Sensitivity of *Pagurus bernhardus* (L.) to substrate-borne vibration and anthropogenic noise

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Abstract

Despite the prevalence of vibration produced by anthropogenic activities impacting the seabed there are few data and little information as to whether these are detected by crustaceans and whether they interfere with their behaviour. Here the sensitivity of unconditioned *Pagurus bernhardus* to substrate-borne vibration was quantified by exposure to sinusoidal vibrations of 5 – 410 Hz of varied amplitudes using the staircase method of threshold determination, with threshold representing the detection of the response and two behavioural responses used as reception indicators: movement of the second antenna and onset or cessation of locomotion. Thresholds were compared to measured vibrations close to anthropogenic operations and to the time in captivity prior to tests. Behaviour varied according to the strength of the stimulus with a significant difference in average threshold values between the two behavioural indicators, although there was overlap between the two, with overall sensitivity ranging from 0.09 – 0.44 m s^{-2} (root mean squared, RMS). Crabs of shortest duration in captivity prior to tests had significantly greater sensitivity to vibration, down to 0.02 m s^{-2} (RMS). The sensitivity of *P. bernhardus* fell well within the range of vibrations measured near anthropogenic operations. The data indicate that anthropogenic substrate-borne vibrations have a clear effect on the behaviour of a common marine crustacean. The study emphasises that these vibrations are an important component of noise pollution that requires further attention to understand the long term effects on marine crustaceans.

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1. Introduction

There is an increasing concern that man-made noise is having a marine ecological impact, hence its inclusion in the OSPAR and HELCOM Regional Seas Conventions and within the European Marine Strategy Framework Directive (2010), which includes noise as a Descriptor to achieve Good Environmental Status (GES) (Borja et al., 2013). Although there has been recent progress, there are still insufficient data on the levels of noise causing injury or responses in fish and invertebrates (Hawkins et al., 2014a; Popper et al., 2014). Within this, the impact of seabed vibration upon marine organisms has been largely neglected even though many activities involve direct contact with the seabed, for example pile driving and drilling. These produce substrate-borne vibrations which can travel as compressional (longitudinal), transverse (shear) or surface (Rayleigh or ‘ground roll’) waves (Aicher and Tautz, 1990; Hazelwood and Macey, 2015; Markl, 1983), with energy being transmitted in one or multiple waveforms depending on the substrate type, boundary layers, and connection to the substrate (Aicher and Tautz, 1990). The energy of low frequency Rayleigh waves in particular, may travel large distances from the source (Brownell, 1977), trapped within the surface seabed with minimal attenuation (Hazelwood and Macey, 2015). Thus animals may detect, and be affected by vibration at large distances from anthropogenic sources. However there are few data on levels of detection and the levels produced by such sources (reviewed in Roberts, 2015), this makes the impacts of such vibrations on marine organisms difficult to ascertain.

Whilst sound comprises both pressure waves and particle motion (water and substrate-borne), crustaceans appear to respond to particle motion only (Breithaupt and Tautz, 1988; 1990; Goodall et al., 1990; Monteclaro et al., 2010; Plummer et al., 1986; Roberts and Breithaupt, 2015; Tautz and Sandeman, 1980). Such detection is likely since sound production is widespread in crustaceans, from snapping shrimp (Johnson et al., 1947; Knowlton and Moulton, 1963; Schmitz and Herberholz, 1998; Versluis et al., 2000) to lobster and crab stridulation (Aicher et al., 1983; Field et al., 1987; Henninger and Watson, 2005; Horch, 1971; 1975; Moulton, 1957; Patek, 2001; Patek et al., 2009), rumbling of mantis shrimps (Order Stomatopoda) (Patek and Caldwell, 2006; Staaterman et al., 2011) and shell rapping in hermit crabs (Briffa and Elwood, 2000).

Substrate-borne vibration detection studies have been predominantly directed towards semi-terrestrial fiddler crabs, which use vibration for communication and courtship (Aicher and Tautz, 1990). Thresholds of sensitivity have been determined using electrophysiological techniques (Aicher and Tautz, 1984; Salmon and Horch, 1973; Salmon et al., 1977) and behavioural observations (Salmon and Atsaides, 1969) or a combination of both (Salmon, 1971; Salmon et al., 1977). These studies have demonstrated greatest sensitivity between 0.02 – 0.07 m s^{-2} (30 – 400 Hz, RMS) and 0.01 – 0.02 m s^{-2} (50 – 90 Hz, RMS) (Salmon, 1971; Salmon and Atsaides, 1969; Salmon and Horch, 1973) for behavioural and electrophysiology work respectively. Of the few data available for aquatic decapod crustaceans exposed to vibration, behavioural work with *Crangon crangon* has indicated thresholds of 0.4 – 0.81 m s^{-2} (20 – 200 Hz, peak) (Berghahn et al., 1995; Heinisch and Wiese, 1987). Thresholds for water-borne particle motion have been found in the range of 0.0002 – 1.4 m s^{-2} (3 – 400 Hz) but work has mostly focussed upon freshwater crayfish such as *Orconectes limosus* and *Procambarus clarkia* (Breithaupt, 2002; Breithaupt and Tautz, 1990; Goodall et al., 1990; Horch, 1971; Offutt, 1970; Tautz and Sandeman, 1980; Wiese, 1976). Most recently, Hughes et al. (2014) demonstrated sensitivity of the mud crab *Panopeus spp.* to water-borne stimuli in the range of 0.025 - 0.2 m s^{-2} (75 – 1600 Hz, RMS).

Establishing the sensitivity of an organism to an acoustic or vibratory stimulus typically involves producing a threshold curve spanning a range of frequencies (Fay and Popper (1974), measuring electrophysiological responses from individual sensory detectors (Breithaupt and Tautz, 1988; Mellon, 1963; Monteclaro et al., 2010; Tautz and Sandeman, 1980) or measuring the auditory evoked potential (AEP). For cephalopods, and some crustaceans, AEP has been successfully applied (Lovell et al., 2005; Mooney et al., 2010), but thresholds determined in this manner are less accurate than those determined by behavioural methodologies (Ladich and Fay, 2013; Sisneros et al., 2015). Response may also be affected by handling time and the possibility of acclimation to background noise levels and disturbance stimuli. This has been demonstrated in fishes (Chapman and Hawkins, 1969; Knudsen et al., 1992; Peña et al., 2013) but needs to be considered for other organisms when investigating behavioural sensory thresholds.

The present study aimed to determine to what extent the common marine intertidal hermit crab, *Pagurus bernhardus L.* (Family Paguridae) is sensitive to substrate-borne vibration, and to fully define the sensitivity range and behavioural responses in relation to levels produced by anthropogenic activities. The data were also related to the sensitivity of other species to vibration. Variation in threshold was investigated in relation to time spent in the laboratory prior to tests.

It is hypothesised that the sensitivities of *P. berhardus* to vibration would fall within the high levels produced by anthropogenic activities and within the range documented for other species. However the precise sensitivity of *P. bernhardus* to vibrations (natural or anthropogenic) is undocumented, although it may be similar to that of semi-terrestrial crabs (Aicher and Tautz, 1990; Salmon and Atsaides, 1969), of marine species such as *Nephrops norvegicus* and *C. crangon* (Goodall et al., 1990; Heinisch and Wiese, 1987) due to similar receptive mechanisms*.*

Hermit crabs were chosen due to the clear anti-predator mechanism (withdrawal into the shell) they undertake in stressful conditions (Chan et al., 2010a; Chan et al., 2010b; Elwood and Briffa, 2001), and their coastal distribution which means they are likely to encounter anthropogenic activities. Small behavioural changes (antenna movement, and changes in locomotion) were used to indicate vibration reception as in studies with other crustaceans (Berghahn et al., 1995; Breithaupt, 2002; Goodall et al., 1990; Heinisch and Wiese, 1987; Tautz, 1987), rather than a conditioning approach.

2. Materials and Methodology

Hermit crabs, *P. bernhardus* occupying *Littorina sp.* shells (shell height 15.9 – 23.3 mm, the total distance between the apical and basal extremities of the shell), were collected from Scarborough shore (54° 16' 15.3"N 0° 23' 17.1"W) and kept in a temperature controlled room with minimal disturbance and a 12 hour light 12 hour darkness regime, with an average water temperature of 11 - 12°C. The crabs were fed every 48 hrs on a diet of mixed shellfish and kept in small groups, and starved for 24 - 48 hours before tests. Partial water changes (25%) were undertaken every 2 - 3 days and water quality was monitored throughout. Within the holding tanks, crabs were free to move and interact. To reduce conflicts, the tanks contained shelters and spare shells. Post-moult individuals and those with missing appendages were not used. A minimum acclimation period of 24 - 48 hours was allowed between collection and testing.

2.1 Experimental setup and threshold determination

The experimental setup consisted of a tank (with external vibration dampening) with a stinger rod descending vertically to the sandy substrate, which transmitted vibrations from an electromagnetic shaker (LDS v101, 8.9 N, 5 - 12,000 Hz) (Fig. 1). Full details of the experimental setup are provided in Roberts et al. (*In press*), Roberts (2015); Roberts and Breithaupt (2015). At the opposite end of the tank, a circular plastic arena (100 diameter, 50 mm height, opaque) was situated, within which the subject moved freely. A camera (Microsoft Lifecam) above the arena allowed behaviour of the subject to be monitored remotely by the experimenter without disturbance. Sine waves of 8 s duration (1 s rise and decay time to prevent signal distortion) were presented at 11 amplitudes (in increments of 6 dB below the maximum level) and seven frequencies (5 - 410 Hz). Signals were generated in AUDACITY (version 2.0.5), exported on an SD card and played back through a Roland R-09HR MP3 recorder connected to an amplifier (JL Audio XD 200/2 200 W, 12 - 22 kHz) and the shaker. The staircase method of threshold determination was used to determine the threshold (Cornsweet, 1962). The procedure consisted of exposing the subject to the signal, observing the response and then selecting the next signal accordingly. A positive response to the signal initiated a reduction of the signal amplitude, and vice versa. This procedure continued until two amplitudes were repeatedly presented, with positive and negative responses consistently i.e. that the staircase reached a plateau (Fig. 2). The average of these two amplitudes, after being presented 10 times, was taken as the threshold value.

[Figure 1]

[Figure 2]

One crab was tested per day with the presentation of frequencies fully randomised, with 10 – 20 minutes between each frequency. An acclimation period of 12 - 14 hours inside the tank was used prior to threshold determination. Each crab was used only once, apart from in the re-test experiments. Amplitudes were presented two minutes apart. Preliminary testing indicated that responses lasted up to 1 - 2 seconds after each stimulus ended. There were no signs of response habituation to repeated stimulation. Control observations were made during each day of experiments, at a random time throughout the day, where behaviour was observed when exposed to five ‘blank’ signatures (i.e.- an 8 s period of no vibration). Results were also compared to known thresholds from the literature (water and substrate particle motion). To enable comparison with anthropogenic values, acceleration threshold values were converted to velocity (see supplemental equation 1).

2.2 Data analysis

Extensive preliminary tests indicated a suite of responses after exposure to vibration, ranging from partial retraction into the shell to smaller antennae responses. As such, two different behavioural indicators were used to calculate threshold values. These were a clear movement of the second antenna, occurring at the onset of the signal and during the signal (indicator 1), and the onset or cessation of locomotion (indicator 2). Only one indicator was used per set of crabs. Threshold values were calculated and plotted against frequency. Comparisons between indicators were undertaken using a Mann Whitney U-test. Data were compared as a whole and subdivided by frequency.

The effect of time in the laboratory prior to tests was investigated by using all data sets which used the same indicator as a response but subdivided into two groups according to duration in the laboratory being 60^+ days and < 10 days. An independent t-test was used to compare values between the two groups both with the data grouped altogether and subdivided by frequency.

The consistency of response was tested in a separate experiment by re-testing a set of crabs. Crabs were tested for the threshold (indicator 2) and then re-tested the following week, to investigate whether sensitivity was consistent within each individual. A paired t-test was used to compare the mean threshold between the first and the second test per crab. Data were analysed as a whole, and subdivided by frequency.

All data sets were tested for normality and equal variance (using Shapiro-Wilks and Levene’s) and log transformed as appropriate to fulfil the assumption of parametric tests. Where this was not possible non-parametric tests were used.

2.3 Stimulus analysis

Full details of stimulus measurement and analysis are provided in Roberts et al. (*in press*) and Roberts (2015). A piezo-electric accelerometer (Brüel & Kjær, type 4333, 20.6 mV/g, with type 2635 charge amplifier) and a 3D geophone system (Sensor Nederland, SM-7 375 ohm, IO, 28.8 V/m/s) were used to measure vibration within the tank continuously and simultaneously throughout experiments. Both sensors were connected to an ADInstrument Powerlab data acquisition system and a laptop computer with CHART 5 software (version 5.5) installed, and were placed adjacent to the arena to avoid contact with the subject. Sensors were calibrated against a Brüel & Kjær accelerometer (type 4370, 80 mV/g).

The stimulus was shown to be of greatest amplitude in the vertical axis, and to have a peak at the desired frequency for each signal with minor variation per day (see supplemental Fig. A1). A sample of background measurements within the tank (RMS) indicated that there was no significant difference in ambient levels during the experiments. For this reason the average background level across the experimental run was compared to threshold values (Roberts et al *in press).*

2.4 Anthropogenic vibration data

Crab sensitivity thresholds were compared to measurements of vibration taken within the vicinity of anthropogenic operations involving contact with the sea or riverbed. Measurements of piling, drilling, dredging, tunnel boring and shell and auger piling were taken on separate occasions using a geophone (Vibrock v901, bolted to a metal plate), which had been calibrated by Vibrock Ltd. to a sensitivity of 0.023 V (mm s^{-1})$^{-1}$. The geophone was lowered to the sea or riverbed by hand from a small vessel nearby to the construction operation being monitored. The cable was weighted close to the geophone in order not to add any additional vibration to the measurements. A custom-made variable gain amplifier (Subacoustech Ltd., 20 – 40 dB) was used to amplify the geophone signal. A sampling rate of 10 kHz or 44.1 kHz was used, well above the frequency bands with the largest amount of energy, with a national instruments ADC of type USB-6216 and storage on a laptop computer. Prior to each set of measurements, the distance from the construction activity being monitored was measured, either by use of a hand held GPS device or a laser range finder. RMS and peak amplitude values were calculated from clips of 10 s, over a window size of 1 s. Where possible the data included here are available as Subacoustech Ltd. reports (East and Collett, 2014; Edwards and Kynoch, 2008; Parvin and Brooker, 2008; Parvin et al., 2007) or as Subacoustech (*unpubl.*).

3. Results

3.1 Behavioural responses to vibration

At onset of the stimuli, or within a second of onset, clear behavioural changes were observed with the type of response varying according to the amplitude of the stimulus. At the lowest levels of exposure, a clear movement of the second antenna occurred at the onset of the signal (indicator 1). The movement consisted of a ‘sweeping’ backwards of both antennae towards the shell, accompanied by ‘flicks’ of the antennules (Schmitt and Ache, 1979) and rapid movement of the maxilliped exopodites “fan organs”, (Breithaupt, 2001). The movement of the second antenna typically occurred once or twice at the onset of the vibration, but the movement of the antennules and fan organs lasted for the duration of the exposure. The movement of these body parts was not accompanied by any other sort of motion.

In some cases a burst of movement was seen (indicator 2), most often at higher amplitudes of vibration. This behaviour occurred at the onset of the vibration (or within 1 – 2 seconds), and consisted of forward movement until the end of the exposure. In animals already moving at the onset of the signal, the vibration induced a cessation of movement for the duration of the signal. As such, regardless of the activity level of the individual, this behavioural indicator was clearly defined. It is of note that indicator 2 was often accompanied by antenna and antennule movements as of indicator 1, however indicator 1 often occurred without indicator 2. Onset and cessation of movement were used as one indicator, but further work could investigate whether the threshold for each was different when considered separately.

Between the two indicators there was a suite of other behaviours which clearly began at the onset of the stimuli; these included a clear ‘flinch’ of all legs, and a sudden burst of digging in the sand. All these changes appeared to be indicative of a response, since non-exposed crabs did not exhibit such clear ‘startle’ type behaviour. In preliminary tests, a semi- or full retraction into the shell was elicited a number of times but was not common during the experiments.

Since the responses were clear, it was possible to find the threshold of sensitivity using the two respective indicators (1 and 2) of behavioural change. Control observations indicated that the experimental setup itself did not appear to affect the animals, that is, there were changes in movement, or bursts of increased antenna flicking during the 8 s control clips.

On a number of occasions crabs appeared to lift the shell from the substrate during the stimulus, and in other cases to exit the shell, examine it thoroughly and return. No crab permanently left the shell, although in preliminary tests involving a stronger stimulus source this response was observed multiple times.

3.2 Threshold determination

A total of 45 hermit crabs were tested for sensitivity (5 – 410 Hz); 35 of those (cheliped width 2.13 - 6.00 mm) were tested using indicator 1. Ten crabs (cheliped width 2.13 - 5.9 mm) were tested using indicator 2, with only 5 of the 7 frequencies tested (20 - 410 Hz) since movement was not elicited at the 2 lowest frequencies. No mortality was observed during the experiments, crabs were active throughout and fed normally afterwards.

An approximately flat response curve was obtained for indicator 1 with average sensitivities between 0.11 – 0.29 m s^{-2} (n = 35, RMS, vertical axis) and greatest sensitivity at 90 Hz. A more irregular curve was seen for indicator 2 with average sensitivities 0.09 - 0.44 m s^{-2} (n = 10, RMS, vertical axis) with greatest sensitivity at 40 Hz, and a larger peak at 210 Hz (Fig. 3). Threshold values varied significantly between the two indicators when all data were grouped (U = 3634, $p < 0.001$) and when subdivided by frequency (U = 66, 102, 129, 142; $p < 0.05$ for 40, 90, 210, 410 Hz respectively), apart from at 20 Hz (U = 216, p = 0.11).

There was no significant difference between the thresholds of re-tested crabs, indicating that the values were representative of the individuals sensitivity in the experimental conditions (t = -0.34, df = 28, p = 0.73, indicator 2, log transformed) and when subdivided by frequency (Table 1). However, there were fewer responses on the re-test in general.

[Figure 3]

3.3 Time in the laboratory

Mean threshold varied significantly depending on duration in the laboratory prior to tests (t = 6.73, df = 270, $p < 0.05$, indicator 1, log transformed, RMS), with crabs held less in the laboratory being most sensitive to vibration (Fig. 4). The same trend was seen when subdivided by frequency (10 Hz t = 3.84, p < 0.05; 20 Hz t = 2.13, p < 0.05; 40 Hz t = 2.13, p < 0.05; 90 Hz t = 4.75, p < 0.01; 210 t = 2.79, p <0.05; 410 Hz t = 3.04, p < 0.05, all df = 38, apart from at 5 Hz t = 1.33, df = 31, p < 0.05).

Since crabs of short duration in the laboratory may reflect the sensitivities of wild crabs more closely (having not become used to laboratory conditions), these thresholds were compared to anthropogenic vibration measurements.

[Figure 4]

3.4 Comparison to anthropogenic values

Each measurement and construction operation was carried out in different conditions, such as water depth and sediment type. In some cases conditions were not fully described and so could not be directly compared. Frequency composition data were not available for all the sources, however for the data that were available indicate that, also similar to the case of underwater noise, most construction operations produce very low frequency vibrations, concentrated at frequencies below 100 Hz (Table 2).

After conversion to velocity, the lowest threshold of sensitivity (from crabs which had spent least time in the laboratory) ranged from 0.00007 – 0.00022 m s^{-1} (RMS). Anthropogenic sources of vibration which typically produce high levels of underwater noise such as blasting produce high levels of ground vibration, and therefore would be detectable up to 296 m from the operation, for example. Operations such as piling and shell auger were measured at a level of 0.0017 m s^{-1} and 0.00009 m s^{-1} (34 and 70 m respectively), well above all the thresholds of detection for frequencies of up to 40 Hz. This is of particular relevance as, with an intertidal distribution, *P. bernhardus* is likely to be close to many anthropogenic activities.

Construction methods which typically produce comparably low levels of underwater noise such as drilling and dredging also produce low levels of vibration, in the region of 0.000023 m s^{-1} at 50 m (Subacoustech Ltd. *unpubl.*). This would put the vibrations below the threshold of detection at all but the higher frequencies, except at small distances from the source (Table 2).

[Table 2]

4. Discussion

4.1 Sensitivity of **P. bernhardus** *to vibrations*

P. bernhardus in this study were sensitive to vibrations in the region of 0.02 – 0.44 m s^{-2} (RMS). Much of the available threshold data is from semi-terrestrial crustaceans rather than marine, making comparisons difficult, and data are often given in different units with varied methodologies. Nevertheless, a comparison of the current results to particle motion sensitivity curves (RMS data only, Fig. 5) indicates that the current values are within the range expected.

In some studies a greater sensitivity to vibration than the current work was demonstrated, which may be attributed to a variation in approach, since electrophysiological methods typically yield greater sensitivities than behaviourally determined values (Ladich and Fay, 2013), as shown when comparing the curves of two *Uca* species (Aicher and Tautz, 1984; Salmon and Atsaides, 1969). For example whilst threshold values obtained from the semi-terrestrial *Uca sp.* are similar to the present work in the 100 Hz region, behavioural tests indicate slightly greater sensitivities for example 0.0175 m s^{-2} at 50 Hz (Salmon and Horch, 1973). However *Uca sp.* may have a greater sensitivity than *P. bernhardus* since this species communicates by 'drumming' the substrate. Such communication has not been observed in hermit crabs, although stridulation (rubbing together of body parts) has been described (Field et al., 1987).

[Figure 5]

The current results indicate a fairly flat response across the frequency range for all data apart from a prominent peak at 210 Hz, which agrees with data for *Orconectes limosus* (Breithaupt and Tautz, 1988) and *Uca sp.* (Salmon and Horch, 1973; Salmon et al., 1977). However if the 410 Hz data are excluded from the present results, the data trend reflects that of curves *U. pugilator* and *O. Limosus* with a gradual reduction of sensitivity with increasing frequency especially above 100 Hz (Aicher and Tautz, 1984; Breithaupt, 2002; Salmon and Atsaides, 1969). A trend such as this has been demonstrated in water-borne particle motion thresholds of cephalopods and fish (Hughes et al., 2014; Packard et al., 1990), and may indicate directionally sensitive cells within a receptor system (Budelmann, 1979; Hughes et al., 2014). Spectral analysis revealed the signals at 210 and 410 Hz to be relatively 'pure' in terms of composition, therefore the two conflicting trends above cannot be explained by problems with the stimulus (Roberts, 2015). A laser Doppler vibrometer could be used in further tests to fully understand the signal on the animal itself, as in Aicher et al. (1983).

Salmon (1971) reported greatest sensitivities of 0.04 – 0.06 m s^{-2} (30 – 60 Hz, RMS) for *U. pugilator* and 0.02 m s^{-2} for *U. minax* (50 Hz, RMS), and Goodall (1988) demonstrated a sensitivity of 0.01 m s^{-2} (20 Hz) for *N. Norvegicus*; all of these values are within the range found in the current work. Berghahn et al. (1995) and Heinisch and Wiese (1987) demonstrated marginally reduced sensitivities for other marine crustaceans compared to the current work, being 0.4 m s^{-2} (20 – 200 Hz) and 0.81 m s^{-2} (170 Hz) respectively (peak). Benthic fishes, such as flatfish, which do not have a swimbladder, appear on the whole to be more sensitive to vibration than *P. berhardus* (Chapman and Sand, 1974; Fay and Simmons, 1998; Karlsen, 1992; Popper and Fay, 2011; Sand and Karlsen, 1986; Sigray and Andersson, 2011), or of similar sensitivity (Berghahn et al., 1995). Similarly, cephalopods sensitivities may be found within the range of 0.0003 – 1.1 m s^{-2} (1 – 280 Hz, peak) (Kaifu et al., 2008; Mooney et al., 2010; Packard et al., 1990).

The particle motion and not the pressure component of an acoustic wave is likely to be the main stimulator in crustaceans since they lack air filled cavities to convert pressure to mechanical displacement (Breithaupt and Tautz, 1990; Goodall, 1988; Hughes et al., 2014; Tautz and Sandeman, 1980). Detection of such motion may involve mechanoreceptors consisting of surface receptors, internal statocysts and the chordotonal organs (Breithaupt and Tautz, 1988; Budelmann, 1992; Goodall, 1988; Wiese, 1976), although the role of each type within detection abilities of vibration is relatively unknown. Cuticular mechanoreceptors have been described, for example sensory hairs on the carapace, chelipeds, antennual flagellae, and second antenna (Breithaupt and Tautz, 1988; Derby and Atema, 1982; Goodall, 1988; Sandeman and Wilkens, 1982; Tautz and Sandeman, 1980; Wiese, 1976). The chordotonal organs located within the joints of appendages may also detect vibration in addition to joint extension (Aicher and Tautz, 1984; Barth, 1980; Budelmann, 1992; Burke, 1954; Horch, 1971; Salmon et al., 1977). Furthermore the statocyst, a fluid-filled chamber with a dense mass (statolith) inside (Budelmann, 1988; Cohen, 1955; Cohen and Dijkgraaf, 1961; Cohen et al., 1953) may enable the detection of particle motion in addition to its role as an equilibrium receptor (Fraser, 1990). As such it may be involved in acoustic detection (Breithaupt and Tautz, 1988; Cohen, 1955; Nakagawa and Hisada, 1990), as in the cephalopods (Budelmann and Williamson, 1994; Kaifu et al., 2008; Maturana and Sperling, 1963; Williamson and Budelmann, 1985). The flat frequency response displayed by hermit crabs here, when vibration thresholds are plotted in acceleration units suggest that it is mediated by an inertial detector such as the statocyst, see Breithaupt and Tautz (1990); Kalmijn (1988). Additionally it is likely that there are vibration receptors in the legs, such as in fiddler crabs (Aicher et al., 1983; Aicher and Tautz, 1984).

4.2 Behavioural responses

Responses here were clear and occurred at onset of the stimulus appearing to take a somewhat predictable pattern (i.e. motion being most likely with stronger signals) varying with the amplitude of the stimulus, allowing use of two distinct behavioural indicators. In crayfish, sweeping movement of the second antennae is common during exploration behaviour (Krång and Rosenqvist, 2006), due to sensory hairs located there to detect tactile and chemo-mechanical cues. Antennae movement in response to vibration has been demonstrated in a range of other crustaceans (Berghahn et al., 1995; Heinisch and Wiese, 1987; Meyer-Rochow, 1982; Tautz, 1987). Postural changes and movement of appendages have also been documented (Breithaupt, 2002; Goodall, 1988; Goodall et al.,

1990) and a similar range of startle-type responses were seen in *Uca sp.* (Salmon and Atsaides, 1969). Crabs were unresponsive during control trials indicating that the experimental setup itself did not have an effect.

The average threshold was higher (i.e. – reduced sensitivity) for indicator 2 than for indicator 1 at 90 and 210 Hz only, otherwise the curves were similar. A difference between the two indicators was expected, since indicator 2 may be described as a more 'energetic' response and as such may require a stronger vibration to be triggered. The use of the two indicators in this way demonstrates how this method could be applied to provide threshold values for a suite of behavioural responses. In several cases crabs were seen lifting their shell from the substrate during vibration exposures, which may have been a method of reducing exposure levels. In stridulating terrestrial hermit crabs, lifting of the shell from the substrate has been shown to reduce vibrations between shell and sand (Field et al., 1987).

The current work used unconditioned animals to determine thresholds. There has been only one documented successful attempt of crustacean conditioning to sound (Offutt, 1970), possibly due to the heart rate being naturally erratic in laboratory conditions (Florey and Kriebelm, 1974). The use of conditioned animals has an advantage in that it reduces the chances of habituation, which has been demonstrated in fishes (Knudsen et al., 1992; Schwarz and Greer, 1984). There are few data available on habituation in crustaceans, however to minimise the chance of habituation in the current work, stimuli were widely spaced and there were large gaps between frequencies (20 minutes); this method was successful since crabs stayed responsive throughout experiments. Although habituation within trials was not demonstrated, the data from the current work may indicate adjustment to background vibration levels across a longer time period, i.e. crabs exhibited reduced sensitivity to vibration after a long duration (weeks) in the laboratory prior to tests. This is important when repeating the current work.

The precise stimulus strength and frequency composition received may have been affected by, for example, the type of shell occupied, the size, volume, and shell wall thickness. For this reason, crabs occupying damaged shells were not used in the experiments. Similarly crabs that moulted within the holding conditions, or that had missing appendages were discounted from tests- particularly since Offutt (1970) noted variation in thresholds after moulting. Furthermore the ‘fit’ of the shell may have had an effect on the resonance of the shells (i.e. whether the crab was in a shell approximately matching its size). In an extension of the present work a significant positive correlation was found between chela size and shell size (Roberts, 2015), which indicated that crabs were in fact occupying shells appropriate to size. Shell resonance was not investigated here but the shells of *Trizopagurus* sp. have been found to amplify certain frequencies, and resonance may differ with shell type and contact area to the substrate (Field et al., 1987).

On a number of occasions individuals were seen exiting the shell, examining it thoroughly before returning. It is possible that these individuals interpreted the ‘tapping’ as initiation of agonistic behaviour by another crab (Briffa et al., 2013; Briffa et al., 2008). Shell rapping is a common behaviour displayed during shell fights and can cause eviction of the defender (Briffa and Elwood 2000). Behaviours such as this illustrate the importance of examining sensitivity thresholds in conditions were the animal is unconstrained. The observation of such behaviours would not have been observed had the crabs been fixed to a point or held in a sling such as in Horch and Salmon (1972), indeed it could be argued that more technical/complex setups would elicit more unnatural behavioural responses.

It is important to determine the consequences of the individual responses to the health and stability of the population and hence the community, although the energetic consequences of the responses detected here are unknown. Frequent bursts of movement may interrupt natural behaviour and change the time energy budget of *P. bernhardus,* which was beyond the scope of this study. Similar time budget disruptions have been seen in reef fishes in response to acoustic playbacks (Picciulin et al., 2010), and pollutants have been shown to effect energy use in *Mytilus edulis* (Widdows et al., 2002; Widdows et al., 1997), but there are few data for crustaceans. The responses seen here may also be accompanied by internal changes- for example heart beat, production of stress proteins and oxygen consumption changes (Celi et al., 2014; Florey and Kriebelm, 1974; Wale et al., 2013b). Movement, feeding, avoidance, agonistic behaviour and habitat choice may also be affected as shown by acoustic studies with fishes (Hawkins et al., 2014b; Simpson et al., 2014; Voellmy et al., 2014a; Voellmy et al., 2014b). Whilst responses of fish may not be directly relevant to crustaceans, there are few data available to allow fair comparisons. As such, further studies are needed to investigate the long term effects of these vibrations on stress levels, growth, and reproduction of crustaceans. While in our study animals indicated reduced sensitivity to vibration after a longer duration in the laboratory (and associated ambient vibration levels) it is unclear whether this promotes or reduces survival and reproductive success. Long term studies are necessary to address and understand the effects that anthropogenic vibrations have on marine communities.

4.3 Relation to anthropogenic vibration levels

The current work demonstrates that the vibration sensitivity of crustaceans is well within the range of substrate disturbances produced by anthropogenic activities. The core acoustic energy of many anthropogenic sources is at low frequencies (Nedwell et al., 2003a; Nedwell et al., 2003b) and within the substrate is predominantly < 100 Hz (Subacoustech Ltd., *Unpubl.*). The current work shows that hermit crabs are sensitive to broad range of frequencies < 410 Hz. The low frequency range is accentuated in the propagation of anthropogenic produced surface waves (Hazelwood, 2012; Hazelwood and Macey, 2015). It is likely that the vibrations summarised in Table 2 are also detectable by other crustacean species, which have similar sensitivities to *P. bernhardus* (Figure). Hence crustaceans are likely to detect such anthropogenic vibrations, but more data are required to investigate the long term repercussions of the responses observed here, at the individual and population level.

There is a shortage of publicly available underwater vibration measurements (Hazelwood, 2012; Hazelwood and Macey, 2015; Miller, 2015), with those available often lacking the details required for comparisons between sources. A modelling approach may be used to estimate seabed vibrations such as from piling (Hazelwood and Macey, 2015; Miller, 2015), but validation must be undertaken in the field. Due to the complexities of underwater sound measurement, a standard protocol involves predominantly pressure data rather than substrate-borne or water-borne particle motion data. On the whole there are no international standards for measuring particle motion, although ISO standards have recently been proposed (ISO, 2014). The measurement of substrate vibration is, at least, easier to measure with three dimensional seismic sensors and directional accelerometers, whereas measurement of water-borne vibration is more complex, with sensors not yet commercially available, although various measurement methods exist (Popper et al., 2005; Zeddies et al., 2010; Zeddies et al., 2012). The lack of data is of importance in the light of the inclusion of underwater noise within the OSPAR (North-East Atlantic) and HELCOM (Baltic) Regional Seas Conventions and within the EU Marine Strategy Framework Directive (Borja et al., 2010; Tasker et al., 2010; Van der Graaf et al., 2012). These require the setting of sound exposure criteria and indicators for marine species, however the inclusion of seabed vibration within this is implicit rather than explicit. The current work highlights the importance of substrate-borne vibration within the assessment of noise sources, allowing it to be considered as of the same importance to water-borne energy.

Levels of vibration from anthropogenic sources fluctuate according to a number of factors, for example, type of source, parameters of the source (for example diameter of pile), depth, propagation conditions, duration of operation (Athanasopoulos and Pelekis, 2000; Kim and Lee, 2000; Thandavamoorthy, 2004). As such, measurements are scenario specific and it is not possible to generalise between sources and conditions. The speed of Rayleigh waves in particular varies with properties of the solid, frequency, the depth of the sediment hard layer and the Poisson ratio (Hazelwood and Macey, 2015). These factors all affect the level of the sound produced, and the frequency spectrum of the signal and laboratory conditions cannot fully replicate the vibroacoustic conditions of the sea shore or the seabed. In translating this information to the field it is necessary to consider the difference in threshold between laboratory and field conditions, especially since thresholds in fish have been shown to vary with background levels (Hawkins and Chapman, 1975), and, as shown here, thresholds vary according to duration in the laboratory, for example.

4.4 Stimulus presentation

It is of note that whilst the energy was predominantly in the vertical axis here the other two axes were of notable strength, which highlights the necessity to measure all three axes to understand the whole signal. It is not possible to determine precisely to which of the three planes the crabs here were sensitive to, however the signal could be described as predominantly vertical. The particles within Rayleigh waves move in an elliptical pathway, hence the waves have some energy in the vertical direction (Brownell, 1977; Lowrie, 2010), as in this study. Such waves have been shown to be detectable by fiddler crabs (Aicher et al., 1983; Aicher and Tautz, 1984; 1990). To increase vertical signal strength, a shaker table could be used to constrain the substrate motion entirely to one axis (Mooney et al., 2010). This system may also help to increase the purity of the stimulus in terms of frequency composition, although on the whole the sinusoidal waves used here had predominant peaks in the region of the intended frequency. In audiometry studies of fishes, waveforms must be as pure as possible (Chapman and Hawkins, 1973) since threshold values may vary with frequency.

There are few studies exposing crustaceans to acoustic signals, such as anthropogenic noise, and yet such stimuli are likely to have strong particle motion components (substrate and water borne) and therefore to be detectable (Hazelwood and Macey, 2015; Popper et al., 2001). Experiments with marine and semi-terrestrial crabs have indicated changes in foraging and anti-predator behaviour after noise exposure (Chan et al., 2010a; Chan et al., 2010b; Wale et al., 2013a; b). However other studies have not demonstrated such adverse effects (Andriguetto-Filho et al., 2005; Parry and Gason, 2006). Variation between laboratory and field results may be attributed to the unpredictable nature of the acoustic field within small laboratory aquaria (Parvulescu, 1964a; b; Rogers, 2015), a factor that must be considered here also. Whilst the stimulus here was predominantly exciting the substrate, it is possible that the signal also created water-borne particle motion, and perhaps even pressure within the tank. However by using a shaker directly contacting the substrate, the pressure and interference phenomena found in small tanks are likely to be minimal. As there is no evidence yet to suggest crustaceans can detect pressure (Goodall, 1988; Popper et al., 2001), the latter may be of little consequence. However further work to fully describe the acoustic and vibratory field within the current setup would be most valuable. A specially designed tank could be used to extend testing to pressure and water-borne particle motion within a controllable acoustic field (Bolle et al., 2012; Breithaupt, 2002; Hawkins and MacLennan, 1975; Plummer et al., 1986). Overall the current setup here was therefore a pragmatic compromise between purity of signal and a tank setup that would allow animals to display natural behaviours.

5. Conclusions

Threshold values and collated measurements of actual anthropogenic vibrations indicate that *P. bernhardus* is sensitive to substrate vibration and may be able to detect anthropogenic vibrations up to 300 m from high vibration sources. This is of importance since many anthropogenic activities involve direct contact with the seabed and other activities may also induce particle motion indirectly. There are few previous data investigating the sensitivity of invertebrates to vibration and acoustic sources, and even fewer focussing upon anthropogenic signatures. As such, future studies must focus upon a range of other species, for example bivalves, in addition to other benthic invertebrates (for *M. edulis* see Roberts et al. *In press.).*

Further work with hermit crabs could determine the threshold required for the animals to exhibit other behaviours, for example to abandon the shell, since such behaviour is likely to induce a physiological stress response and increase the susceptibility to predation. Most importantly, the consequences of the behaviours demonstrated here must be assessed on an individual and population level. Background vibration levels here were below average threshold values, however a valuable next step would be to vary background levels using white noise and study the variation in threshold. Here, time in the laboratory prior to testing was shown to significantly raise the threshold (i.e. reduce sensitivity to vibration) although further investigation would be beneficial. Additionally, the directionality of response could be measured since benthic organisms may be able to use surface waves for directional orientation (Hazelwood and Macey, 2015).

When considering anthropogenic energy it is not sufficient to focus solely upon substrate vibration since disturbance, for example pile driving, also has a pressure component and a water-borne particle motion, both of which would reach the seabed indirectly. In order to fully investigate the response to such sources and to separate natural and anthropogenic pressure effects, exposures must be undertaken in the field with actual sources. Even sophisticated playback systems, as used by Hawkins et al. (2014b) cannot, nor do they aim to, replicate the strong ground borne component produced by many activities. Laboratory work could also be extended to include a suite of different stimuli and a greater frequency range.

The recent large amount of research effort directed towards modelling and measuring the effects of underwater noise on fish and marine mammals now requires repetition to assess whether high levels of seabed vibration have a significant impact upon benthic organisms. The effects of substrate transmission should be included in assessing the effects of noise pollution on the marine environment.

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Glossary of abbreviated terms

GES Good Environmental Status as defined in the European Marine Strategy Framework Directive; RMS root mean squared- defined as the square root of the sum of the squared amplitude of the points; AEP- Auditory Evoked Potential technique; ISO- International Organisation for Standardisation.

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FIGURE CAPTIONS

Figure 1 Schematic of experimental setup (not to scale), consisting of electromagnetic shaker and stinger rod (1), underwater camera (2), experimental arena (3), layered base made up of mixed hard and soft insulation and concrete (4), wooden support structure (5), steel frame completely separate from the base (6), experimental tank with needlepoint legs and 30 mm sandy substrate (7), position of geophone system (8), position of accelerometer (9). [BLACK AND WHITE]

Figure 2 Example data for a typical sensitivity threshold by the staircase-method. Amplitude of the signal is reduced with every positive response (black dot), and increased when a negative response is observed (cross), this continues until there are consecutive iterations of positive-negative (shown by the last six points). An average of ten iterations is used to calculate the threshold of response. [BLACK AND WHITE]

Figure 3 Average behavioural thresholds for *P. bernhardus* (n = 35, +/- SE, RMS) to substrate vibration in terms of vertical acceleration (m s^{-2}). Average background levels are denoted by a dashed line. Two behavioural indicators were used, a ‘flick’ of the antenna (indicator 1), and a burst or cessation of movement (indicator 2). Average background levels are denoted by a dashed line. [BLACK AND WHITE]

Figure 4 Average behavioural thresholds for P. *bernhardus* (n = 10 per group, +/- SE, RMS, indicator 1) to substrate vibration given in terms of vertical acceleration (m s^{-2}), for two groups with different amounts of time in the laboratory prior to tests. Average background levels are denoted by a dashed line. [BLACK AND WHITE]

Figure 5 Behavioural thresholds to vibration (water and substrate-borne) for crustaceans (mixed species), values taken from the literature and compared to those of the present work (RMS, data presented for 5- 410 Hz only, crabs of short duration in the laboratory). Data from Aicher and Tautz (1984); Breithaupt (2002); Breithaupt and Tautz (1990); Horch (1971); Hughes et al. (2014); Salmon and Atsaides (1969); Salmon and Horch (1973) and the current work (dashed line, thresholds of crabs of shortest time in captivity prior to tests). [IN COLOR ONLINE]

TABLES

Table 1 Total number of responses between *P. bernhardus* (n = 10) tested for the threshold (using a burst of movement as the response) with a ten day gap between re-tests, plus associated statistics.

Frequency (Hz)	Test 1	Test 2	t	df	p
20	8	9	0.70	6	0.51
40	10	3	-0.42	4	0.70
90	9	6	-0.87	4	0.43
210	10	10	-0.36	7	0.73
410	7	6	0.39	3	0.72
Sum	44	34			

Table 2 Summary of the vibration levels measured in the vicinity of anthropogenic sources, provided in terms of the maximum amplitude across all three axis (RMS or peak m s^{-1}). Dashes- unavailable parameters. Values that fall within/above the thresholds found for *P. bernhardus* in the current work are denoted in bold italics.

Activity	Distance (m)	Vibration levels (ms^{-1}) (RMS)	Vibration levels (m s^{-1}) (peak)	Background (m s$^{-1,}$ RMS)	Background levels (m s$^{-1,}$ peak)	Frequency range (Hz)	Details	Water Depth (m)	Location	Sea/Riverbed type
Drilling	23	***1.0E-04 – 7.0E-04***	-	-	-	Primarily <100	Unknown	3 – 4	-	Loose, primarily mud, some sand
Shell and auger piling	70	3.7E-05 – ***9.4E-05***	-	-	-		Unknown			
	109	1.20E-005	-	-	-					
Shell and auger piling and drilling	23	***2.7E-03 – 6.0E-03***	-	-	-	-	Unknown	-	-	-
	64	7.7E-06 – ***6.7E-05***	-	-	-					
Pile driving	17	-	***4.10E-003***	-	-	Primarily 5 - 50	0.9 m diameter pile	1 – 2	Mersey River (UK)	Loose, primarily mud, some sand
	34	-	***1.70E-003***	-	-					
Auger piling	29	3.90E-005	***1.38E-004***	1.60E-005	7.00E-005	-	0.75 m diameter auger to 30 m deep.	-	River Usk (UK)	-
	38	1.60E-005	4.60E-005							
	47	1.40E-005	2.3E-005							
Drilling	22	2.20E-005	8.20E-005	3.00E-006	7.00E-005	-	Experimental kind of impact drilling	40	Vobster Quay (UK)	-
Backhoe dredging	5	***7.80E-005***	***3.80E-004***	-	-	-	Vessel: Dinopotes. Length: 37.8 m. Max power: 699 kW.	-	Mersey River (UK)	-
	50	2.30E-005	***2.60E-004***	-	-					
	175	1.30E-005	***2.90E-004***	-	-					
	220	3.00E-006	***1.50E-004***	-	-					
Tunnel boring machine (TBM)	5.5 - 12 m above machine	***6.80E-005***	***3.90E-004***	3.00E-006	2.20E-005	-	Internal diameter of tunnel: 3.5 m. Motors: two 140 kW motors. Length: 140 m.	0.6	Sruwaddacon bay (Ireland)	Sand
Blasting	24.25	-	***6.00E-002***	-	-	-	Charge weight of 6.25 kg	-	Ben Schoeman Dock (South Africa)	Stone dock
	296.75	-	***< 1E-03***	-	-					

Figure 1

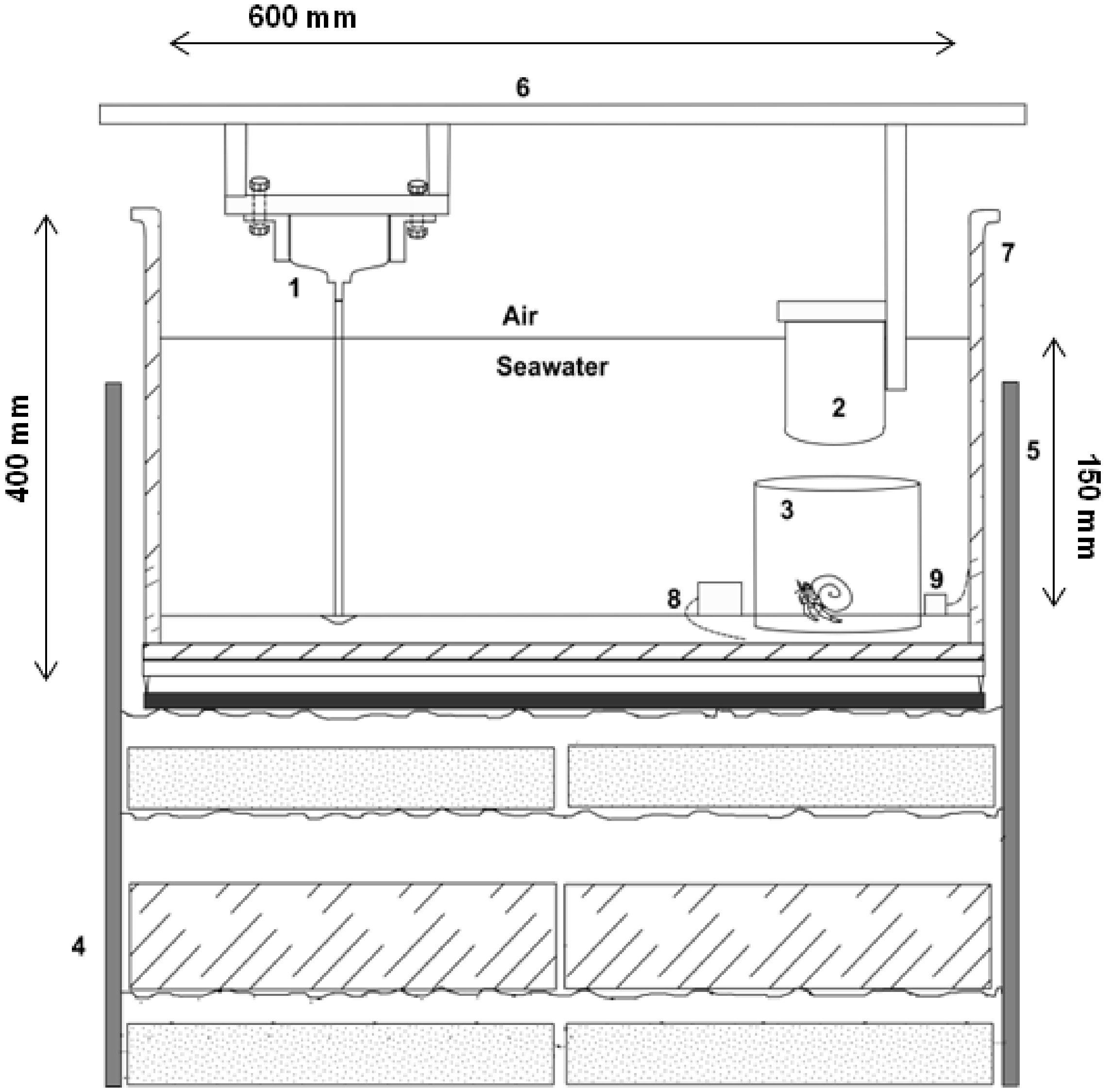


Figure 2

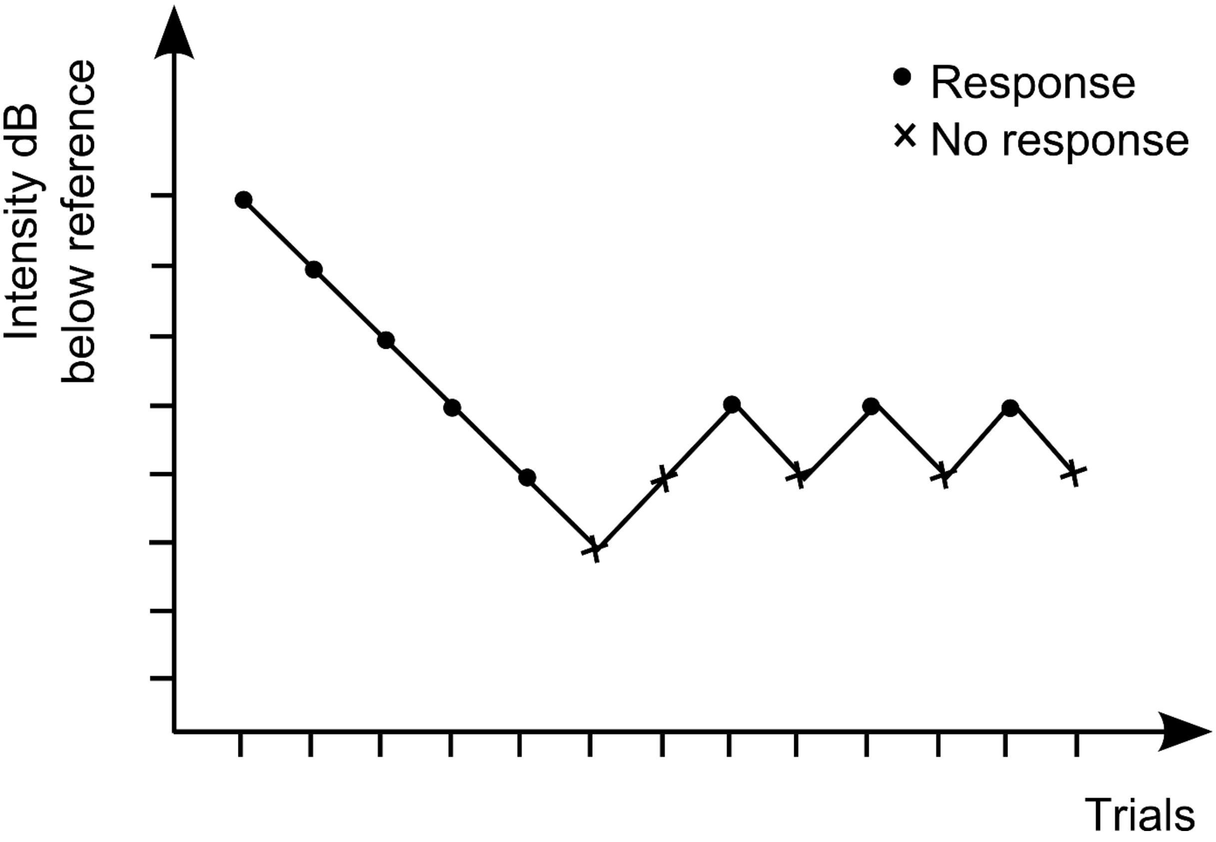


Figure 3

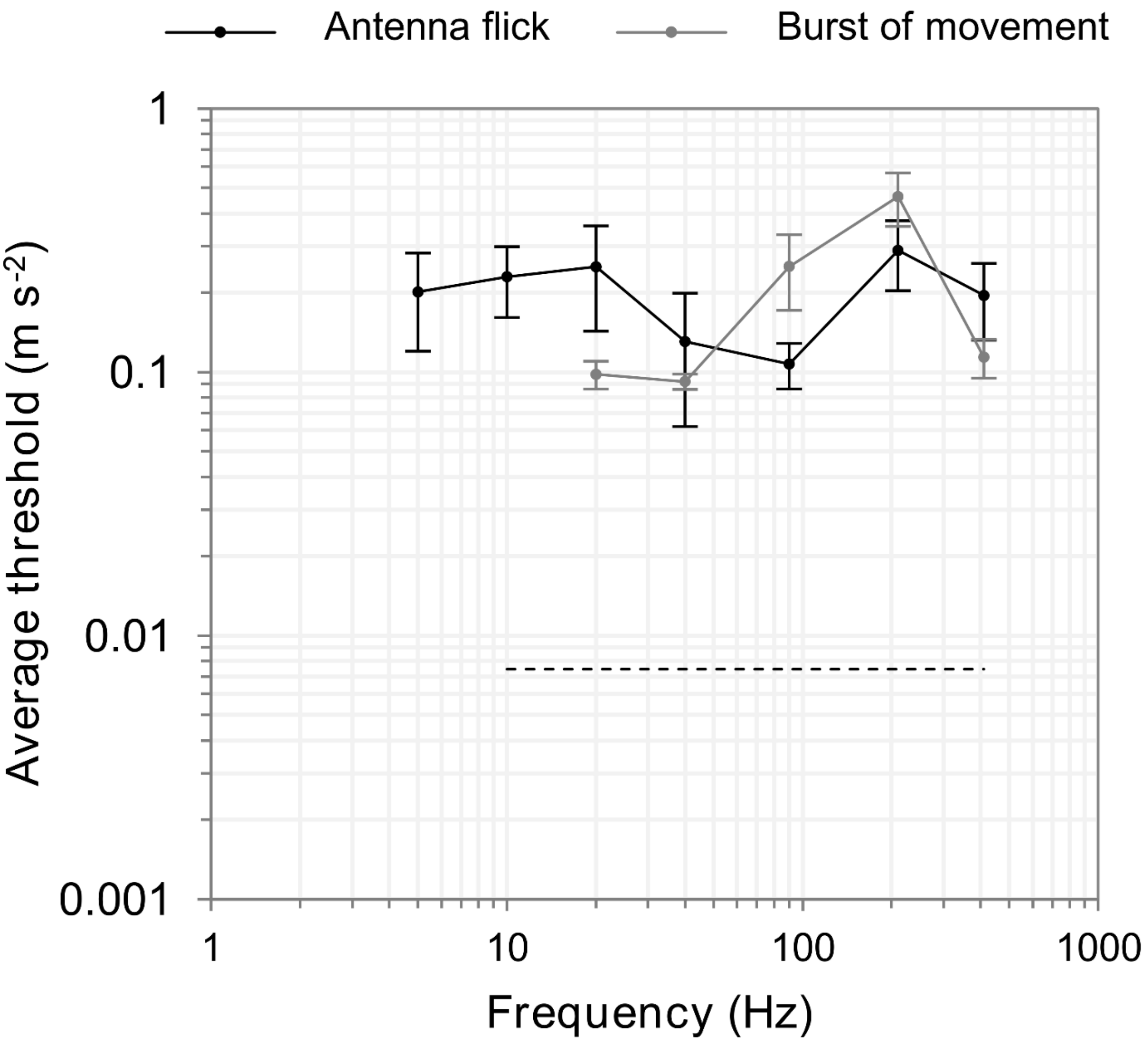

Antenna flick
Burst of movement
Average threshold (m s^{-2})
1
0.1
0.01
0.001
1
10
100
1000
Frequency (Hz)

Figure 4

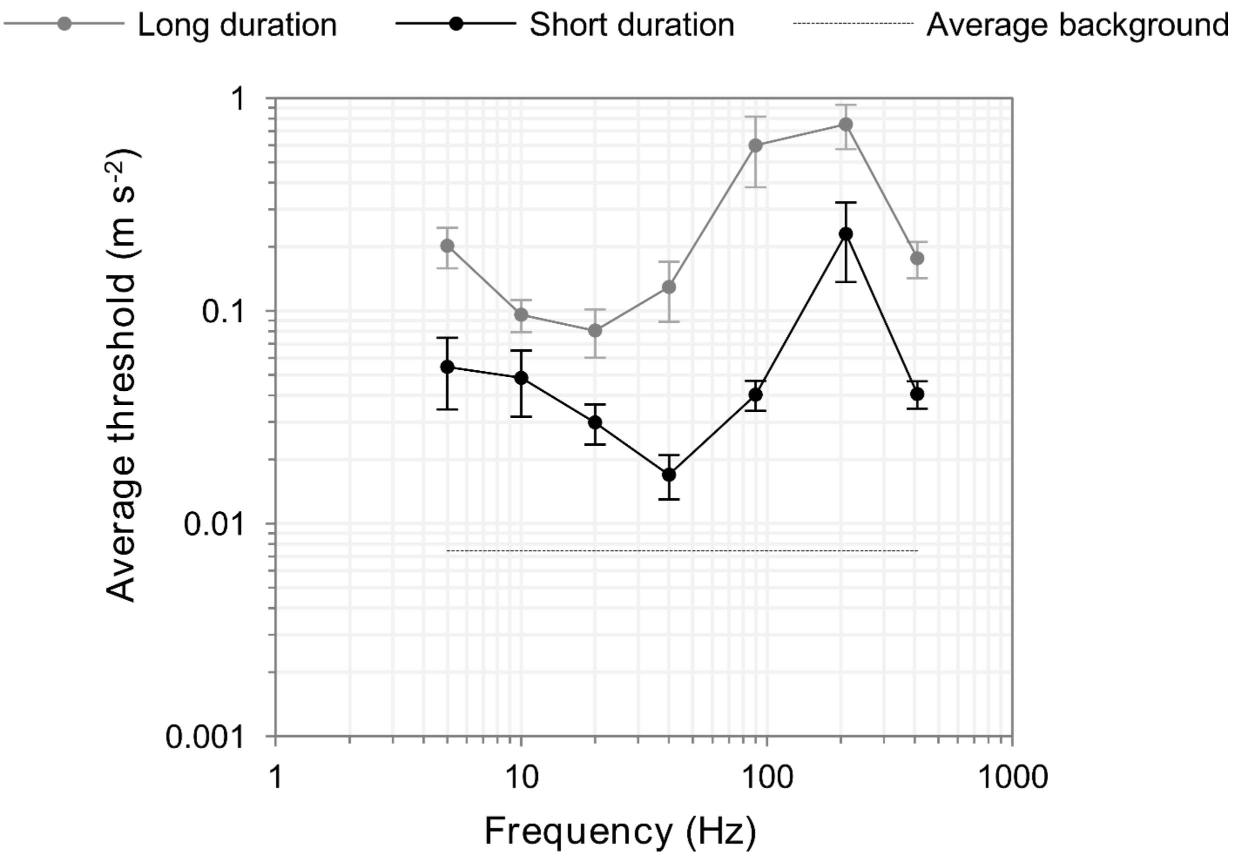
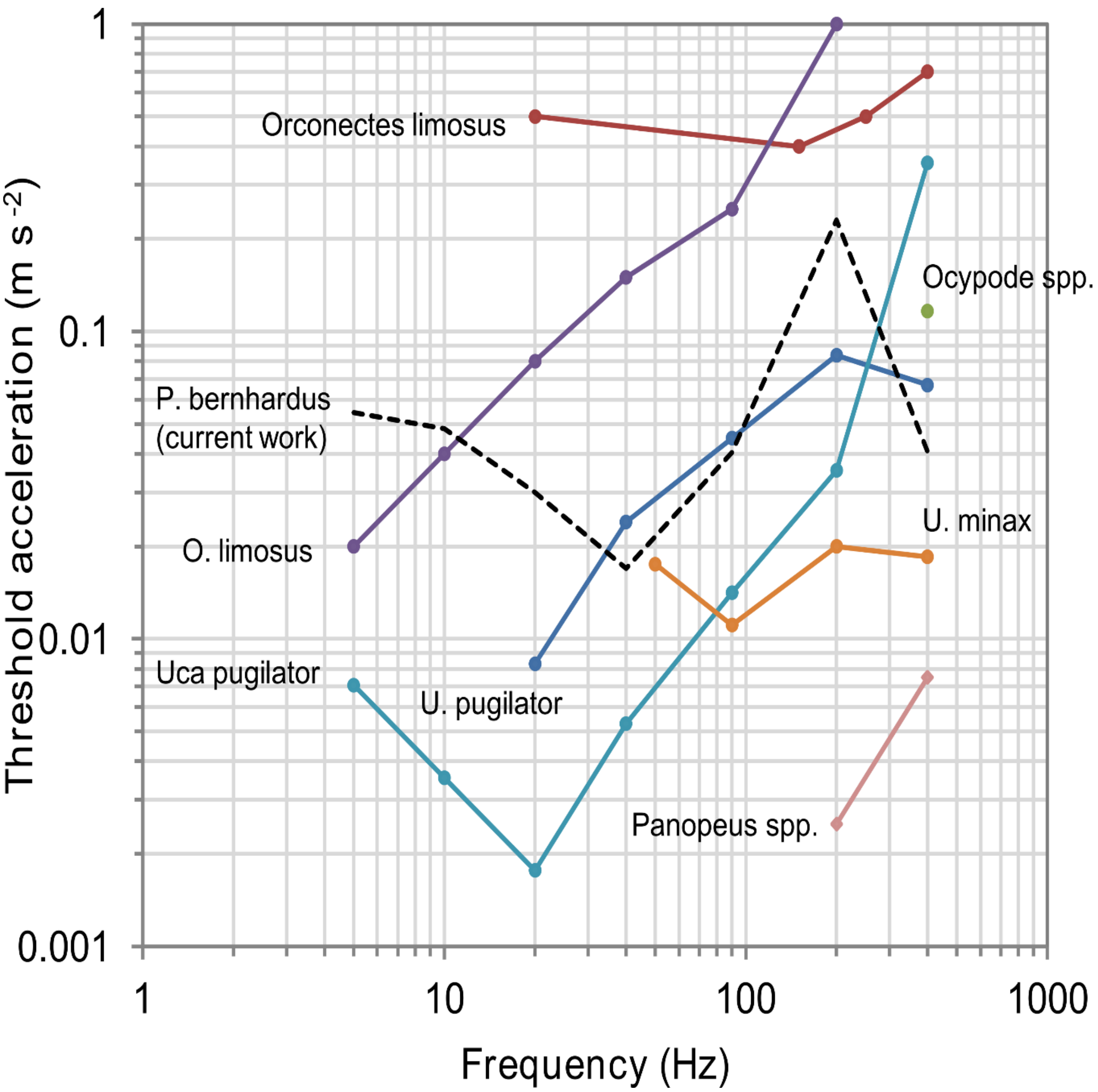

Long duration
Short duration
Average background
Average threshold (m s^{-2})
1
0.1
0.01
0.001
1
10
100
1000
Frequency (Hz)

Figure 5



1
0.1
0.01
0.001
Threshold acceleration (m s -2)
Orconectes limosus
Ocypode spp.
P. bernhardus
(current work)
O. limosus
U. minax
Uca pugilator
U. pugilator
Panopeus spp.
1
10
100
1000
Frequency (Hz)