# Chapter 120
# A Brief Review of Cephalopod Behavioral Responses to Sound

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**Abstract** Sound is a widely available cue in aquatic environments and is used by many marine animals for vital behaviors. Most research has focused on marine vertebrates. Relatively little is known about sound detection in marine invertebrates despite their abundance and importance in marine environments. Cephalopods are a key taxon in many ecosystems, but their behavioral interactions relative to acoustic stimuli have seldom been studied. Here we review current knowledge regarding (1) the frequency ranges and sound levels that generate behavioral responses and (2) the types of behavioral responses and their biological relevance.

**Keywords** *Sepia officinalis* • Cuttlefish • Sensory ecology • Hearing • Squid

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## 1 Introduction

Sounds are abundant in the ocean. They are produced by a range of organisms (e.g., fish, crustaceans, mammals) and by abiotic conditions (e.g., wind, waves, rain, earthquakes). Underwater sounds travel relatively fast (~1,500 m/s), can be detected over long distances (Urick 1983), and are often available when sensory cues such as light or chemical stimuli may be limited (Popper and Hastings 2009). It is well established that many marine vertebrates detect and use sound for vital activities such as navigation, foraging, predator detection, and reproduction (Fay and Popper 1999; Au et al. 2000). The ability of marine invertebrates to detect and potentially use sound is far less understood, which is somewhat surprising given their relative abundance and central role in many aquatic ecosystems (Budelmann 1992a, b; Boyle and Rodhouse 2005).

Sound detection in cephalopods was first reported by Baglioni (1910), who noted that octopuses reacted to low-frequency acoustic vibrations and water movements. Later publications included the description of behavioral (Dijkgraaf 1963; Komak et al. 2005), physiological (Kaifu et al. 2007), conditioned (Packard et al. 1990), and neurological (Hu et al. 2009; Mooney et al. 2010) responses to sound stimuli of different frequencies and intensities.

The organs generally thought to enable sound detection in cephalopods are the statocysts (Hanlon and Messenger 1996; Kaifu et al. 2008). These are paired organs located in the cartilage below the brain. They consist of a fluid-filled cavity containing a macula-statolith system for the detection of linear acceleration (e.g., gravity) and a crista-cupula system for the detection of angular acceleration (e.g., movement; Budelmann 1975). Polarized hair cells are found in both the macula and the crista systems (Budelmann 1979). The component of a sound field likely perceived by cephalopods is particle acceleration, not sound pressure (Packard et al. 1990; Mooney et al. 2010). In addition to the statocysts, *Sepia officinalis* (European common cuttlefish) also has lines of epidermal hair cells running over the head and arms that detect local water displacement (Budelmann et al. 1991; Hanlon and Messenger 1996). Their contribution to sound detection is poorly understood.

In the past decades, the development and greater use of the ocean have led to a concurrent increase in anthropogenic noise (National Research Council 2005). This noise may stem from many sources including shipping and vessel traffic, sonar systems, seismic air guns, and oil drilling. Our increased awareness of the influences of anthropogenic noise on the marine environment has led to several scientific studies addressing its potential impacts on diverse marine life (e.g., Mooney et al. 2009; André et al. 2011; Fewtrell and McCauley 2012).

Cephalopods play an important role in ecosystems and are a key component of food webs, providing a vital link from smaller invertebrates and fish to marine megafauna, birds, and humans (Boyle and Rodhouse 2005). It is therefore important to investigate the potential impact of increased anthropogenic noise on cephalopods. Changes in the behavior and distribution of cephalopod populations could have substantial impacts on the survival and distribution of top predators such as marine mammals, sharks, and sea birds; such changes would also impact commercial fisheries (Boyle and Rodhouse 2005). In this paper, we review research regarding cephalopod behavioral responses to sound, placing these studies in the context of potential noise impacts. In particular, we address the frequency and sound level ranges that generate behavioral responses in cephalopods, the types of behavioral responses elicited, and their biological relevance.

## 2 Behavioral Responses to Various Acoustic Stimuli

Cephalopods have a broad behavioral repertoire, including body movements (arms, mantle), body pattern changes, locomotor responses (jetting, fin movements), and inking (Hanlon and Messenger 1996). Multiple ethograms have been published (e.g., Hanlon and Messenger 1988; Hanlon et al. 1999 and references therein) and these provide the framework for future experiments in which behavioral responses to acoustic stimuli can be observed, recognized, and categorized in a quantitative manner.

Figure 120.1 summarizes the cephalopod responses to sound. Dijkgraaf (1963) reported jetting, darkening of the skin, and narrowing of the pupils in *S. officinalis* in response to taps on the tank walls. Body patterning changes were observed when using 180-Hz tones. Juvenile cuttlefish exhibited changes in body patterning, displacements, and burrowing when exposed to local sinusoidal water motion from 20 to 600 Hz (Komak et al. 2005). Certain frequencies generated substantially higher levels of activity in juvenile animals. Unfortunately, the stimulus intensities (measured as sound pressure level or particle motion) were not reported. Recently, using acoustic stimuli ranging from 80 to 1,000 Hz and a range of sound levels (measured in both sound pressure and particle acceleration), Samson et al. (2014) categorized the behavioral responses of *S. officinalis* to different tones. The responses included fin movements, body pattern changes, startle, jetting, and inking. Reactions considered

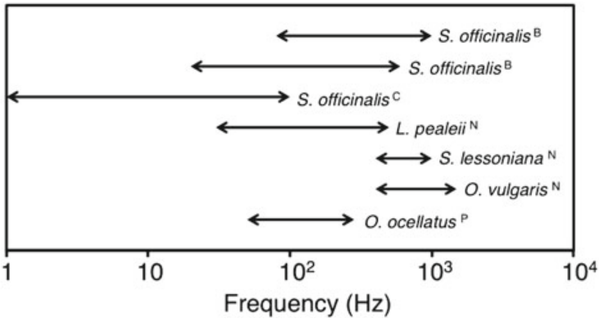

**Fig. 120.1** Sound detection ranges for several cephalopod species determined using behavioral (*B*), conditioned (*C*), or neurological (*N*) responses. References: Samson et al. (2014); Komak et al. (2005); Packard et al. (1990); Mooney et al. (2010); Hu et al. (2009); Kaifu et al. (2008)

to be escape and/or startle behavior (blanching, jetting, inking) mostly occurred at low frequencies and high sound levels. The average sound level needed to elicit a certain response varied for each sound frequency.

Similar escape responses have been observed in squid, *Sepioteuthis australis*, exposed to seismic air gun noises. The animals showed inking and jetting behaviors and increased swimming speed and swam upward, possibly to benefit from the sound shadow near the water surface (McCauley et al. 2000; Fewtrell and McCauley 2012). In *Octopus ocellatus*, Kaifu et al. (2008) reported changes in respiratory rates during exposure to sounds of 50–283 Hz. Although octopuses are also capable of body pattern changes, jetting, and inking, those behaviors were not mentioned in the literature as responses to sound stimuli.

## 3 Potential for Habituation to Acoustic Stimuli

Studies on the potential for habituation of cephalopods to any kind of stimulus are scarce; most research on the learning capabilities of these animals has focused on memory and spatial learning (e.g., Karson et al. 2003; Agin et al. 2006). Visual habituation to a predator model has been observed in the squid *Lolliguncula brevis* (Long et al. 1989); the squid showed a decrease in body pattern changes and jetting with repeated presentation of the fish models. Visual and tactile habituation were also demonstrated in *Octopus vulgaris*; the animals showed long-term habituation to visual stimulation using a prey model and a decrease in object handling over time (Kuba et al. 2006).

Cephalopod habituation to acoustic stimuli has yet to be addressed in detail. Only a few notes on the subject, collected en passant during previous studies on sound detection in cephalopods, have been found in the scientific literature. Dijkgraaf (1963) mentioned a very quick habituation to a 180-Hz tone in *S. officinalis*; after only one exposure, the animals would not react to the stimulus anymore. Using juvenile *S. officinalis*, Komak et al. (2005) obtained opposite results: no habituation was observed to repeated stimuli of different frequencies ranging from 40 to 600 Hz.

After behavioral tests to different sound frequencies and levels, Samson et al. (2014) exposed *S. officinalis* to repeated sound exposures at 200 Hz and different sound levels. A potential for habituation was observed; response intensity decreased, but response extinction was not reached during the time of the experiments.

## 4 Future Research Directions

Studying behavioral responses along with physiological, conditioned, or neural responses is a productive way forward to determine the function of sound in cephalopod life history. Physiological responses, for example, can provide information on

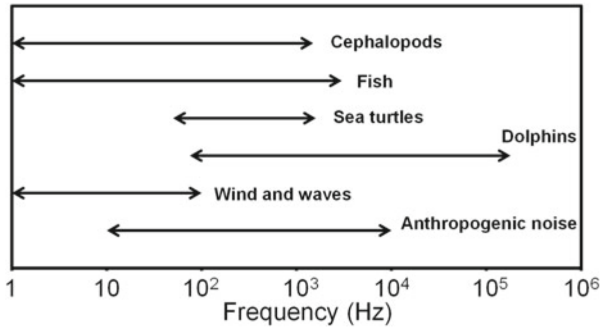

**Fig. 120.2** Hearing ranges of several marine organisms in comparison to two important abiotic sound sources in the ocean. References for cephalopods are listed in Fig. 120.1. References: Popper and Hastings (2009); Piniak et al. (2012); Au et al. (2000); Wenz (1962)

the detection ranges and thresholds (Hu et al. 2009; Mooney et al. 2010) but not on the use of sound by organisms and the role it plays in vital behaviors such as feeding, defense, or reproduction. Behavioral responses may also reveal cephalopod functional use of sound stimuli. Moreover, knowing how animals respond to sound is important from an ecological point of view (Hanlon and Shashar 2003) and should enable us to predict the disruptive effects of anthropogenic sounds on population behaviors (e.g., migration, spawning) and ecosystems because there is substantial overlap among the hearing ranges of many key organisms and the range of anthropogenic noise in the ocean (Fig. 120.2). It is unclear which type of acoustic information influences cephalopod ecology given the low frequencies to which they react and the absence of behavioral responses to ultrasonic clicks typical of odontocetes, a prominent group of cephalopod predators (Wilson et al. 2007).

Microscopic studies have shown that the hair cells in the statocysts and epidermal lines of *S. officinalis* and other cephalopods are polarized (Budelmann 1979; Budelmann et al. 1991). This characteristic of the hair cells could be the anatomical basis for directional hearing and sound location in cephalopods. The ability to sense the direction of acoustic stimuli and the location of acoustic sources has likely functions in defense but could also play roles in other behaviors including navigation. Investigating these potentials in cephalopods might shed light on important aspects of their sensory ecology.

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