THE HEARING ABILITIES OF THE PRAWN *PALAEMON SERRATUS*

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1 INTRODUCTION

The oceans are virtually transparent to sound, and opaque to light and radio waves. At a wavelength of 1 m (1,500 Hz), water is nearly 1,000,000 times more transparent to sound than to radio signals [1]. This fact underlies the intense interest currently being directed toward the acoustical exploration of the ocean. Naturally produced sounds arise from a number of sources, such as breaking waves, heavy rain, volcanic activity, or from marine animals (bio-acoustic sources). Vocalisations such as whale song, along with the grunts and whistles from sonic fish are especially relevant for communication purposes and during predator prey interactions [2]. There are several types of anthropogenic sources used routinely that produce intense levels of noise, such as the Low Frequency Active Sonar (LFA) used by the military in anti-submarine warfare, or from the airgun arrays used during a seismic survey of the substrate beneath the seafloor by the petroleum industry. Seismic airgun arrays can generate noise levels in excess of 253 dB (re 1 µPa at 1 m) [3] and are comparable to the noise levels generated by a seafloor volcanic eruption, which can produce a source level of in excess of 255 dB (re 1 µPa at 1 m) [4]. Recent concerns regarding the impact of these anthropogenic sounds on fish and other marine animals has prompted a number of investigations into the effects of intense noise exposure on the hearing systems of marine mammals [5,6,7]. Additionally, several studies of the behaviour of free living fish when exposed to intense noise have been conducted [3,8,9,10] and includes the examination of log books from fishing vessels operating within 5 km of a concurrent seismic survey [11].

It is known that several crustacean species produce sound; for example, the pistol shrimp (*Alpheus spp*) produces a loud click by rapid closure of a specially adapted claw [12]. The spiny lobster (*Palinurus vulgaris*) and the rock lobster (*P. longipes*) make alarm sounds by drawing the base of the antenna across scale like ridges below the eyestalks [13,14]. Additionally, *P. longipes* has been shown to take longer emerging from a hide, when feeding was preceded by a white noise [14]. The female cricket (*Gryllus bimaculatus*) has the ability to localise and respond to male chirp sounds [15,16], using specially adapted acoustic receptors (tympanum), located in the forelegs below the knee [17]. On hearing the chirp, a receptive female will orientate itself toward the sound using a behavioural response known as phonotaxis [16]. The ability of an organism to orientate itself in the 3-D marine environment requires the presence of a suitable gravity receptor. These receptors occur in many diverse organisms throughout the marine environment and include cephalopods [18,19], crustaceans [20,21,22,23], and fish [24,25]. In crustaceans the statocyst is located either at the anterior end of the animal in the basal segment of each antennule, or posteriorly within the uropods, abdomen or telson [26,27,28]. It has been well established that the crustacean statocyst functions as an equilibrium organ by initiating corrective movements to maintain the animal's position in the water column [27,28,29,30]. In this work, we study the electrophysiological response of the statocyst in an underwater sound field, using the Auditory Brainstem Response (ABR) recording technique, originally developed for use in clinical neurophysiology. Until now, this method of acquiring hearing ability has only been applied in the auditory assessments of vertebrates [31], though the presence of afferents in the statocyst and existence of a neural pathway terminating in the supraesophageal ganglion, indicates that the physiology of *Palaemon serratus* is suitable for an ABR type investigation. An ABR waveform is acquired by averaging conglomerate responses of peak potentials, arising from nuclei in the auditory pathway during acoustic stimulation [31,32]. The sweep records the generation of neural waveforms over a user-defined time span termed the sweep velocity and measures activity prior to, during and after stimulation of the receptor organ. Additional waveform generation by neural

activities other than those associated with hearing combined with muscular movements, ensure that recordings have to be repeated over 1000 to 2000 presentations before clear results can be obtained [33,34]. The recorded waveforms resulting from each sweep are averaged together and produce a recognisable ABR waveform. Two ABR recordings are made at each intensity, which are then overlaid to show that the evoked potentials are repeatable.

The aim of the present paper is to examine the morphology of the statocyst receptor array of the prawn (*Palaemon serratus*), using both scanning and transmission electron microscopy (SEM & TEM); the full results of this experiment can be found in Lovell et al. (2005) [35]. The nerves associated with the statocyst and the pathway taken to the neuropil of the antennule in the supraesophageal ganglion was examined by the principle author, to provide a detailed description of how acoustic signals are perceived and transmitted by the neuronal pathways. Measurements of the electrophysiological response of the statocyst and Central Nervous System (CNS) to acoustic stimuli were also made and by ablation, it was demonstrated that the evoked response was generated in the statocyst organ.

2 MATERIALS AND METHODS

One hundred specimens of the prawn (*Palaemon serratus*) Phylum Crustacea and Class Eumalacostraca of mixed sex, and ranging in length from 27 mm (0.1 g) to 71 mm (1.9 g) were obtained from wild stock in the South West of England using a dip net. Once captured, the prawns were transferred to a marine tank divided by a fine mesh screen into four equal sized compartments of 50 litres each. An Eheim type 2013 biological filter with a flow rate of 390 litres per hour maintained water quality and provided aeration by spraying filtered seawater back into the tank via the filter outlet pipe located 60 mm above the water surface. The ambient noise within the holding tank was measured using a hydrophone and the sound pressure level was calculated to be 102 dB (re. 1 µPa at 1 m), with the Eheim pump active. Sounds generated by the prawns that could be detected above the ambient pump noise were generally broad band clicks and snaps up to 158 dB (re. 1 µPa at 1 m) (peak to peak), produced when feeding and swimming. It is noted here that the pistol shrimp *Alpheus spp* can produce a snap sound as loud as 215 dB (re. 1 µPa at 1 m) [12], though high intensity clicks were not recorded from *P. serratus*. In all of the experiments, and in the holding tank, the ambient water was kept at a temperature of 18° C and a salinity of 34 psu. When not under experimental protocols, the prawns were provided with 14 hours of light per day from a fluorescent tube controlled by a mains timer switch. Prior to any experimentation the prawns were divided by size into three populations, and fed on a granulated feed at a daily rate of 6 g for the large prawns, 4 g for the medium and 2.5 g for the small.

2.1 Preparation methodology for electron microscopy

The pathway taken by the innervating nerves of the statocyst to the supraesophageal ganglion or brain was revealed by the anatomical investigation of a 54 mm *P. serratus*. The prawn was first immersed in 70% ethanol for 18 hours, to “fix” the specimen prior to the investigation. Exposure of the brain and statocyst was achieved by the dissection and removal of the dorsal-rostral section of carapace, the dorsal cuticle layer of the peduncle, the left eye, and the stomach. In decapod crusteacea, the lateral antenular and otic nerves extend with bi-lateral symmetry from the neuropil of the antennule; a region located centrally in the brain [20], to the statocyst and tactile bristles of the antennules. Examination of the brain of *P. serratus* reveals that it lies close to the rostral extremities of the carapace, ventral to the eyestalks and posterior to the antennules. On leaving the anterior region of the brain, the lateral antennular and otic ganglia project forward, and enter the antennule close to the inside edge of the peduncle. From there, the otic ganglia branches outward away from the main antennular nerve, which continues to project forward to the tactile receptors.

The statocyst capsules were removed by dissection from 12 of the specimens, and placed in a conical dish containing 2.5 ml of 0.9 % sodium chloride. The capsules were opened by making a lateral incision around the statocyst chamber using a fine scalpel. Needlepoint tweezers were used to lift the upper section of the capsule, thus exposing the sand granules and ultrastructure. The sodium chloride solution was removed using a pipette and replaced with a solution of 2.5 % S-Carboxymethyl-L-Cysteine in sodium chloride, which was used to hydrolyse the mucus surrounding

the statocyst receptors. The contents of the dish were gently agitated for two minutes, after which the solution was removed and replaced with chilled fixative (2.5% glutaraldehyde in 0.1 M cacodylate buffer with 3.5% sodium chloride). The statocyst capsules were then dehydrated through a graded ethanol series ranging from 35% through 50%, 70% and 90% to absolute ethanol, prior to desiccation using the critical point drying method. Fully desiccated statocyst capsules were subsequently mounted on a specimen stub using a carbon tab, and coated with c. 8 nm of gold in an Emitech K 550 sputter coater (working at approximately 5 x 10-6 Torr). Finally, the processed specimens were investigated and photographed using a JEOL JSM 5600 scanning electron microscope operated at 15 kv, and a 15 mm working distance. Images of the ultrastructure were captured using the JEOL software, which saved the micrographs in a bitmap format.

2.2 ABR methodology

In order to concisely answer the question of hearing by crustaceans, twelve prawns were stimulated with sound ranging in the frequency domain between 100 Hz to 3000 Hz, presented at sound pressure levels of between 132 dB (re 1 µPa at 1m) to below 90 dB (re 1 µPa at 1 m). The response of the prawn to acoustic stimulation was measured using a well established audiometry technique, with the results expressed as an audiogram or limen of sound spectral sensitivity. The ABR measurements of hearing threshold were made using a proprietary control and analysis programme, written in a LabView 7 environment. This programme both generated the stimulus signals and captured and analysed the response and was installed onto the PC shown in Figure 1.a. The stimulus used was a sine train (sine wave pulse) which was presented to *P. serratus* at a given frequency and sound pressure level, not exceeding 130 dB (re 1 µPa at 1 m) for each of the frequencies tested. For ABR recordings to be clear, it requires that short duration tone bursts are used, especially for the low frequencies. Kenyon et al (1998) [33] used a two cycle burst for frequencies between 100 and 300 Hz, a five cycle burst with a 2 cycle attack decay for frequencies between 400 and 3000 Hz. Amplification of the sound was achieved using a Pioneer type SA-420 amplifier and a 200 mm Eagle L032 loudspeaker with a frequency response range of 40 Hz to 18000 Hz. Additionally, the loudspeaker was placed inside a Faraday cage and connected to a centralised earth point located in an adjacent room where the PC, amplification, and analysis equipment was set up. Connecting wires were fed through a 100 mm port in the partitioning wall.

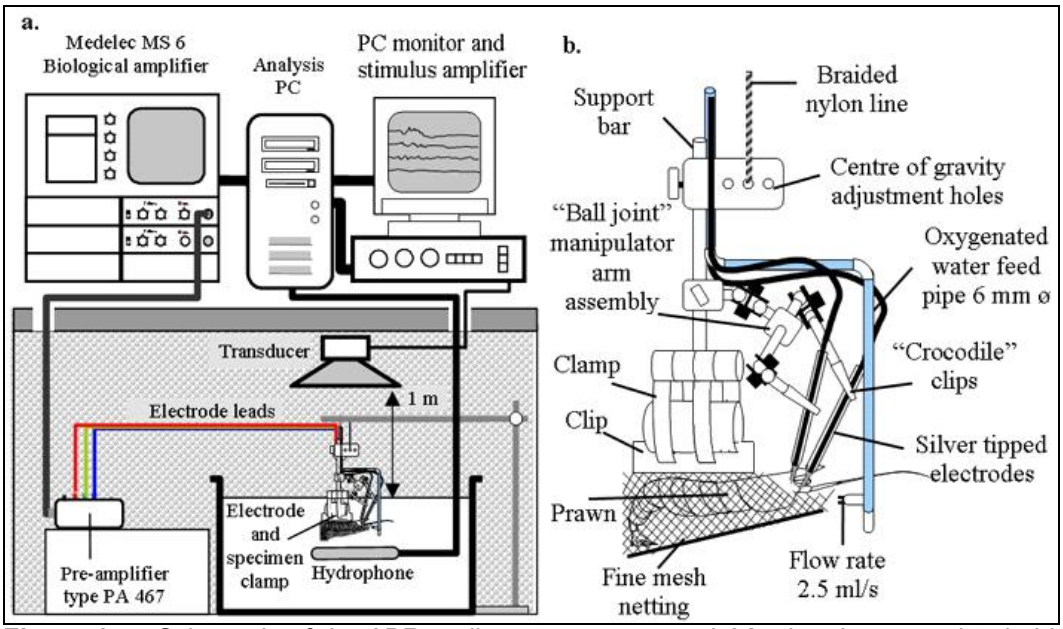

Figure 1.a. Schematic of the ABR audiometry system, and **1.b.** the clamp used to hold the prawn in position and manipulate the electrodes during the audiological tests

The procedure used to acquire the acoustically evoked potentials was approved by the United Kingdom Home Office 11.03.03. The test subjects were placed into a flexible cradle formed from a

soft nylon mesh rectangle saturated with seawater. Oxygenated water kept at a temperature of 18° C was gravity fed at an adjustable flow rate of 3 millilitres per second and directed toward the gills. The water was held in an aerated reservoir positioned in an adjacent room, and fed to the prawn through a 4 mm diameter plastic tube. The prawn was first placed lengthwise and centrally on an 80 mm x 60 mm rectangle of fine nylon netting, which was wrapped firmly around the cephalothorax and pleon, and the two sides of the net were held together using the clip shown in Figure 1.b. The evoked response was amplified and digitised to 12 bits resolution and recorded. This process was repeated up to 2000 times and the response averaged to remove electrical interference caused by neural activities other than audition, and the myogenic noise generated by muscular activity. Each measurement was repeated twice; this aids in separating the evoked response, which is the same from trace to trace, from the myogenic noise, which varies in two successive measurements. After the averaging process, the evoked potential could be detected, following the stimulus by a short latency period of 5 milliseconds or so. The latency is accounted for by the time it takes the sound in air to travel the 1 m to the prawn, plus 1 to 2 milliseconds response latency.

The properties of the sound field are especially relevant when comparing the audio capabilities of both pressure sensitive and motion sensitive fish in the near field. In a small laboratory set-up, the complexities associated with independently measuring sound pressure and particle motion are compounded by the reflectivity of the tank sides and base. For this reason, a number of experiments have used air-mounted transducers to successfully generate sounds underwater [33,34,35,36]. The principle advantage of such a system is that as the sound source is located at a distance of 1 m from the air/water interface, the moving part of the transducer does not contact the water and generate near-field displacements. In this situation the pressure and motion of the water adjacent to the ear can be considered as being equal (Hawkins 1981). The stimulus tones presented from the loudspeaker to the prawn were calibrated using an insertion calibration. A calibrated Bruel and Kjaer Type 8106 Hydrophone (Serial Number 2256725) was placed in the tank and positioned adjacent to the shrimp cephalothorax region. The signal from the hydrophone was amplified using a PE6 preamplifier and digitised using a National Instruments DAQ-6062e interface card at a sample rate of 300 kB/s. In case of non-proportionality of the response amplitude of the loudspeaker, measurements of the sound pressure were taken for each amplitude and frequency setting used.

3 RESULTS

3.1 Electron Microscopy

The examination of the complete statocyst revealed ultrastructural cell projections extending into an elliptical mass of sand granules (the statolith), cemented to the tips of the projections by mucus. The sand granules are collected from suitable substrate and carefully positioned in the antennule by the prawn, following each moult cycle. For ease of viewing the ultrastructure, prawns selected for histological examination were denied sand and other particulate matter that could be used to build the statolith, thus keeping the cell tips clear. The inertial interaction between the dense statolith mass and the less dense supporting statocyst provides the central nervous system with accelerational and gravistatic information. The motion sensitive cells project from small apertures in the statocyst floor about 7 µm in diameter; through which the receptor connects to the peripheral fibres of the otic ganglion. At a distance of 2 µm from the base, the cell widens and forms a bulb which has a diameter of 9 µm at its widest point, and displays a series of longitudinal ridges that run around the bulbous structure. The uppermost portion of the cell base narrows to 0.8 µm and forms a fulcrum point from where a 3.5 µm diameter hair shaft extends 40 µm into the lumen of the statocyst. The tips of the hair shafts are embedded in the sand granules and mucous forming the statolith. More than 70 of these vertical cell projections are arranged in a row shaped like a crescent, covering 0.073 mm^2 of statocyst (Figure 2.b) and form a mesh cradle that supports the statolith. Each hair cell is orientated toward a common central region (cr), and the shortest hairs (< 120 µm) were found proliferating in a band running down the left side of the array, whilst the longest hairs (> 170 µm) were found in the right caudal quadrant. The statocyst capsule is elliptical in shape, and the walls (Figure 2.b) symmetrically curve inward toward the base, where the receptor cells are located on a mound rising 40 µm from the floor of the capsule. From the crest of the mound, the receptor hairs project upward into the lumen of the statocyst at angles of between 27°

and 74° from the horizontal plane. Behind the hair cells, in the space between opposing receptors, the mound flattens and forms a plateau (pl), which is void of any ultrastructure.

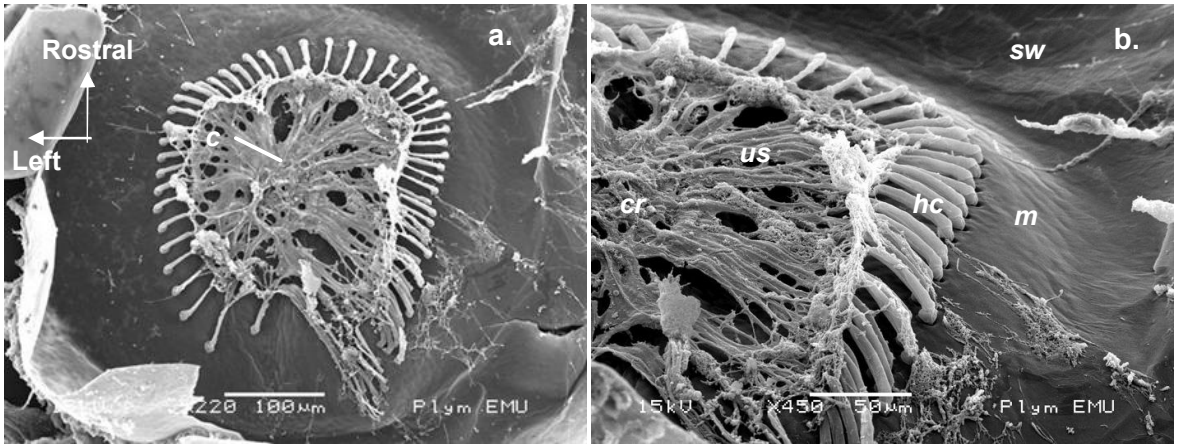

Figure 2.a. Dorsal view of the statocyst from a 55 mm prawn denied sand for 7 days post moulting. cr. central region, and Figure **2.b.** Lateral view of the statocyst. cr. central region, hc. hair cell, m. mound, sw. statocyst wall, us. upper tapering section of hair cell

3.2 Electrophysiological response to auditory stimuli

In order to concisely answer the question of hearing by crustaceans, twelve prawns of mixed sex were stimulated with sound ranging in the frequency domain between 100 Hz to 3000 Hz, presented at sound pressure levels of between 130 dB (re 1 µPa at 1 m) to below 90 dB (re 1 µPa at 1 m). The Auditory Brainstem Response (ABR) recording technique has been successfully applied in the auditory assessments of both mammalian and non-mammalian vertebrates and invertebrates [36]. An ABR waveform is acquired by averaging conglomerate responses of peak potentials, arising from nuclei in the auditory pathway during acoustic stimulation. Figure 3 shows ABR waveforms evoked from *P. serratus* in response to a 500 Hz tone burst, presented initially at between 120 to 132 dB (re 1 µPa at 1 m), and attenuated in steps of 4 dB (re 1 µPa at 1 m) ordinarily, and 2 dB (re 1 µPa at 1 m) as the hearing threshold was approached.

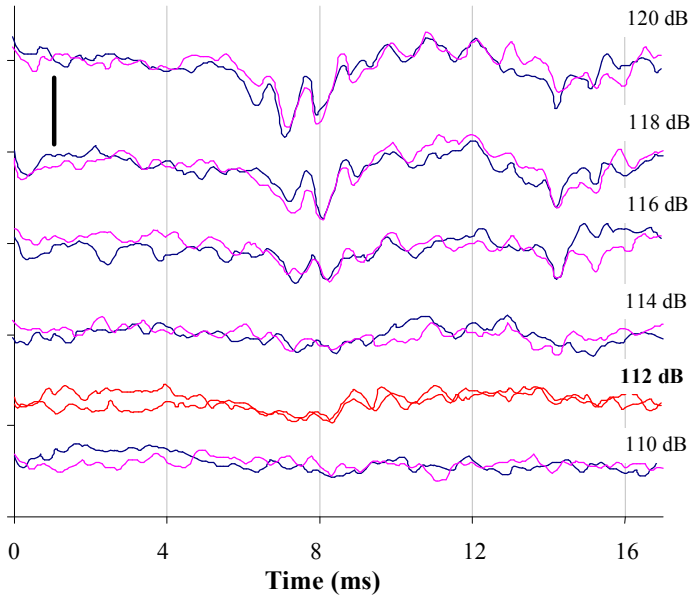

Figure 3. ABR waveforms from *P. serratus* in response to a 500 Hz tone burst attenuated in 2 dB steps. Averaged traces of two runs (2000 sweeps each), for each intensity are overlaid and arranged sequentially. Bar = 1 µV (ABR response)

3.3 Audiogram for *P. serratus*

Threshold responses from twelve 50 mm to 55 mm (medium) prawns were determined visually from the sequentially arranged waveforms for each frequency tested, in accordance with Kenyon et al (1998). When two replicates of waveforms showed opposite polarities (see 110 dB traces in Figure 3), the response was considered as being below threshold. The audiogram shown in Figure 4 was produced using sequential ABR waveform threshold data, acquired from frequencies of 100 Hz to 3000 Hz, presented in steps of between 200 Hz to 500 Hz. The hearing thresholds of 12 mixed sex *P. serratus* was measured, and follows a ramp like profile, determined by calculating the lowest intensity stimulus sounds (recorded underwater using the hydrophone located adjacent to the antennule) that evoked a repeatable ABR response (112 dB in Figure 3). The profile follows a steady downward gradient to 100 Hz (the lowest frequency tested), and indicates that the "best" frequency in terms of threshold could be below this frequency.

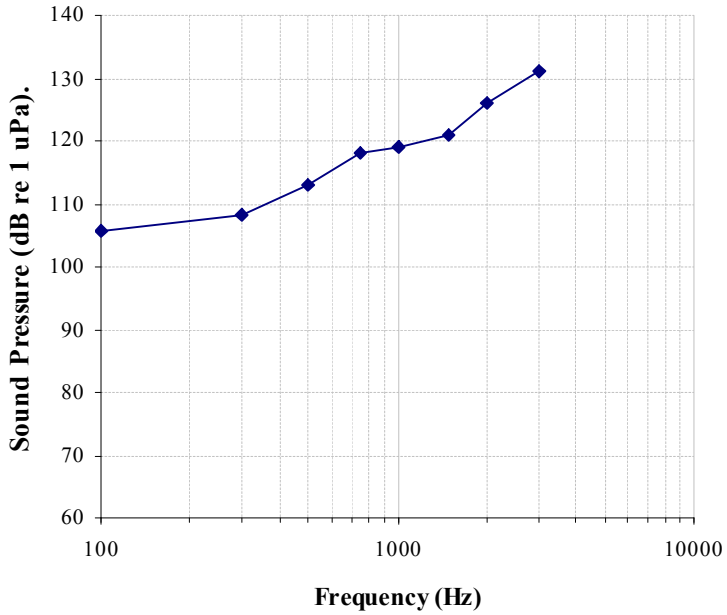

Figure 4. Audiogram for *P. serratus*, determined visually from the sequential ABR waveform data, and by calculating the RMS of threshold SPL values of the stimulus sounds, presented at 100 Hz, 300 Hz, 500 Hz 750 Hz, 1000 Hz, 1500 Hz, 2000 Hz and 3000 Hz tone bursts

4 Discussion

The hearing ability of the prawn (*Palaemon serratus*) has been clearly demonstrated by this work using ABR audiometry, and offers conclusive evidence of low frequency sound detection of frequencies ranging from 100 Hz to 3000 Hz by an invertebrate from the sub-phylum crustacea. For hearing in the strictest sense to be attributed to an organism, the physiological response sound should be initiated by a specialised receptor mechanism [2], shown by this work to be generated in the statocyst. Current literature states that this organ is purely responsive to angular rotations and strong vibrations propagated directly through a solid medium and is not responsive to sounds propagated in either air or water [27]. It is highly probable that Cohen and Dijkgraaf [27] did not find evidence of hearing due to masking of the AEP by neural activities other than audition and from myogenic noise generated by muscular activity. To produce clear waveforms of an auditory response, it is recommended that AEP recordings be averaged for at least 1000 to 2000 stimulus presentations [33,34]. The amplitude and shape of the electrophysiological response from *P. serratus* shown in Figure 3, bear a remarkable similarity to AEP's generated by fish and higher vertebrates [31,33].

The two statocyst organs found in *P. serratus* lie adjacent to one another with medial symmetry, in the basal peduncle segment of the antennule. The statocyst is innervated by the otic ganglion, which emanates from a bed of peripheral nerve fibres lying under the mound (Figures 2.a,b) directly beneath the receptor array. The otic nerve terminates in the neuropil of the antennule, which is located in the ventral/anterior region of the brain. The total length of the neuronal pathway taken by the otic nerve, from the centre of the statocyst organ to the centre of the supraesophageal ganglion is approximately 600 µm in a 54 mm prawn. However, the direct distance between the neuropil and the peripheral nerve fibres located below the statocyst, was found to be 500 µm. This is due to the

curved pathway taken by the otic nerve, which first projects forward with the lateral antennular ganglion along the inside edge of the peduncle for 300 µm. From here, the otic ganglion branches away from the antennular ganglion at angles approaching 45° either side of the midline, from where it extends for a further 300 µm to the centre of the peripheral otic nerve bed.

It is clear by the evidence presented in this work, that the perception of sound in the frequency domain by *P. serratus* is similar in range to hearing in many marine fish, which are reported to be capable of both hearing and responding to sounds within a frequency bandwidth of 30 Hz to around 2000 or so Hz [37]; hearing is reliant on the phase variance between the three otolithic organs and the surrounding flesh to stimulate the sensory hairs of the inner ear [38]. The audiogram presented in Figure 4 follows a similar ramp like profile to those obtained from the cichlid *A. ocellatus*, which is considered to have most sensitive hearing at a frequency of 100 Hz [33]; however, lower frequencies were not tested.

We therefore conclude that at least one species from the invertebrate sub-phylum of crustacea, is sensitive to the motion of water particles displaced by low frequency sounds ranging from 100 Hz up to 3000 Hz. Although a number of physiological and behavioural experiments have been conducted on fish to assess the impact of noise on the auditory system none have, so far, been directed toward the crustaceans, a major link in the oceanic food chain. The long-term effects of intense low frequency sounds on the shrimp hearing ability and ecology is not known, but the data presented here shows that there is a need to include crustaceans in such an assessment, in order to gain a more insightful view of the effect of intense noise on the marine ecosystem.

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