

Article

Mechanoreceptors found on larval and juvenile stage of *Squilla empusa* Say 1818 (Stomatopoda: Squilloidea)

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Abstract

The mechanoreceptors found on the larval stages and juvenile stage of squilloid stomatopods are investigated using photomicrographs and scanning electron micrographs. The frequency which may be detected by a sensillum is related to its length and the thickness of the boundary layer. Early stage alima larva, the larval form of the Squillidae, have paired peg sensilla on the distal margins of the annuli of the antennule flagella. These sensilla are potentially capable of detecting nearfield sound energy at frequencies ≥ 2.0 kHz. In the later alima larval stages, the peg sensilla are present in both paired and triple sets. The triple sets of sensilla are potentially capable detecting nearfield sound energy at frequencies ≤ 0.02 kHz. In both early and late alima larva the distal margin of each antennule flagella annuli is found to have a tactile sensilla. In the late alima larval stage, there are ten sensilla at the distal end of the coxa of the antennules. The scale of the antenna is armed with numerous peg sensilla potentially capable of detecting nearfield sound energy at frequencies greater than ≤ 0.02 kHz. Peg sensilla are also found on the posterior margins of the walking legs. The flagella of the juvenile stage of *Squilla empusa* Say have a tuft of sensilla on the distal margins of each annulus. Six sensilla are found on the walking legs of the juvenile stage. A tympanum-like structure similar in shape and location to that reported in the literature on the stomatopod *Ostratosquilla* is found on the coxa of the juvenile stage of *Squilla empusa* Say.

Keywords *Squilla empusa*; bioacoustics; sensilla; tympanum; alima larva.

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1 Introduction

The ability of members of the Stomatopoda to produce sounds by means of stridulating structures located on the uropods and telson of squilloid mantis shrimp has been recognized in the scientific literature from the late 1800s (Brooks, 1886b; Kemp, 1913; Ahyong, 1997). More recently sound production by muscular vibrations of the carapace in *Hemisquilla californiensis* has been studied and documented (Staaterman et al., 2011;

Staaterman et al., 2012). The ability to produce sounds by the actions of the second maxillipeds has been studied by (Patek and Caldwell, 2005; Fornshell, 2020). The ability to detect near field sound has been recognized and documented (Heitler et al., 2000; Popper et al., 2001). There is disagreement as to the ability to detect far field sound by the Stomatopoda. Popper et al. (2001) assert that only near field sound is detected by sensilla in arthropods and possibly by means of the statocyst. Derby et al. (2003) also asserted that while the crustacean statocyst can detect near field sound also asserted that “There is no evidence of the presence of a statocyst in the stomatopod *Neogonodactylus oerstededii*”. Popper et al. (2001) and Derby et al. (2003) and Tidau and Briffs (2016) assert that members of the Stomatopoda do not have pressure sensing organs and therefore cannot detect far field sound energy. Alternatively, Tirmizi and Kazmi (1984) reported on sound pressure detecting organs in the Stomatopoda and record the presence of a tympanum on the stomatopod, *Ostratosquilla*. Ng (2000) reported the presence of a tympanum-like structure on the merus of the chela of the deep-sea swimming crab *Benthochascon schmitti*. Ramadan (1936) similarly described the presence of a tympanum-like structure on the merus of the last walking leg of the crab *Dotilla sulcata* (Forsk., 1775).

Based on studies involving the rearing of stomatopod larva to the juvenile stage, the alima larva has been found to be the larval form of the genus *Squilla* (Brooks, 1881; Ahyong et al., 2014). The alima larva in the Natural History Museum’s collections are assumed to be the larva of squilloid stomatopods. The larvae of this family hatch as Pseudo zoea having pedunculate eyes and biflagellate antennules and only two pairs of maxillipeds. The Pseudo zoea, which last for 2 to 3 molts, remain in the benthic in what is often called the propelagic phase (Payne, 1972; Ahyong et al., 2014). The next phase or pelagic phase is when the alima larvae undergo several molts, up to nine, before metamorphosing into the post-Larval stage. The alima larvae have pedunculate eyes and triflagellate antennules. The alima larvae are motile and found in the plankton. The post larval stage is in many ways morphologically similar to the juvenile stage (Ahyong et al., 2014).

Arthropod larvae have been shown to respond to acoustic cues from the marine environment (Simpson et al., 2011; Stanley, 2012). Also, there are characteristic acoustic signatures for different marine benthic environments (Stanley, 2012; Staaterman et al., 2013). The development of mechanoreceptors capable of detecting sound energy, either near field or far field is fundamentally important in the understanding of larval and juvenile behavior and habitat selection.

2 Materials and Methods

In this study the presence of sound detecting organs on alima larva and juveniles of *Squilla empusa* Say 1818 are described from electron micrographs. Specimens archived in the collections of the U. S. National Museum of Natural history which had been stored in 70% ethanol were used. The specimens used in this study were progressively dehydrated in 75%, 90%, and 100% ethyl alcohol solutions, critical point dried and coated with gold palladium alloy before the making the scanning electron micrographs using a Zeiss EVO MA15 Electron Microscope (Zeiss, Tokyo, Japan). The photomicrograph images used in this study were made using a ScopePhoto MI-DC1300 digital camera Home Science Tools (665 Carbon Street, Billings MT 59102 USA). The dimensions of the mechanoreceptors, sensillum, were measured from electron micrographs.

3 Results

Photomicrographs, like the line drawings typical of the literature describing stomatopod larvae (Brooks, 1886; Kemp, 1913) show early stage alima larva as having paired mechanoreceptors on the annulated flagella of the antennules (Fig. 1). The early instars, pseudo zoea or third or fourth instars of the alima larva viewed in electron micrographs are seen to have paired peg sensilla on the three flagella of the antennules. The sockets of the paired peg sensilla are 4 µm in diameter and the sensilla are 24 to 45 µm long (Fig. 2). This would indicate

that these sensilla can only detect near field sounds at frequencies of ≥ 2.0 kHz (Fletcher, 1992; Barth, 2004). Late post hatching stage alima larva have both paired and triple peg sensilla on the annulated flagella of the first antennules. In addition to the paired sensilla there is a tactile sensilla at the distal margin of each annulus with a single socket eight μm in diameter. The tactile sensilla is 207 μm long (Fig. 2).

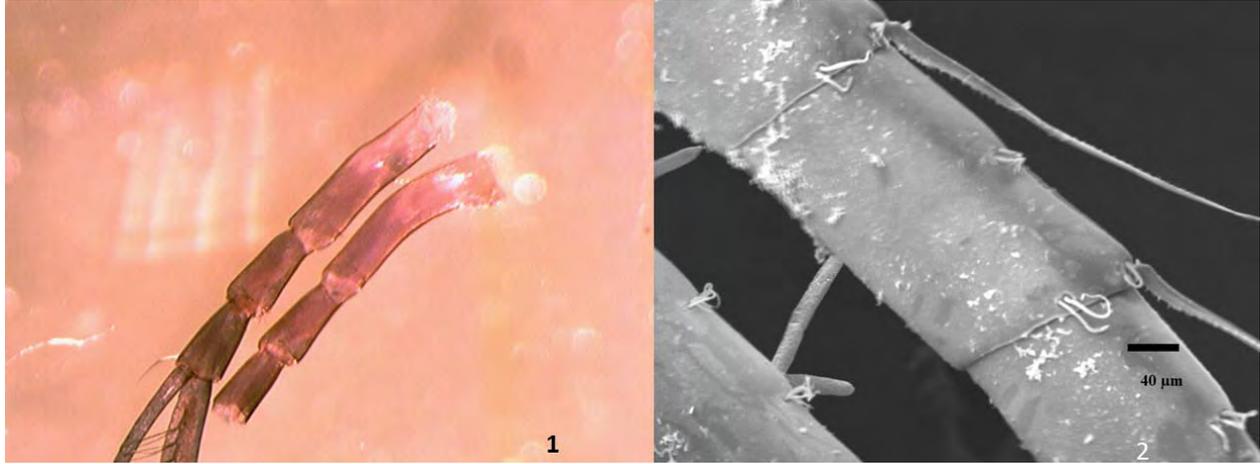


Fig. 1 A photomicrograph of an alima larva antennule.

Fig. 2 An electron micrograph showing the paired sensilla at the distal margin of the annuli on the flagella of the antennules of an early post hatching stage of an alima larva.

The later instars of the alima larva also have paired peg and triple sensilla on the three flagella of the antennules (Fig. 3). The sockets of the paired peg sensilla are thirteen μm in diameter and the peg sensilla are 300 to 320 μm long. This would indicate that they can detect near field sounds at frequencies ranging from tens of kHz to ≤ 0.02 kHz (Fletcher, 1992; Barth, 2004; Fornshell, 2022). Based on photomicrographs and electron micrographs, the alima larva antennular coxa lacks a tympanum-like structure, but it does have ten individual sensilla 53 to 100 μm long at the distal end of the coxa of the antennules analogous to similar structures described by Tirmizi and Kazmi (1984)(Fig. 1 & 4). This pattern was described by Tirmizi, and Kazmi (1984) as occurring on adults of *Ostratosquilla*.

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In the juvenile stage the three flagella of the antennules are annulated with about 33 annuli each (Fig. 7). At the distal margin of each annulus there is a tuft of sensilla varying in length from 17 μm to 140 μm (Figs. 8 & 9). The legs of the juvenile stage of *Squilla empusa* have 6 sensilla approximately 650 μm long. The socket diameter is sixty μm . The mechanoreceptors on the posterior margin of the waling legs of *Squilla empusa* juveniles are plumose in form (Fig. 10). The morphology of these sensilla on the legs indicates that they are tactile in function (Figs. 8 and 9).

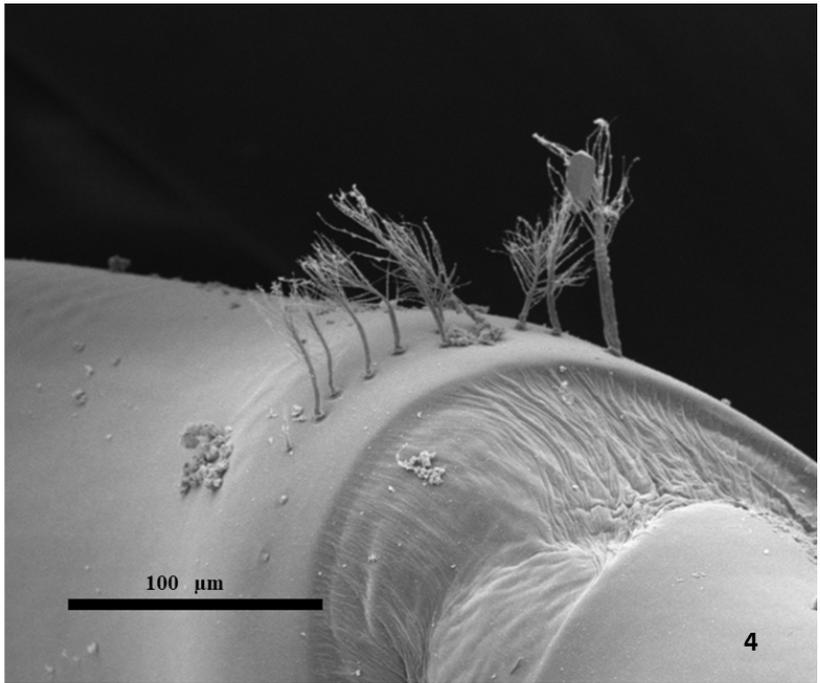


Fig. 3 Late stage alima larva with both paired and triplet peg sensilla and the annulated flagella of the antennules. **Fig. 4** A tuft of sensilla at the distal margin of the coxa of the first antennule of an alima larva.

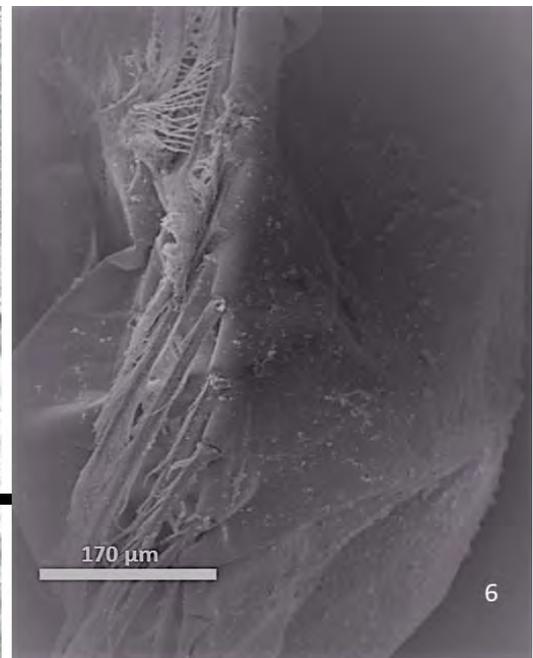
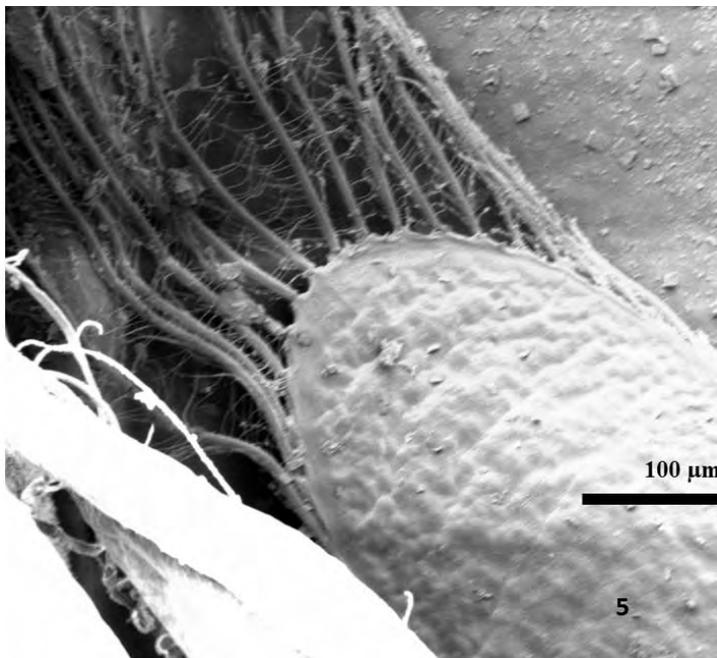


Fig. 5 Elongated Peg sensilla on the margin of the antennal scale of a late stage alima larva.

Fig. 6 Sensilla on the walking legs of an alima larva.

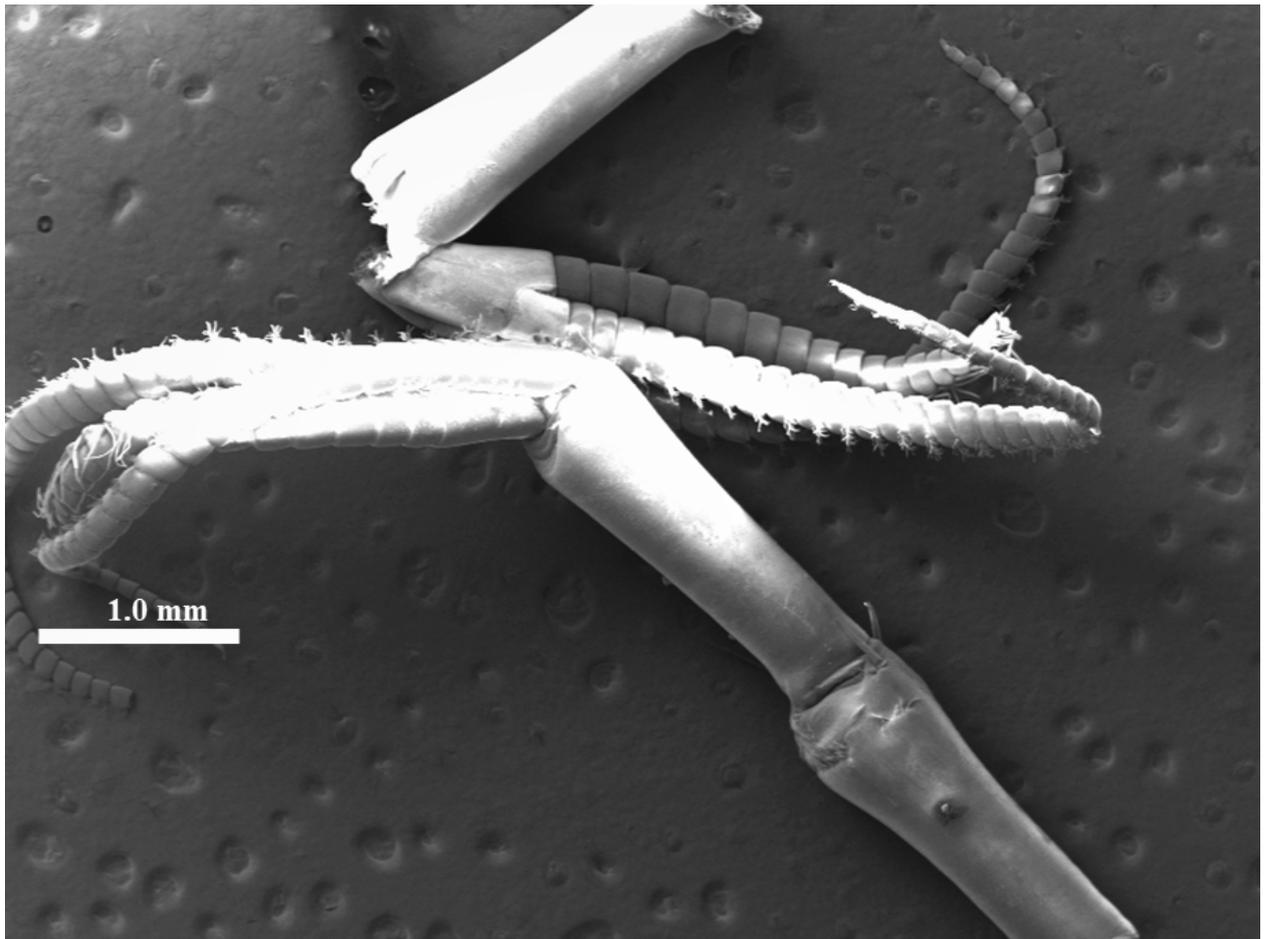


Fig. 7 Antennule of juvenile *Squilla empusa*.



Fig. 8 Tufts of peg sensilla on the distal margins of the flagella annuli. There are typically thirteen sensilla in each tuft with lengths varying from 17 to 140 μm.



Fig. 9 A single tuft of sensilla on the distal margin of the antennular flagella.

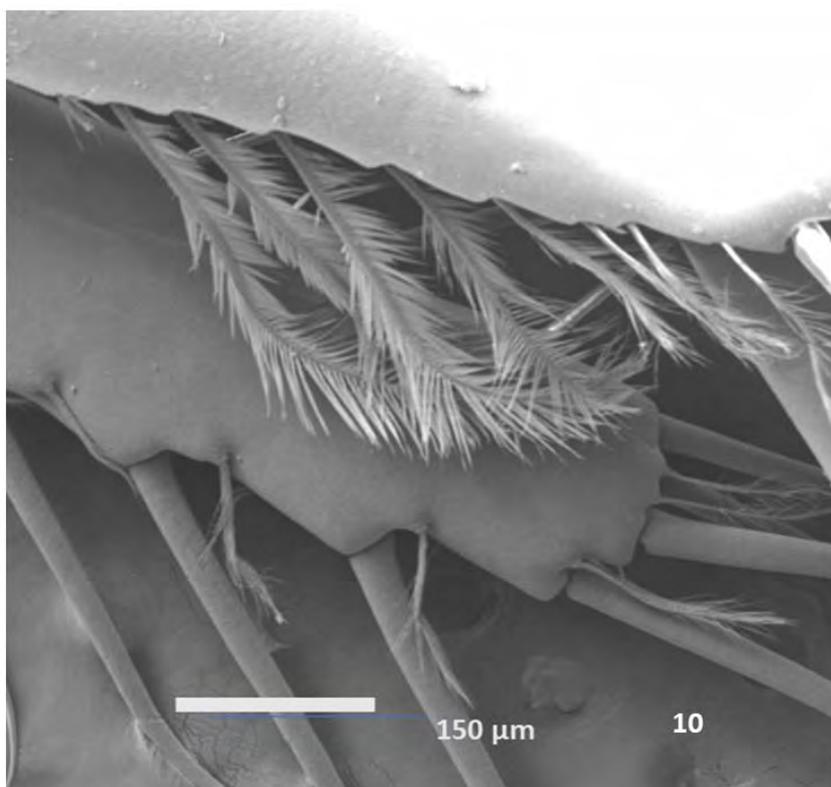


Fig. 10 Sensilla on the walking legs of a juvenile *Squilla empusa*.

In the juvenile stage of *Squilla empusa*, there is a tympanum-like structure on the coxa of the antennule. This tympanum-like structure is @ 47 μm in diameter (Figs. 7, 11 & 12). The sensilla seen in the alima larval stage at the distal end of the coxa is also present, but now the length is 90 μm. This would indicate that the peg sensilla on the flagella of the antennules can only detect near field sound energy with frequencies ≥ 2.0 kHz.

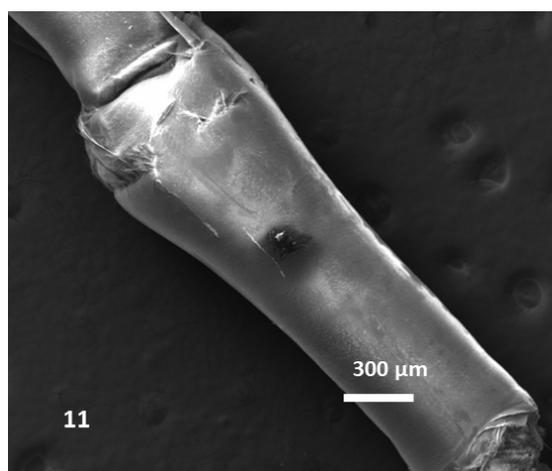


Fig. 11 The coxa of the antennule shows the tympanum-like organ on the coxa of the antennule of a juvenile animal.

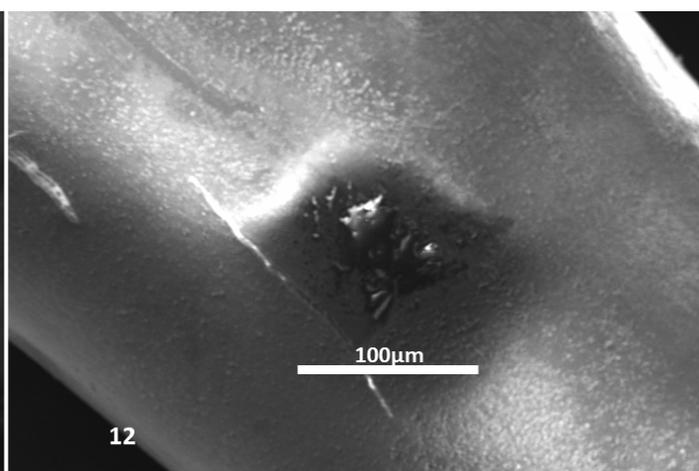


Fig. 12 An enlarged image of the tympanum-like organ of the antennule of a juvenile animal.

4 Discussion

The sensilla found on the alima larva are like those found on other crustaceans adapted to detecting near field sound, which is particle motion. This form of sound energy dominates at ranges of about one-half the wavelength. The sensilla must extend above the boundary layer for particle motion in sea water (Fletcher, 1992; Devarakonda et al., 1996; Barth, 2004; and see graphs 1 and 2 in Fornshell (2022)). The thickness of this boundary layer is a function of the kinematic viscosity and the frequency of the sound. It is equal to $[\text{kinematic viscosity}/\text{sound frequency}]^{1/2}$ (Fletcher, 1992; Devarakonda et al., 1996; Barth, 2004; Fornshell, 2022).

The larva of marine animals, invertebrates and fish have been shown to use acoustic cues to locate a suitable habitat and/or avoid an unsuitable habitat (Fletcher, 1992; Simpson et al., 2011; Stanley et al., 2012). The alima larva has mechanoreceptors on the three flagella of the antennules, on the Scale of the antenna and on the posterior margin of the larval stage walking legs. Based on their length (Table 1) these mechanoreceptors have the potential of detecting sound energy only if they extend above the boundary layer for particle motion in sea water (Fletcher, 1992; Devarakonda et al., 1996; Barth, 2004; Fornshell, 2022). This would indicate that they can detect sounds of ≥ 2.0 kHz in the case of the sensilla on the early alima stage antennule flagella. The sensilla on the antennules at least in the early larval stage would have little value for navigation due to the extremely short ranges at which they could detect sound sources, ≤ 0.75 m. In the case of the late stage alima antennule flagella sensilla this would decrease to frequencies as low as 0.10 kHz and would be capable of detecting near field sound at ranges of about 7.5 meters. Thus, they might be useful in navigation to favorable or from unfavorable habitats. The sensilla on the scale of the antenna at 400 μm are capable of detecting exceptionally low frequencies, ≤ 0.02 kHz and therefore ranges ≥ 37.5 meters. As such the alima larva may be capable of using sounds to orientate its behavior.

Table 1 Mechanosensory organs on larval squilloid mantis shrimp.

Location of sensilla	socket diameter	length of sensilla	Number of sensilla present
Antennule flagella Early stage alima	paired sockets 4 μm	24 and 45 μm	present in pairs
Antennule flagella Late stage alima	paired socket 13 μm	300 μm	present in pairs
Antennule flagella tactile setae on the distal margin Each annulus of The antennule flagella	single socket 8 μm	207 μm	single sensilla
Scale of the antenna	single socket 8 μm	400 μm	eighteen sensilla
Coxa of antennules	10 individual sensilla	53 to 100 μm	individual sensilla
Alima walking leg	single socket 4 μm	300 μm	sensilla?

Localized habitats have been shown in some cases to have distinct sound signatures. As such the presence of peg sensilla on the flagella of the antennules and scale of the antenna would potentially facilitate habitat selection by late alima larvae and juvenile stages of stomatopods (Radford et al., 2010; Stanley, 2012).

Table 2 Mechanosensory organs on juvenile squilloid mantis shrimp.

Location of sensilla	socket diameter	length of sensilla	Number of sensilla present
Juvenile antennule	@ 5 μm	20-100 μm	13 sensilla on annuli
Juvenile walking leg	@ 60 μm	600 μm	6 sensilla
Tympanum-like structure on coxa of antennule @ 47 μm in diameter.			

The mechanoreceptors on the juvenile stage antennule flagella are actually shorter than those in the late stage alima larva. As such they are only capable of detecting sounds of frequencies greater than 0.5 kHz. The fact that there are sensilla of different length, the juvenile is potentially capable of differentiating between different frequencies ≥ 0.50 kHz

As noted in the introduction Popper et al. (2001) and Derby et al. (2003) assert that crustaceans lack a sound pressure sensing ability. Three carcinologists have, however, reported the presence of a tympanum-like organ on a crustacean (Ramadan, 1936; Tirmizi and Kazmi, 1984; Ng, 2000). These authors report the presence of a tympanum on the merus of the last walking leg of the land crab *Dotilla sulcata* (Forskal, 1775) (Ramadan, 1936). The presence of a tympanum has been reported on the stomatopod *Ostratosquilla*, providing a line drawing. In the genus *Ostratosquilla* an oval membrane-the tympanum found halfway from the base on the median margin of the basal segment of the antennular peduncle is regarded as auditory in function. A tuft of special setae is also found in its proximity. To some sensory setae an auditory function has also been attributed.” (Tirmizi and Kazmi, 1984). Finally, Ng (2000) described and provided a photomicrograph of a tympanum-like organ on the crab *Benthochascon*. In the present study a tympanum-like organ has been found on the coxa *S. empusa*. Because none of these observed tympanum-like organs has been shown experimentally to be a functional tympanum one cannot conclude definitively that a tympanum is found on crustaceans. The behavioral studies showing that stomatopods can recognize other stomatopods in their burrows indicates the possibility of having a sound pressure sensing capability (Vetter and Caldwell, 2015). This is an area of bioacoustics research which needs further work.

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