Methods in Ecology and Evolution

British Ecological Society

Methods in Ecology and Evolution 2016 doi: 10.1111/2041-210X.12544

Particle motion: the missing link in underwater acoustic ecology

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Summary

1. Sound waves in water have both a pressure and a particle-motion component, yet few studies of underwater acoustic ecology have measured the particle-motion component of sound. While mammal hearing is based on detection of sound pressure, fish and invertebrates (i.e. most aquatic animals) primarily sense sound using particle motion. Particle motion can be calculated indirectly from sound pressure measurements under certain conditions, but these conditions are rarely met in the shelf-sea and shallow-water habitats that most aquatic organisms inhabit. Direct measurements of particle motion have been hampered by the availability of instrumentation and a lack of guidance on data analysis methods.

2. Here, we provide an introduction to the topic of underwater particle motion, including the physics and physiology of particle-motion reception. We include a simple computer program for users to determine whether they are working in conditions where measurement of particle motion may be relevant. We discuss instruments that can be used to measure particle motion and the types of analysis appropriate for data collected. A supplemental tutorial and template computer code in MATLAB will allow users to analyse impulsive, continuous and fluctuating sounds from both pressure and particle-motion recordings.

3. A growing body of research is investigating the role of sound in the functioning of aquatic ecosystems, and the ways in which sound influences animal behaviour, physiology and development. This work has particular urgency for policymakers and environmental managers, who have a responsibility to assess and mitigate the risks posed by rising levels of anthropogenic noise in aquatic ecosystems. As this paper makes clear, because many aquatic animals senses sound using particle motion, this component of the sound field must be addressed if acoustic habitats are to be managed effectively.

Key-words: accelerometer, aquatic invertebrates, bioacoustics, fish, paPAM, Particle motion, sound analysis programme, underwater acoustics

Introduction

Auditory cues are particularly useful in aquatic habitats, as sound travels relatively far and relatively fast in water (Ainslie 2010). For this reason, a large number of aquatic organisms have evolved ways of detecting and producing sound (Song, Collin & Popper 2015) and aquatic bioacoustics has been an active field of study for many decades (Au & Hastings 2008). Audiometric studies have long recognized the significance of particle-motion detection in fishes and invertebrates (e.g. Chapman & Hawkins 1973; Fay 1984; Popper, Salmon & Horch 2001), yet investigations of acoustic phenomena in the ecology of aquatic systems have previously focused on only one component of the sound field: sound pressure (see for exception Banner 1968; Sigray & Andersson 2011).

From an ecological perspective, there are several key reasons why we need to better understand the particle-motion component of underwater sound. First, while aquatic mammals use sound pressure, all fish and many invertebrates (i.e. most acoustically receptive aquatic organisms) detect and use the particle-motion component of sound (Popper, Salmon & Horch 2001; Bleckmann 2004; Kaifu, Akamatsu & Segawa 2008). The role that particle motion plays in the biology and ecology of these species is largely unknown. (Particle motion is also important in terrestrial bioacoustics for invertebrates; however, its measurement is better established (see Morley, Jones & Radford 2014). Second, fish and invertebrates are socio-economically important and form the basis of many food webs (Béné, Macfadyen & Allison 2007). Third, anthropogenic (man-made) sounds can have detrimental effects on marine fauna, and are increasingly recognized as a global challenge (Popper & Hastings 2009; Slabbekoorn *et al.* 2010). While there is mounting evidence and accompanying

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legislation surrounding the impacts of anthropogenic noise on fishes and invertebrates, until now the focus has been on sound pressure, even though many (if not most) of these species cannot directly sense this component of sound.

In some cases, particle motion can be calculated from sound pressure. However, sound pressure and particle motion are directly related only under specific conditions, which are not generally met in the shelf seas and shallow waters that most aquatic life inhabit. To characterize particle motion in these habitats, it is therefore necessary to make measurements using a particle-motion sensor. Instruments to measure particle motion have only recently become commercially available, and their use in tank experiments and field studies is still in its infancy (Popper *et al.* 2014; Merchant *et al.* 2015; Martin *et al.* 2016). As the uptake of these novel sensor technologies gathers pace, there is a growing need for user-friendly guidance on the methods, instrumentation, and underlying physics of particle-motion measurement to ensure broad understanding of – and participation in – this research effort. The relevant sectors extend from researchers to consultants to environmental managers, who are beginning to address the rising influence of anthropogenic noise on aquatic ecosystems. It is therefore important that the significance of particle-motion measurement is clearly articulated for non-specialists.

Here, we provide a brief introduction to underwater particle motion in an ecological context. We begin with an accessible overview of the physics of particle motion and the detection of particle motion by fishes and invertebrates. To help inform new studies, we offer practical guidance on instrumentation and data analysis techniques for particle-motion measurement, as well as software in MATLAB (Mathworks, Natick, MA, USA) to analyse particle-motion data, including tutorial materials and example data. Finally, we identify several key knowledge gaps related to particle-motion in aquatic environments, which warrant further research.

Physics of particle motion

Sound is propagated vibratory energy (Gans 1992). Put simply, a sound wave propagates because particles next to a vibrating source are moved backwards and forwards in an oscillatory motion; these particles then move the particles next to them and so on, resulting in the propagation of vibratory energy. The particles of the medium do not travel with the propagating sound wave, but transmit the oscillatory motion to their neighbours. This *particle motion* contains information about the direction of the propagating wave. Particle motion can be expressed as displacement (m), velocity (m s^{-1}) or acceleration (m s^{-2}). These three quantities are directly related in a frequency-dependent way (see Box 1).

Sound pressure is the variation in hydrostatic pressure caused by the compression and rarefaction of particles as the sound wave propagates. If a sound can be assumed to be propagating as a *plane wave* (see below), then there is a simple relationship between sound pressure and particle velocity (Box 2). Particle acceleration and particle displacement can then be derived from the particle velocity if required (Box 1). A plane wave occurs where the wavefront can be considered flat: this is generally far from the sound source and far from boundaries where reflections could influence the shape of the wavefront (the definition of 'far' here depends on the wavelength of sound and the dimensions of the source; see Appendix S1). These conditions are typically not met in coastal and shelf-sea habitats at the low acoustic frequencies commonly used by fish and invertebrates, meaning there is not a reliable way to derive particle motion from sound pressure measurements. Although the relationship between particle motion and sound pressure can, in theory, be derived for more complicated wavefronts (e.g. by assuming an idealized geome-

Box 1. Relationships between particle velocity, particle acceleration and particle displacement

Particle velocity, acceleration and displacement are always linked by the following equations:
Velocity and acceleration:

$$a = u \times 2\pi f, \qquad \text{Eqn 1.1}$$

where a = acceleration (m s^{-2}), u = particle velocity (m s^{-1}) and $2\pi f$ = angular frequency (f = frequency in Hz).
Velocity and displacement:

$$\xi = \frac{u}{2\pi f}, \qquad \text{Eqn 1.2}$$

where ξ = displacement (m), u = particle velocity (m s^{-1}) and $2\pi f$ = angular frequency (f = frequency in Hz).

Box 2. Calculating particle motion from sound pressure

In a plane wave, sound pressure is directly related to particle velocity:

$$u = \frac{P}{\rho c'} \qquad \text{Eqn 2.1}$$

where u = particle velocity (m s^{-1}), P is acoustic pressure (Pa), ρ = density of the water (kg m^{-3}) and c = sound speed (m s^{-1}) (ρc is also known as characteristic acoustic impedance). This is only applicable in a plane wave or where a plane wave is a suitable approximation (i.e. in the free field). Particle acceleration or displacement can be calculated from velocity using equations in Box 1.
In the near field of a point source, far from any boundaries that could lead to the wave not propagating due to the cut-off frequency, or reflections that could interfere with the propagating wave, the following equation can be used to calculate particle displacement from sound pressure:

$$\xi = \frac{p}{2\pi f \rho c}\left[1 + \left(\frac{\lambda}{2\pi r}\right)^2\right]^{\frac{1}{2}} \qquad \text{Eqn 2.2}$$

where ξ = displacement (m), p = pressure (Pa), f = frequency, ρ = density of the water (kg m^{-3}), c = sound speed (m s^{-1}) and r = distance to sound source (m). Particle acceleration or velocity can be calculated from displacement using equations in Box 1 (Chapman & Hawkins 1973).

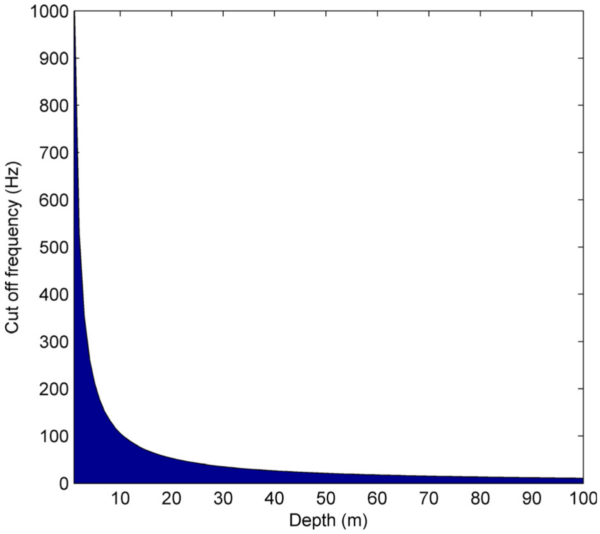

Fig. 1. Cut-off frequency as a function of depth, calculated for a coarse silt bottom with a sound speed of 1593 ms^{-1} and density of 1693 kg m^{-3}, assuming that sound speed in water is 1500 ms^{-1} and water density is 1026 kg m^{-3}. Sounds below the cut-off frequency will not propagate as a plane wave and particle motion cannot be calculated from pressure; thus, it should be measured. Cut-off frequency (f_c) is calculated using the equation: $f_c = (\pi - \rho_{sed}/\rho_w)/(2\pi \sin\psi_c)\ (c/H)$ where ρ_{sed} = sediment density, ρ_w = water density, $\psi_c = \arccos\ (c/c_{sed})$, c = sound speed in water, c_{sed} = speed of sound in the sediment and H = water depth (Ainslie 2010).

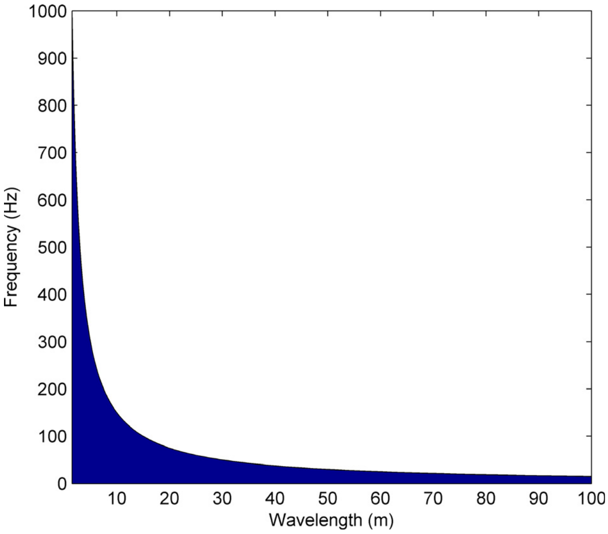

Fig. 2. Wavelength as a function of frequency, calculated for an assumed sound speed in water of 1500 ms^{-1} using $\lambda = 1500/f$, where λ = wavelength and f = frequency in Hz.

try such as a spherical wavefront), for realistic scenarios direct measurement of particle motion is the only reliable method.

Note that in addition to the distance to the sound source and the proximity of boundaries, whether the plane-wave approximation is valid can be affected by other factors, such as: the size of the sound source; the cut-off frequency, which is related to the water depth (see Fig. 1); the wavelength of sound; and variations in the sound-propagation environment (e.g. sound speed variations in the water column and seabed, determined by temperature, density and salinity). As a rule of thumb, particle-motion measurement should be considered at depths of less than 100 m and frequencies less than 1 kHz, and at distances from the source of less than the Fraunhofer distance (distance where the near field transitions to the far field) or one wavelength (Fig. 2), whichever is greater. The calculator provided in the 'tools' section of Appendix S1 (with instructions in user guide Appendix S1) allows a user to enter frequencies, depths and information about the sound-propagation environment and provides advice about whether particle-motion measurement is necessary, along with a tool for predicting particle-motion levels when measurement is not necessary. In tank measurements, near-field effects, resonant frequencies and reflections will lead to a complex relationship between particle motion and pressure; thus, particle motion should always be measured directly.

Hearing of particle motion

Hearing is the detection of propagated vibratory energy by the ear (Gans 1992). All hearing is based on mechanosensory hair cells transducing vibrations into electrical signals. Particle oscillations can either be detected directly by hair cells that protrude into the medium (air or water), or by the relative motion between the body and a solid structure in the ear to which the hair cells are attached (Gans 1992). The bodies of fish and aquatic invertebrates, being composed mainly of water, are coupled directly to the medium (water). Thus, the whole body vibrates as a sound wave passes through. Denser calcareous structures in the inner ears, such as the otoliths and statocysts, lag behind the vibration of the body due to their impedance difference (being denser). Chordontal organs are also found in the legs of some crabs and allow detection of sounds propagating in the substrate by sensing leg movement (Popper, Salmon & Horch 2001). Hearing in fish and invertebrates seems to be focused in the lower frequencies; although some fish can hear up to over 100 kHz, most have a peak sensitivity under 1·5 kHz (Popper & Fay 1993; Popper & Hastings 2009; Fay & Popper 2012). The hearing of particle motion in fishes is relatively well understood (see e.g. Fay 1984; Radford *et al.* 2012), but until recently, the availability of instrumentation for use in the field has hindered our understanding of the ecology of particle motion underwater.

Instrumentation

Although measuring particle motion has been possible for decades, instruments to record particle motion have only recently become available commercially. There are three main methods of measuring particle motion underwater: (i) calculating the pressure gradient between two hydrophones; (ii) measuring with velocity sensors; and (iii) measuring with accelerometers (Martin *et al.* 2016). To measure particle motion using pressure gradients, it is necessary to calibrate the phase response of the hydrophones accurately (Zeddies *et al.* 2010). While this method has been applied successfully (e.g. Zeddies *et al.* 2010), it requires costly hydrophones, which can make highly accurate phase measurements, in addition to the necessary expertise for phase calibration. Velocity sensors (geophones) typically have a very low resonance and are only useful up to a few tens of Hertz. While geophones make better sensors for seismic measurements, accelerometers are more appropriate for acoustic measurements. As frequency increases, acceleration magnitude increases in relation to velocity magnitude, meaning the signal-to-noise ratio is better with an acceleration-based sensor. Given the limitations of the geophone and pressure-gradient approaches, the accelerometer will normally be the best option for particle-motion measurements in the frequency ranges relevant to fishes and invertebrates.

Accelerometers work in a similar fashion to fish ears: they measure the relative motion between the body of the device and a denser structure within. Thus, the coupling between the device and the water must be understood for accurate measurements to be made. Ideally, the accelerometer should be neutrally buoyant, meaning that it behaves in the same way as the surrounding water (e.g. Leslie, Kendall & Jones 1956). However, neutrally buoyant devices can be difficult to position and orientate as they drift with water movement. Negatively or positively buoyant devices are more practical as they can be suspended from the surface, the seabed, or some other platform. The effect of gravity can then be filtered out as part of the instrument calibration, although there may still be some effect on the vertical axis (Sigray & Andersson 2011), which needs testing.

The accelerometer functions by transducing changes in proper acceleration (‘g-force’, i.e. acceleration relative to free fall) in the x, y and z directions into current fluctuations, which are converted to voltages before being recorded by a digital device. The digital recorder must also be calibrated. This can be carried out by recording a signal such as a sine wave (or ‘pure tone’), which has a known voltage. The recorded voltage is then compared with the known voltage to establish the effect of the device on the voltage. Step-by-step instructions for calibrating recorders can be found in Appendix S1 (note that the same method can be used for recorders that are used with hydrophones or microphones). Manufacturers of recorders should provide information on the bandwidth over which a recorder has a flat frequency response. This is the range that a calibration of a single tone will be valid, provided the tone lies within this bandwidth. Alternatively, a frequency-dependent calibration can be carried out by measuring sine waves at several frequencies within the range of interest. It is advisable to calibrate recorders regularly (e.g. once per field season or year), as slight changes can occur with age, climate or travel. It is also advisable to measure the noise floor of the instrument (the self-noise generated when no sound is present, e.g. in an acoustically isolated chamber) to assess whether measured particle motion levels are due to instrument self-noise.

Data analysis

There are no current standard methods for analysing particle-motion data. We provide a user-friendly tutorial (Appendix S1) and analysis programme (Appendix S2) for each of the steps needed to analyse data recorded from triaxial accelerometers or particle velocity sensors. Here, we present a non-technical outline of the analyses appropriate to recordings of different sound types.

When making recordings from an accelerometer, digitally recorded voltage fluctuations represent changes in particle acceleration that occur as a result of the particle motion in a sound wave. A plot of these fluctuations is called a ‘waveform’; values exceed 0 when the wave is ‘pushing’ away from the source (when the phase of the wave is between 0 and 180°) and are below 0 when the wave is ‘pulling’ towards the source (when the phase of the wave is between 180 and 360°) (see Fig. 3). Using calibration information, these voltage fluctuations can be converted back to represent particle acceleration. Various analyses can then be applied to waveforms to quantify the sounds they represent, thus allowing us to summarize and compare sounds.

Impulsive and continuous sounds are typically quantified in different ways (Hawkins, Pembroke & Popper 2015). For impulsive sounds, the peak or peak-to-peak amplitude, rise time, crest factor and sound exposure level (SEL) are appropriate measures. For continuous sounds (or sounds that are longer lasting and thus better summarized using approximations to continuous sounds), it is more useful to average amplitudes over time. The simple mean level from the waveform would result in 0; thus, the root mean squared (RMS) is used.

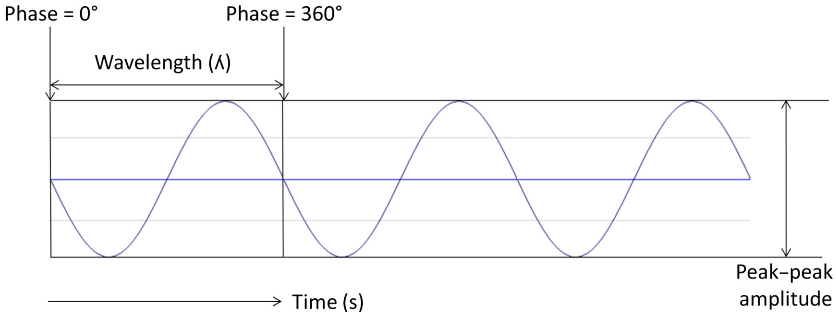

Fig. 3. Schematic of a sine wave illustrating phase, wavelength and peak–peak amplitude. Time is on the *x*-axis. The *y*-axis could apply to pressure (for sound pressure levels), particle velocity, particle acceleration, or particle position in space (for particle displacement), or voltage (the language of instruments that measure any of the above).

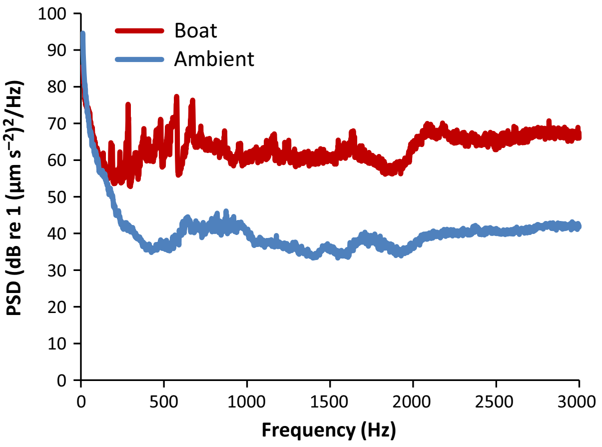

Fig. 5. Example power spectral density figure created in excel from spreadsheet output of mean values from recordings of ambient and boat noise. Mean over 60 s. FFT length = fs, giving a frequency resolution of 1 Hz.

One way to assess the variability in sound over time is to measure consistency; the amount of time that the RMS exceeds a predefined sound level (Gill *et al.* 2015).

Impulsive sounds can have enough energy that they cause physical injury such as barotrauma in fish (Halvorsen *et al.* 2012), although this is not always the case (Kane *et al.* 2010). Sound energy from outside the hearing range of the animal concerned can also contribute to injury. For this reason, energy at all frequencies measured is usually included in impulse measurements when impulses may be loud enough to cause injury. It is thus important to consider the frequency response of equipment used to measure impulses, because conclusions could be compromised if recording equipment does not have a flat frequency response across the range of frequencies encompassing the peak frequencies of the pulse (Merchant *et al.* 2015).

For sounds that do not have enough energy to cause physical injury, the hearing range of the species of interest affects the frequencies of recorded sounds that are relevant. If the auditory sensitivity of the species of interest is known (rare, even in the pressure domain, but see Casper & Mann 2007; Radford *et al.* 2012 for exceptions), frequencies outside the range of hearing can be filtered out before calculating impulse metrics or RMS levels. Another useful way to account for the fact that different animals have different auditory abilities is to look at the energy present across the frequency spectrum, for example, at 1 Hz resolution. This information can either be plotted over time in a 3-D spectrogram (Fig. 4), where amplitude is coded by colour, or averaged over time by RMS and plotted on a 2-D power spectral density plot (PSD, Fig. 5). Variability in sound levels over time can be represented on a PSD by percentiles or ‘exceedance levels’ in addition to the mean.

There are currently no internationally agreed standard units for particle-motion measurement. Here, we use the following units in lieu of such standards (M. Ainslie, pers. comm.): displacement (dB re 1 pm), velocity (dB re 1 nm s^{-1}), acceleration (dB re 1 µm s^{-2}). From a technical viewpoint, velocity, acceleration and displacement are equally valid representations. All three can be found in the literature (e.g. Banner 1968; Fay & Popper 1974; Radford *et al.* 2012). We consider that the acceleration is the most relevant, as it is closest to the way that fish and invertebrate auditory systems function (Au & Hastings 2008; Mooney *et al.* 2010). The analyses outlined above can all be carried out using the software provided in Appendix S2.

Discussion

It has been known for decades that fishes and invertebrates hear particle motion (e.g. Cahn, Siler & Wodinsky 1969). However, although many papers written about sound and fishes and/or invertebrates have acknowledged the importance of particle motion (e.g. Wale, Simpson & Radford 2013; Kunc *et al.* 2014; Neo *et al.* 2015; Simpson, Purser & Radford 2015), very few have reported particle motion measurements, particularly in field studies, but see for exceptions (Chapman & Hawkins 1973; Nedelec *et al.* 2014, 2015). Published examples

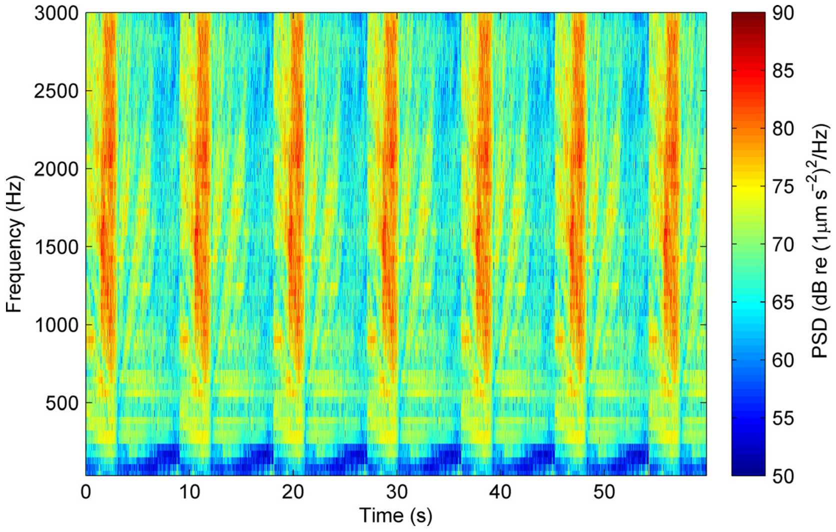

Fig. 4. Example spectrogram output from a recording of a motorboat passing multiple times. Window = Hamming, window length = 1024, overlap = 50%.

of measurements of ambient underwater particle motion are also rare (see Banner 1968; Lugli & Fine 2007 for exceptions). The major obstacle to scientific progress in this area has been the availability of appropriate equipment and the expertise to apply it in laboratory and field studies. Here, we have highlighted the recent availability of commercial instruments and their potential to make particle-motion measurement more accessible to researchers. We are optimistic that the analysis tools provided in the supporting information will encourage others to participate in this research effort.

We have laid out some priorities for particle-motion measurements in Box 3. particle-motion measurement may play a role in answering important biological and ecological questions relating to fishes and invertebrates. From a methodological perspective, there are several related topics that warrant further attention. Deviations between sound pressure and particle motion can be high in the near field (near sound sources), meaning sound cues such as vocalizations are likely to be detectable at different ranges via particle motion compared with sound pressure. This is also the case for anthropogenic noise sources, such as pile driving and shipping, which may have near-field effects on fishes and invertebrates that scale with particle motion rather than sound pressure. Methods to measure and model the particle-motion field at close ranges are needed to understand better the behavioural and evolutionary implications for acoustic communication, and the potential effects of noise on aquatic fauna. A related subject is the role of directionality in these effects: sound pressure signals do not contain directional information, whereas particle motion is inherently directional, which gives information about source direction. To what extent this information is used by fish and invertebrates, and by what mechanism these animals resolve the 180° ambiguity in source direction are as yet uncertain (Bleckmann 2004). Finally, there is the inclusion of particle motion in remote sensing and modelling of acoustic habitats. Measurements of particle motion could improve eco-hydro-acoustic models for environmental impact assessment where fish and invertebrates may be affected by anthropogenic noise (e.g. Rossington *et al.* 2013; Bruintjes *et al.* 2014). More generally, the use of remote sensing to monitor and model acoustic habitats is a growing area in relation to sound pressure (Gill *et al.* 2015; Merchant *et al.* 2015), and the extension of these techniques to include the particle-motion component of sound would further improve our understanding of natural and human-influenced soundscapes and their interactions with aquatic ecosystems.

Box 3. Priorities for particle motion measurements

1) Comparison of different suspension methods on calibration of accelerometers constrained in the vertical axis.
2) Comparisons between measured sound pressure levels, sound velocity levels, sound acceleration levels and modelled sound velocity and acceleration levels. With varying
  i Source type
  ii Source distance
  iii Water depth
  iv Bottom type
3) Comparisons of effects of sounds on fish where the pressure is maintained constant, but particle-motion levels are varied (can be achieved by adjusting speaker volume and distance). Conduct with
i Species that cannot detect pressure (i.e. do not possess a swim bladder)
ii Species that can detect pressure (i.e. possess a swim bladder)
4) Maps of areas where models cannot predict particle motion from pressure. Overlay with species presence or biomass.
5) Mechanisms used for sound source localization
i Are fish able to localize sound sources in the far field?
ii How do invertebrates localize sound sources?
6) Does particle motion allow a release from masking for nearby signals in distant noise? This information should be incorporated into models predicting impacts of anthropogenic noise, which are thus far only based on pressure measurements.
7) Effect of accelerometer size on particle-motion measurements in small tanks.

Acknowledgements

We thank Michael Ainslie, Hans Slabbekoorn and Innes Cuthill for helpful comments on a draft of this manuscript and Geospectrum for providing us with an accelerometer and associated logistical support.

Data accessibility

This paper does not use data.

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Received 14 October 2015; accepted 5 January 2016
Handling Editor: Diana Fisher

Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. paPAM. User Manual for version 8.7.

Appendix S2. paPAM software v0.872.