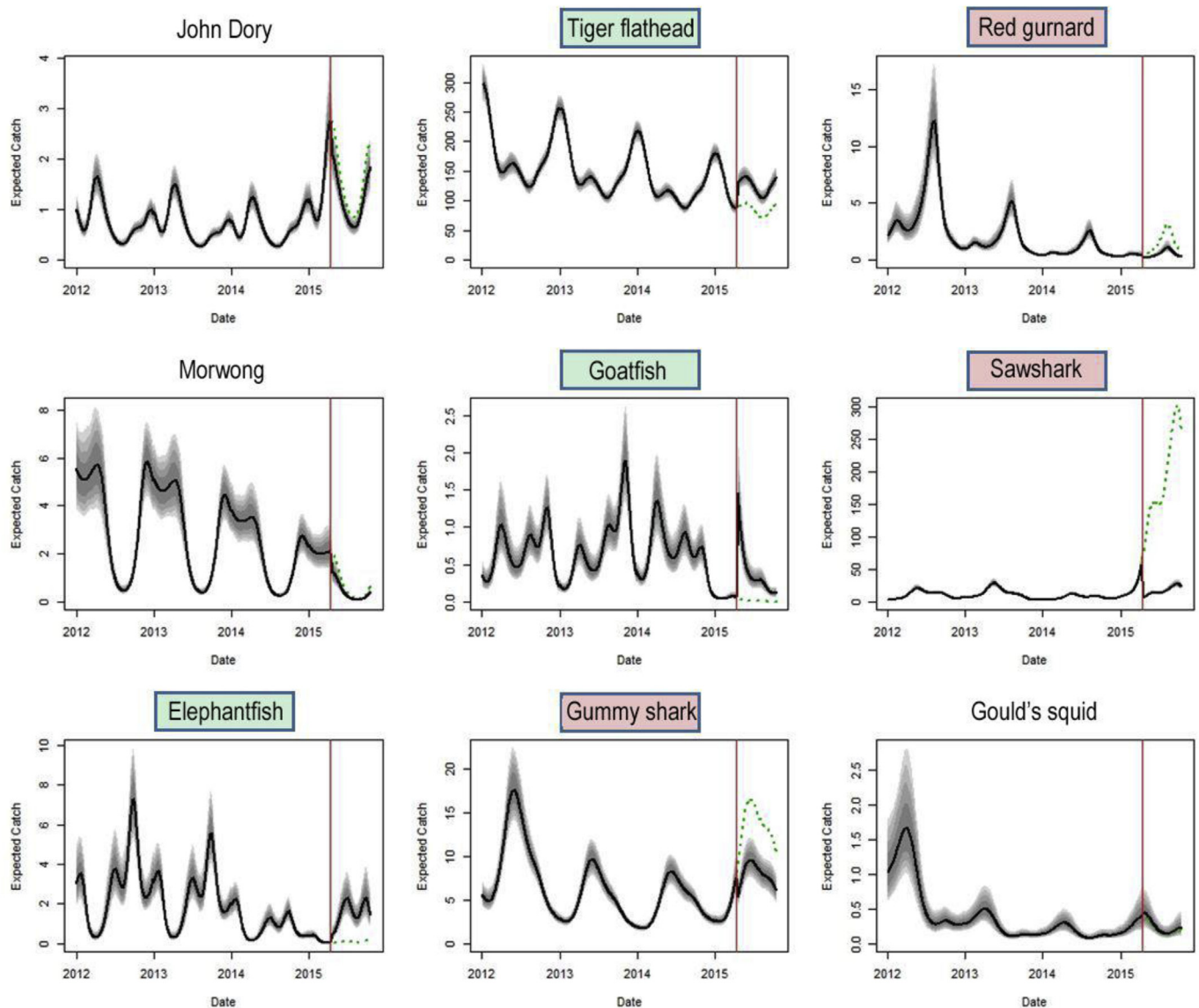
Fig. 6. Predicted catch from Danish seine for a randomly chosen vessel. The timing of the seismic survey is indicated by the vertical red line. Black line is the expectation for the observed catch history including the seismic survey. Grey shaded areas around the expected catch are confidence intervals (60%, 80%, 90% and 95%). Green dashed line is the predicted catch if the survey had not taken place. Red boxes identify species where the catch was significantly less than expected after the seismic survey; green boxes indicate catch was significantly higher than expected (p < 0.05). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

An increase in movement events has previously been reported for some species prior to seasonal departure (Andrews et al., 2010), and it is possible that the increase in flathead activity after the survey reflected an impending movement away from the area as part of a normal seasonal cycle (Jordan, 1998). There was, however, no indication that tiger flathead departed the experimental area as a result of the seismic survey itself. This is in contrast to the findings of Paxton et al. (2017) where a reduction in fish abundance during a seismic survey was presumed to indicate fish had left a reef in response to seismic airgun activity.

Overall, behaviour consistent with a possible response to the seismic survey operations was observed as an increase in flathead swimming speed during the seismic survey period. This may indicate a startle response, similar to those previously documented in other finfish species (e.g. Wardle et al., 2001, Kastelein, 2008), as well as possibly sharks (Myrberg et al., 1978). Vertical movement rather than horizontal movement of fish could be a short-term reaction to seismic sound (Chapman and Hawkins, 1969; Slotte et al., 2004). Nevertheless, the

range of flathead movement was not sufficient to generate a significant displacement. Thus, although flathead provide some evidence for moving faster during the seismic survey period, the distance over which this occurred was relatively short and within the acoustic range of individual receivers. A similar lack of displacement was recently recorded in Southern Bluefin Tuna in which broad-scale observations of their movement in the Great Australian Bight suggested that tagged individuals remained in the regions during periods of geophysical surveys (Evans et al., 2017).

4.2. Commercial catch rates

Our catch rate analysis indicated changes in catch rate over the six month period after the seismic survey in nine out of the 15 species examined across both fishing types, but these were not consistently negative. Rather, six species reflected increases in catch rates after the seismic survey, whereas three species showed reductions relative to the predicted catch rate. These results support previous studies that have
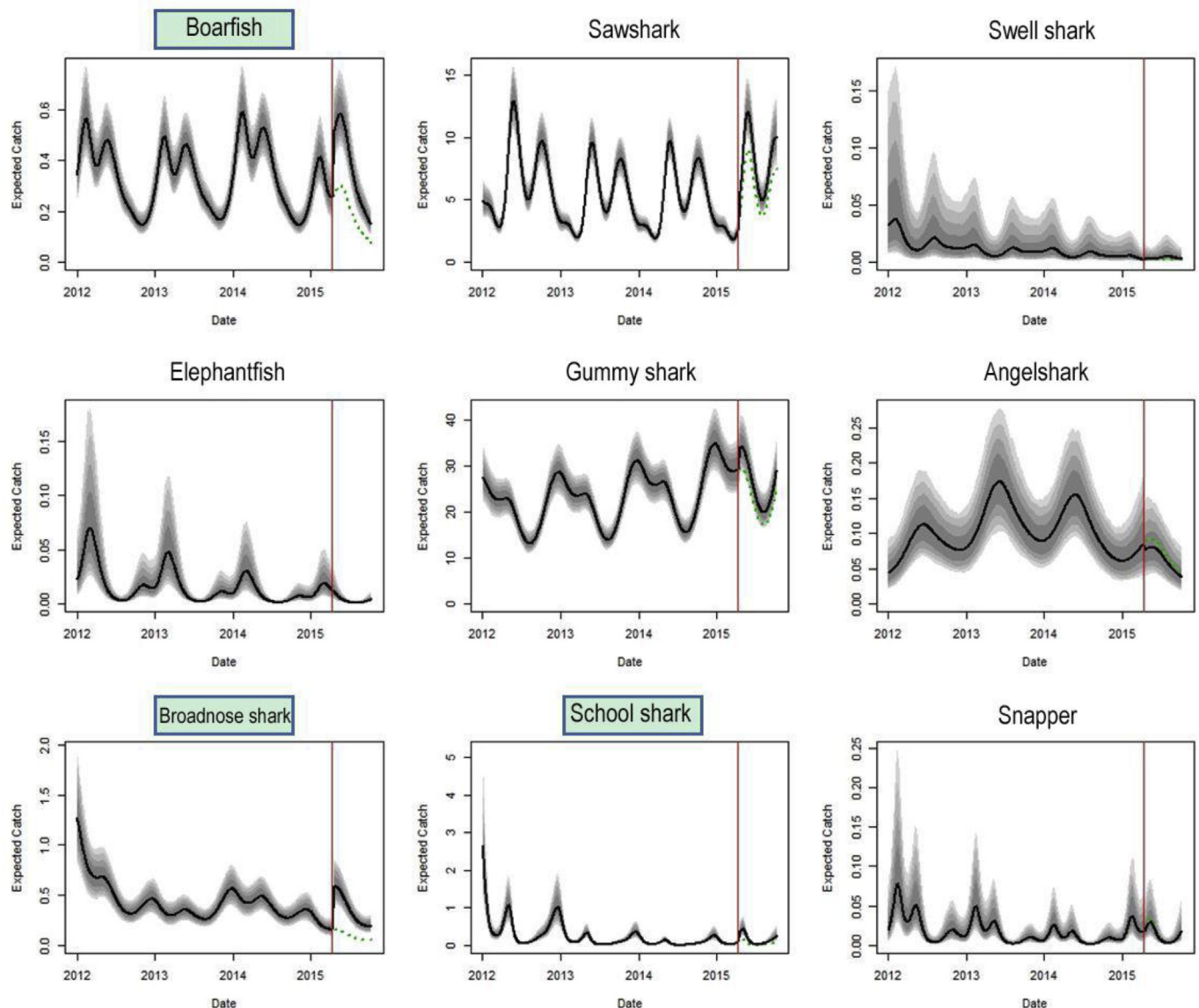
Fig. 7. Predicted catch from demersal gillnet for a randomly chosen vessel. The timing of the seismic survey is indicated by the vertical red line. Black line is the expectation for the observed catch history including the seismic survey. Grey shaded areas around the expected catch are confidence intervals (60%, 80%, 90% and 95%). Green dashed line is the predicted catch if the survey had not taken place. Red boxes identify species where the catch was significantly less than expected after the seismic survey; green boxes indicate catch was significantly higher than expected. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

used fishing logbooks to show no (Parry and Gason, 2006) or inconsistent (Thomson et al., 2014) relationships between catch rate and seismic surveys. Importantly, changes in catch rates were both species- and gear-specific, with no single species showing a consistent pattern in their variation in catch between gear types. For example, the reduction in gummy shark and sawshark captures and the increase in elephantfish captures recorded in the Danish seine sector were not reflected by similar changes in the demersal gill-net catch data.

Many factors can account for changes in logbook recorded catch rates including differences in fishing practices, market forces influencing the retention of catch and environmental effects influencing the distribution and catchability of species (Thomson et al., 2014). A more refined approach to our analyses would be to look concurrently at a control fishing area outside of possible influences of the seismic survey via a Before-After-Control-Impact (BACI) approach. In such an approach, catch rates (aboard vessels with standardised methods of catching) before and after the seismic survey would be compared across regions exposed to the seismic survey (experimental) and those that

were not (control). In this study, the major difficulty with the BACI approach when looking at existing commercial fisheries data was that we were not able to identify an appropriate control region to the experimental region (physical and biological). The problem was further exacerbated in that the method of catch could not be standardised. In the current analyses we therefore took our 'control' to be displaced in time, i.e. looking at catch rates across the region retrospectively to 2012 and seeing if there was a change in the 2015 pattern. A similar approach was adopted by Streever et al. (2016).

There is evidence, however, of possible confounding factors that may have influenced the before and after seismic survey catch analysis in at least one species. Sawshark catch rate in the Danish seine sector increased sharply prior to the seismic survey, with recorded catches being higher than in previous years. This is likely to have inflated the predicted catch rates for the period after the survey, leading to a greater perceived decrease in catch from 'expected' after the survey than might otherwise have been the case. Interestingly, similar deviations in sawshark catch rates were not reflected in the demersal gill-net fishery

across the region. We have no way of reconciling this anomaly given the available data, and thus urge caution in interpreting the result for this species. No obvious changes were observed in catch rates for other species in the lead up to the seismic survey suggesting that the interpretation of other species' catch rate changes are more robust.

5. Conclusion

This is the first study to use a combined field and desktop approach to investigate the potential impacts of seismic surveys on fish behaviour and catch. By using acoustic telemetry, fish were monitored in a natural environment with the full spectrum of targeted behavioural responses able to be expressed (e.g. displacement is not able to be measured in caged studies). The catch rate analysis complemented the field study by focussing on a commercially important metric (catch per unit effort) underpinned by fish behaviour. Overall, we found little evidence of consistent behavioural responses (excluding flathead movement) or catch rate changes induced by the seismic survey in the targeted species, although behavioural data were limited because many sharks left the acoustic receiver array prior to the commencement of the seismic survey.

Acknowledgements

Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.marenvres.2018.05.005.

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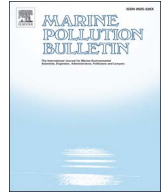
Multiple field-based methods to assess the potential impacts of seismic surveys on scallops

Rachel Przeslawski[a,*], Zhi Huang[a], Jade Anderson[b], Andrew G. Carroll[a], Matthew Edmunds[c], Lynton Hurt[a], Stefan Williams[d]

[a] National Earth and Marine Observations Branch, Geoscience Australia, GPO Box 378, Canberra, ACT, Australia
[b] Energy Systems Branch, Geoscience Australia, Australia
[c] Marine Ecology Pty Ltd, 82 Parsons St, Kensington, VIC 3031, Australia
[d] Australian Centre for Field Robotics, University of Sydney, Sydney, 2006, NSW, Australia

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ABSTRACT

Marine seismic surveys are an important tool to map geology beneath the seafloor and manage petroleum resources, but they are also a source of underwater noise pollution. A mass mortality of scallops in the Bass Strait, Australia occurred a few months after a marine seismic survey in 2010, and fishing groups were concerned about the potential relationship between the two events. The current study used three field-based methods to investigate the potential impact of marine seismic surveys on scallops in the region: 1) dredging and 2) deployment of Autonomous Underwater Vehicles (AUVs) were undertaken to examine the potential response of two species of scallops (*Pecten fumatus, Mimachlamys asperrima*) before, two months after, and ten months after a 2015 marine seismic survey; and 3) MODIS satellite data revealed patterns of sea surface temperatures from 2006–2016. Results from the dredging and AUV components show no evidence of scallop mortality attributable to the seismic survey, although sub-lethal effects cannot be excluded. The remote sensing revealed a pronounced thermal spike in the eastern Bass Strait between February and May 2010, overlapping the scallop beds that suffered extensive mortality and coinciding almost exactly with dates of operation for the 2010 seismic survey. The acquisition of *in situ* data coupled with consideration of commercial seismic arrays meant that results were ecologically realistic, while the paired field-based components (dredging, AUV imagery) provided a failsafe against challenges associated with working wholly in the field. This study expands our knowledge of the potential environmental impacts of marine seismic survey and will inform future applications for marine seismic surveys, as well as the assessment of such applications by regulatory authorities.

1. Introduction

An important part of managing marine petroleum resources is mapping the geology beneath the seafloor using seismic surveys. Marine seismic surveys involve the use of airgun arrays that are towed behind vessels and produce high-intensity, low-frequency impulsive sounds at regular intervals (McCauley et al., 2000). These sounds are directed down towards the seafloor and are used to generate detailed images of its underlying geological formations. These images are then interpreted by geologists and geophysicists to identify potential oil and gas reservoirs (Rollet et al., 2012), assess risk from activities such as CO_2 sequestration (Borissova et al., 2013), or understand geological history (Kolarsky et al., 1995). Responsible planning of marine seismic surveys involves understanding and mitigating associated environmental impacts. Without certainty about presence or magnitude of

impacts, several countries have adopted precautionary principles in their seismic survey approvals process (Brêthes et al., 2004; Dalen et al., 2007). These policies restrict the timing, location, and duration of seismic exploration and can be a source of conflict between fisheries, the petroleum industry and other groups using marine resources (Knuckey et al., 2016; Lewandowski, 2015).

In southeast Australia, a marine seismic survey was blamed for a mortality event towards the latter half of 2010 involving scallops and other benthic invertebrates (Hall, 2010). In particular, fishermen pointed to the fact that western and eastern scallop beds within the seismic survey area were devastated, while a southern scallop bed ~50 km from the seismic survey was healthy (J. Semmens, personal communication). Spatial and temporal variability of scallops has been a challenge to the fishing industry, and the causes of recruitment failures and mortality events often remain unknown (Dredge et al., 2016) but

can include disease (Levesque et al., 2016), high water temperatures (Caputi et al., 2016), freshwater influx (Courtney et al., 2015), fishing (Stokesbury et al., 2011), predation (Marino et al., 2009), sedimentation (Szostek et al., 2013), and ontogenetic factors (i.e. self-thinning) (Frechette et al., 2013). Several studies have addressed the potential impact of seismic surveys on scallop mortality by using observational or manipulative field experiments with scallops. Two of these found no short-term effects two months after a commercial seismic survey was completed (Harrington et al., 2010; Parry et al., 2002). Another study, however, found evidence of seismic impacts in scallops from transplanted populations (increased mortality, inability to maintain homeostasis, reflex changes, depressed immune response) after they had been exposed to an airgun operated in shallow water (< 10 m) (Day et al., 2016; Day et al., 2017). As noted by the authors, the ecological relevance of these results requires further investigation, particularly as they relate to potential impacts on fisheries.

The aim of this study was to use multiple field-based methods to investigate the potential impact of marine seismic surveys on scallops in the Bass Strait, specifically as related to a standard seismic survey conducted in the region in April 2015 and the 2010 scallop mortality event. Many sound impact studies use experimental cages or tanks (reviewed by Carroll et al., 2017), but assessing seismic impacts from these is challenging due to experimental artefacts (Gray et al., 2016; Rogers et al., 2016) that may lead to misinterpretation of impact in field settings (e.g. Aguilar de Soto et al., 2013). In contrast field studies may offer more ecological realism but may be associated with environmental unpredictability, spatiotemporal variability, and difficulty finding and tracking individual organisms. In the current study, dredging and Autonomous Underwater Vehicles (AUV) were used to examine the potential response of two species of scallops (*Pecten fumatus, Mimachlamys asperrima*) before, two months after, and ten months after a 2015 marine seismic survey, while satellite data was used to investigate patterns of sea surface temperatures from 2006 to 2016 in study areas affected by the 2010 mortality event. By using *in situ* populations and an industry-scale seismic survey, results from the current study will provide a field-based complement to those from Day et al., 2017, thereby expanding our knowledge of invertebrate responses to marine seismic surveys. Our findings may also assist the development, or further refinement, of precautionary policies according to the best information on species-specific responses to known exposure levels of low-frequency sound (Lucke et al., 2016; Parsons et al., 2009).

2. Methods

2.1. Study area & environmental surveys

The Gippsland Basin overlaps the Bass Strait in Australia and forms much of eastern Victoria's offshore region. It is a hub of marine resource activity, including petroleum exploration and production, as well as both Commonwealth and state fisheries (Fig. 1). Three environmental surveys were undertaken in the Gippsland Basin, timed to collect data three weeks before (29 March–3 April 2015), two months after (19–24 June 2015), and ten months after (18–23 February 2016) a seismic survey. For each survey, scallops were collected, an Autonomous Underwater Vehicle (AUV) was deployed to collect seafloor imagery, and fish were tagged and released in experimental and control zones. The fish tagging component will be the subject of a separate paper and is included in Przeslawski et al. (2016a). The lack of prior information about scallop distributions and abundances meant that the first environmental survey was tasked with not only collecting appropriate baseline (i.e. 'before' data) but also with identifying sites with scallop beds suitable for dredging. Wherever possible, dredge tows and AUV sites overlapped locations in which *P. fumatus* had previously been collected in 2014 by fishermen (S. Richey, personal communication) or collected in 2010 during a census (J. Semmens, personal communication). Neither of these sources identified dense beds of scallops in our

study area. For the 'short-term after' survey, site selection was also informed by bathymetry acquired during the seismic survey and dredging conducted during the 'before' survey which helped identify potential locations of scallops.

2.2. Seismic survey

In April 2015, a 2-D marine seismic survey was undertaken over part of the western Gippsland Basin (Fig. 1) as part of the Australian Government's National CO_2 Infrastructure Program investigating targeted offshore basins as potential CO_2 geosequestration sites. The *M.V. Duke* was used to tow a single 2530 cubic inch airgun array (BOLT Long Life Array), comprised of 16 airguns towed at 6 ± 1 m depth. Airguns had varying chamber sizes to optimise the array for power, primary-to-bubble ratio and frequency content (2×40 LLX, 1×70 LLX, 1×80 LLX, 2×100 LLX, 4×150 LLX, 2×200 LLX, 2×250 LLX and 2×300 LLX units in cubic inches). The array was operated at a working pressure of 2000 psi, with a lower acceptable limit of 1800 psi. The locations of seismic lines are shown in Fig. 1, and the seismic acquisition times can be found in Table 1 of Przeslawski et al. (2016b). The airgun array and survey line spacing were the same as those used in commercial seismic surveys.

The study area included two zones based on their spatial proximity to this seismic survey area: an experimental zone located 0–1 km from airgun operations and a control zone located > 10 km from seismic airgun operations. The control zone was chosen based on a compromise between previous Bass Strait scallop studies (control zone < 4 km away in Harrington et al., 2010, 20 km away in Parry et al., 2002), logistics (survey duration precluded a further zone), and sound propagation modelling (Supplementary Material B). Moored hydrophones recorded the highest SEL per seismic shot of 146 dB re 1 μPa^{2}s at 51 m depth when the airguns were operating 1.4 km away, and sound propagation modelling estimated maximum SEL received one metre above the seafloor with airguns directly overhead to be 170 dB re 1 μPa^{2}s, extending 200–250 m from the receiver depending on water depth and directionality (Supplementary Material A). In addition, the highest modelled peak particle velocity was 171 dB re 1 nm/s at 40 Hz and 166.7 dB re 1 nm/s at 80 Hz, both values at 100 m from the sound source (Supplementary Material A). Although all fish can detect particle motion, this aspect of sound is highly applicable to impact assessments on elasmobranchs (i.e. sharks and rays) and invertebrates since these groups are sensitive only to particle motion (Hawkins and Popper, 2016).

2.3. Study species

The dredging and AUV components of this study focused on the commercial scallop (*Pecten fumatus*), as well the doughboy scallop (*Mimachlamys asperrima*), a potential biological surrogate (Mellin et al., 2011) with similar habitat and life history (Shumway and Parsons, 2016). The commercial scallop *Pecten fumatus* typically spawns from June to November in Tasmanian and Victorian waters (Dredge et al., 2016), and peak settlement of larvae occurs in mid-late September (Hortle and Cropp, 1987). After two years, commercial scallops reach maturity and can grow to about 70 mm and then grow slowly (Edgar, 2000; Young and Martin, 1989). Healthy scallops recess their convex right valve beneath the sediment such that the flat left valve is level or slightly below the sediment surface. They are strongly associated with finer sediments, as well as with depth, seastar abundance, shell and macroalgae cover (Mendo et al., 2014).

The doughboy scallop *Mimachlamys asperrima* typically spawns in late September to mid-October in the D'Entrecasteaux Channel in Tasmania, with scallops growing to 80 mm in 3.4 years (Zacharin, 1995). Unlike commercial scallops, they attach to a substrate using their byssal threads throughout their entire lives, although they can break these threads and move if needed, often in response to a predator
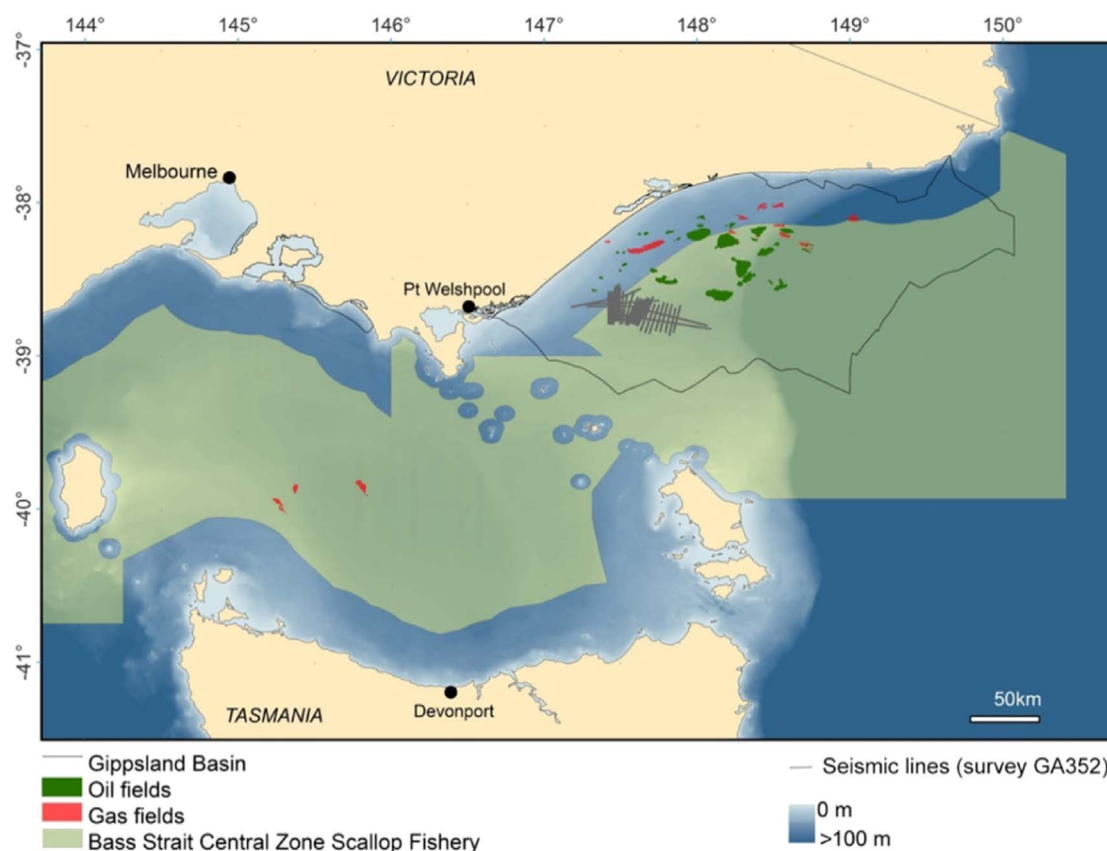
Fig. 1. Map of the offshore Gippsland Basin, overlaid with Commonwealth scallop fishery and petroleum industry infrastructure. The Victorian and Tasmanian scallop fisheries operate in the waters between their respective states and the BSCZS fishery.

Table 1
Summary of scallop data that were acquired from before, short-term after, and long-term after) surveys. C = commercial scallop (*P. fumatus*). D = doughboy scallop (M. asperrima).

Data type	Collection method	Species	Before	Short-term	Long-term	Reason for exclusion
Number of live scallops	Dredged samples	C,D	Yes	Yes	Yes	n/a
Shell assemblages	Dredged samples	C	No	Yes[1]	Yes[1]	Shells from only one tow were recorded on 'before' survey. Doughboy shell assemblages not recorded.
Morphometrics (shell length, height)	Dredged samples	C,D	Yes	Yes	Yes	n/a
Morphometrics (adductor muscle, gonad)	Dredged samples	C	Yes	Yes	Yes	Doughboys not opened for internal morphometrics
Scallop condition ((live, clapper, dead shell, unknown)	Seafloor imagery	C,D	No	Yes	Yes	AUV did not acquire suitable images for analysis on 'before' survey

[1] To account for spatial variation of dredges among surveys, a sub-set of dredges undertaken adjacent to each other was analysed (see Fig. 2 insets).

(Chernoff, 1987). Populations of doughboy scallops can reach high densities, with "an immense mobile population of dwarf animals 20–40 mm in length…present in the deeper waters of Bass Strait" (Edgar, 2000). Doughboy scallops often have an association with different species of epizootic sponges which may protect them from predation by seastars (Chernoff, 1987; Pitcher and Butler, 1987).

2.4. Dredging

A standard commercial box dredge (4.26 m wide with 46 × 70 mm mesh) was deployed for ~500 m from the *Dell Richey II* at various locations in control and experimental zones during the three environmental surveys (before, short-term, long-term) (Fig. 2). All tows were on the seabed for ~500 m except for dredge numbers 33 and 34 which were retrieved early due to small rocks and outcrops on the seafloor.

Upon completion of each dredge tow, live scallops were counted and photographed to quantify size. At least ten *P. fumatus* (if available) from each dredge were opened and photographed to examine various metrics of scallop condition (Supplementary Material C). For the short-

and long-term surveys, *P. fumatus* shells (i.e. dead scallops) were counted based on five categories as adapted from Harrington et al. (2010): Clappers in which both scallop valves are connected, but the animal is gone; newly dead shell in which the inside of a single shell has no notable discoloration or fouling organisms, old dead shell in which the inside of a single shell is intact but has a dull discoloured appearance or some fouling organisms, very old dead shell in which the inside of a single shell is heavily fouled or beginning to break apart due to age, broken shell in which fragments of shell were separated. For the last category, individuals could not be counted so weight was instead recorded. After each survey, the software package Image J-Fiji (http://imagej.nih.gov/ij/index.html) was used to extract data from *P. fumatus* images, including upper valve (i.e. flat shell) height and length, adductor muscle (AM) diameter, gonad area, and gonad stage (Supplementary Material C). Due to resource limitations (e.g. equipment issues, insufficient time), not all analyses included scallop data from before, short-term, and long-term surveys (Table 1).

The metrics used in the current study (Table 1) were included based on other studies suggesting that seismic airguns may cause scallop
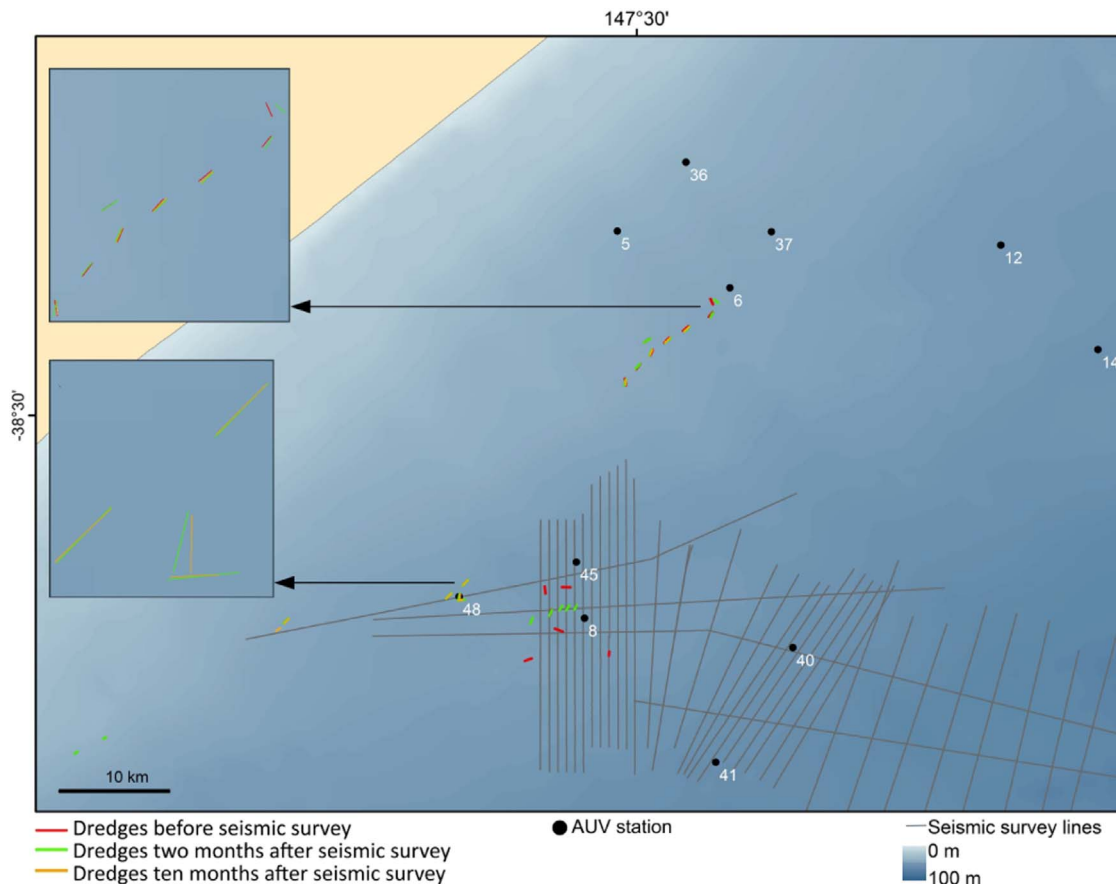
Fig. 2. Map of dredging and AUV operations. AUV operations were conducted in the same location among all surveys, while dredging locations changed among surveys to optimise scallop collection. Insets magnify regions with multiple dredges adjacent to each other from which shell assemblages were analysed.

mortality or reduced growth (Aguilar de Soto et al., 2013; Day et al., 2017), as well as anecdotes from fishermen that seismic surveys may be linked to poor meat quality (i.e. adductor muscle, gonad) (Hall, 2010).

2.5. Seafloor imagery

As with dredge tows, AUV sites were haphazardly chosen both in control (> 10 km from seismic lines) and experimental (0–1 km from seismic lines) zones based on previous scallop distribution. The transect shape was designed as a right-angled figure-eight (Supplementary Material D), rather than the traditional grid formation often used in AUV studies (Foster et al., 2014). This was done to increase the number of habitat types covered, as we had very little prior knowledge about current scallop locations in the Gippsland region and wanted to max-imise the chances of imaging scallops. The transect shape was also designed with two cross-over points (loop closures) to assist in refining vehicle position estimates during data post-processing.

The AUV deployed on the 'before' survey yielded low-quality images so an alternative platform (*AUV-Phoenix*) was deployed on the 'short-term after' and 'long-term after' surveys. Stereo image pairs were ac-quired at a rate of 2 Hz with a target altitude of 2 m above the seabed and speed of 1 m s-1 (2 knots). Post-processing included image colour-balancing and simultaneous localisation and mapping (SLAM) proces-sing of the stereo imagery to improve georeferencing. Further details on the AUV platforms and online links to imagery data can be found in Supplementary Material D.

Data were extracted from images using the online annotation plat-form Squidle (https://squidle.acfr.usyd.edu.au) which allowed an analyst to categorise georeferenced images. Approximately every 4–5 images were annotated, depending on the speed of the AUV, such that a

continuous but non-overlapping series of images were annotated. Both commercial and doughboy scallops were counted and assigned modi-fiers based on the position of their valves (open, closed, indeterminate) and their location in the sediment (fully, partially, or un-buried). Dead or disarticulated scallop shells were also scored. Categorisation of scallops based on these classifiers allowed for the determination of scallop condition and overall health within each site (live, dead (shell), dead (clapper), unknown).

2.6. Satellite imagery

Sea surface temperature (SST) time-series imageries were derived from MODIS (Moderate Resolution Imaging Spectroradiometer) sa-tellites. Six study areas were generated to provide different spatial scales for the analysis. Area 1 represents the southern zone scallop bed with minimal impact in 2010, and areas 2–3 represent eastern and western zones in which scallop mass mortalities were detected (S. Richey, personal communication). Area 4 includes both the 2010 and the 2015 seismic surveys, and Area 5 covers the entire Bass Strait. Area 6 includes the 2015 seismic survey and associated environmental survey (control and experimental zones in current study). The mean SST values in Areas 1–6 were extracted from the monthly data layers between Jan 2006 and August 2016. The positive and negative anomalies of SST were defined as above or below the ten-year average (2006–2015) for each month, respectively. Conductivity-temperature-depth (CTD) data collected during the sound monitoring component of the project confirmed that vertical mixing was strong enough to allow applicability of our SST modelling to the seabed (Supplementary Material E).

2.7. Statistical analyses

Biological data were square-root transformed to reduce the influence of abundant taxa (e.g. doughboy scallops in Site 06). Two or three-factor permutational multivariate analysis of variance (PERMANOVA) tests were used for dredging and AUV data, with fixed factors being zone and time and random nested factors varying among metrics. For shell assemblages from dredging, there were no nested factors as each dredge tow yielded one datum; in this analysis a sub-set was used including only dredges undertaken adjacent to each other among surveys to account for spatial variation. For metrics related to shell size, gonads, and adductor muscle, dredge tow was nested within zone. For AUV imagery, site was nested within zone. All images with no scallops were excluded from the PERMANOVA because this multivariate procedure cannot incorporate zeroes across all variables (Clarke and Warwick, 2001). PERMANOVAs were undertaken with permutation of residuals under a reduced model using a fully partial analysis; this conservative approach is recommended for unbalanced designs (i.e. Type III Sum of Squares) (Anderson et al., 2008). The software package PRIMER 6 (v. 6.1.13) with PERMANOVA + (v. 1.0.3) was used to perform all statistical analyses (Anderson et al., 2008).

To account for spatial variation of dredges among surveys, a sub-set of dredges undertaken adjacent to each other was analysed (see Fig. 2 insets).

3. Results

3.1. Dredging

There were no signs of ill health in live scallops. Specifically, *P. fumatus* remained tightly closed during handling, and all scallops that were opened required force to separate valves. All opened scallops had normal meat except for those collected from three dredges (13, 15, 16) in which meat was watery and low quality based on the assessment of commercial scallop fishermen and previous definitions of Harrington et al. (2010). These dredge tows were all from the control zone and included large numbers of doughboy scallops (Fig. 3b), suggesting *P. fumatus* being outcompeted for food by *M. asperrima* (Sievers et al., 2013).

There was extremely large variation in catch among some of the dredge tows in the control zone for both species (Fig. 3). In general, *P. fumatus* catch increased over time (Fig. 3a), but this was almost certainly due to growing awareness of commercial scallop bed locations in the area as the surveys progressed.

P. fumatus shell assemblages from a sub-set of dredges within the same area (Fig. 2) revealed a significant interaction between time and zone (Pseudo F = 13.436, p = 0.001). Pairwise comparisons showed differences between shell assemblages from short- and long-term surveys in the control zone but not in the experimental zone. These were driven by more live scallops and new dead shells collected in the control zone during the long-term survey. In addition, the experimental zone had consistently more very old dead shells than the control zone (Supplementary Material F).

For *P. fumatus*, there was no detectable impact due to seismic activity on *P. fumatus* shell size (growth), adductor muscle diameter, gonad size, or gonad stage. This was confirmed by PERMANOVA tests in which 'zone' (control, experimental) and 'time' (before, short-term after, long-term after) did not show a significant interaction for any metric measured (Supplementary Material F). There was a significant effect of zone, with scallops in the control zone showing smaller shells, adductor muscles, and gonads than those in the experimental zone; this relationship existed before and after the seismic survey (Fig. 4). Time had a significant effect on size of adductor muscles and gonads, with scallops collected from the 'long-term' survey showing significantly smaller gonads than those from the previous surveys, and scallops collected from the 'before' survey showing significantly larger adductor

muscles than those from the subsequent surveys (Fig. 4). Dredge tow had the most universal effect on *P. fumatus*, with strong differences among tows for all metrics (p = 0.001).

In contrast to commercial scallops, the size of *M. asperrima* was affected by a significant interaction between zone and time (height: Pseudo F = 7.3604, p = 0.006; length: Pseudo F = 6.9485, p = 0.002), but this was not associated with adverse effects from the seismic survey. Both control and experimental zones showed similar patterns, with larger doughboy scallops collected from both the short- and long-term surveys compared to the before survey, although there was a much larger difference in the experimental zone between scallops collected before the seismic survey and those collected two months after (Fig. 5). As with commercial scallops, dredge tow had a strong effect on doughboy shell size (p = 0.001).

3.2. Seafloor imagery

Based on the 9349 images that were annotated (Supplementary Material D), there was no interaction between zone (experimental, control) and time (short-term, long-term) on *P. fumatus* classes (live, clapper, dead shell, unknown) (Pseudo F = 1.5143, p = 0.3). This indicates that no long-term effects attributable to the seismic survey were detected on commercial scallops, although short-term or moderate effects could not be tested due to lack of AUV data before the seismic survey. There were no differences in scallop types between experimental and control zones (Pseudo F = 2.091, p = 0.193), but there was a significant effect of time (Pseudo F = 8.3949, p = 0.023), with scallops from the short-term survey dominated by a higher proportion of disarticulated shells compared to those from the long-term survey (Fig. 6a,b).

There was a significant interaction between zone (experimental, control) and time (short-term, long-term) on doughboy scallop types (live, clapper, dead shell, unknown) (Pseudo F = 4.0485, p = 0.02). Pair-wise comparison PERMANOVA tests showed that in the experimental zone, there were differences in scallop types between the short-term and long-term surveys; there were no such differences in the control zone. This was attributed to more doughboy scallops with unknown viability observed the short-term survey (site 45) and more live doughboys observed in the long-term survey (sites 08 and 41) (Fig. 6c,d). Importantly, there were very few dead doughboys (clappers and shells) detected in the experimental zone during short- or long-term survey (Fig. 6c,d) which would have indicated potential adverse impacts of the marine seismic survey on this species.

3.3. Satellite imagery

Positive temperature anomalies (> 0.5 °C) occurred in late summer-autumn (when SSTs are warmest) sporadically from 2006 to 2016 (Fig. 7a). Between Feb 2010 and May 2010, a large positive temperature anomaly occurred (up to 1 °C), especially for areas 2 and 3 (Fig. 7b) which overlapped scallop beds subject to the 2010 mortality event. For the current study (area 6), there were no high temperature anomalies during the before or short-term surveys (Fig. 7c). In contrast, large positive temperature anomalies occurred between the two latter surveys, with the largest spike occurring just two weeks prior to the last survey (Fig. 7c). Fig. 8 shows SST images of the study area to provide an indication of inter-annual variability for March. These data confirm higher SST values in March 2010 (Fig. 8d) and March 2016 (Fig. 8f) than other years.

4. Discussion

No adverse effects on scallops that could be linked to the 2015 marine seismic survey were detected based on dredged samples or AUV imagery, and satellite data confirmed SST fluctuations within normal ranges (< 1 °C anomaly) in times preceding the 2015 environmental
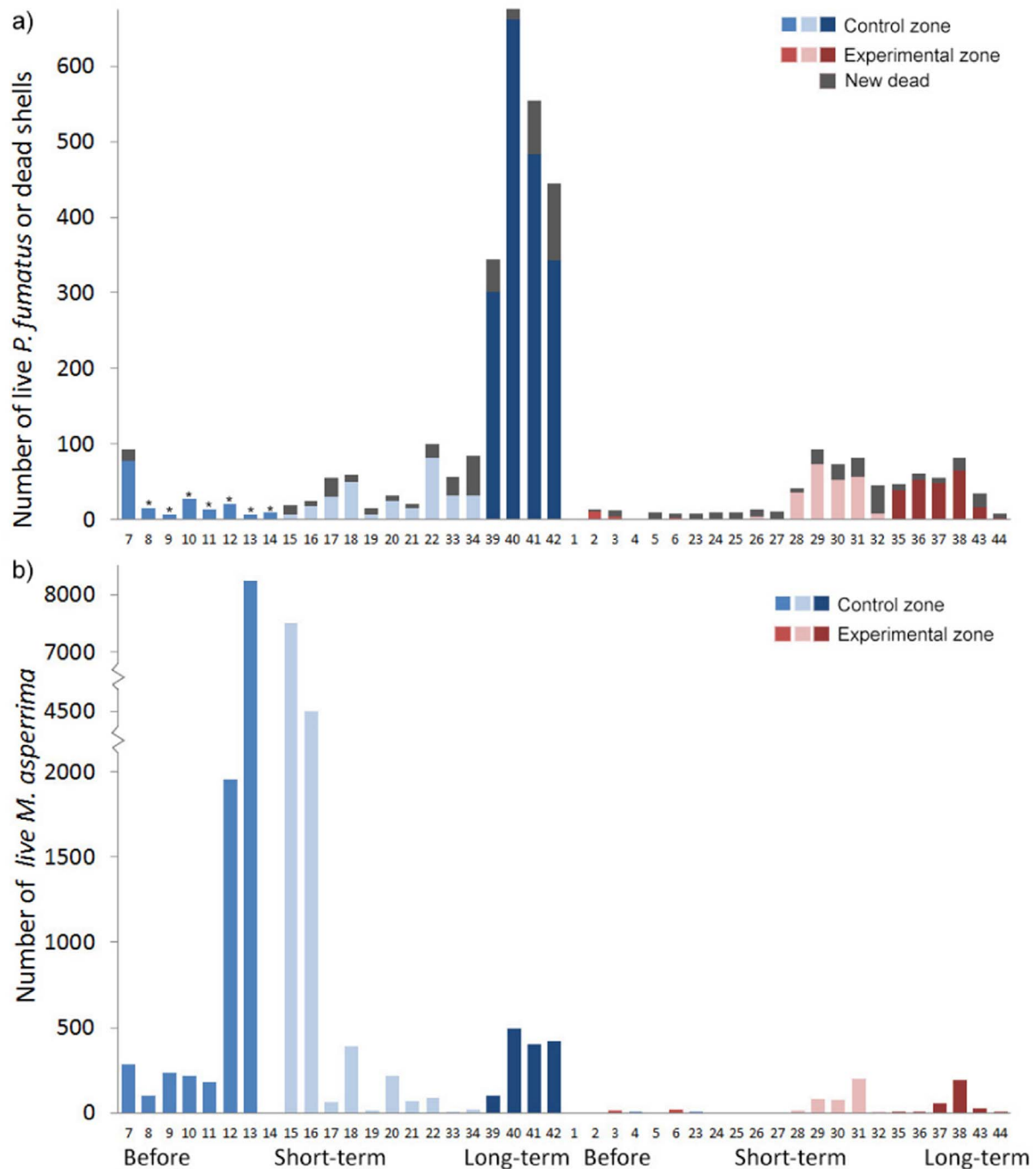
Fig. 3. Catch for a) commercial scallops and b) doughboy scallops for each dredge (numbered) towed in control (blue) and experimental zones (red). Dredges were undertaken before (medium shading), two months (light shading), and ten months (dark shading) after a seismic survey in the Gippsland Basin. Numbers on the x-axis identify individual dredge tows. 'New dead' is defined in the text. Clappers were only collected in dredge tows 39 and 42, and each clapper was included as two 'new dead' shells here. Dead shells were only recorded from commercial scallops, and asterisks show dredge tows where this information was not recorded. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

surveys. However, there were possible effects noted on doughboy size. Specifically, doughboy scallops exposed to the seismic survey were larger than unexposed scallops two months after completion of the survey (Fig. 5). Reasons for this remain unknown, but may reflect the high densities of doughboys in the control zone compared to the experimental zone which could limit growth due to competition for food (MacDonald and Thompson, 1986).

Our results must be interpreted in the context of other research in the region, as well as the larger body of international research (Carroll et al., 2017; Hawkins et al., 2015; McCauley et al., 2000; Popper et al.,

2003). To date, there are three other scientific studies that have examined the effects of seismic surveys on adult scallops (Day et al., 2017; Harrington et al., 2010; Parry et al., 2002). None of these indicate that seismic surveys can cause catastrophic or short-term mortality in scallops. However, Day et al. (2017) showed that exposure to noise from an airgun at < 10 m depth can adversely impact scallops through behavioural or physiological change, as well as an increase in long-term mortality rates. These contrasting findings may reflect experimental differences such as sound exposure or environmental conditions. Alternatively, the intense history of fishing and seismic surveying in the
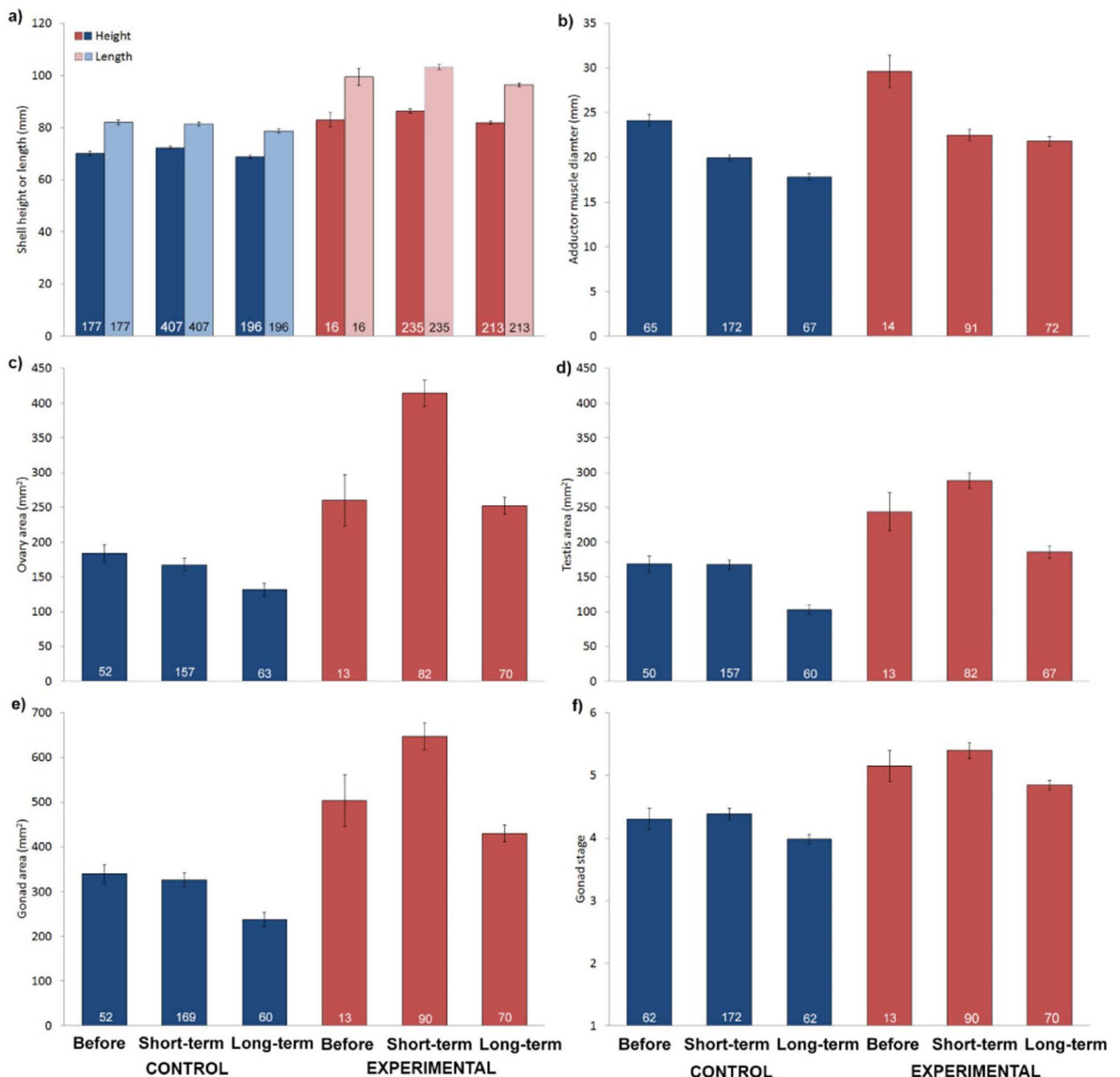
Fig. 4. Commercial scallop metrics averaged from control and experimental zones before, two months after (short-term) and ten months after (long-term) a seismic survey in the Gippsland Basin: a) shell height and length, b) adductor muscle diameter, c) ovary area, d) testis area, e) total gonad area and f) gonad stage. Numbers over the bars indicate sample sizes, and error bars are standard error of the mean.

region may have resulted in a small population of scallops locally adapted to noise exposure in the current study (Sanford and Kelly, 2011). In the interests of clarity and resolution, it is tempting to simplify studies as showing impact or no impact, but there is then the associated danger of 'cherry-picking' data to support particular agendas. Instead, the reality seems much more complex and warrants an avoidance of simplified or sensationalised claims, as well as mechanistic research to identify conditions in which marine seismic surveys may impact certain organisms and their natural populations.

The 2010 scallop mortality event was the reason for concern about seismic impacts on scallops, and the causes of this mass mortality remain unknown. Nonetheless, the environmental modelling clearly shows a pronounced thermal spike in the eastern Bass Strait between February and May 2010, coinciding almost exactly with the dates of operation for the seismic survey (Fig. 7) and overlapping study areas 2 and 3 in which the mortality event occurred. High temperatures have been linked to saucer scallop death in Queensland (Courtney et al., 2015) and Western Australia (Caputi et al., 2015) and are known to affect survival, behaviour and a range of physiological functions (Hao et al., 2014). The tolerance of scallops to high temperatures has been shown to vary according to their reproductive cycle with recently spawned scallops showing marked reduction in the expression of heat-shock proteins (Brokordt et al., 2015). Further research using both observational and manipulative approaches is recommended to investigate the role of temperature in scallop population sizes and catch rate fluctuations in the Bass Strait.
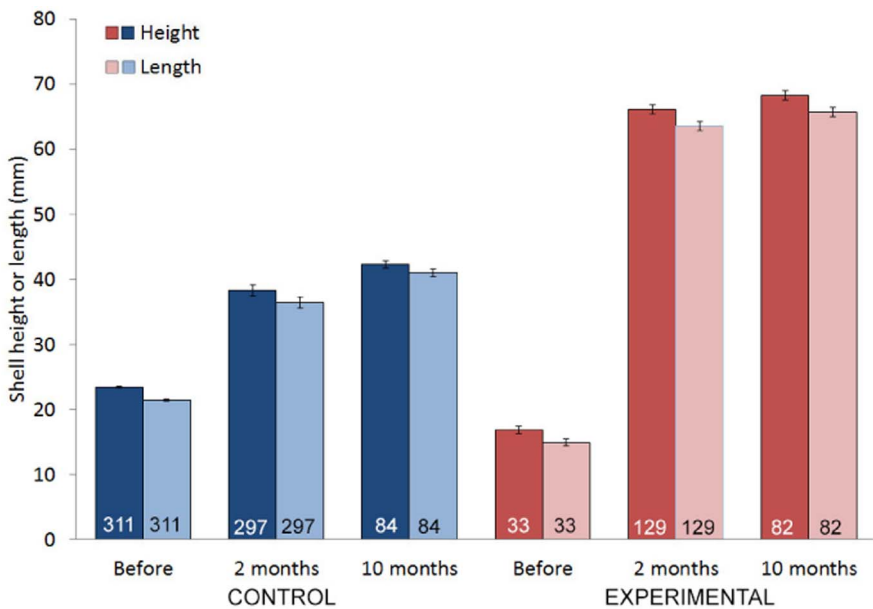
Fig. 5. Doughboy shell size averaged from control and experimental zones before, two months after (short-term) and ten months after (long-term) a seismic survey in the Gippsland Basin. Numbers over the bars indicate sample sizes, and error bars are standard error of the mean.
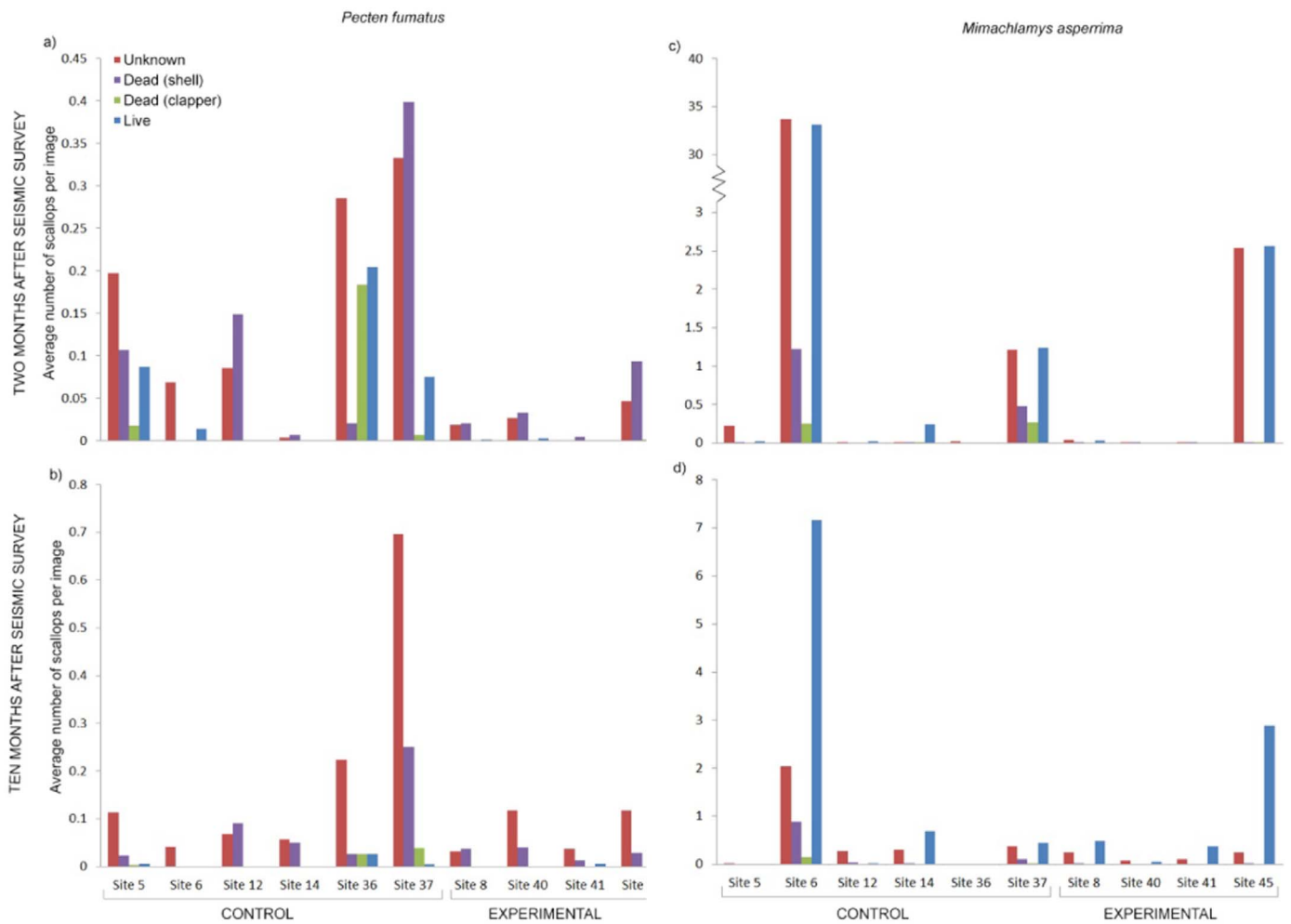

Fig. 6. Average numbers of commercial scallops observed per image acquired from the AUV a) two months after the seismic survey (short-term) and b) ten months after the seismic survey (long-term), as well as average numbers of doughboy scallops c) two months and d) ten months after the seismic survey. Total number of annotated images is listed in Supplementary Material D, and locations of AUV stations is in Fig. 2.
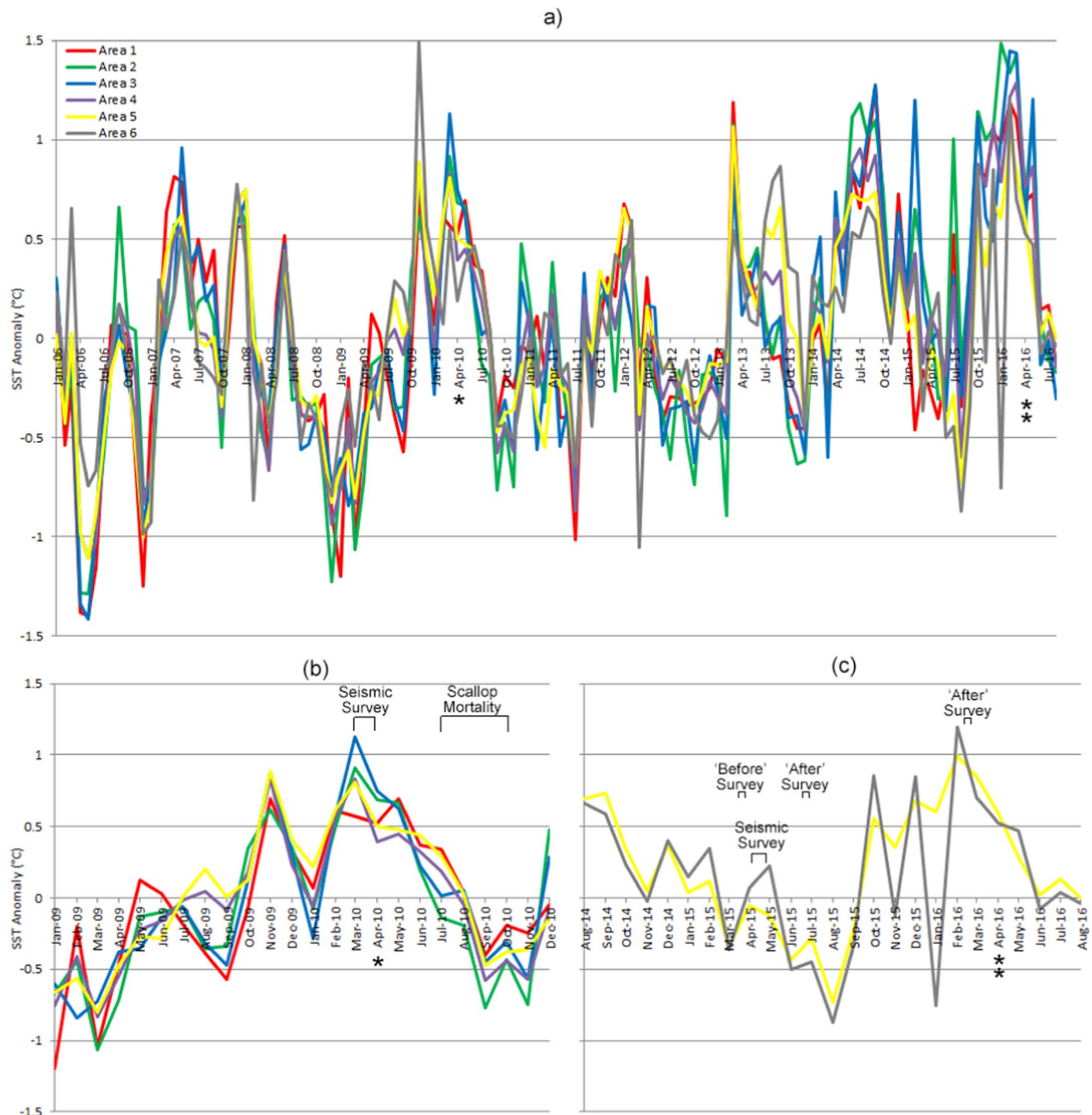
Fig. 7. SST anomaly plot between (a) Jan 2006 and July 2016, with asterisks indicating focus on b) the 2010 scallop mortality event and c) 2015–16 environmental surveys from the current study. Coloured lines indicate SST data from areas defined in Fig. 8, with b) and c) showing only areas relevant to specified events.

One of the most interesting hypotheses stemming from the current study is that multiple stressors may lead to a tipping point at which impacts of seismic surveys may then be observed. Temperature is perhaps the most justifiable concurrent stressor to target due to its possible role in the 2010 mortality event. Globally, 2015 was the warmest year on record, with the average global temperature across ocean surface areas 0.90 °C above the 20th century average of 13.9 °C (NOAA, 2016). Eastern Australia is a known climate warming hotspot (Oliver et al., 2013), with marine range shifts and community cascades already evident (Johnson et al., 2011). Stress associated with experimental conditions may also interact with low-frequency sound exposure. For

example, the scallops reared by Day et al. (2017) in suspended lantern nets were not kept in their natural environment (i.e. not buried beneath sediment), and cultured suspended scallops previously have shown higher mortality rates compared to benthic populations (Yu et al., 2010). The additional stress of being cultured in suspension may have acted as a tipping point at which seismic sound exposure produced biological impacts. To test such hypotheses, research should focus on low-frequency sound in the context of other stressors, including if seismic surveys contribute to synergistic interactions (i.e. the effects of two or more stressors are greater than the sum of their individual effects).
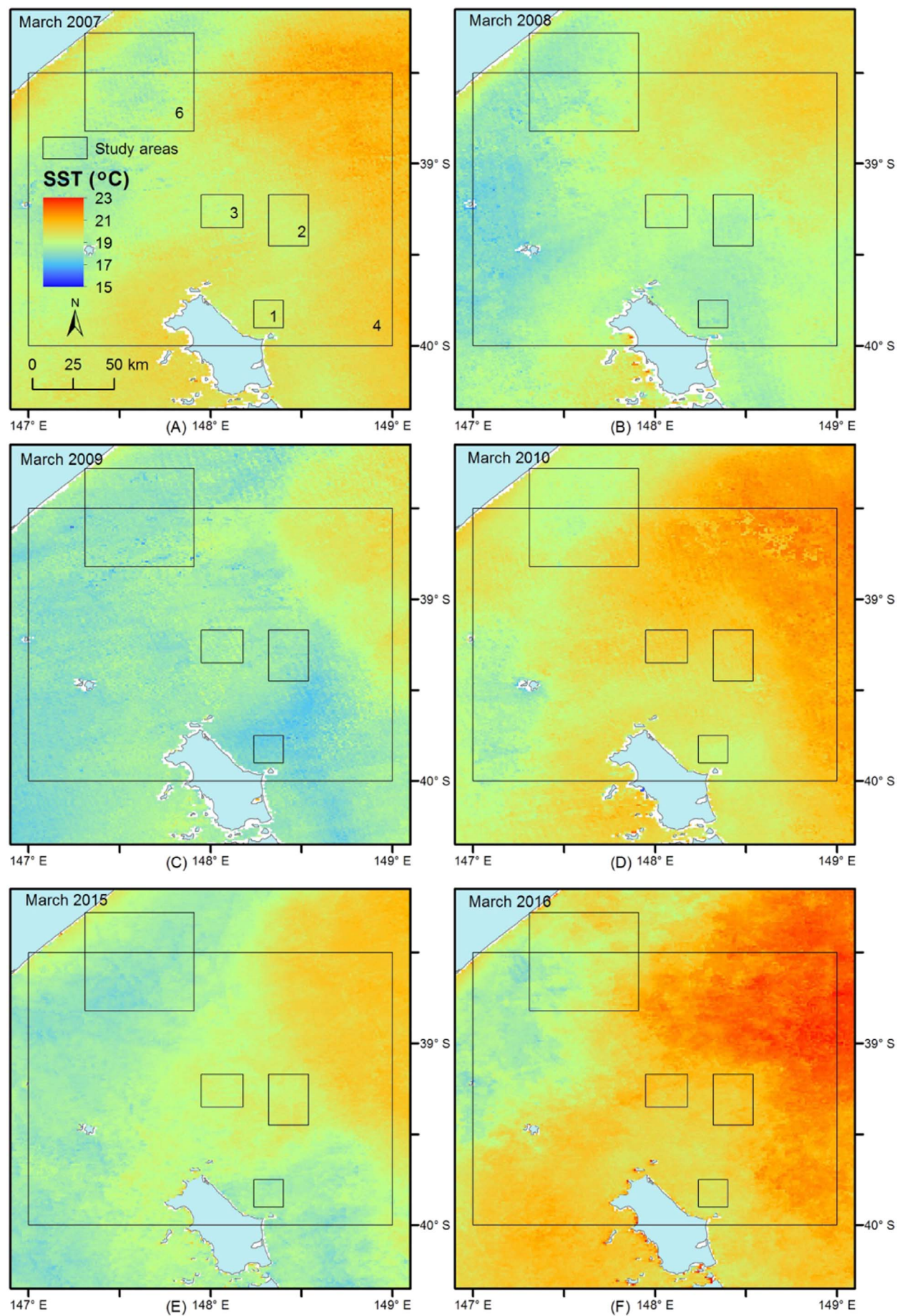
(caption on next page)

Fig. 8. SST images showing inter-annual variability. Rectangles represent study areas that are labelled in (A); study area 5 is not shown but includes all other areas and the rest of the Bass Strait. Areas 2 and 3 overlap scallop beds that showed mass mortality in 2010.

One of the main strengths of this study is its use of open water environments and industry-scale seismic surveys (e.g. Morris et al., 2018). By using the organisms' actual habitat, we observed natural responses to seismic airguns and avoided artefacts that can be introduced by aquaria or cages (Carroll et al., 2017). However, fieldwork obviously has its own challenges, and here these manifested as missing data (i.e. AUV data missing from 'before' survey), variable sample sizes (i.e. scallop catch was low on 'before' survey in experimental zone), and spatiotemporal variation in sample sites (i.e. dredge locations not balanced among zones and times). The two direct sampling methods used here (dredging and AUV) complemented limitations of the other in showing that mass mortality, such as that seen in 2010, was observed neither in images nor specimens. Future field observational studies can reduce such risk by the following:

- Undertake a preliminary marine survey to establish population distributions and densities of target organisms, as well as establishing appropriate equipment parameters if using imagery or complex monitoring technology.
- Adopt a multi-experimental approach, integrating the controlled aspects of laboratory studies with the ecological realism of field studies; this will likely provide a more comprehensive assessment of stressors than either approach alone (e.g. Thomsen et al., 2013).
- Consider large mesocosm experiments as an intermediate approach, incorporating the best aspects of manipulative laboratory and observational field studies (Sagarin et al., 2016).

This study represents an important step in expanding our understanding of the potential impacts of seismic surveys on marine invertebrates. Results from this study will be of direct use to a range of stakeholders, including fisheries industry to better understand the potential impacts of competing industries on future stocks and the oil and gas industry to develop best practice techniques. In conjunction with related research, our results will inform future environmental plans seeking approval to undertake a seismic survey, as well as the assessment of environmental plans by regulatory authorities (Prideaux and Prideaux, 2016).

Author contributions

RP conceived, conducted and analysed the study. ZH led the satellite imagery analysis. ME and SW led the AUV image acquisition, and AC, JA, and LH annotated and analysed imagery. RP and ZH wrote the paper.

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Appendix A. Supplementary data and text

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Review

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

A.G. Carroll [a,*], R. Przeslawski [a], A. Duncan [b], M. Gunning [c], B. Bruce [d]

[a] National Earth and Marine Observations Branch, Geoscience Australia, GPO Box 378, Canberra ACT 2601, Australia
[b] Centre for Marine Science and Technology, Curtin University, GPO Box U1987, Perth WA 6845, Australia
[c] Energy Systems Branch, Geoscience Australia, GPO Box 378, Canberra ACT 2601, Australia
[d] Commonwealth Scientific and Industrial Research Organisation, GPO Box 1538, Hobart TAS 7001, Australia

A B S T R A C T

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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* Corresponding author.
  E-mail address: andrew.carroll@ga.gov.au (A.G. Carroll).

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

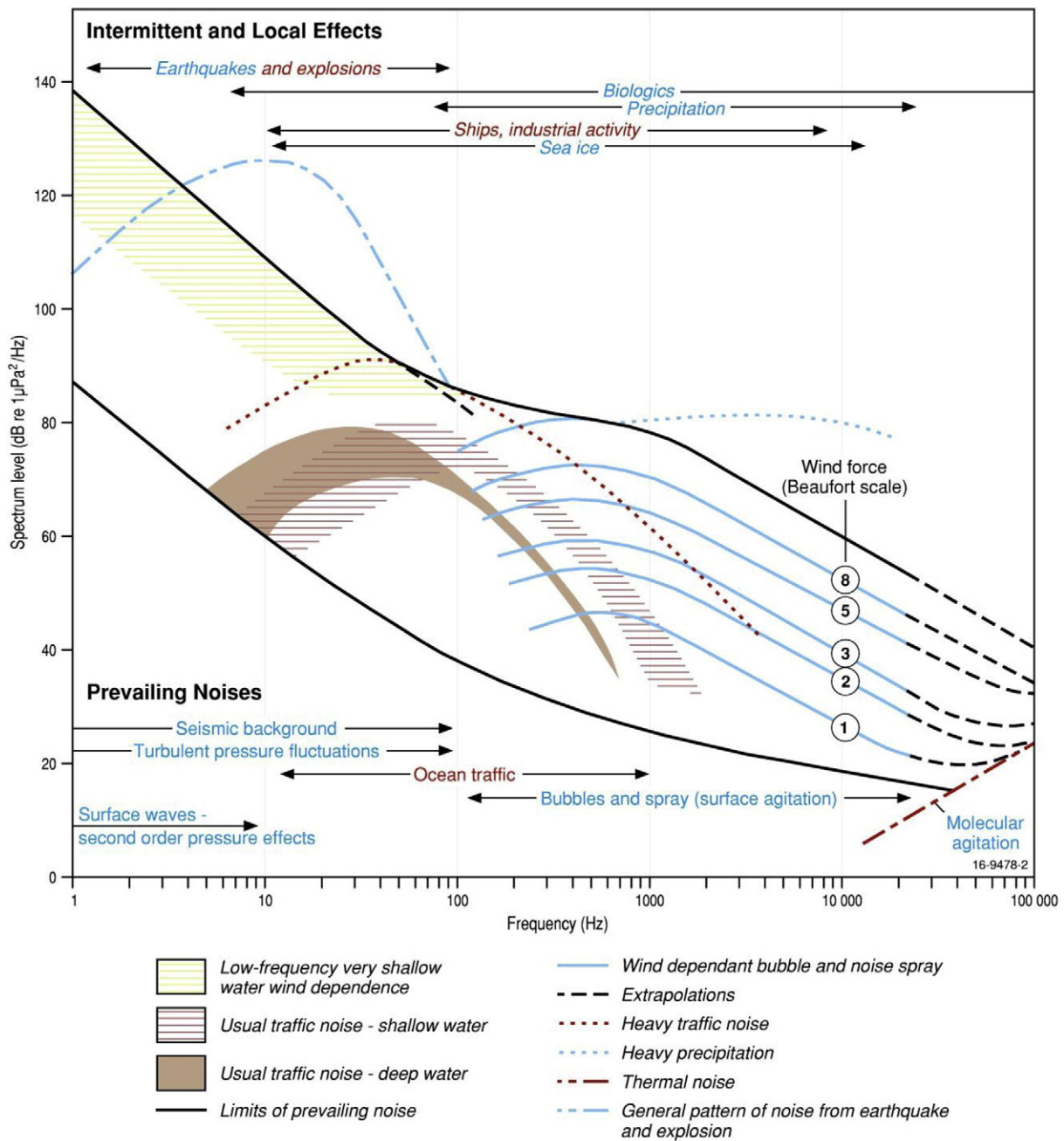**Fig. 1.** Diagram of ambient noise spectra levels (commonly referred to as the Wenz curves) in a marine environment showing pressure spectral density levels of marine ambient noise from precipitation, wind, geological activity, and anthropogenic sources (commercial shipping and seismic activity). Horizontal 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 (saccule, 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 saccule, 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.
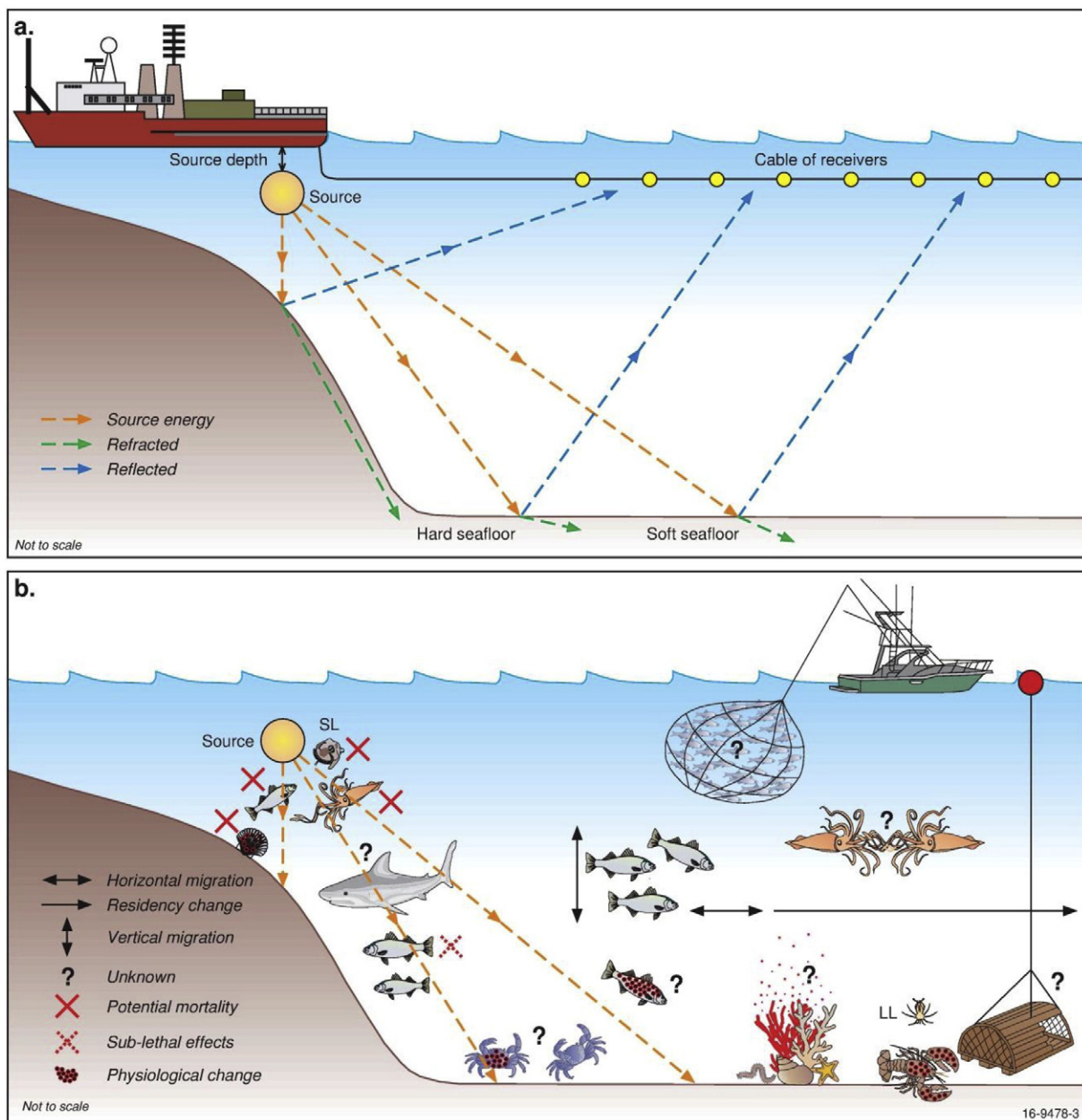
Fig. 2. Conceptual models showing a) physical characteristics and variation regarding sound propagation through the water column and seabed, and b) potential biological impacts of low frequency sound exposure as described in main text. SL = Scallop larvae; LL = Lobster larvae. References can be found 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 otophysic 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 μPa) 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 μPa 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 μm 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 1μPa 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,

	Adult/juvenile fish		Fish eggs/larvae		Elasmobranchs
PHYSICAL					
Swim bladder damage	1,2				*(not applicable)*
Otolith/inner ear damage	3	4			
Temporal Threshold Shift	5	1a,3a			
Permanent Threshold Shift	5				
Organ/tissue damage	1,2,6				
Mortality	1,2,6-11		12-14	13,15	
BEHAVIOURAL					
Startle/alarm response	1,8a	6,7,8a,9,16,17			
Sound avoidance/migration*	9,18-20	7,12,16-18,21-23,24a	18		
Other changes in swimming	20				
Predator avoidance					
Foraging					
Reproduction					
Intraspecific communication					
PHYSIOLOGICAL					
Metabolic rates					
Stress bio-indicators	16	6a	10a		
Metamorphosis/settlement					
CATCH EFFECTS					
Catch rates /abundance	7,19,25,26	21-23	12,18,23,27,28		28

1= Popper et al. 2005*, 2 = Popper et al. 2016*, 3 = Song et al. 2008*, 4 = McCauley et al. 2003, 5 = Hastings and Miksis-Olds 2012, 6 = Santulli et al. 1999, 7 = Hassel et al. 2004, 8 = Boeger et al. 2006, 9 = Wardle et al. 2001, 10 = Radford et al. 2016*, 11 = McCauley and Kent 2012, 12 = Dalen and Knutsen 1987, 13 = Booman et al. 1996, 14 = Payne et al. 2009, 15 = Kostyuchenko 1973, 16 = McCauley et al. 2000, 17 = Pearson et al. 1992, 18 = Løkkeborg et al. 2012, 19 = Pickett et al. 1994, 20 = Peña et al. 2013, 21 = Skalski et al. 1992, 22 = Slotte et al. 2004, 23 = Engås et al. 1996, 24 = Chapman and Hawkins 1969, 25 = Miller and Cripps 2013, 26 = Thomson et al. 2014; 27 = Løkkeborg and Soldal 1993, 28 = Przeslawski et al. in prep.

1a: Statistically significant hearing loss immediately upon exposure of freshwater adult Northern Pike to 5 pulses at 400 Hz and exposure of Lake Chub to 5 and 20 pulses at 200, 400 and 1600 Hz. Recovery within 18 hrs. A shift was observed only in adults and not in juvenile Pike.

3a: Adult freshwater Northern Pike and Lake Chub exhibited temporary hearing loss, but no damage to the sensory epithelia studied in any of the otolithic end organs, demonstrating that hearing loss in fishes is not necessarily accompanied by morphological effects on the sensory hair cells.

8a: Repeated exposure to air guns resulted in increasingly less obvious startle responses in effected fish, indicating possible habitation to the disturbance.

10a: 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.

24a: Free ranging Whiting school responded to airgun sound by shifting downward, temporary habituation was observed after one hour of continual sound exposure.

* Includes changes in vertical/horizontal distribution.

*Freshwater/brackish species.

KEY

⬛ (red)	Response at realistic exposure levels	⬛ (blue)	Possible response (conflicting results)
⬛ (yellow)	Response at unrealistic/unknown exposure levels	⬛ (dark grey)	No data, has not been tested
⬛ (green)	No response at either realistic or unrealistic exposure levels	⬛ (light grey)	Not applicable

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								
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 a; 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 = Fewtrell 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 2013, 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 = Filiciotto et al 2014, 31 = Branscomb and Rittschof 1984, 32 = Andriguetto-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 superseded 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 (Andriguetto-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 μPa whereas no response was observed vermilion (*S. miniatus)* or brown (*S. auriculatus)* rockfish up to the maximum exposure of 207 re 1 μPa 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 μPa. 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 μPa 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 μPa rms and 0.01 m·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* supressing their respiration at 50–150 Hz (120 rms dB re 1μPa) (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 haeomolymph 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 glocuse 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-pomacentridae 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 μPa² 0-peak) did not result in increased larval mortality (Bolle 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 Materia 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 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) (Bolle 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; Andriguetto-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

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