Review on behavioral impacts of aquatic noise on crustaceans

Svenja Tidau, and Mark Briffa

Citation: Proc. Mtgs. Acoust. **27**, 010028 (2016); doi: 10.1121/2.0000302

View online: https://doi.org/10.1121/2.0000302

View Table of Contents: https://asa.scitation.org/toc/pma/27/1

Published by the Acoustical Society of America

Proceedings of Meetings on Acoustics

Volume 27 http://acousticalsociety.org/

Fourth International Conference on the Effects of Noise on Aquatic Life

Dublin, Ireland
10-16 July 2016

Review on behavioral impacts of aquatic noise on crustaceans

Svenja Tidau
Marine Biology and Ecology Research Centre, Plymouth University, Davy Building, Plymouth, PL48AA, UK
Marine and Freshwater Research Centre, Galway-Mayo Institute of Technology, Dublin Road, Galway, Ireland; svenja.tidau@plymouth.ac.uk

Mark Briffa
Marine Biology and Ecology Research Centre, Plymouth University, Davy Building, Plymouth, PL48AA, UK mark.briffa@plymouth.ac.uk

This review identified eleven peer-reviewed articles on behavioral impacts of noise on aquatic crustaceans, examining one freshwater species and several marine species, of which all are decapod crustaceans. Research incorporated noise sources such as low-frequency pile driving and airgun exploitation for seismic surveys, ship, and boat noise as well as white noise and pure tones. The studies suggest a variety of biological and ecological impacts ranging from increase in some behaviors (for instance locomotion) and stress, reduced and slower antipredator behavior, changes in foraging, suppressed behaviors with an ecological function (bioirrigation), and changes to intraspecific behavior (for instance agonistic encounters). More research on crustaceans and clearer reporting on the methods used to expose them to noise during experiments are needed. This would allow for consistent methods and ready comparison of results across studies.

Published by the Acoustical Society of America

[DOI: 10.1121/2.0000302]
Proceedings of Meetings on Acoustics, Vol. 27, 010028 (2016)

1. INTRODUCTION

Over the last decade there has been increasing interest in the impacts of noise pollution on marine life (Radford *et al.*, 2016), with studies focusing in particular on marine mammals (Southall *et al.*, 2007) and fishes (Popper *et al.*, 2014). In contrast, our understanding of the potential effects on invertebrates is relatively underdeveloped (Morley *et al.*, 2014; Hawkins *et al.*, 2015). However, assessing the impacts on invertebrates will be crucial if we are to develop a rounded view of how noise pollution may impact marine ecosystems.

In this review we focus on behavioral impacts of noise on aquatic crustaceans (covering freshwater and marine species). Some of the most extensive studies on crustaceans, their auditory systems, and sensitivity to sound, have been conducted on adult decapods such as crayfish and lobster species (see for instance Breithaupt and Tautz, 1990; Goodall *et al.*, 1990; Budelmann, 1992). With regard to sound production in crustaceans snapping shrimp species have been the main focus of research (Schmitz, 2002). In addition to adult crustaceans, the effects of natural sounds and anthropogenic noise on larval behavior have increasingly been investigated across a range of taxa (Stanley *et al.*, 2012).

Besides entirely aquatic species, there are also a number of studies on sound perception, including the effects of anthropogenic noise, on semi-terrestrial crustaceans. While aquatic and semi-terrestrial species have homologous auditory sensory systems, the soundscapes that they experience are likely to differ. Although semi-terrestrial ghost and fiddler crabs have been used as model systems for studies of how crustaceans use air-borne sound and vibration (Salmon, 1971; Popper *et al.*, 2001; Chan *et al.*, 2010; Stahlman *et al.*, 2011) their relevance to this review on aquatic noise pollution may be limited.

This review first gives an overview of underwater sound and the auditory systems of aquatic crustaceans (although the focus is on marine species). We then discuss sound production mechanisms and sensitivity to sound in crustaceans, and consider the use of sound cues by crustacean larvae. The behavioral impacts of aquatic noise on adult crustaceans are then discussed in detail.

2. UNDERWATER SOUND AND THE AUDITORY SYSTEM OF CRUSTACEANS

Sound has a pressure wave component and a particle motion component. As the density of crustacean bodies (for instance crayfish 1000kg/m^3) is nearly the same as the density of seawater (1100kg/m^3) (Breithaupt and Tautz, 1990) and as crustaceans lack an air-filled chamber, it is highly unlikely that they can detect sound pressure (Breithaupt and Tautz, 1990; Goodall *et al.*, 1990; Budelmann, 1992; Popper *et al.*, 2001; Breithaupt, 2002), although see Patek *et al.* (2009). Crustaceans have a specialized body plan allowing them to detect particle motion and respond to impinging sound fields through hydrodynamic receptors as part of their auditory system (Budelmann, 1992; Popper *et al.*, 2001; Breithaupt, 2002). While sound pressure is a water-borne noise source, particle motion can also be caused by substrate-borne vibration, for instance through pile driving and drilling (Hazelwood and Macey, 2016). Experiments on the crayfish *Orconectes spp.* and *Procambarus spp.* (Breithaupt and Tautz, 1990) and the European hermit crab *Pagurus bernhardus* (Roberts *et al.*, 2016) have shown that crustaceans are sensitive to vibration.

The auditory system of crustaceans has been studied for more than 150 years (for instance Farre, 1843). While the detection of sound in aquatic crustaceans is widespread and well documented, the intentional production of sound (i.e., signaling) is relatively unknown (Budelmann, 1992). In a narrow definition of hearing, however, this sense would be almost absolutely absent in most aquatic crustaceans; conversely, in the broadest definition, almost all crustaceans are able to detect sounds (Budelmann, 1992).

Electron microscopy techniques provide direct evidence of auditory structures in crustaceans (Cohen and Dijkgraaf, 1961; Heinisch and Wiese, 1987). For instance, Heinisch and Wiese (1987) used scanning electron microscopy (SEM) to delineate the structure of auditory organs in the North Sea shrimp *Crangon crangon*. Three external and internal structures work together to detect mechanically stimulated changes in hydrodynamic flows: setae hair-like cells on the body surface, a statocyst receptor system and chordotonal organs (Budelmann, 1992; Breithaupt, 2002; McCauley and Fewtrell, 2008).

Extensive arrays of sensory hairs ranging from 50 µm to 2000 µm cover most of the bodies of aquatic crustaceans (Heinisch and Wiese, 1987; Budelmann, 1992). Some of these hairs are solely mechanoreceptive while others also receive chemoreceptive stimuli (Derby, 1982). A single receptor has either a singular cuticular hair or bundle of hairs both with a flexible basis associated to one and up to four sensory cells. Mechanical disturbance, like acceleration and hydrodynamic flows as low as 0.05 to 300 Hz, has been shown to stimulate these hairs by bending them (Budelmann, 1992; Popper *et al.*, 2001).

The chordotonal organs are associated with the joints of flexible body appendages and connected to the central nervous system (Popper *et al.*, 2001). These organs are found for instance at the basal segment of the semi-terrestrial Giant hermit crab *Petrochirus diogenes*, at the large and small antenna of several lobster species such as the European spiny lobster *Palinurus elephas*, and the first and second antenna of the Danube crayfish *Astacus leptodactylus* (Budelmann, 1992).

Statocysts perform a similar function as otoliths in fish and thus have been assumed to be the main sound detection organ in crustaceans. It has been suggested that they are able to detect particle motion in an analogous way to the otolith-loaded inner ear in vertebrates (Popper *et al.*, 2001). Statocysts are internal receptors located at the basal segment of the antennule, within head region, and the posterior of the uropods, abdomen, or telson (Cohen and Dijkgraaf, 1961). Statocysts perform a number of important functions such as control of the antennules, triggering the righting movement (since they are the gravity sensors in crustaceans), and enable the animal to compensate for movement of the eyes and locomotion. Thereby statocysts allow the animal to maintain its position in the water column (Cohen and Dijkgraaf, 1961; Popper *et al.*, 2001; Breithaupt, 2002).

3. SOUND PRODUCTION IN AQUATIC CRUSTACEANS

Some aquatic crustaceans have sound producing structures (Popper *et al.*, 2001). In other cases the sounds produced by crustaceans are likely to be incidental to the behaviors observed. For example, hermit crabs such as the European hermit crab produce sounds when an attacking individual raps its shells against the defender to advertise the attacker’s fighting ability (Briffa *et al.*, 2003). The actual sound produced, however, is unlikely to be important to the crabs. Likewise, barnacles (Cirripedia) produce a crackling sound when they scrape their appendages on their calcareous shells when feeding (Budelmann, 1992). The Californian mantis shrimp

Hemisquilla californiensis produces a rumbling sound when they make contact with their raptorial appendage to a prey between the uropod and the telson (Staaterman *et al.*, 2011).

Crustaceans produce acoustic signals over a wide range of frequencies. At the lower end, the Californian mantis shrimp emits rumblings at a dominant frequency of 167 Hz (Staaterman *et al.*, 2011) and American lobster *Homarus americanus* at an average range of 87-261 Hz (Henninger and Watson, 2005). At the upper range of the bandwidth, crustaceans generate ultrasonic frequencies such as the European spiny lobster at a peak frequency of 19.52 ± 6.7 kHz (Buscaino *et al.*, 2011) and the big-claw snapping shrimp *Alpheus heterochaelis* beyond 200 kHz in some instances (Schmitz, 2002).

Macrurans such as lobsters and snapping shrimp also produce some of the most powerful sounds of aquatic crustaceans. Lobsters have specialized sound producing structures and seem to use these intentionally in intraspecific interactions (Patek *et al.*, 2009). Spiny lobsters such as the California spiny lobster *Panulirus interruptus* employ a plectrum (a basal extension of each antenna) over a file (located on the antennular plate below the eyes), which is similar to a stick–slip system as in bowed-stringed instruments (Patek, 2001; Patek *et al.*, 2009). This mechanism allows them to produce loud, abrasive rasps, which are potentially used as a startling deterrent when interacting with predators (Meyer-Rochow *et al.*, 1982; Patek, 2001). Experiments European spiny lobster showed rasps and screeches of a peak amplitude of 119.82 ± 8.44 dB re 1 μPa (Buscaino *et al.*, 2011).

Snapping shrimp have been shown to respond to the water jet they eject when closing their claw but not to playback of recorded snaps as discussed by Schmitz (2002). For example, the big-claw snapping shrimp produces a loud click by rapid closure of a specially adapted claw, which also emits a fast water jet (Schmitz and Herberholz, 1998). The signaling mechanism in snapping shrimp is the formation and collapse of cavitation bubble and a high velocity water jet perceived by conspecifics (Versluis *et al.*, 2000). Thus, the sound produced might simply be a by-product of the water jet (Schmitz, 2002). This behavior has been suggested to be a tool to defend a shelter or territory from conspecifics (Schmitz and Herberholz, 1998) and to stun or kill prey (Versluis *et al.*, 2000). Snapping shrimp have shown to generate some of the broadest spectra with peak-to-peak sound pressure levels up to 183-189 dB re 1 μPa for *Synalpheus paraneomeris* (Au and Banks, 1998) and 215 dB re 1 μPa for *A. heterochaelis* (Schmitz, 2002) both at 1 m distance from the hydrophone in a tank.

These biological sounds form an inherent part of the natural ambient soundscape in many coastal marine habitats and the chorus of snaps, squeaks, hums, grunts, and rasps has important biological functions. Pelagic post-larval fish and crustaceans are guided to settle and choose habitats based on distinct acoustic profiles associated with suitable reefs (Simpson *et al.*, 2016). Indeed, most fish at the settlement stage select habitats with high frequency reef sounds mainly produced by invertebrates, for example sea urchins and snapping shrimp (Radford *et al.*, 2008; Simpson *et al.*, 2008).

4. SENSITIVITY TO SOUND IN AQUATIC CRUSTACEANS

The sensitivity of crustaceans to detect sound can be studied by behavioral measures and also through electrophysiological techniques such as auditory evoked potentials (AEP). Electrophysiological techniques can determine relative rapidly the detectable range of frequencies (bandwidth) and the lowest detectable stimulus level of an animal (Ladich and Fay, 2013). Initial application of electrophysiological audiograms focused on marine mammals but more recently the approach has been applied to fishes (Ladich and Fay, 2013) and to the common prawn *Palaemon serratus* (Lovell *et al.*, 2005). However, audiograms obtained through electrophysiological techniques only measure the sensory and neural components of hearing and can differ from those obtained through behavioral measurements (reviewed for instance in Ladich and Fay, 2013; for an overview of the rise of electrophysiological techniques over behavioral assays since the 1970s see Sisneros *et al.*, 2016). As a tendency, auditory thresholds based electrophysiological measurements are suggested to indicate higher thresholds at lower frequencies and lower thresholds at higher frequencies in comparison to behavioral tests (Ladich and Fay, 2013). Due to these differences, AEPs are recommended to be used with caution (Popper *et al.*, 2014). However, such sensitivity audiograms can serve as a starting point to approach behavioral impacts of noise on crustaceans.

The most extensive studies on the sensitivity of decapod crustaceans to sound are based on experiments with crayfish and lobster species as model systems (Budelmann, 1992; Popper *et al.*, 2001). The following section gives an overview of several crustacean species and their electrophysiologically determined frequency bandwidth.

Heinisch and Wiese (1987) showed that the North Sea shrimp *Crangon crangon* has its maximum sensitivity at 170 Hz and acceleration of 81 cm/ s^2 corresponding to 0.7 µm amplitude of particle displacement. An upper end to the detectable bandwidth of crayfish species has been found at up to 2500 Hz by activating structures such as fibers of hair-pit organs, antennal flagella, and statocysts in the spinycheek crayfish *Orconectes limoses*, and the fibers of hair receptors at the telson in the red swamp crayfish *Procambarus clarkii* (Breithaupt and Tautz, 1990).

The Norway lobster *Nephrops norvegicus* exposed to pure tones of frequencies between 20 and 200 Hz and a displacement threshold of 0.888 µm at a distance of 0.09 m during laboratory and field experiments showed extension and movement of the abdomen and legs, beating of the swimmerets, and waving of the claws and antennae (Goodall *et al.*, 1990). Although the sound pressure was identical at 0.09 m and 1 m, responses were only observed when the source was 0.09 m away from the animal. This led the researchers to conclude that the Norway lobster is sensitive to particle motion rather than sound pressure.

Recent studies demonstrated in the common prawn that its statocysts are sensitive to particle motion in water at frequency range between 100 and 3000 Hz (Lovell *et al.*, 2005), substantially higher than the previously measured thresholds. Sensitivity to substrate-borne vibration was determined for the European hermit crab *Pagurus bernhardus* through sinusoidal vibrations of 5 to 410 Hz of varied amplitudes (Roberts *et al.*, 2016).

Despite these examples, the acoustic sensory system in decapod crustaceans remains understudied (Popper *et al.*, 2001) and few hearing threshold curves and audiograms have been established so far (Hawkins *et al.*, 2015). The existing audiograms suggest that species differ in their hearing thresholds and differences between studies in how the sensitivity to sound had been tested and measured make formal comparisons between the different species even more difficult.

5. SOUND AND BEHAVIOR OF CRUSTACEAN LARVAE

Research on the impact of ocean noise on marine crustaceans at the larval stage has emerged rather recently. To get the full picture of noise impacts on crustacean behavior, this review provides a brief overview into the behavioral impacts on crustacean larvae. It has long been suspected that pelagic larvae of crustaceans (and fish) use acoustic cues to orient towards settlement sites as underwater sounds travel long distances with relatively little attenuation

(Radford *et al.*, 2008). This possibility has only relatively recently been experimentally demonstrated (Jeffs *et al.*, 2003; Montgomery *et al.*, 2006; Radford *et al.*, 2007).

A study by Simpson *et al.* (2011) with nearly 700,000 individual crustacean larvae showed that the response to reef sounds varied across taxa and at different life stages. The sample included reef-settling Brachyura in the two larval developmental stages (zoea and megalopa), the two pelagic taxa Copepoda and Hyperiidea, and the five taxa Caridea, Cumacea, Gammaridea, Mysidae, and Ostracoda, of which the latter tend to emerge mainly during the night. In general, those species which require reefs for settlement were attracted to the corresponding sound while pelagic species avoided reef sound (Simpson *et al.*, 2011). A similar influence of sound in directing swimming behavior has been found in the post-larval stages of five crab species which are common in New Zealand (Radford *et al.*, 2007). In addition to using sound for directional cues, sound also influences the time to metamorphosis in crustaceans (Stanley *et al.*, 2011). Species showed varying sensitivity to sounds levels and regarding the spatial range in which they were able to detect suitable sound, with some showing metamorphosis in response to a sound source as far away as 40 km (Stanley *et al.*, 2011). The main components of these reef sounds are fishes and invertebrates, for instance snapping shrimp of the genera *Alpheus spp.* and *Synalpheus spp.* and sea urchin *Evechinus chloroticus* (Radford *et al.*, 2008).

An effect of anthropogenic noise on crustaceans has also been shown during larval settlement, the process that in many cases directly precedes metamorphosis. Noise from wind and tidal turbines delayed median time to metamorphosis and discouraged larval settlement in two common estuarine crabs in New Zealand, the tunneling mud crab *Austrohelice crassa* and the hairy-handed crab *Hemigrapsus crenulatus* (Pine *et al.*, 2012). The researchers concluded that noise is likely to mask natural acoustic settlement cues and that such a disruptive effect is most likely when larvae are simultaneously subjected to a range of frequencies rather than a single intensity (Pine *et al.*, 2012). In the case of fish larvae, the masking effect of small-boat noise has been shown to produce maladaptive behavior during the settlement stage (Simpson *et al.*, 2016). Larvae subjected to small boat noise spent greater time in the planktonic phase and this may lead to an increase in predation risk. Experiments with fish larvae have thus shown that noise has the potential to impact survival.

Such studies show that larvae can extract detailed information from sound and that sound influences crucial behaviors during development. Sound serves as an orientation cue for the pelagic larvae of reef fishes and decapod crustaceans and triggers the induction of settlement in crab megalopae (Jeffs *et al.*, 2003; Montgomery *et al.*, 2006; Stanley *et al.*, 2011; 2012). This suggests that the use of acoustic cues could be more prevalent across taxa then assumed (Simpson *et al.*, 2011).

6. REVIEW ON BEHAVIORAL IMPACTS OF AQUATIC NOISE ON ADULT CRUSTACEANS

For this review on behavioral impacts of noise on crustacean, eleven articles have been identified (Table 1). Only peer-reviewed articles are incorporated, which examine clear whole animal behavioral responses in the broadest sense. For instance, we included studies based on field observations of changes in species density as a measure of avoidance behavior. On the other hand, studies that only documented that species were sensitive to sound are not part of this review. The identified studies cover mainly marine species (10 out of 11) and one freshwater crayfish, all of which are decapod crustaceans. Experiments with semi-terrestrial hermit crabs exposed to water-borne noise or vibration are not contained as described earlier.

Table 1 Overview about peer-reviewed articles on behavioral impacts of noise on aquatic crustacean

Authors	**Species common name**	**Species scientific name**	**Noise source**
Andriguetto-Filho *et al.* 2005	Southern white shrimp Southern brown shrimp Atlantic seabob	*Litopenaeus schmitti* *Farfantepenaeus subtilis* *Xyphopenaeus kroyer*	Seismic survey (airguns)
Celi *et al.* 2013	Red swamp crayfish	*Procambarus clarkii*	White noise
Filiciotti *et al.* 2014	European spiny lobster	*Palinurus elephas*	Ship, boat
Filiciotti *et al.* 2016	Common prawn	*Palaemon serratus*	Ship, boat
Meyer-Rockow *et al.* 1982	Marine rock lobster	*Panulirus longipes*	Pure tone
Nousek-McGregor and Mei 2016	European hermit crab	*Pagurus bernhardus*	Ship, boat
Parry and Gason 2006	Rock lobster	*Not provided*	Seismic survey (air guns)
Payne *et al.* 2008	American lobster	*Homarus americanus*	Seismic survey (airguns)
Solan *et al.* 2016	Norway lobster	*Nephrops norvegics*	Pile driving, ship, boat
Spiga 2016	Snapping shrimp	*Athanas nitescens,* *Alpheus macrocheles* *Alpheus glaber*	Pile driving
Wale *et al.* 2013	Common shore crab	*Carcinus maenas*	Ship, boat

Three studies cover the impact of airgun exposure for seismic surveys on crustaceans (Table 2). Research on the American lobster suggests a significant increase in food intake several weeks post airgun exposure in laboratory and experiments (Payne *et al.*, 2008). Under laboratory conditions the airgun reached an average peak-to-peak pressure of around 202 dB at 144-169 dB re 1 µPa^2/ Hz; in the field, the average exposure reached 227 dB peak-to-peak and had an average peak energy density of 187 dB re 1 µPa^2/ Hz. Payne *et al*. (2008) make the interesting point that similar a result of increased food intake after brain trauma and stress has also been observed in humans. A similar mechanism could explain the behavior of American lobster.

The statistical analysis of seismic surveys coinciding with changes in commercial catch rates of rock lobster (species not indicated) in western Victoria between 1978 and 2004 suggests no effect on the distribution of this species (Parry and Gason, 2006). The authors point out, however, that in some regions fishing before and after seismic surveys was low. Moreover, these rock lobsters tend to be fished in water less than 50-70 m while most seismic surveys occur in water deeper than 50 m causing a spatial separation between high intensity fishing habitats and seismic survey areas. Thus, given the data available, it appears difficult to draw robust conclusions about the effects of seismic surveys on lobsters.

Andriguetto-Filho *et al.* (2005) measured the density and catch rates of a commercially important shrimp species in 92 trawl hauls 36 hours after the airgun employment with a peak pressure of 196 dB re 1 µPa at 1m. They found no significant decrease in either density or catch rates in any of the target species (Southern white shrimp *Litopenaeus schmitti*, Southern brown shrimp *Farfantepenaeus subtilis*, and Atlantic Seabob *Xyphopenaeus kroyer*). The authors suggest that these decapods are resilient to airgun exposure. However, they also acknowledge that they were unable to measure immediate effects as the sampling trawling took place 12-36 hours after the airgun use, which does not allow them to draw long-term conclusions or extrapolate their findings beyond its locality. Furthermore, a report on the impact of seismic surveys on invertebrates points out that catch rates following airgun explosions are difficult to interpret as species may have been attracted by dead or injured animals to feed on (Moriyasu *et al.*, 2004).

Table 2 Peer-reviewed articles covering behavioral impacts of seismic surveys (airguns) on crustacean

Species	**Noise characteristics**	**Behavioral response**	**Authors**
Southern white shrimp *Litopenaeus schmitti* Southern brown shrimp *Farfantepenaeus subtilis* Atlantic seabob *Xyphopenaeus kroyer*	peak pressure 196 dB re 1 µPa at 1m	• no significant decrease in density and catch rates ~ 36 hours after air-gun employment	Andriguetto -Filho *et al.* 2005
American lobster *Homarus americanus*	Lab: p-p averaged ~202 dB at 144-169 dB re 1 μPa^2/ Hz Field: p-p average 227 dB at 187 dB re 1 μPa^2/ Hz	• increased food consumption often several weeks post-exposure	Payne *et al.* 2008
Rock lobster *Not provided*	*Varied, see article for details*	• no statistical coincidence between seismic surveys and changes in catch rates	Parry and Gason 2006

Two experiments showed behavioral effects of pile driving on snapping shrimp chorus and the Norway lobster on its sediment dwelling behavior (Table 3). Pile driving exposure altered the chorus of temperate snapping shrimp species *Athanas nitescens, Alpheus macrocheles,* and *Alpheus glaber*. There was an overall increase in the number and amplitude of acoustic signals during the highest level of noise playbacks (152 ± 0.00 dB re 1 µPa p-p) at two out of the three sites (Spiga, 2016). At the third site, the playback at a level of −10 dB of the highest noise level increased the mean snap amplitudes. Overall, 96 controlled experimental exposures have been carried out. An increase in snap numbers and intensity is likely to cause a higher energy need and thus, altered foraging behavior.

Norway lobster showed repressed burying, bioirrigation behavior, and reduced locomotion when exposed to impulsive pile driving broadband sound with an sound exposure level of 150 dB re 1 μPa^2s (Solan *et al.*, 2016). There was no effect on surface sediment reworking activities or on the depth of sediment mixing. The experiment revealed intraspecific differences in bioturbation behavior and increased variability within individuals. It is suggested that variation in exposure history, environmental context, or physiological condition could explain these differences. As the Norway lobster has an important role in mixing the upper sediment and preventing suspension feeding any sound induced changes in its behavior could have wider ecosystem impacts (Solan *et al.*, 2016).

Table 3 Peer-reviewed articles about the impact of pile driving on crustacean behavior

Species	**Noise source**	**Behavioral response**	**Authors**
Snapping shrimp *Athanas nitescens, Alpheus macrocheles, Alpheus glaber*	p-p high: 152 ± 0.00 dB re 1 μPa -10 dB 145 ± 1.06 dB re 1 μPa -20 dB 137 ± 1.71 dB re 1 μPa	• increased number of snaps during noise at two site • increased amplitude of acoustic signals during playbacks at two site • increased mean snap amplitudes at a level of −10 dB at site 3 during playback • no increased snaps after playbacks	Spiga 2016
Norway lobster *Nephrops norvegicus*	SEL 150 dB re 1 μPa^2 s 100 Hz - 2 kHz	• repressed burying behavior • repressed bioirrigation • reduced locomotion activity • no effect on surficial sediment reworking • no effect on depth of sediment mixing	Solan *et al.* 2016

In five experiments, crustaceans showed altered behavior when exposed to ship or boat noise (Table 4). An experiment with 12 European hermit crabs suggests longer mean latency of first antipredator response (described as flee, freeze, hide) in the presence of ship and boat noise, with the change being more marked in the presence of ship compared to boat noise (Nousek-McGregor and Mei, 2016). The duration of noise exposure and latency of the first antipredator response showed a significant positive correlation. The response latency and emergence time are more variable during both noise treatments. For response latency and either hermit crab size or day of trial there was no significant correlation. As a result these findings suggest that noise could increase the risk of predation for hermit crabs.

Exposed to continuous broadband ship noise at 135-140 dB re 1 μPa, Norway lobsters showed the same behavioral response as for impulsive pile driving broadband sound (Solan *et al.*, 2016). Exposed individuals repressed burying and bioirrigation, reduced locomotion activity but showed no response regarding surficial sediment reworking activities and the depth of sediment mixing. As mentioned before, due to their ecosystem engineering function, behavioral change of Norway lobsters in mixing the sediment could alter the habitat conditions for other species.

Common shore crabs *Carcinus maenas* exposed to ship noise (148-155 dB RMS re 1 μPa) showed disrupted feeding behavior, slower retreat into shelter during simulated predator attack, and faster righting times (Wale *et al.*, 2013). These findings suggest that ship noise has the potential to increase the risk of starvation and predation.

When exposed to boat noise, individuals of the common prawn spent more time outside the shelter and more time resting (Filiciotto *et al.*, 2016). When placed into groups, the encounters between individuals decreased in the presence of boat noise. There was, however, no difference in startle response duration. Again, more time outside the shelter could also decrease survival in this species. The single and grouped European spiny lobsters significantly increased locomotion behavior and, similar to the common prawn, showed lower proximity between grouped individuals (Filiciotto *et al.*, 2014). Grouped animals increased the distance and speed of movement (measured as mean distance cm/s moved from the center point of the subject).

Table 4 Peer-reviewed articles about the impact of boat and ship noise on crustacean behavior

Species	**Noise source**	**Behavioral response**	**Authors**
Common prawn *Palaemon serratus*	Boat $SPL_{max.}$ 86 dB RMS re 1 µPa 0.1-3 kHz	• less encounters between subjects • individuals spent more time outside the shelter • more time spent resting in individuals • no difference in startle response	Filiciotti *et al.* 2016
European spiny lobster *Palinurus elephas*	Boat *No detail provided*	• increase in locomotion time in singles and groups • increase in distance moved in grouped animals • increased velocity in grouped animals • lowered proximity in grouped lobsters	Filiciotti *et al.* 2014
European hermit crab *Pagurus bernhardus*	Ship SPL 58 dB re 1 µPa Boat SPL 50 dB re 1 µPa 1-3 kHz	• longer mean latency of first antipredator response to ship noise not boat • duration of exposure correlates with latency of first antipredator response • more variable response latency and emergence time in both noise treatments	Nousek-McGregor and Mei 2016
Norway lobster *Nephrops norvegicus*	Ship 135-140 dB re 1 µPa 100Hz-2kHz	• repressed burying behavior • repressed bioirrigation • reduced locomotion activity • no effect on surficial sediment reworking • no effect on depth of sediment mixing	Solan *et al.* 2016
Common shore crab *Carcinus maenas*	Ship 148-155 dB RMS re 1 µPa	• disrupted feeding • slower retreat into shelter to simulated predator • righted up faster after being turned on back	Wale *et al.* 2013

Two experiments using white noise were identified (Table 5), including the only one on a freshwater crustacean. Celi *et al.* (2013) studied red swamp crayfish and found a lower number of encounters and decreased fights and tail flips in comparison to the control measurement under a linear sweep tone with a peak amplitude of 148 RMS dB re 1 µPa at 12 kHz. No significant differences in treatments were shown for motility and avoidance behavior. However, the authors acknowledge that this might be due to reverberation and/or reflection in the experimental tank, which may have prevented detection of the noise source by the crayfish. Agonistic encounters may be decisive in the competition for the access to resources. Reduced engagement in such encounter may therefore impact the distribution of resources within the population.

Four marine rock lobster *Panulirus longipes* exposed to white noise (no details given) showed slightly longer antennule flicks, needed approximately 50% longer to emerge from their shelter, and searched longer for food (Meyer-Rochow *et al.,* 1982). Nevertheless, the authors suggest that some individuals might compensate for increased hiding by performing other activities at a greater rate once they emerged from their shelters.

Table 5 Peer-reviewed articles about the impact of sine tones on crustacean behavior

Species	**Noise source**	**Behavioral response**	**Authors**
Red swamp crayfish *Procambarus clarkii*	Linear sweep: peak amplitude 148 RMS dB re 1 µPa at 12 kHz frequency: 0.1-25 kHz	• lower number of encounters • decreased fights and tail flips • no significant differences in motility • no avoidance behavior	Celi *et al.* 2013
Marine rock lobster *Panulirus longipes*	White noise *No details provided*	• slightly longer to antennule flicks • significant approximately 50% longer to emerge from their hide • longer to search for food and reach goal • Some individuals caught up with the delay	Meyer-Rockow *et al.* 1982

7. DISCUSSION

The reviewed studies suggest some common patterns but also some clear differences in conclusions among studies. Two field surveys on the catch rates of different shrimp species and American lobster after airgun exposure, which could indicate avoidance (or mortality), have not shown any obvious effect (Andriguetto-Filho *et al.*, 2005; Parry and Gason, 2006). In contrast, in laboratory experiments the American lobster showed increased food intake (Payne *et al.*, 2008). Andriguetto-Filho *et al.* (2005) suggest that substantial limitations in the data that can be collected in the field as a potential reason for such discrepancies between results from laboratory and field based studies.

The increased food intake in American lobster is suggested to be a response to stress (Payne *et al.*, 2008). However, Meyer-Rockow *et al.* (1982) found delayed search for food in marine rock lobster and Wale *et al.* (2013) disrupted feeding behavior of common shore crab under ship noise. The latter two behaviors would imply higher energetic costs in the presence of noise. Further indications for increased energetic costs are likely for snapping shrimp, which increased the amplitude and number of snaps during pile driving noise (Spiga, 2016). Single and grouped European spiny lobster increased locomotion time, distance, and velocity (Filiciotto *et al.*, 2014) and shrimp increased locomotion (Filiciotto *et al.*, 2016). These serve as further examples on potential impacts of anthropogenic noise on animal behavior and hence physiology.

Other experiments suggest distraction of crustaceans in crucial behaviors, which could have implications for survival. Norway lobster repressed bioirrigation and burying behavior in the presence of pile driving and ship noise (Solan *et al.*, 2016). The European hermit crab increased latency of first antipredator response (Nousek-McGregor and Mei, 2016) and the common shore crab responded slower to predators during ship noise (Wale *et al.*, 2013). These behaviors suggest that distraction could lead to a higher risk of predation due to increased latency in antipredator behavior.

Noise could also change and suppress intraspecific behavior. Grouped common shrimp showed reduced social behavior (Filiciotto *et al.*, 2014). Under white noise, red swamp crayfish reduced agonistic encounters (Celi *et al.*, 2013). In another experiment, marine rock lobsters took longer to emerge from shelter when exposed to a pure tone, which was set at the same frequency and amplitude to the noises made by conspecifics (Meyer-Rochow *et al.*, 1982).

8. CONCLUSION

The studies identified suggest a variety of biological and ecological implications to noise exposure. These range from increase in behavior (for instance locomotion), stress responses, reduced and slower antipredator behavior, changes in foraging, suppressed behaviors with an ecological function (bioirrigation), and changes to intraspecific behavior (for instance agonistic encounters). Studies have also shown behavioral impact on crustacean larvae relying on acoustic cues for settlement and metamorphosis.

Current knowledge, however, is based on few studies and sometimes these have low sample sizes. In addition to behavioral change, aquatic noise pollution (including ocean noise pollution) may impact upon underlying physiological traits, either directly or as an indirect result of the behavioral changes such as reduced foraging. Therefore, future research, which combines both behavior and its physiological underpinnings, may reveal impacts that would otherwise remain unknown.

To facilitate more research in this field, more detailed reporting on methods and noise treatment would allow increased reproducibility of experimental set-ups and hence a better comparison of results. Advancement in methods and equipment such as affordable accelerometers will contribute to the growing research field of the impacts of noise on crustaceans and their crucial role in aquatic ecosystems.

ACKNOWLEDGMENTS

This review evolved from the PhD project “Driven to distraction: behavioural impacts of ocean noise on European hermit crab *Pagurus bernhardus*” at Plymouth University, UK, and Galway-Mayo Institute of Technology, Ireland, funded by the European Commission as part of the Joint Doctoral Programme on Marine Ecosystem Health & Conservation.

REFERENCES

Andriguetto-Filho, J. M., Ostrensky, A., Pie, M. R., Silva, U. A., and Boeger, W. A. (**2005**). "Evaluating the impact of seismic prospecting on artisanal shrimp fisheries," Continental Shelf Research **25**, 1720-1727.

Au, W. W. L., and Banks, K. (**1998**). "The acoustics of the snapping shrimp *Synalpheus parneomeris* in Kaneohe Bay," The Journal of the Acoustical Society of America **103**, 41-47.

Breithaupt, T. (**2002**). "Sound Perception in Aquatic Crustaceans," in *The Crustacean Nervous System*, edited by K. Wiese (Springer, Berlin, Heidelberg), pp. 548-558.

Breithaupt, T., and Tautz, J. (**1990**). "The sensitivity of crayfish mechanoreceptors to hydrodynamic and acoustic stimuli," in *Frontiers in Crustacean Neurobiology*, edited by K. Wiese, B. Mulloney, W. D. Krenz, J. Tautz, and H. Reichert (Birkhauser Verlag, Basel), pp. 114-120.

Briffa, M., Elwood, R. W., and Russ, J. M. (**2003**). "Analysis of multiple aspects of a repeated signal: power and rate of rapping during shell fights in hermit crabs," Behavioral Ecology **14**, 74-79.

Budelmann, B. U. (**1992**). "Hearing in crustacea," in *The Evolutionary Biology of Hearing*, edited by D. B. Webster, A. N. Popper, and R. R. Fay (Springer, New York), pp. 131-139.

Buscaino, G., Filiciotto, F., Gristina, M., Bellante, A., Buffa, G., Di Stefano, V., Maccarrone, V., Tranchida, G., Buscaino, C., and Mazzola, S. (**2011**). "Acoustic behaviour of the European spiny lobster *Palinurus elephas*," Marine Ecology Progress Series **441**, 177-184.

Celi, M., Filiciotto, F., Parrinello, D., Buscaino, G., Damiano, M. A., Cuttitta, A., D’Angelo, S., Mazzola, S., and Vazzana, M. (**2013**). "Physiological and agonistic behavioural response of *Procambarus clarkii* to an acoustic stimulus," Journal of Experimental Biology **216**, 709-718.

Chan, A. A. Y.-H., David Stahlman, W., Garlick, D., Fast, C. D., Blumstein, D. T., and Blaisdell, A. P. (**2010**). "Increased amplitude and duration of acoustic stimuli enhance distraction," Animal Behaviour **80**, 1075-1079.

Cohen, M. J., and Dijkgraaf, S. (**1961**). "Mechanoreception," in *Physiology of Crustacea*, edited by T. H. Waterman (Academic Press, New York), pp. 65-108.

Derby, C. D. (**1982**). "Structure and function of cuticular sensilla of the lobster *Homarus americanus*," Journal of Crustacean Biology **2**, 1-21.

Farre, A. (**1843**). "On the organ of hearing in crustacea," Philosophical Transactions of the Royal Society of London **133**, 233-242.

Filiciotto, F., Vazzana, M., Celi, M., Maccarrone, V., Ceraulo, M., Buffa, G., Arizza, V., de Vincenzi, G., Grammauta, R., Mazzola, S., and Buscaino, G. (**2016**). "Underwater noise from boats: Measurement of its influence on the behaviour and biochemistry of the common prawn (*Palaemon serratus*, Pennant 1777)," Journal of Experimental Marine Biology and Ecology **478**, 24-33.

Filiciotto, F., Vazzana, M., Celi, M., Maccarrone, V., Ceraulo, M., Buffa, G., Di Stefano, V., Mazzola, S., and Buscaino, G. (**2014**). "Behavioural and biochemical stress responses of *Palinurus elephas* after exposure to boat noise pollution in tank," Marine Pollution Bulletin **84**, 104-114.

Goodall, C., Chapman, C., and Neil, D. (**1990**). "The acoustic response threshold of the Norway Lobster, *Nephrops Norvegicus (L.)* in a free sound field," in *Frontiers in Crustacean Neurobiology*, edited by K. Wiese, W. D. Krenz, J. Tautz, H. Reichert, and B. Mulloney (Birkhäuser, Basel), pp. 106-113.

Hawkins, A. D., Pembroke, A. E., and Popper, A. N. (**2015**). "Information gaps in understanding the effects of noise on fishes and invertebrates," Reviews in Fish Biology and Fisheries **25**, 39-64.

Hazelwood, R. A., and Macey, P. C. (**2016**). "Intrinsic Directional Information of Ground Roll Waves," in *Effects of Noise on Aquatic Life II*, edited by A. N. Popper, and A. Hawkins (Springer-Verlag Berlin, Berlin), pp. 447-453.

Heinisch, P., and Wiese, K. (**1987**). "Sensitivity to movement and vibration of water in the North Sea shrimp *Crangon crangon L*," Journal of Crustacean Biology **7**, 401-413.

Henninger, H. P., and Watson, W. H. (**2005**). "Mechanisms underlying the production of carapace vibrations and associated waterborne sounds in the American lobster, *Homarus americanus*," Journal of Experimental Biology **208**, 3421-3429.

Jeffs, A., Tolimieri, N., and Montgomery, J. C. (**2003**). "Crabs on cue for the coast: the use of underwater sound for orientation by pelagic crab stages," Marine and Freshwater Research **54**, 841-845.

Ladich, F., and Fay, R. R. (**2013**). "Auditory evoked potential audiometry in fish," Reviews in Fish Biology and Fisheries **23**, 317-364.

Lovell, J. M., Findlay, M. M., Moate, R. M., and Yan, H. Y. (**2005**). "The hearing abilities of the prawn *Palaemon serratus*," Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology **140**, 89-100.

McCauley, R. D., and Fewtrell, J. (**2008**). "Marine invertebrates, intense anthropogenic noise, and squid response to seismic survey pulses," Bioacoustics **17**, 315-318.

Meyer-Rochow, V. B., Penrose, J. D., Oldfield, B. P., and Bailey, W. J. (**1982**). "Phonoresponses in the rock lobster *Panulirus longipes* (Milne Edwards)," Behavioral and Neural Biology **34**, 331-336.

Montgomery, J. C., Jeffs, A., Simpson, S. D., Meekan, M., and Tindle, C. (**2006**). "Sound as an orientation cue for the pelagic larvae of reef fishes and decapod crustaceans," in *Advances in Marine Biology* (Academic Press), pp. 143-196.

Moriyasu, M., Allain, R., Benhalima, K., and Claytor, R. (**2004**). "Effects of seismic and marine noise on invertebrates: A literature review," (Department of Fisheries and Oceans), p. 50.

Morley, E. L., Jones, G., and Radford, A. N. (**2014**). "The importance of invertebrates when considering the impacts of anthropogenic noise," Proceedings of the Royal Society B-Biological Sciences **281**.

Nousek-McGregor, A. E., and Mei, F. T. L. (**2016**). "Does noise from shipping and boat traffic affect predator vigilance in the European common hermit crab?," in *The Effects of Noise on Aquatic Life II*, edited by N. A. Popper, and A. Hawkins (Springer, New York), pp. 767-774.

Parry, G. D., and Gason, A. (**2006**). "The effect of seismic surveys on catch rates of rock lobsters in western Victoria, Australia," Fisheries Research **79**, 272-284.

Patek, S. N. (**2001**). "Spiny lobsters stick and slip to make sound," Nature **411**, 153-154.

Patek, S. N., Shipp, L. E., and Staaterman, E. R. (**2009**). "The acoustics and acoustic behavior of the California spiny lobster (*Panulirus interruptus*)," The Journal of the Acoustical Society of America **125**, 3434-3443.

Payne, J. F., Andrews, C. D., Fancey, L. L., Guiney, J., Cook, A., and Christian, J. R. (**2008**). "Are seismic surveys an important risk factor for fish and shellfish?," Bioacoustics **17**, 262-265.

Pine, M. K., Jeffs, A. G., and Radford, C. A. (**2012**). "Turbine sound may influence the metamorphosis behaviour of estuarine crab megalopae," PLOS ONE **7**, e51790.

Popper, A. N., Hawkins, A. D., Fay, R. R., Mann, D. A., Bartol, S., Carlson, T. J., Coombs, S., Ellison, W. T., Gentry, R. L., Halvorsen, M. B., Løkkeborg, S., Rogers, P. H., Southall, B. L., Zeddies, D. G., and

Tavolga, W. N. (**2014**). "Effects of Sound Exposure," in *ASA S3/SC1.4 TR-2014 Sound Exposure Guidelines for Fishes and Sea Turtles: A Technical Report prepared by ANSI-Accredited Standards Committee S3/SC1 and registered with ANSI* (Springer International Publishing), pp. 17-21.

Popper, A. N., Salmon, M., and Horch, W. K. (**2001**). "Acoustic detection and communication by decapod crustaceans," Journal of Comparative Physiology A **187**, 83-89.

Radford, A. N., Purser, J., Bruintjes, R., Voellmy, I. K., Everley, K. A., Wale, M. A., Holles, S., and Simpson, S. D. (**2016**). "Beyond a simple effect: Variable and changing responses to anthropogenic noise," in *Effects of Noise on Aquatic Life II*, edited by A. N. Popper, and A. Hawkins (Springer, New York), pp. 901-907.

Radford, C. A., Jeffs, A. G., and Montgomery, J. C. (**2007**). "Directional swimming behavior by five species of crab postlarvae in response to reef sound," Bulletin of Marine Science **80**, 369-378.

Radford, C. A., Jeffs, A. G., Tindle, C. T., and Montgomery, J. C. (**2008**). "Temporal patterns in ambient noise of biological origin from a shallow water temperate reef," Oecologia **156**, 921-929.

Roberts, L., Cheesman, S., Elliott, M., and Breithaupt, T. (**2016**). "Sensitivity of *Pagurus bernhardus (L.)* to substrate-borne vibration and anthropogenic noise," Journal of Experimental Marine Biology and Ecology **474**, 185-194.

Salmon, M. (**1971**). "Signal characteristics and acoustic detection by fiddler crabs, uca rapax and uca pugilator," Physiological Zoology **44**, 210-&.

Schmitz, B. (**2002**). "Sound production in crustacea with special reference to the Alpheidae," in *The Crustacean Nervous System*, edited by K. Wiese (Springer, Berlin, Heidelberg), pp. 536-547.

Schmitz, B., and Herberholz, J. (**1998**). "Snapping behaviour in intraspecific agonistic encounters in the snapping shrimp (*Alpheus heterochaelis*)," Journal of Biosciences **23**, 623-632.

Simpson, S. D., Meekan, M. G., Jeffs, A., Montgomery, J. C., and McCauley, R. D. (**2008**). "Settlement-stage coral reef fish prefer the higher-frequency invertebrate-generated audible component of reef noise," Animal Behaviour **75**, 1861-1868.

Simpson, S. D., Radford, A. N., Holles, S., Ferarri, M. C. O., Chivers, D. P., McCormick, M. I., and Meekan, M. G. (**2016**). "Small-boat noise impacts natural settlement behavior of coral reef fish larvae," in *The Effects of Noise on Aquatic Life II*, edited by N. A. Popper, and A. Hawkins (Springer, New York), pp. 1041-1048.

Simpson, S. D., Radford, A. N., Tickle, E. J., Meekan, M. G., and Jeffs, A. G. (**2011**). "Adaptive avoidance of reef noise," PLOS ONE **6**, e16625.

Sisneros, J. A., Popper, A. N., Hawkins, A. D., and Fay, R. R. (**2016**). "Auditory evoked potential audiograms compared with behavioral audiograms in aquatic animals," in *The Effects of Noise on Aquatic Life II*, edited by N. A. Popper, and A. Hawkins (Springer, New York), pp. 1049-1056.

Solan, M., Hauton, C., Godbold, J. A., Wood, C. L., Leighton, T. G., and White, P. (**2016**). "Anthropogenic sources of underwater sound can modify how sediment-dwelling invertebrates mediate ecosystem properties," Scientific Reports **6**, 20540.

Southall, B. L., Bowles, A. E., Ellison, W. T., Finneran, J. J., Gentry, R. L., Greene Jr., C. R., Kastak, D., Ketten, D. R., Miller, J. H., Nachtigall, P. E., Richardson, W. J., Thomas, J. A., and Tyack, P. L. (**2007**). "Marine mammal noise exposure criteria: Initial scientific recommendations," Aquatic Mammals **33**, 411- 521.

Spiga, I. (**2016**). "Acoustic response to playback of pile-driving sounds by snapping shrimp," in *Effects of Noise on Aquatic Life II*, edited by A. N. Popper, and A. Hawkins (Springer, New York), pp. 1081-1088.

Staaterman, E. R., Clark, C. W., Gallagher, A. J., deVries, M. S., Claverie, T., and Patek, S. N. (**2011**). "Rumbling in the benthos: acoustic ecology of the California mantis shrimp *Hemisquilla californiensis*," Aquatic Biology **13**, 97-105.

Stahlman, W. D., Chan, A. A. Y.-H., Blumstein, D. T., Fast, C. D., and Blaisdell, A. P. (**2011**). "Auditory stimulation dishabituates anti-predator escape behavior in hermit crabs (*Coenobita clypeatus*)," Behavioural Processes **88**, 7-11.

Stanley, J. A., Radford, C. A., and Jeffs, A. G. (**2011**). "Behavioural response thresholds in New Zealand crab megalopae to ambient underwater sound," PLOS ONE **6**.

Stanley, J. A., Radford, C. A., and Jeffs, A. G. (**2012**). "Location, location, location: Finding a suitable home among the noise," Proceedings of the Royal Society B-Biological Sciences **279**, 3622-3631.

Versluis, M., Schmitz, B., von der Heydt, A., and Lohse, D. (**2000**). "How Snapping Shrimp Snap: Through Cavitating Bubbles," Science **289**, 2114-2117.

Wale, M. A., Simpson, S. D., and Radford, A. N. (**2013**). "Noise negatively affects foraging and antipredator behaviour in shore crabs," Animal Behaviour **86**, 111-118.