Article

A brief analysis of progress in mantis shrimp bioacoustics

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Abstract
The historical study of bioacoustics of mantis shrimp (Stomatopoda) is used as an example for the progress made in the study of bioacoustics in general. In the preceding 139 years biologists have published 80 manuscripts documenting the acoustics of the Stomatopoda. The number of scientific publications is taken as a quantitative measure of the increase of our knowledge of stomatopod bioacoustics. The first eighty years were characterized by anecdotal studies and records with a scientist to publication ratio of 1:1. The fifty year period from 1960 to 2010, which resulted in an exponential increase in our knowledge of bio-acoustics, were characterized by the increasing use of electronic recording instruments, hydrophones, underwater imaging devices, computers for spectral analysis and laboratory experiments, with a scientist to publication ratio of approximately 2:1. The following fourteen years saw decrease in the publications, i.e., acquisition of new knowledge, and a near doubling in the ratio of scientists to publications ratio to 3.25:1 scientists to publication.

Keywords bio-acoustics; sensilla; Stomatopoda; hydrophones; stomatopod rumble; stridulations.

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1 Introduction

The study of sounds produced by living animals began when people first began to interact with animals on land and the sea. At first this was purely anecdotal in nature with hunters learning the sounds produced by their prey and recognizing the need to avoid making noises which might be heard by the object of their hunt. In the case of marine life, fishermen learned the sounds produced by the marine animals which they were seeking. For example, New England whalers called sperm whales, *Physeter macrocephalus*, carpenter fish, because of the tapping sounds they made when surfacing.

Looking at the subject of bio-acoustics for the whole of the animal kingdom would involve an extremely large body of scientific publications. The bio-acoustics of the mantis shrimp, Stomatopoda, is chosen in part because these animals have been the subject of well documented research and is typical of both the trends in technology and biology present in the study of marine bio-acoustics globally. Also, the author has some firsthand experience with the study of bio-acoustics of these animals, having published two manuscripts in referred scientific journals. Brooks (1886) was the first to record sounds produced by mantis shrimp in the scientific literature. He observed that the mantis shrimp, *Squilla impusa* Say 1818, makes sounds by rubbing the serrated spine of the swimmeret across theridge on the ventral surface of the telson. “The noise which is thus made under water can be clearly heard above the surface.” Kemp (1913) and Ramadan (1936) observed the presence of what they called a tympanum on a stomatopods and decapods . They did not record the detection of any sounds. Before the 1960s, Stomatopod acoustics research was restricted to sounds detected by the human ear and visual observations of potential sound detecting and producing organs.

In the 1960s biologists studying the behavior of mantis shrimp and other arthropods, *Panulirus, Gonodactylus, Alpheus,* and *Synalpheus*, established that they produced specific sounds when defending territory and during acts of aggression (Hazlett & Winn, 1962; George & Main, 1967; Dingle & Caldwell, 1969). As in the earlier work,the human eye and ear were the methods of observing and recording sound production and response to sounds in the animal’s environment. The use of electronic recording devices was to begin in the coming decades.

The use of acoustic recording devices was first introduced by Australian biologist studying larval movements using experimental methods to identify and quantify the response of animals to acoustic cues in the tropical marine environment (Payne, 1972; Montgomery et al., 1974; Cato, 1978). These studies mark the beginning of the use of hydrophones for the detection and recording of sounds produced by animals as well as their response to bioacoustics signals and environment noises not produced by living creatures.

The 1980s brought the use of active Sound Navigation and Ranging, SONAR, to identify the acoustic signatures of plankton in the marine environment (Greenlaw & Johnson, 1982). The role of the statocyst in sound detection by arthropods was identified (Budelmann, 1988). Wales & Ferrero (1987) also introduced the study of proprioception as a sensory mode for detecting low frequency vibrations in the substrate of benthic marine animals.

In the 1990s the role of sensilla in arthropod sound detection was studied by Wolfrum (1992) Devarakonda et al. (1996), Fletcher (1992) and Schiff & Hendrickx (1997). This work further increased the knowledge of the importance of near field sound detection in stomatopods as well as other arthropods. The morphology of sound production and detection was also shown to have phylogenetic significance for the Stomatopoda (Ahyong, 1997).

The first decade of the twenty first century witnessed a doubling of the number of stomatopod bioacoustics publications as well as a similar increase in the number of research workers in the field. During this decade bioacoustics began to be used to study and understand the mechanisms of conspecific interaction in the marine environment (Popper et al., 2001). The use of video imagery to connect animal behavior with acoustic signals began with Heitler et al. (2000) showing the escape behavior of *Squilla mantis* in response to both visual and acoustic stimulation. The morphology of near field sound detecting organs of the Caribbean stomatopod *Neogonodactylus oerstededii* was further investigated by (Derby et al., 2003). Montgomery et al. (2009) added to our understanding of signal detection by mechanoreceptors. The sounds produced by marine animals such as stomatopods were found to contribute to the distinct sound scapes of marine habitats (Radford et al., 2010). Also, a review of fossil morphology of the Stomatopoda showed that the ability to produce sounds was present in Mesozoic and Paleozoic times (Stentor, 2008).

Laboratory studies of the mechanisms of far field sound production in stomatopods was also begun during this decade. The sounds produced by the maxillipeds of *Odontodactyluss cyllarus* when attacking prey organisms were documented by Patek & Caldwell (2005). Low frequency sound production in *Hemisquilla californiensis*by vibrations of the carapace was also described by (Patek & Caldwell, 2006). This work was further extended to *Panulirus interruptus* in the marine environment linking behavior with sounds produced by stomatopods (Patek et al., 2009). Marine benthic animals such as *Squilla mantis* were found to have distinct acoustic signatures in active SONAR studies (Fornshell et al., 2010).

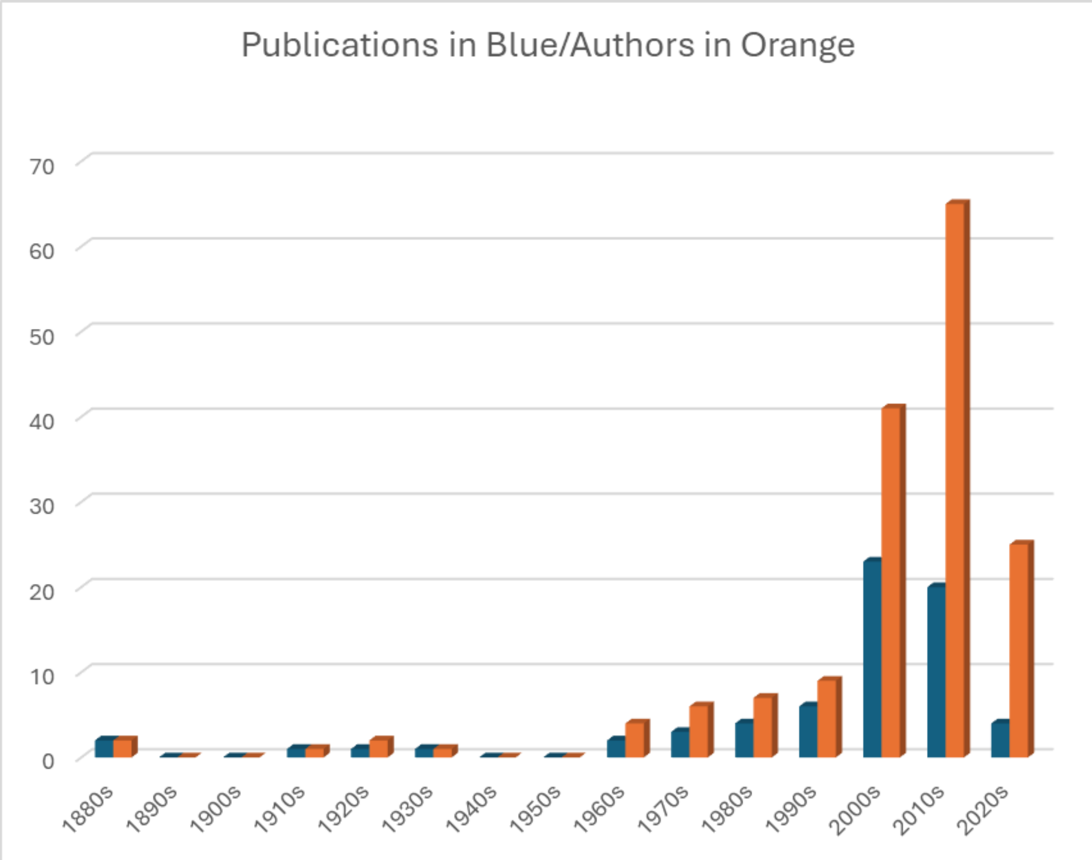

Table 1. This table shows the number publications in scientific journals per decade and the number of scientists working on the study of bioacoustics. The blue columns represent the publications produced during the decade. The orange columns represent the number of research workers conducting the research. The columns shown for the 2020s only include data for the first four years of this decade but clearly show the continuation of the trend.

The second decade of the twenty first century saw a 50% increase in the number of research scientists published in the scientific literature accompanied by a decrease in the number of research publications. The study of the behavioral response of benthic animals in the marine environment to local sound scape variations using hydrophones and modern sampling gear continued (Simpson et al., 2011; Stanley et al., 2012; Staaterman et al., 2013; Staaterman et al., 2013; Au 2016). Conspecific behavioral response to acoustic signals was also studies (Vetter & Caldwell, 2015). In addition several projects addressing the impact of anthropogenic noise on stomatopod behavior were conducted (Morley et al., 2014; Tidau & Briffs, 2016; Edmonds et al., 2016; Larsen & Radford, 2018;).

Experimental studies of the mechanisms of sound production by members of the Stomatopoda continued including the acoustic ecology of the California mantis shrimp *Hemisquilla californiensis* (Staaterman et al., 2011; Staaterman et al., 2012). The functioning and morphology of stomatopod sensilla including the hydrodynamics of their detection of the particle motion associated with near field sound was further advanced (Hartline & Békésy, 2014). A strictly morphological study of the sound producing organs of the Stomatopoda was conducted by Fornshell (2020). Patek (2019) continued the study of the physics associated with the feeding actions of the second maxillipeds.

The first four years of the third decade of the twenty first century saw 25 research scientists producing four publications. Two of these publications addressed the morphology and function of sound production by larva of *Squilla empusa* Say 1818 and adult stomatopods (Fornshell, 2023; Craig et al., 2023). A third addressed the effects of ambient sound, both anthropomorphic and natural of stomatopod behavior (Sole et al., 2023). The fourth was an experimental study of the distortions of sounds in studies of arthropods in tanks (Jézéquel et al., 2022).

2 Discussion

Biological scientists were aware of the production of and detection of sounds by marine organisms in the ocean from the latter part of the nineteenth century. Little progress was made in the study of bioacoustics for the 80 years, 1880s to 1960. The typical research publication containing bioacoustics information in this period was a single author paper, which is a 1:1 ratio of publications to scientists. The methods used in the research were restricted to anecdotal studies.

When bio-acousticians began to make use of electronic measurement devices, hydrophones and visual/video observations of animals when making sounds or exposed to sounds the rate of advancement increased exponentially from 1960 to 2010. Bioacousticians were beginning to make use of technology that had been developed in the preceding half century by scientists and engineers working on ocean acoustics, primarily in areas with applications to defense such as active and passive SONAR (Sound Navigation And Ranging). During this period of exponential growth of our knowledge there was a fairly consistent 2:1 ratio of research scientists to published results. This seems to be the most efficient. The use of hydrophones, electronic recording devices and computerized analysis of the sounds produced were vital to the advancement of the field of bio-acoustics.

The contribution of marine organisms to the sound scape was one of the first significant advances in bio-acoustics in the 50-year period from 1960 to 2010. The identification and description of sound producing and detecting organisms was also being advanced in this period. The use of active SONAR as a tool for studying plankton began to see. The use of active and passive SONAR to study marine life is more fully documented in the review paper by Fornshell et al. (2010) and Fornshell and Tesei (2013). The role of bioacoustics in behavioral processes as related to conspecific interactions and the response of animals to environmental acoustic cues began to be investigated in this time period (Dingle & Caldwell, 1969; Payne, 1972).

From 2010 to 2019 advances in the use of passive acoustic monitoring in the marine environment are well documented in Au's book, "Listening in the sea" published in 2016, and in the experiments of Hartline, & Békésy (2014) working in a laboratory setting extended our knowledge of near field sensing organ structure and function in arthropods. A new branch of study in bioacoustics, response to ambient noise, both natural and anthropomorphic, began to attract attention.

In the first four years of the third decade of the twenty first century progress was made in the study of sound generating and detecting organs in the Stomatopoda (Fornshell, 2020; Radford & Stanley, 2023). Sole et al. (2023) extended the study of the effects of ambient anthropogenic noise on marine animals. The study of acoustics in the laboratory was also being advanced with attention being given to the distortions of broadband sounds resulting from the acoustics of the tanks in which the recordings are being made.

In the second decade of the twenty-first century the ratio of scientist to publications increased to 3.5:1 and the actual number of publications decreased. This trend is continued into the first four years of the third decade of the twenty-first century approaching 5:1, Scientists: publications.

A ratio of 2:1 researchers working on a particular project seems to be the optimum for scientific advancement. The rate, however, at which bioacoustic knowledge increases is not as closely related to the number of active researchers working in the field as one might expect. The use of modern technology and innovative research methods is obviously particularly important. It is difficult to identify any reason for the decreased productivity with an increase in research workers involved in a given research project.

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