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Teaching acoustics in an interdisciplinary context with ‘singing’ fish

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Abstract

This article describes a novel and interdisciplinary context for learning about real-world sound waves. The ‘song’ of the plainfin midshipman fish consists of an acoustical wave that is periodic but not sinusoidal. This acoustical signal is the focus of active research in sound source localization by fishes, the effects of hormones on hearing systems and the elucidation of neural mechanisms involved in social acoustic communication. In this paper, we introduce the reproductive biology and bioacoustics of the midshipman fish. We describe the use of the advertisement ‘song’ of the male fish to visualize and interpret the dramatically different displacement, velocity and acceleration waveforms, to explore the roles of pressure and particle motion in production and detection of acoustical waves and to apply Fourier analysis to understand the implications of the frequency spectrum in the production, transmission and reception of sound in an aquatic environment.

Supplementary material for this article is available [online](#)

Keywords: physics education, acoustics, biophysics, interdisciplinary



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(Some figures may appear in colour only in the online journal)

Introduction

A model to explain wave phenomena is a fundamental idea in science. The wave model is an essential component for understanding light, sound and communication technologies. Waves are an integral part of many physics topics and are becoming more important in all science disciplines as science education becomes more interdisciplinary, therefore, it is critical to help students develop and understand a wave model that is intuitive, flexible and interdisciplinary. University physics students should have opportunities to apply the wave model to disciplines outside of physics including the life sciences. Such opportunities can promote the application of the wave model to complex, real-world phenomena that can be both exciting and rewarding to students across a broad range of science disciplines. These opportunities can also help budding physicists and engineers prepare to apply their knowledge to real-world problems outside of their own disciplines.

Most introductory university physics courses feature a unit on waves using sound waves as specific examples. Several decades of research have revealed both learner resources and challenges associated with understanding wave phenomena [1–4]. The Mechanical Waves Conceptual Survey was developed to provide a research-based assessment of student understanding [5]. Several research-based curricula have been designed to help students construct a model for waves that allows them to

- characterize the wavelength of periodic waves;
- relate and differentiate frequency, period, wavelength and wave speed; and
- distinguish wave propagation and particle motion.

Although these curricula can provide students with an excellent foundational understanding of waves, their scope is limited. Most curricula rely heavily, if not solely, on sinusoidal waves as examples of periodic waveforms. Even when non-sinusoidal, periodic waves are presented, they are often limited to geometric waves (square, triangle, sawtooth, etc) and are rarely associated with sound waves. Many introductory textbooks provide a mathematical relationship between acoustic pressure and particle motion for sound waves because sound can be described in terms of either sound pressure or particle motion. But since these presentations focus entirely on sinusoidal waves, the resulting displacement, velocity and acceleration waveforms all have the same sinusoidal shape with differences in phase and amplitude.

Several excellent, educationally oriented articles have been written that provide Fourier analysis of non-sinusoidal sound waves. Some articles explore sound waves with a well-defined harmonic structure (instrument strings [6], pipes [7], etc). In other studies, the sound source has a less predictable set of resonant frequencies (wineglasses [8], brass instruments [9], etc). We are not aware, however, of another educationally oriented article contextualizing and analyzing a periodic, non-sinusoidal sound wave that is naturally produced during animal communication. Yet, as we will see, among non-sinusoidal sound waves, the difference between periodic and non-periodic waveforms has profound implications for the interpretation of harmonics.

While not well known to the public, the plainfin midshipman fish (*Porichthys notatus*), the subject of active neuroscience research for the past 30 years, offers an exceptionally rich context for interdisciplinary acoustic studies. Specifically, the midshipman model provides students with novel opportunities:

- (i) To explore natural periodic waves that are not sinusoidal and are used in the context of social communication.
- (ii) To visualize and interpret the dramatically different displacement, velocity and acceleration waveforms for non-sinusoidal waves.
- (iii) To recognize how pressure and particle motion play distinctly different roles in the production and detection of sound waves.
- (iv) To understand how Fourier analysis and harmonics have different implications in the production, transmission and reception of sound in different acoustic environments.

In this paper, we will describe specific activities at the advanced high school or university level that support these learning opportunities in an interdisciplinary context. Teachers who want to explore the acoustic communication of the midshipman with their students can access an interactive lecture tutorial along with acoustical data sets (see supplementary materials available online at stacks.iop.org/EJP/40/025801/mmedia).

Plainfin midshipman: crooners of the intertidal

Introduction to the reproductive biology and bioacoustics of the midshipman fish

The plainfin midshipman (*Porichthys notatus*) is a marine fish native to the eastern Pacific ocean, ranging along the coast of North America from southeast Alaska to Baja, California [10]. Named for the distinctive pattern of bioluminescent photophores distributed on its underside (which resemble the pattern of brass buttons on a naval uniform), the midshipman is perhaps best known for its ability to produce sound or ‘sing’, earning it the nickname of ‘California singing fish’. Typically found in deep water, these fish are primarily nocturnal, resting in the substrate during the day and then rising into the water to feed on crustaceans and smaller fish at night [11–13]. This behavior changes radically at the onset of the reproductive season when they migrate from deep waters into the intertidal zone to spawn as shown in figure 1.

Midshipman fish have three types of reproductive adult morphs: the female and two types of males as shown in figure 1(c). Type I or ‘singing’ males build nests under rocky shelters in the intertidal zone and produce relatively loud (153–161 dB re 1 μ Pa at approximately 10 cm from the source), long-duration (minutes to hours) advertisement calls or ‘hums’ to attract mates at night. These calls can be loud enough to annoy local human populations [14]. The fundamental frequency of a midshipman hum is established by the rapid contraction of sonic muscles that surround the swim bladder in type I males as shown in figure 2. This advertisement call attracts gravid females, which use the social signal to locate calling mates [15].

Once in the nest, the females lay their eggs on its roof, and the eggs are fertilized by the nesting male. After spawning, females return to deeper waters while type I males remain in the nest to care for the young as shown in figure 1(d). Nesting type I males may spawn with multiple females during a single breeding season and will continue to guard their nests until their young are free swimming, a period of approximately 30–40 d post fertilization [16]. Type II or ‘sneaker’ males employ a different reproductive tactic that does not involve guarding nests or ‘singing’ to attract mates. Instead, they ‘sneak’ spawn in nests, trying to steal fertilizations from the mates of type I males [17].

Midshipman have been the focus of research investigations of sound source localization by fishes, the effects of hormones on hearing systems, and the elucidation of neural mechanisms involved in social acoustic communication. We now suggest that midshipman



Figure 1. (Clockwise from top left). (a) Type I male midshipman in his nest during low tide. Note the bed of orange-yellow eggs on the underside of the nest roof (see top arrow), which has been exposed to reveal the nest-guarding male (see bottom arrow). (b) A cluster of four nests (see arrows) with roofs removed in the rocky intertidal zone at low tide. (c) From left to right, all three reproductive adult morphs of the plainfin midshipman: type II male, type I male, female. (d) Type I male guarding hatched embryos (see arrow) in the nest. Reproduced with permission from Margaret Marchaterre.

bioacoustics provide an ideal context for developing a flexible, interdisciplinary acoustical wave model for advanced high school and undergraduate university students.

The periodic, non-sinusoidal, advertisement ‘hum’ of a male midshipman

Although type I male midshipman are capable of producing short-duration ‘grunt’ trains and ‘growls’, [17] their most significant vocal-acoustic signal is their long-duration multi-harmonic ‘hums’ to attract gravid females for reproduction. The fundamental frequency of these relatively long-duration hums varies between 79 and 105 Hz with water temperature. Following a brief transient period, both the waveform shape and the fundamental frequency of the call remain consistent for the duration of the call [18], resulting in a remarkably stable waveform. We recorded the natural advertisement call or ‘hum’ from a type I male midshipman calling from a semi-natural nest in an indoor tank at the University of Washington’s Friday Harbor Laboratories on San Juan Island, WA. The waveform of the hum shown in

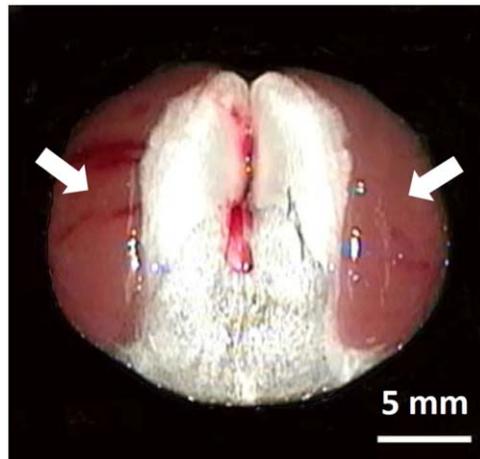


Figure 2. Dissected swim bladder from a type I male plainfin midshipman. Note the enlarged red sonic muscles (see white arrows) attached to the swim bladder which are used to produce the reproductive advertisement call. Scale bar = 5 mm.

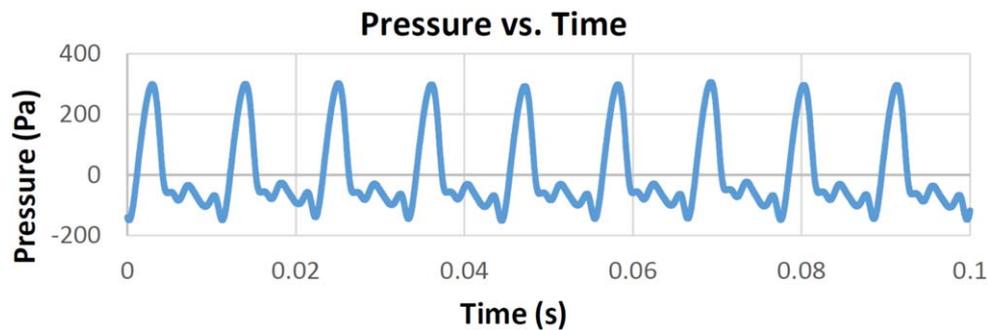


Figure 3. Representative pressure waveform of the advertisement call or 'hum' produced by the type I male plainfin midshipman.

figures 3 and 4 was recorded using a mini-hydrophone (model 8103, Bruel and Kjaer) placed near the nest entrance of the calling male and the acoustic signal was amplified using a conditioning amplifier (model 2692-C, Bruel and Kjaer).

Complex periodic sound waves

A Google image search for 'sound wave pressure' quickly reveals that the overwhelming majority of sound waves presented in educational materials are sinusoidal. Students can describe sinusoidal waves with simple mathematical functions and readily construct graphical representations of the waveforms. Nevertheless, over reliance on sinusoidal waves may leave learners with the impression that either all sound waves are sinusoidal or all periodic waves are sinusoidal, thus neglecting a great deal of the complexity of sound in nature. Anyone who has recognized that different vowel sounds can have the same pitch should realize that non-sinusoidal sound waves are fundamental to our auditory experience.

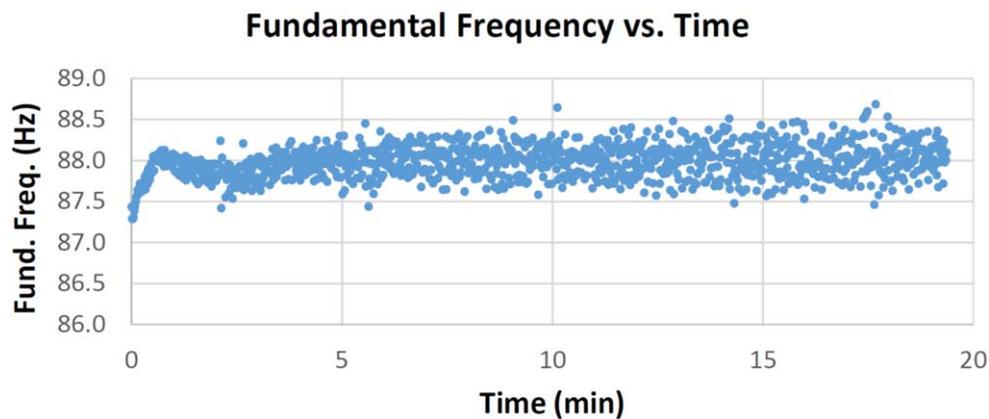


Figure 4. Stability of the fundamental frequency of the male midshipman advertisement call as a function of time.

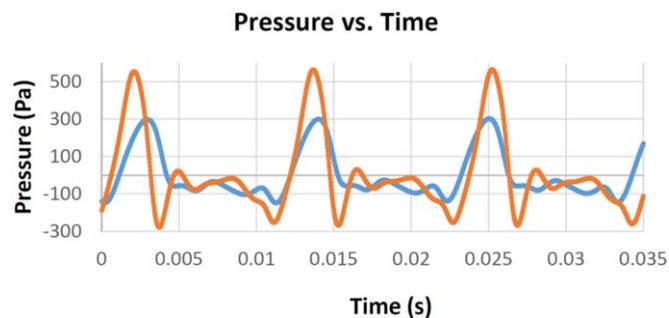


Figure 5. Comparison of the vocalization of two male fish at similar fundamental frequencies.

Midshipman vocalizations provide consistent and scientifically relevant examples of natural periodic, non-sinusoidal sound waves. The advertisement call of the midshipman can be described as either a complex periodic wave or a combination of Fourier components. The complex shape of the call's waveform reveals details of the sound production mechanism for individual fish. Figure 5 shows the vocalizations of two male fish at nearly the same fundamental frequency. The detailed shape of the waveform from an individual fish appears to depend on subtle structural differences in the swim bladder and sonic muscles shown in figure 2.

To the extent that any waveform is periodic and non-sinusoidal, it will have Fourier components or harmonics that occur at integer multiples of the fundamental periodicity of the wave. This is true for all periodic, non-sinusoidal waveforms but it may be surprising or even counterintuitive to many learners. Students may believe that harmonics are always produced by various resonant modes of the sound source. Although this idea applies in the many common educational examples such as a guitar string or an organ pipe, it does not apply in general to all sound production systems. As long as a male fish contracts their swim bladder muscle with a precise fundamental frequency, the resulting complex waveform must include harmonics at integer multiples of that frequency. The Fourier spectrum of a midshipman hum

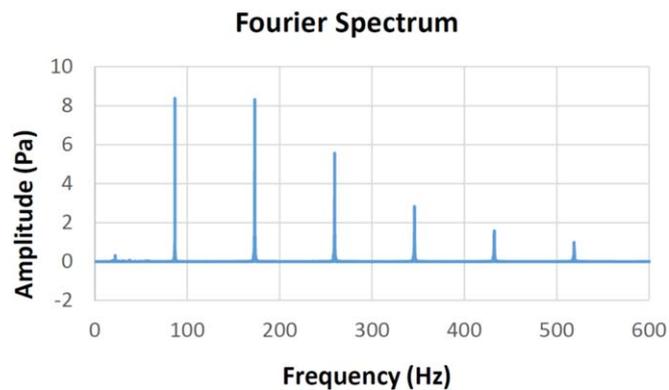


Figure 6. Fourier spectrum of a midshipman hum.

is shown in figure 6 and illustrates this principle. Note that the Fourier peaks are precisely spaced at even intervals. The fundamental frequency of this call is 86.44 Hz. The harmonics occur at 172.88 Hz, 259.33 Hz, 345.77 Hz, 432.21 Hz, 518.66 Hz, respectively. More significantly, the ratios of each harmonic frequency to the fundamental frequency are 2.0001, 3.0001, 4.0002, 5.0002, and 6.0002, respectively. To three significant figures, the harmonics occur at integer multiples of the fundamental frequency. The swim bladder does not have resonant modes at precise integer multiples of the fundamental frequency. Rather, the fish contracts his swim bladder periodically. The response of the bladder to each contraction is nearly identical, which results in an almost perfectly periodic acoustical waveform. Because the waveform is both periodic and non-sinusoidal, it is a mathematical necessity that the harmonics occur only at integer multiples of the fundamental frequency. Like an acoustical fingerprint, the amplitude and relative phase of these harmonics are determined by details of the swim bladder structure for a particular fish.

The fact that harmonics do not correspond to resonant modes of the swim bladder does not mean that the harmonics in the resulting waveform are not real and important. Lower frequencies will propagate further in a deep water, free-field environment. The higher harmonics are important because they propagate further in the shallow, intertidal waters where midshipman nest and breed [19].

Particle motion: hearing in a completely different way than mammals

Physics textbooks introduce the idea that sound waves can be described either by oscillating pressure or oscillating particle motion, which results from a mechanical disturbance. In addition, various instructional materials allow students to visualize the pressure and particle motion associated with sound waves [20]. The implications of particle motion for acoustical measurement and perception, however, are often not explored in detail. This is not surprising, considering that human ears and most microphones are designed to detect only sound pressure oscillations. Like other fish, however, midshipman are able to detect sound through either pressure or particle motion, providing an excellent opportunity for students to explore the structure and function of a complex vocal-acoustic system that has been engineered through natural selection. How can midshipman hear sound when the pressure variations are less than 0.1% of atmospheric pressure? How can midshipman detect particles moving by displacements of less than a micrometer? Why would these fish need to detect both pressure

and particle motion? Can fish get any information from particle motion that they could not get from pressure? At the nexus of biomechanics, sensory neuroscience and evolution, these types of questions are relevant to professional scientists along with students of biology, physics and engineering.

The mechanisms that fish use to detect pressure and particle motion are completely different. Changes in pressure cause the swim bladder to expand and contract, which can be detected in some fish, like female midshipman, because their swim bladder extensions project close to the sacculle, which is its main organ of hearing. The close proximity of the swim bladder to the inner ear in females is thought to allow the saccular end organ to detect local particle motion produced by pressure-wave induced vibrations of the swim bladder when exposed to sound. This indirect mechanism for sound pressure detection is posited to increase the overall auditory sensitivity of the fish [21]. All fishes are thought to be sensitive to the particle motion component of sound via their otolithic end organs (inner-ear end organs containing otoliths made of dense calcium carbonate, also known as ‘ear stones’) that essentially function as inertial accelerometers [22, 23]. This common mode of hearing in fishes enables them to detect particle motion—the directional vector component of sound—as opposed to sound pressure, which is a scalar quantity containing no directional information. As inertial accelerometers, the otoliths are set in motion by the motion of the medium and the body of the fish moves with the same displacement, direction, and phase as the water because fish tissue has about the same acoustic properties as water. Otoliths are denser than water and will thus move with smaller amplitude and lag in phase relative to the fish’s body. The resulting net movement of the otolith relative to the saccular hair cells generates neural impulses which are sent to the brain where the auditory information is later decoded to perceive sound. The mechanism described above is very similar to the way otolithic end organs in the human vestibular system function [24].

Developing an intuitive model linking particle motion to sound pressure

We have created an interactive lecture tutorial that teachers can use to guide learners through a multi-step analysis of a midshipman waveform (see supplementary materials). This activity enables learners to work through a conceptual analysis linking sound pressure to particle acceleration, velocity and displacement. Midshipman vocalizations provide an ideal context for this analysis because they represent a real physics example of a waveform for which both pressure and particle motion are significant. Furthermore, they are not symmetrical in time, and they produce visibly different waveforms for acceleration, velocity and displacement. This activity supports learners in the following conceptual learning goals:

- Translating waveforms between the time domain and the spatial domain.
- Relating particle acceleration to spatial gradient in pressure.
- Translating between graphs of acceleration, velocity and displacement.

Figure 7 illustrates the various waveforms that learners explore as they work through this activity. In these figures and in the tutorial materials, several locations (d_1 through d_4) and corresponding times (t_1 through t_4) have been labeled to allow learners to focus on significant features of the waveform. A set of slides, instructor’s notes and data files are included as supplementary materials.

In addition to practicing the conceptual learning goals listed above, learners can also gain new insights into the particle motion associated with a travelling sound wave in water. Specifically, they can see that the average particle velocity in a sound wave, shown in

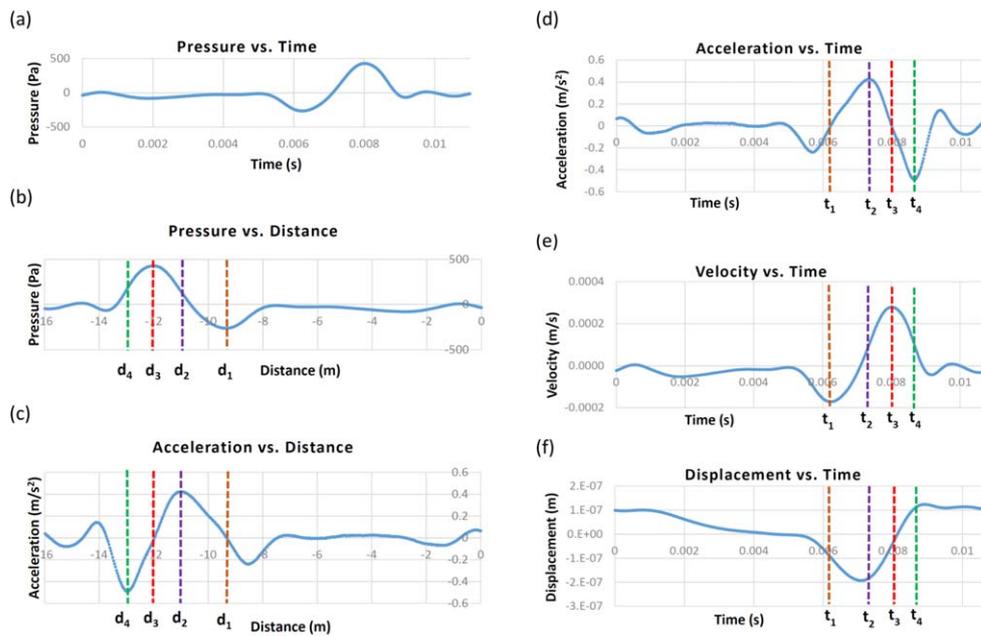


Figure 7. (a) Pressure as a function of time. (b) Pressure as a function of distance in front of the hydrophone. (c) Acceleration as a function of distance. (d) Particle acceleration as a function of time. (e) Particle velocity as a function of time. (f) Particle displacement as a function of time.

figure 7(e), is directly proportional to the pressure, shown in figure 7(a). Pressures above the ambient pressure are associated with regions where the particle velocity is in the same direction as the wave propagation. Students can readily correlate this relationship between pressure and particle velocity with results from a simulation of a traveling sound wave [25]. They can also consider the very small average particle velocity ($\sim 3 \times 10^{-4} \text{ m s}^{-1}$) and particle displacement ($\sim 3 \times 10^{-7} \text{ m}$) associated with a midshipman hum. Finally, they can also recognize that the maximum particle velocity is exceedingly small compared to the disordered thermal motion of the water molecules.

Conclusions

We have described a novel context for exploring naturally occurring periodic sound waves. The non-sinusoidal waveforms associated with midshipman vocalizations provide an ideal context for exploring relationships between pressure and particle motion in a sound wave. Students can analyze real waveforms to identify the direct relationship between pressure and locally averaged particle velocity. They can recognize that pressures above the ambient pressure are associated with regions where the particle velocity is in the same direction as the wave propagation. By exploring the complex relationships between acceleration, velocity and displacement of particles, students can also gain a quantitative appreciation for the magnitude of these quantities in a naturally occurring sound wave. These learning opportunities are encountered in an interdisciplinary context that lies at the cutting edge of neuroscience research.

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