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Marine invertebrates and noise

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Within the set of risk factors that compromise the conservation of marine biodiversity, one of the least understood concerns is the noise produced by human operations at sea and from land. Many aspects of how noise and other forms of energy may impact the natural balance of the oceans are still unstudied. Substantial attention has been devoted in the last decades to determine the sensitivity to noise of marine mammals—especially cetaceans and pinnipeds—and fish because they are known to possess hearing organs. Recent studies have revealed that a wide diversity of invertebrates are also sensitive to sounds, especially *via* sensory organs whose original function is to allow maintaining equilibrium in the water column and to sense gravity. Marine invertebrates not only represent the largest proportion of marine biomass and are indicators of ocean health but many species also have important socio-economic values. This review presents the current scientific knowledge on invertebrate bioacoustics (sound production, reception, sensitivity), as well as on how marine invertebrates are affected by anthropogenic noises. It also critically revisits the literature to identify gaps that will frame future research investigating the tolerance to noise of marine ecosystems.

KEYWORDS

marine invertebrates, marine noise pollution, sound production, sound detection, noise effects, statocyst, sound pressure, particle motion

1 Introduction

Marine invertebrates represent a hugely diverse taxa, playing a central role in food webs and ecosystem services, as well as constituting an important economical resource. Invertebrates make essential contributions to global biodiversity and provide major ecosystem functions (e.g., water filtering, habitat creation, organic matter processing, carbon transfer through food webs and nutrient recycling) (Collier et al., 2016). Many marine invertebrate species also have important intrinsic value to human society, including as food resources (shellfish protein), for health purposes (protection form algae eutrophication), as coastal protection from natural disasters and ocean acidification, through ornamental and recreational value, and in tourism.

Some agents of biodiversity decline in marine ecosystems (e.g., water pollution, overexploitation, habitat degradation, invasive species and climate change) have been analysed extensively (Collier et al., 2016). However, it is only relatively recently that noise and other forms of energy, like anthropogenic electromagnetic fields, have been considered critical stressors of the natural balance of the oceans. These pressure elements can have detrimental impacts on the survival and reproduction of individuals, with consequences for entire populations and species (van der Graaf et al., 2012; Hutchison et al., 2020; Popper et al., 2020). Recent findings have shown that marine invertebrates can be sensitive to anthropogenic noise and indicated that this sensitivity may have influence ocean biodiversity (André et al., 2011; Aguilar de Soto, 2016; Edmonds et al., 2016; Sordello et al. 2020), placing them as direct indicators of ocean health.

Ocean soundscapes are composed of a combination of biological, geological and anthropogenic sounds produced from a variety of sources (Pijanowski et al., 2011; Lindseth and Lobel, 2018; Duarte et al., 2021). As with other marine species, invertebrates have evolved around the extraction of information from soundscapes. Invertebrates are mainly sensitive to the particle motion of sound, rather than the sound pressure. As many of them live close to the seabed they are often affected by substrate vibration, which usually involves particle motion (Hawkins et al., 2021). Changing soundscapes due to a decrease of sound-producing animals and the introduction of man-made noises may thus alter vital invertebrate sensory abilities. Sources of marine underwater anthropogenic noise that generate vibration, include shipping (fishing boats, recreational motorboats, jet skis, trade vessels), oil and gas exploration and operation, the construction and operation of offshore wind farms and other renewable energy devices, dredging, construction of bridges and harbours, commercial and military sonar, and underwater explosions for construction or ordnance disposal. There are some natural sources of substrate vibration, including volcanos, earthquakes and breaking waves, animal movements/interactions and objects falling or rolling onto the seabed. Seabed substrates can propagate some seismic interface waves well, with particle motion existing in both the water and the sediment. Underwater sound sources can extend over large periods of time (continuous; e.g., shipping (Van der Graaf et al., 2008) and result in an increase in low-level background noise, or can be short and intense (tonal/impulsive; e.g., sonar, pile driving, air guns (Rako-Gospić and Picciulin, 2019). Impulsive sounds have a fast rise time reaching a maximum value followed by a fast decay. Impulsive sounds may be much higher in amplitude near the source than continuous sounds, but their energy decreases faster with distance (Hawkins and Popper, 2016). It is important to note that sound is not limited to just the water column but that the near-surface seabed can respond vigorously to in-water sound and the seabed transmits low-frequency energy well (Nedelec, 2021).

Impulsive sounds can be expressed in terms of their peak levels, but in some cases (e.g., seismic airguns) that is not sufficient for characterizing the energy. An alternative is the sound exposure level (SEL) – the time integral of the pressure squared for a single event – a measure reflecting the total acoustic energy received by an organism (Slabbekoorn et al., 2010). The metrics applied for continuous sounds are the root-mean-square sound pressure (RMS) and the peak sound pressure (Hawkins and Popper, 2016; Hawkins and Popper, 2017). In general it is accepted that the assessment of the sound sources and its potential impact on marine fauna needs to consider cumulative (repetition of a particular source) and aggregate (combined effects of different type of sources (Hawkins and Popper, 2016).

Sound can affect marine organisms depending on sound pressure level at the source, the pitch (frequency) and the distance between source and receiver (Richardson et al., 1995). Table 1 provides a summary of the typical characteristics of different common anthropogenic sound sources in the marine environment.

Given the increasing introduction of anthropogenic noise to the oceans, it has become essential to design tools to monitor and regulate the effects of sounds on marine fauna. Anthropogenic noise is recognized as a major component of environmental change in the 21st Century and a pollutant of international concern, featuring prominently on international directives and agendas. Although additional scientific and technical progress is still required to support the further development of criteria related to acoustic impact on marine environment (including in relation to impacts of introduction of energy on marine life, relevant noise and frequency levels), two indicators were published for Descriptor 11 (Noise/energy) of the Marine Strategy Framework Directive (MSFD EU, 2008) in the EC Decision 2010/477/EU on criteria and methodological standards on GES of marine waters (Dekeling et al., 2014):

Indicator 11.1 Distribution in time and place of loud, low and mid frequency impulsive sounds.

- Proportion of days and their distribution within a calendar year, over areas of a determined surface as well as their spatial distribution, in which anthropogenic sound sources exceed level that are likely to entail significant impact on marine animals, measured as Sound Exposure Level (in dB re 1µPa2.s) or as peak sound pressure level (in dB re 1µPa-peak) at one meter, measured over the frequency band 10 Hz to 10 kHz.

Indicator11.2 Continuous low frequency sound.

- Trends in the ambient noise level within the 1/3 octave bands 63 and 125 Hz (centre frequency) (re 1µPa^2; average noise level in these octave bands over a year) measured by a statistical representative sets of observation stations and/or with the use of models if appropriate.

TABLE 1 Acoustic properties of some anthropogenic noises.

Sound	Source level (dB re 1 µPa-m) *	Bandwidth (Hz)	Major amplitude (Hz)	Duration (ms)	Directionality	Sound type
TNT (1-100 lbs)	272–287 Peak	2–1000	6–21	~ 1–10	Omnidirectional	Tonal/ impulsive
Pile driving	228 Peak/ 243–257 P-to-P	20–>20 000	100–500	50	Omnidirectional	Tonal/ impulsive
Offshore industrial activities						
Dredging	168–186 rms	30–>20 000	100 - 500	Continuous	Omnidirectional	Continuous
Drilling	145–190 rms**	10–10 000	< 100	Continuous	Omnidirectional	Continuous
Wind turbine	142 rms	16–20 000	30 - 200	Continuous	Omnidirectional	
Shipping						
Small boats and ships	160 –180 rms	20–>10 000	>1 000	Continuous	Omnidirectional	Continuous
Large vessels	180–190 rms	6–>30 000	>200	Continuous	Omnidirectional	Continuous
Sonar						
Military sonar low- frequency	215 Peak	100 –500	_	600–1 000	Horizontally focused	Tonal/ impulsive
Military sonar mid-frequency	223–235 Peak	2800–8200	3 500	500–2 000	Horizontally focused	Tonal/ impulsive
Echosounders	235 Peak	Variable	Variable 1500 – 36 000	5–10 ms	Vertically focused	Tonal/ impulsive
Seismic surveys						
Airgun array	260–262 P-to-P	10–100 000	10–120	30–60	Vertically focused*	Tonal/ impulsive
Other activities						
Acoustic deterrent/harassment Devices	132–200 Peak	5 000–30 000	5 000–30 000	Variable 15–500 ms	Omnidirectional	Tonal/ impulsive
Tidal and wave energy devices***	165–175 rms***	10–50 000	_	Continuous	Omnidirectional	Continuous

* Nominal source, ** Higher source levels from drill ships use of bow thrusters, *** Projection based on literature data with levels back-calculated at 1 m (Modified from Götz, 2009).

In this review, we provide a synthesis of the peer-reviewed literature published from the late 1960s to 2022 reporting marine invertebrate bioacoustics (detection and production of sound) and responses to anthropogenic noise in different life stages, in populations and ecosystems. This work documents prominent trends in research topics and methods, the kinds of noise sources that have been studied, the measurements used to characterise them, and the gaps and perspectives in research coverage that merit attention in future research. We outline the necessity/utility of existing scientific information concerning anthropogenic noise effects on marine invertebrates for predicting potential consequences of noise exposure. We also scale up to influences on ecological and evolutionary processes, and consider how this information is important for biodiversity conservation and the implementation of meaningful mitigation measures.

2 Marine invertebrate bioacoustics

Sound travels about five times faster in water (ca. 1500 m/s) than in air (ca. 340 m/s) because the density of water is greater, and also attenuates less over the same distance. This characteristic allows long-distance communication in water, but also implies a long-distance impact of noise on aquatic animals (Slabbekoorn et al., 2010). Particle motion is an important component of sounds travelling through the water and it is detected by invertebrates (Popper & Hawkins, 2019). Sound is an important sensory modality for marine organisms, especially because other senses (vision, smell or taste) may be limited due to information loss in marine ecosystems (Popper and Hawkins, 2019). The scientific knowledge of the biological significance of sound perception and production in marine invertebrates is scarce. Animals produce acoustic signals for communication about, for instance, predators, prey, territorial defence, social and sexual behaviour, and identity. They have evolved to detect sounds both as part of communication and to make use of acoustic cues in the environment, aiding in, for instance, settlement and habitat choice. In this section, we summarize the current knowledge regarding marine invertebrate bioacoustics including analysis methods, receptor organs, sound detection and production.

2.1 Measurements: Imaging, electrophysiology, respirometry, biochemistry

The different techniques used to study invertebrate bioacoustics are summarized and described below.

2.1.1 Imaging techniques

Scientific and diagnostic imaging allow visual representations of invertebrate sensory structures, organs or tissues for various purposes such as the study of normal anatomy and function, or the diagnosis of the effects of sound on these structures. Imaging techniques include Electron Microscopy and 3D imaging techniques (Figure 1).

Electron microscopes have a higher resolution than light microscopes and are capable of a higher magnification (up to 2 million times) (Rudenberg and Rudenberg, 2010), allowing the visualization of structures that would not normally be visible by optical microscopy. There are two major types of electron microscopes used in invertebrate bioacoustics: Transmission Electron Microscopes and Scanning Electron Microscopes. Scanning Electron Microscopy produces images of a sample by scanning it with a focused beam of electrons that interact with atoms in the sample, providing information about its surface topography and composition (Butterfield et al., n.d.) and achieving resolution better than 1 nanometre (Suzuki, 2002). In invertebrates, this technique allows description of the surface of sensory epithelium and effects of noise upon it (Figures 1A–E) (Solé et al., 2013a; Solé et al., 2013b; Day et al., 2016; Solé et al., 2016; Solé et al., 2018; Day et al., 2019). In Transmission Electron Microscopy, a beam of electrons is passed through an ultrathin specimen and an image is formed from the interaction of the electrons transmitted through it. This technique is used in the description of invertebrate ultrastructural sensory epithelia, allowing the inner cellular organelles to be visualised and analysis of the effects of sound on them. (Figure 1F) (Solé et al., 2013b)

Magnetic Resonance Imaging (MRI) is a non-invasive imaging technique that allows creation of a 3D image of a body's internal organs using powerful magnetic fields and radio waves. This technique has been used to construct models of the morphological structure of invertebrate sensory systems (Ziegler et al., 2018). Computer tomography (CT) relies on differences in X-ray attenuation of biological tissues to do a 3D reconstruction of them. Major molluscan organs have been visualized using CT techniques (Ziegler et al., 2018).

2.1.2 Electrophysiology

Auditory evoked potential recordings have been used in a variety of invertebrate taxa as a measurement of sound sensitivity (Figure 2A). The evoked potential technique for hearing was popularized by Hong Yan's work on fishes before to spreading it among invertebrates (Yan, 2002). This method involves measuring responses from neurons associated with sound detection and the resulting conduction of responses toward a brain or central set of ganglia (Hall, 2007). Recording may be thus from nearby sensory organs, such as the statocyst, or if sound detection comes from more peripheral hair cells or organs, it may occur nearby the brain/central ganglia area (Jezequel et al., 2021). While evoked potential methods have been widely applied to measure hearing abilities in many aquatic vertebrates e.g., (Supin et al., 2001; Kastak et al., 2005; Nachtigall et al., 2007; Mooney et al., 2012; Piniak et al., 2016; Jones et al., 2021), it has

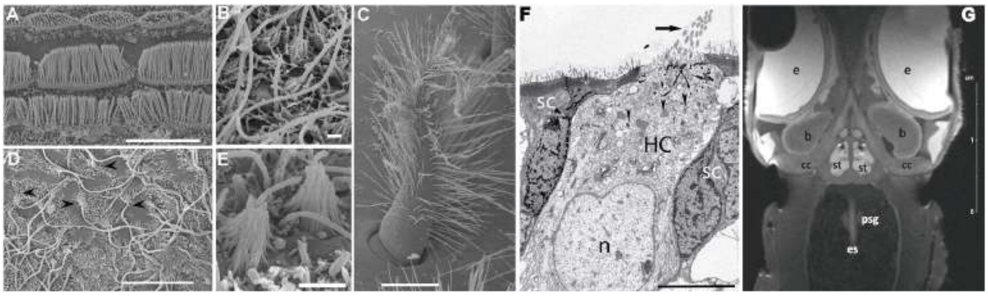

FIGURE 1
Imaging Techniques. **(A–E)**: Scanning Electron Microscopy. **(F)**: Transmission Electron Microscopy. **(G)**: Magnetic Resonance Imaging. **(A–F)**: Different types of sensory epithelia (hair cells) depending on the marine invertebrate group (**A, F**: Cephalopods. **(B, E)**: Cnidarians. **C**: Crustaceans. **D**: Gastropods). **(A)**: View of three rows of hair cells (bundle of kinocilia) in statocyst *crista* epithelium of *Sepia officinalis*. **(B)**: Statocyst sensory epithelium of the jellyfish *Cotylorhiza tuberculata*. Hair cells carry an only nonmotile kinocilia surrounded by a short crown of stereocilia (Solé et al., 2016). **(C)**: A seate (bearing hairs) of the medial group sensory epithelia in the hermit crab *Dardanus calidus* statocyst. Setae are typical hair cell on crustaceans. **(D)**: Apple snail (*Pomacea maculata)* inner statocyst sensory epithelia. Arrowheads point to the hair cells exhibiting their lonely kinocilia surrounded by a crown of stereocilia. Between them microvilli of the supporting cells is visible (Solé et al., 2021a). **(E)**: Statocyst sensory epithelia of the sea anemone *Calliactis parasitica*. Similarly to other groups of cnidarians **(B)** their hair cells present a solitary kinocilia surrounded by a crown of stereocilia. **(F)**: Apex of a *S. officinalis* hair cell (HC) in between two supporting cells (SC). The HC shows kinocilia (arrow), nucleus (n) and cytoplasmic mitochondria (arrowheads) (André et al., 2011). **(G)**: Coronal view -anterior section- of squid (*Loligo vulgaris*) head (B: Brain, cc: cranial cartilage, e: eye, es: oesophagus, m: mouth, psg: posteror salivary gland, st: statocyst. (Solé et al., 2013b). Scale bar: **(G)** = 2 cm. **(C)** = 25 µm. **(A)** = 10 µm. **(D, F)** = 5 µm. **(E)** = 2 µm. **(B)** = 1 µm.

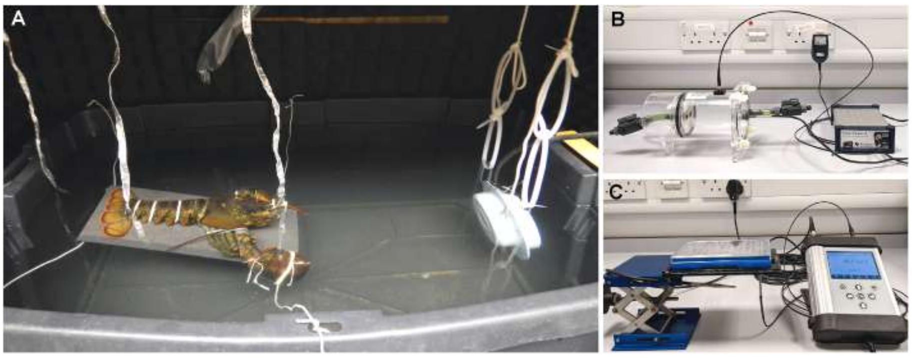

FIGURE 2
(A) Electrophysiology. **(B, C)**: Respirometry. **(A)**: Evoked potential hearing test of an American lobster (*Homarus americanus*) **(B)**: Respiration set-up for adult invertebrates; calibrated volume sealed respiration chamber connected to a fibox 3 trace v3 fibre-optic trace oxygen meter (Presens – Precision Sensing, Regensburg, Germany) *via* fibre-optic cable to a PSt3 oxygen sensor spot (detection limit: 0.03% oxygen, 15ppb). **(C)**: Plate set-up used for larvae and gametes; 64 well plate with PSt7 oxygen sensor spots (detection limit: 0.03% oxygen, 15ppb) attached to a fibox 4 trace hand held oxygen meter (Presens – Precision Sensing, Regensburg, Germany). Both (**B, C** use non-destructive oxygen measurements, measuring luminescence decay time by stimulating an immobilised luminophore with monochromic light.

only been sparingly applied to invertebrates, including squid (Mooney et al., 2010), prawns (Lovell et al., 2005), snapping shrimp (Dinh and Radford, 2021), lobsters (Jezequel et al., 2021) and other crustaceans (Hughes et al., 2014; Radford et al., 2016). Some of its advantages include that it can be applied to a variety of taxa, including wild caught animals, and it can be non-invasive. Although often times it is a more invasive method involving sedation, needle electrodes and surgery to access nerve structures. Evoked potential methods are generally cost-effective and permit to reach a relatively high animal sample size of (i.e. > 10), that is higher than psychophysical methods, and whole audiograms can be measured quickly (tens of minutes to a few hrs).

2.1.3 Respirometry

There are a number of techniques used to assess the effects of a stimulus on the metabolic rate of an organism. One such method, respirometry, provides an indirect calorimetric approach to the measurement of metabolic heat changes through monitoring and measurement of variations in oxygen uptake (Figures 2B, C). For marine invertebrates, changes in respiration rate are observed indirectly through changes in the dissolved oxygen of the surrounding water. Animals are encapsulated in a sealed, water-filled chamber and dissolved oxygen is measured either at the start and end points of the exposure using an oxygen probe, or continuously throughout the exposure using an oxygen sensor. During long exposures, intermittent flow respirometry may be used (Steffensen et al., 1984; Steffensen, 1989) when periodic flushing of the respirometry chamber is performed to maintain sufficient oxygen saturation. In both static and intermittent-flow respirometry, oxygen consumption is calculated accounting for bacterial respiration, water volume, exposure time and environmental conditions, and calibrated against the animal's mass to allow comparability between individuals and across species. Respirometry has been used to investigate the effects of anthropogenic noise on decapods (Regnault and Lagardere, 1983; Wale et al., 2013b; Ruiz-Ruiz et al., 2020), bivalves (Shi et al., 2019; Wale et al., 2019) and cephalopods (Woodcock et al., 2014).

2.1.4 Cellular–biochemical–molecular aspects

Several techniques for the assessment of invertebrate stress are based on cellular, biochemical and molecular aspects. It is possible to determine the physiological state of an animal using stress analysis after sound exposure. Stress bioindicators can be measured in invertebrate haemolymph. Total haemocyte count (THC), heat shock protein 27 (Hsp27) expression in haemocyte lysate, total protein concentration (PT) and phenoloxidase activity (PO) in cell-free haemolymph, were considered potential biomarkers of stress (Filiciotto et al., 2014; Celi et al., 2015).

In aquatic invertebrates, the homeostasis of total haemocyte density and composition may be considered an important well-being predictive parameter. Decreases of total haemocyte count (THC) under stressful conditions, usually carried out with cell counter chambers, have been reported for several aquatic crustacean species (Le Moullac et al., 1998; Sánchez et al., 2001; Mercier et al., 2006), suggesting the possibility of immune depletion as well as an increased risk of infection (Filiciotto et al., 2014; Celi et al., 2015). Although the variation in differential haemocyte count in the presence of different stressors is not well understood, it has been used as a stress indicator in crustaceans (Jussila et al., 1997; Johansson et al., 2000; Filiciotto et al., 2014) (Figure 3). The measurement of this parameter is easily feasible under the microscope after on slide cell fixation and stain.

Another parameter useful to evaluate the disturbance of the homeostatic balance of animals is the measurement of glucose haemolymphatic. Hyperglycemia is a primary response typical of many aquatic animals to different stressors (Lorenzon, 2005; Fazio et al., 2013; Faggio, 2014). Glucose haemolymphatic, which can be measured in haemolymph using commercial kits, increases in marine invertebrates under exposure to acoustic stimulu (Filiciotto et al., 2014; Vazzana et al., 2016). In the haemolymph, it is possible to measure the total protein concentration. This parameter is non-destructive, easy, cheap and measurable through fluorimetric methods. It can be used as a "warning" of poor environmental conditions such as noise (Filiciotto et al., 2014; Vazzana et al.,

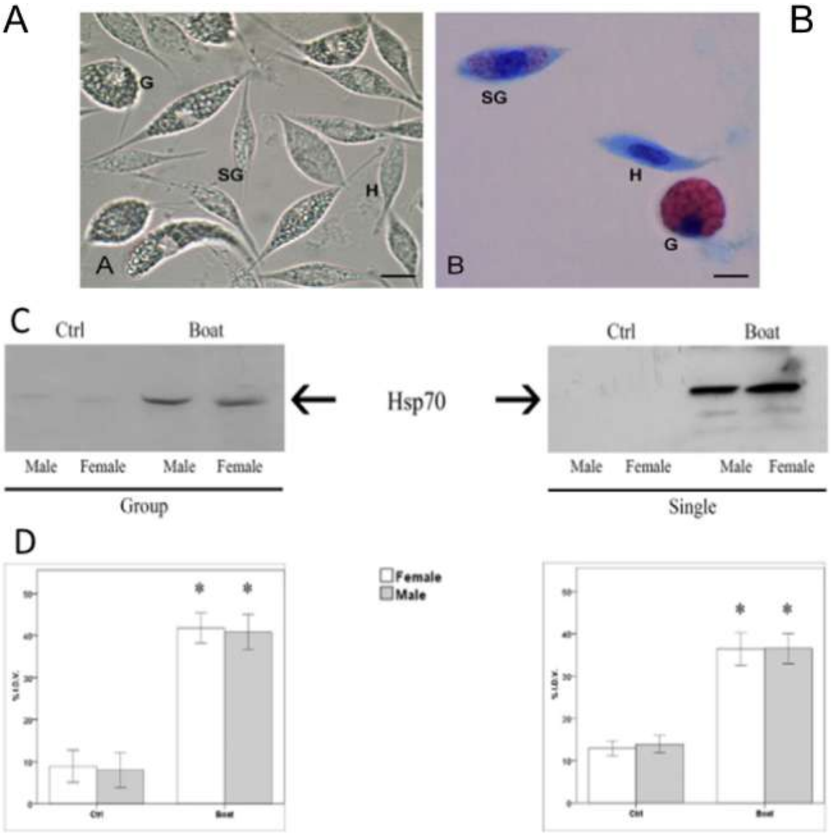

FIGURE 3
Light Microscopy. Haemocytes of the spiny lobster *Palinurus elephas* **(A)** no staining and **(B)** stained with May–Grünwald–Giemsa. H: hyalinocytes; SG: semigranulocytes; G: granulocytes. Scale bars: **(A, B)** = 8 µm. Effect of the acoustic stimuli on the expression levels of the protein Hsp70 in *P. elephas*; **(C)** Representative western blot of Hsp70 levels in single and grouped animals. **(D)** Integrated density value (% IDV) of the Hsp70 protein bands. Data are the means ± standard error (N = 18 control and N = 18 test specimens). Asterisks represent significant differences between CTRL and BOAT condition (*= $p < 0.01$). (Filiciotto et al., 2014).

2016). A further indicator of the negative effect of altered conditions on invertebrates is a change in enzyme activities. There are still few studies on the variations of enzymes in stressed invertebrates, but some have shown a modulation of peroxidase, alkaline phosphatase and esterase activity measured through rapid colorimetric methods (Vazzana et al., 2016; Vazzana et al., 2020a; Vazzana et al., 2020b) after acoustic stimulus. Among bioindicators of stressful conditions in crustaceans is also included expression of heat shock proteins (Snyder and Mulder, 2001; Liberge and Barthelemy, 2007). Some authors showed, through the use of western blot analysis and Real-Time PCR (RT-PCR), that, in marine invertebrates exposed to acoustic stimuli, occurs a protein and gene overexpression of the Hsp70 (Filiciotto et al., 2014; 2016; Vazzana et al., 2016; 2020a). The latter aspect is useful to understand better the variations of the complex cellular–biochemical–molecular network of organism in stress condition.

2.1.5 Measurement of underwater sound

In a sound wave, particles of the medium (e.g., water) oscillate around a point of origin ('particle motion') causing local compressions and expansions ('sound pressure') that transfer the sound energy to neighbouring particles (ISO 18405:2017; Gray et al., 2016). Thus, all sound involves both pressure and particle motion fluctuations. The number of oscillations per second is the frequency in Hertz (Hz). Sound pressure fluctuations are omnidirectional and are measured as force per unit area in Pascals (Pa), typically using piezoelectric hydrophones, which have been readily available for many years (ISO 18405:2017, Robinson et al., 2014). Sound particle vibrations are directional and are described by displacement (m), velocity (ms^{-1}) or acceleration (ms^{-2}); three metrics that have a frequency-dependent relationship to one another (Nedelec et al., 2016, ISO 18405:2017). The directional information is described by angles relative to references such as magnetic north and gravity. Particle acceleration can be measured using capacitive, piezoresistive or piezoelectric accelerometers, while particle velocity can be measured using geophones, all of which are proof-mass instruments (a proof mass is a known quantity of mass used in a measuring instrument as a reference for the measurement of an unknown quantity) that are becoming more readily available (Nedelec, 2021). Particle acceleration can also be measured using a pressure gradient between hydrophone pairs (Chapuis et al., 2019). Finally, in simplified acoustic conditions (deep water and far from the source relative to wavelength), particle velocity magnitude but not direction can be estimated from pressure measured by a single hydrophone (Nedelec, 2021). Underwater sound is often reported in decibel units (dB), which are represented on a logarithmic scale relative to 1 µPa for pressure, 1 pm for displacement, 1 nm s^{-1} for velocity and 1 um s^{-2} for acceleration (ISO 18405:2017).

The statolith organs of many invertebrates measure the relative motion of the body of the animal to the dense statocyst, which moves with a lag due to its greater mass and inertia, creating a biological analogue of a proof-mass instrument (Packard et al., 1990; Kaifu et al., 2011). Therefore, measuring the whole-body vibration of animals is of interest because it links acoustic stimulus and sound detection. Piezoresistive accelerometers that measure acoustic vibrations of solid objects they are fixed to exist, however their scale relative to the bodies of aquatic invertebrates means that the accelerometers themselves would alter the vibration of the whole body. Recently, the availability of non-contact laser Doppler vibrometer techniques, that have already been applied to research on hearing in several amphibian, reptile and crustacean species (Hetherington and Lindquist, 1999; Hetherington, 2001), has opened the possibility of measuring whole-body vibration of aquatic animals. Whole-body vibrations of cephalopods and scallops that were exposed to air borne sound (<360 Hz) were successfully measured using a laser Doppler vibrometer, confirming the hypothesis that particle motion can vibrate the whole body of invertebrates (André et al., 2016). However, to report the particle motion levels measured by an instrument, it is necessary to calibrate the instrument for its coupling to the medium in which the sound is to be measured. The coupling of animal bodies to the water column remains poorly understood, thus measuring whole-body motion gives us a limited understanding of responses to particle motion levels in the water. Further advancement of measurement techniques on whole-body vibration of aquatic animals elicited by propagating acoustic waves will improve understanding of particle motion reception in invertebrates. This will involve calibrating the animals themselves as well as any accelerometers that are attached to them.

2.2 Detection of sound: Vibration, reception and sensitivity

2.2.1 Physical aspects: Acoustic pressure vs particle motion

The motion of the 'particles' that make the medium (e.g., air, water, or solid substrate) is an intrinsic aspect of sound. Sound pressure can be described by its magnitude and its temporal and frequency characteristics, but at a single point, sound pressure does not contain directional information. Particle motion can be described by its magnitude, temporal and frequency characteristics, but additionally it always contains directional information because of its inherent 'back and forth' action (Hawkins and Popper, 2017). Many aquatic invertebrates sense and use particle motion, including to detect the direction of the source, (André et al., 2016; Nedelec et al., 2016). Particle motion and sound pressure are proportional in 'plane wave' conditions (far from the source and from any boundaries that may cause reflections relative to the wavelength). Close to the source in the 'near field', particle motion is higher than would be expected from equivalent pressure in plane wave conditions in the 'far field' due to interactions between the wavelength, frequency and distance from the source. This interaction, which causes additional particle motion near to the source decreases with inverse proportion to the distance from the source until it can be treated as negligible after approximately one wavelength. A good rule of thumb is therefore that the boundary of the near field region with additional particle motion is one wavelength from the source. Therefore, particle motion is present wherever there is sound and a good rule of thumb is that the boundary of the near field region with additional particle motion is one wavelength from the source. Sensory hair cells in the sensory systems (see below) are stimulated by mechanisms that respond to particle motion and convert these motions to electrical signals that stimulate the nervous system. Because aquatic invertebrates lack gas-filled cavities, it seems that they mostly perceive the particle motion of the sound. But recent experiments put this statement in question: particle motion may not be the sole component implied in sound lesions in invertebrates (Solé et al., 2017).

2.2.2 Receptor systems

2.2.2.1 Cilia-based mechanosensory systems

Mechanoreceptors are sensory cells (hair cells) detecting mechanical forces that usually bear specialized cilia (Figure 1). These mechanosensory cells are the starting point of mechanotranduction processes in which the hair cells express transmembrane channels that convert force into cellular signal. Hearing, proprioception or gravity mechanisms are based in these mechanosensory cells (Bezares-Calderón et al., 2020). These receptor systems can be found on the body surface of animals or enclosed in fluid-filled cavities. Hair cells possess unique features including the presence of cilia (microtubule with a basal body which contains organelles) that can be motile or not and, a tuft of stereovilli (actin-filled microvilli). Unlike vertebrates that are characterized by the presence of a single cilia with a 9 + 2 axoneme and a group of stereovilli, invertebrates generally have kinocilia (with an internal structure of 9 x 2 + 2 microtubules in the axoneme) in their hair-cell-based receptor systems. The number of kinocilia per cell varies according to the group of invertebrates (e.g., cnidarians: monociliary cells with a concentric or eccentric bundle of stereovilli; cephalopods: multiciliary cells with microvilli; crustaceans: monociliary cells without microvilli; Figure 1). Some mechanosensory systems present accessory structures (statolith, statoconia, cupula) above the hair cells which stimulate the underlying sensory epithelia. The kinocilia are mechanically directly or indirectly (via a cupula) coupled with the surrounding fluid. An external stimulus causes the movement of an accessory structure or fluid which leads to the mechanical deflection of the cilia, and stimulates the sensory cells. These hair cells may appear in the form of primary (specialized neurons with an axon leaving the cell) or different types of secondary sensory cells (without an axon) that make afferent synaptic contacts with first-order afferent neurons. Hair cells and neurons receive numerous efferent endings (Budelmann, 1989) and are responsible from the information transmission to the nervous system. Depending on the direction of deflation of the kinocilia, the amount of neurotransmitter release will be different, causing an excitation or inhibition response and serving to regulate a wide range of behaviours.

Invertebrates can detect underwater sound (i.e., of mechanical disturbance of water) through three types of sensory systems: the body superficial receptor systems, the internal statocyst receptor system and the chordotonal organs (Budelmann, 1992b) (Figure 4).

2.2.2.2 Superficial receptor systems

Epidermal detector systems for vibration and other local water movements known as "hydrodynamic receptor systems" are found all over the external body surface and are analogous structures to fish and amphibian lateral lines (Budelmann, 1992b) (Figure 5). Their

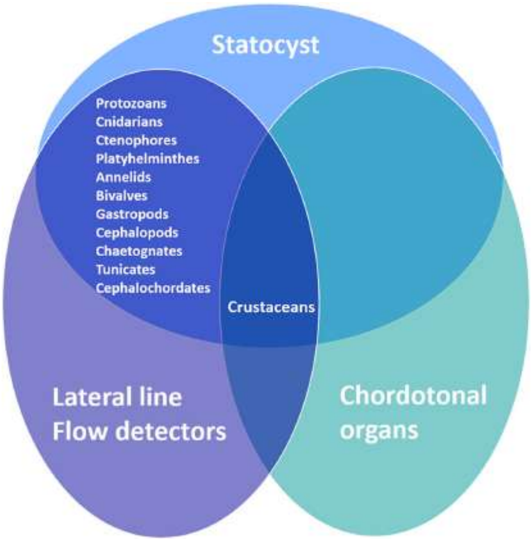

FIGURE 4
Marine Invertebrate sound sensory systems.

receptor cells are epidermal sensory cells carrying kinocilia that can be mechanically deflected by local movements that occur relative to the animal's body surface. In some cases, the cilia are embedded in an accessory cupula structure (Budelmann, 1989) (Figure 5).

Some species of **protozoans** respond to vibrations and water disturbances (Kolle-Kralik and Ruff, 1967). Unicellular organisms commonly respond to mechanical stimuli impinging upon them. Motor responses in ciliated cells result from alterations in motility of the cilia. The resulting behaviour is cellular contraction or alteration in locomotion (Budelmann, 1992b).

Cnidarians are sensitive to low-frequency water oscillations. Horridge (Horridge, 1966) showed sensitivity to low-frequency oscillations by the hydromedusa *Eutonia*. The sea anemone *Sagartia* reacts to water currents (Frings, 1967). The sensory structures are monociliary hair cells with a concentric bundle of stereovilli (Budelmann, 1989). Cnidarian's polyp and medusa stages

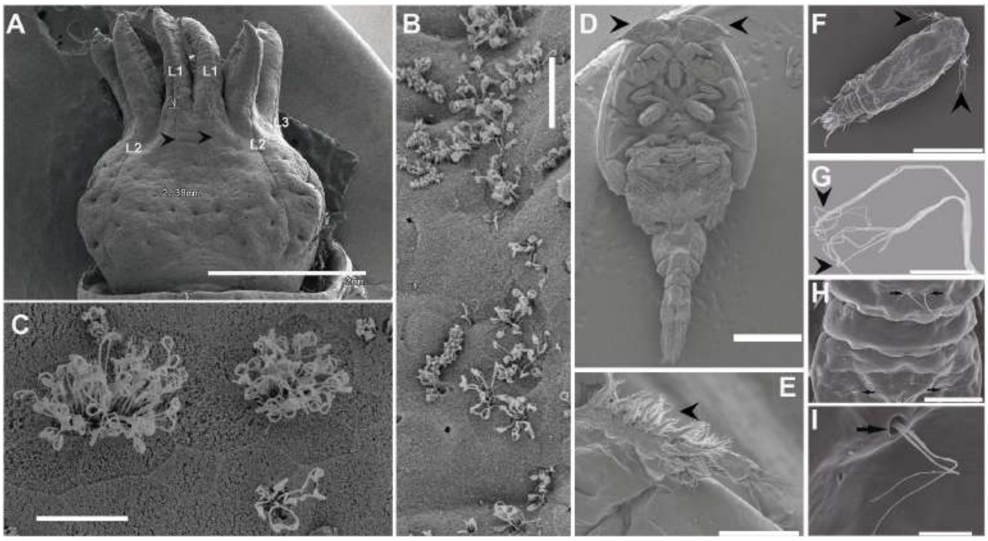

FIGURE 5
Scanning Electron Microscopy. (**A–C**: Cephalopod. **D–I** Crustacean). (**A**): Epidermal lines (lateral line analogue) on the head of *Sepia officinalis* larva. Lateral lines on three arms and above the eye (L1–L3) that run in anterior/posterior direction are visible. White arrows show the length of the lateral line L1 (black arrowheads). (**B**): Epidermal line L1. (**C**): Detail from (**B**). Hair cells' kinocilia of L1. (**D**): Ventral view of an adult whole body of sea lice (*Lepeophtheirus salmonis*) showing the first antenna (arrowheads) responsible from the sound perception. (**E**): First antenna of an adult of *L. salmonis*. (**F**): Dorsal view of a *L. salmonis* copepodid showing the first antenna (arrowheads). (**G**): Detail from the first antenna setae showing their irregular branching tips. (**H**): Dorsal view of the *L. salmonis* copepodid abdomen showing some paired setae (arrows). (**I**): Detail from H showing the structure of a birrame setae (arrow). (**A–C**: Solé et al., 2022; **D–I**: (Solé et al., 2021b). Scale bar **(A, D)** = 2 **mm**. **(F)** = 300 µm. **(E)** = 100 µm. **(H)** = 30 µm. **(B, C, G)** = 10 µm. **(I)** = 5 µm.

to detect vibrations in water associated with prey movement. Hydrozoan and Cubozoan polyps show mechanoreceptors bearing specialized cilia located in their tentacles (Golz and Thurm, 1993; Golz and Thurm, 1994; Bouillon et al., 2006; Tardent and Schmid, 1972) which inform the animals about surrounding environment changes. Albert (Albert, 2011) described light, touch, gravity, chemicals, sound pressure waves, direction, vibration and hydrostatic pressure receptors in medusa. Behavioural observations in *Aurelia labiata* under turbulent water evidenced its sensitivity to sound pressure waves and vibration mediated by sensory ciliary hairs (Albert, 2007).

Ctenophores possess sensory organs able to detect vibrations in water associated to prey movement (Tamm, 2014). The comb jelly *Leucothea* and the sea walnut *Pleurobrachia* are sensitive to water oscillations. The receptor cells are monociliary hair cells with a specialized basal body (Budelmann, 1992b).

Platyhelminthes have many sensory cells that sense local water movements. In flatworms, each cell has a single kinocilium surrounded by either a collar of eight separate stereovilli or a collar with eight columnar ridges, closely filled with microfilaments (Budelmann, 1989).

The receptor organs for water movements and vibrations on **annelids** are the “segmental sensilla” which are disk-like-sensory buds containing three types of ciliated epidermal cells distributed all over the body surface, tentacular cirri and palps (Budelmann, 1989). When low-frequency vibrations stimulate their tentacles, tube worms withdraw into their tubes (Laverack, 1968).

Among **Mollusks, Cephalopods** also have superficial receptor systems sensitive to local water movements. These receptors are analogous in structure and function to the amphibian and fish lateral lines. Late embryonic stages and hatchlings of cephalopods have epidermal lines (Villanueva and Norman, 2008), consisting of ciliated primary sensory hair cells that carry cilia (Hanlon and Budelmann, 1987) and non-ciliated accessory cells, running in anterior-posterior direction and located on the arms, head, anterior part of dorsal mantle and funnel (Figures 5A–C). Cuttlefish present eight, and squids ten, “epidermal lines” of ciliated sensory cells (Budelmann, 1992b; Solé et al., 2018) which are sensitive to local water oscillations (0.5–400 Hz) and are able to perceive hydrodynamic pressure. In addition to the epidermal lines in the head and arms, on cephalopods, there are others ciliated cells with shorter cilia that occur on the body surface, also involved in the detection of water movements (Budelmann, 1992b; Preuss and Budelmann, 1995).

In **gastropods**, several types of receptor endings were identified in the skin of the tentacles, lips, dorsal surface of the head and mouth region of the pond snails *Lymnaea stagnalis* and *Vivipara viviparus* (Zaitseva and Bocharova, 1981). The **bivalve** abdominal sense organ (ASO) of scallop *Patinopecten yessoensis* is highly sensitive to water-born vibrations (Zhadan and Semen’kov, 1984; Zhadan et al., 2004). It is the largest of the mechanosensory organs studied, containing about 4 million sensory cells (Haszprunar, 1983; 1985).

Chaetognathes are predators of marine plankton. They wait motionless until the water oscillation produced by a prey or another source of vibration arrives (Budelmann, 1992b; Feigenbaum, 2011). Chaetognates exhibit “ciliary fences” on the body surface, consisting of stiff kinocilia polarized in the same direction. All fences together are able to detect the direction of water movements (Horridge and Boulton, 1967; Budelmann, 1992b).

The sessile ascidians (**Tunicates**) are sensitive to water movements through cupular organs present in the exhalent siphon of the animal (Bone, and Ryan, 1978; Mackie and Singla, 2004). The cupular organ exhibit primary sensory cells embedded in a gelatinous cupula, structure considered an analogue of neuromasts in vertebrates. In ascidians, mechanoreceptors of the oral area are involved in monitoring the incoming water flow. In the coronal organ of the oral siphon, the sensory cells present different morphologies depending on the species (*Enterogona* order show multiciliate cells, *Pleurogona* present one or two cilia accompanied by stereovilli). The coronal organ presents a line of secondary sensory cells with a hair bundle also comprising graded stereovilli. These hair cells resemble vertebrate hair cells for morphology, embryonic origin and arrangement, and this organ is considered homologous to the vertebrate octavo-lateralis system (Burighel et al., 2011). *Molgula socialis* presents a coronal organ with a few associated rows of sensory cells running the whole length of the oral velum and the tentacles (Caicci et al., 2007). *Oikopleura* exhibit another organ sensitive to water oscillations, the Langerhans receptor (with monociliary cells that lack a cupula) on either side of the trunk (Bone and Ryan, 1979).

Two types of ciliated sensory cells sensitive to water movements are shown in the lancelet Branchiostoma (*Amphioxus*) (**Cephalochordates**) (Bone and Best, 1978). On the buccal cirri, the hair cells carry a normal kinocilium. On the velar tentacles, the sensitive cells bears a shorter and thicker modified cilium (Burighel et al., 2011).

Crustaceans exhibit superficial receptor systems sensitive to water disturbances over the body surface. The receptors systems can present a single cuticular hair (“sensillum”) or a group of hairs. The structure of the hair(s) consists of one to four sensory cells with a flexible basal joint. When the water oscillations bend the hairs the sensory cells are mechanically stimulated (Budelmann, 1992a). Decapod crustaceans, especially lobsters and crayfish, present cuticular cells on their carapace and over the body surface, on the two large and small antennae and on the telson (Budelmann, 1992a; Jezequel et al., 2021). In addition to sensory sensilla distributed around the body surface, some planktonic crustaceans present sensory sensilla responsible for the water disturbance and sound perception on the antenna (Solé et al., 2021b) (Figures 5D–I).

2.2.2.3 Statocyst receptor systems

Invertebrate statocysts can be defined as internal receptor systems, analogous to the vertebrate inner ear (otolith organ), that act as equilibrium receptor systems, although most are thought to be gravity receptor systems only (Anken and Rahmann, 2002). In addition, statocysts of cephalopods and decapod crustacea include angular acceleration detector systems (Budelmann, 1988; Budelmann, 1992a). In these groups, the statocyst as linear accelerometers can also detect acoustic particle motion (since the whole animal vibrates together with the water column) and are involved in underwater hearing (Budelmann 1992a; Budelmann 1992b).

Statocysts present different range of complexity from the simplest gravity receptor systems to the more complex organs of cephalopods which show receptor systems for linear and angular accelerations (Budelmann, 1992b). However, all these different systems have only two basic structural elements: a mass, the statolith or statoconia, the position of which varies as a function of the forces applied; and sensory elements (hair cells that carry kinocilia in contact with the mass) that are mechanically affected by the position of the mass (Figure 6). Changes in orientation cause the movement of the statolith into the statocyst and thereby the stimulation of different groups of hair cells. In some cases, the heavy mass is surrounded by, or included in, the sensory cell lacking kinocilia (Budelmann, 1992b).

In **cnidarians**, statocysts can be external or internal pendulum-like projections bearing internally the mass (Budelmann, 1988; Solé et al., 2016). The position of the pendulum is monitored by one or several hair cells. Scyphozoan medusae shows marginal sense organs bearing statocysts (Werner, 1993). Numerous small crystals collected in sac-like statocyst are located at the distal ends of their rhopalia (sensory organs associated with pulsing, swimming, orientation and gravireception) (Passano, 1982) (Figure 6E). Statocysts lacking hair cells occur in cnidarian polyp *Corymorpha* (Campbell, 1972), in the nemertine worm *Ototyphlonemertes* (Brüggernann and Ehlers, 1981), and in some flatworms (Ferrero, 1973). The process of stimulus detection in the statocyst is mediated by the differential contact of the statolith and the surrounding sensory cell(s), or alternatively by membrane distortions (Budelmann, 1988).

Ctenophores have only a single statocyst containing a single large statolith in the aboral organ (apical organ). The frequencies of the eight locomotory comb rows are controlled by four compound motile mechanoresponsive cilia (balancers), which support the statolith, and consequently regulate the position of the animal respect to gravity perception (Budelmann, 1992b; Tamm, 2014).

Lacking on the sessile adults, the **ascidian tunicate** *Ciona* present a unique statocyst in their its larvae, consisting in a single cell carrying a large pendulum-like projection without cilia (Budelmann, 1992b).

Bivalve, scaphopod mollusks and most **gastropods** exhibit the “typical” invertebrate statocyst. (Figure 6D) (Cragg and Nott, 1977; Budelmann, 1992b) that is shown from the pediveliger stage (Cragg and Nott, 1977). It is a sphere filled with endolymph which walls are lined by between 10 and 3,000 hair cells, each bearing kinocilia and contains either a single statolith or a mass of statoconia (Budelmann, 1988).

With the exception of the **Nautiloids**, which present a simplest statocyst that resemble gastropod and bivalve molluscs equilibrium organs, all **cephalopods** have a couple of statocysts generally located within the cephalic cartilage. The cephalopod statocysts are sophisticated balloon-shape bodies filled with endolymph that contain the sensory hair cells which lie on the inside wall of the inner sac and are grouped into two main areas of sensory epithelium (macula and crista). In **octopods**, the statocyst is a sphere-like sac. It contains a single gravity receptor system, the macula plate with a compact attached statolith. The angular acceleration receptor system is a ridge of cells that runs along the inside of the statocyst sac, divided into nine crista segments. Either a large or a small cupula is attached to each segment (Budelmann, 1988). In **decapods**, such as cuttlefish and squid, the statocysts are even more complex (Figures 6A–C). Its

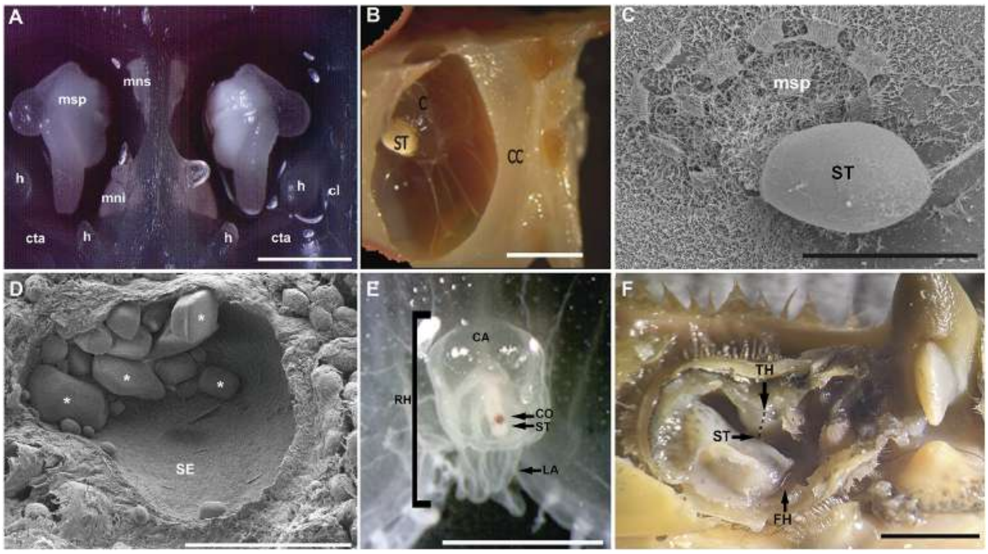

FIGURE 6
Invertebrate marine statocyst (**A–C**: Cephalopods. **D**: Gastropods. **E**: Cnidarians. **F**: Crustaceans). **(A,B, E, F)**: Photomicrograps**. (C, D):** SEM. **(A)**: *epia officinalis* statocyst cavities opened transversally (Anterior view). Each cavity shows the three macula-statolith systems (msp, mns, mni) and two of the crista-cupula systems (cta, cl)(Solé et al., 2017). **(B)**: Lateral view of the interior of a *Octopus vulgaris* statocyst. The spherical inner sac is suspended in the cephalic cartilage cavity by fibrous strands. The statolith is attached to the macula. The crista lies on the inside wall of the sac-like structure (André et al., 2011). **(C)**: *Illex coindetii* hatchling inner statocyst morphology. The transversally opened statocyst cavity shows the statolith attached to the macula statica princeps. Note the hair cell kinociliary groups arranged in nearly concentric rings around a center (Solé et al., 2018). **(D)**: Inner cavity of apple snail (*Pomacea maculate)* statocyst covered by sensory epithelium. Some aragonite crystals are visible (asterisk) (Solé et al., 2021a). **(E)**: Anterior view of the jellyfish *Aurelia aurita* rhopalium bell margin. There is a mass of sensory cells with a single layer of pigment cells (pigment-cup ocellus) on the oral side near the statocyst (Solé et al., 2016). **(F)**: Transversally opened statocyst cavity of a blue crab (*Callinectes sapidus*). Arrows point to the location of the different ciliary areas (ST, TH, FH). TH hair cells run following a line distribution as it is shown in the image (Solé et al., 2023) (ca, rhopalar canal; C, Crista; CC, Cephalic cartilage; cl, crista longitudinalis; co, pigment-cup ocellus; cta, crista transversalis anterior; FH, Free-hook hairs; h, hamuli lobe; LA, lappet; mni, macula neglecta inferior; mns, macula neglecta superior; msp, macula statica princeps; RH, rhopalium; SE, Sensory epithelium; ST, statolith; TH, Thread hairs). Scale bars: **(A, B)** = 2 mm. **(F)** = 0,5 mm. **(E)** = 400 µm. **(D)** = 200 µm. **(C)** = 20 µm.

angular acceleration receptor system is subdivided into only four segments. Its gravity receptor system is subdivided into three systems. Each system has a unique pattern of morphological and physiological polarization of its hair cells, depending on the position of the basal foot structure and the internal tubuli content of its kinocilia (Budelmann, 1979). One of these three systems is covered by a large calcareous statolith, whereas the others are covered by statoconial layers. In cephalopods statocysts, the sensory hair cell organization is highly complex and receive a high degree of efferent innervation (Colmers, 1981).

Crustaceans are sensitive to low frequency acoustic stimuli (Salmon and Horch, 1972; Goodall et al., 1990; Roberts et al., 2016). Mechanical disturbances of water/sediment (associated to sound waves) are detected by a pair of statocysts (Figure 6F), chordotonal organs linked to joints of antenna or legs (Figure 7) and internal and external sensilla (Figure 5) (Popper et al., 2001; Breithaupt, 2002). The statocyst in **crustaceans** shows a similar basic structure among all species and can be located on the basal segment of the antennule (in decapods) and the uropod or telson of the tail (mysids and isopods). The statocyst presents cuticular sensory hairs polarized in one particular direction due to its asymmetric basal joint. They have an overlying statolith mechanically connected to the cuticular hair which stimulates three sensory hair cells. Depending on the species the cuticular hairs per statocyst is variable but in general they are arranged in two to four rows and are polarized towards the centre (Budelmann, 1992a; Rose and Stokes, 1981).

2.2.2.4 Chordotonal organs

Chordotonal organs which are associated with flexible articulations of the appendages, are common among **crustaceans** (Bush and Laverack, 1982; Cooper, 2008; Atkins et al., 2021) (Figure 7). The oscillations of the water column stimulate the chordotonal sensory cells sited in the appendages. The hermit crab *Petroehirus* exhibit chordotonal organs with sensory cells in the basal segment of the antennal flagellum. The rock and the spiny lobster present a similar organs in the large and small antenna and, the crayfish *Astaeus* in intersegmental joints of the first and second antenna (Laverack, 1964; Rossi-Durand and Vedel, 1982). The chordotonal organ is a proprioceptive organ that monitors joint movement, direction of movement and static position and in some cases could be related with sound perception (Figure 7). Fiddler and ghost crabs present specialized Barth's myochordotonal organs (Bart's MCO) located on each walking leg; these resembles a distinct, thin-walled "window" in the exoskeleton. The males of these species produce acoustic signals detected by their females. Thanks to Barth's myochordotonal organs, ghost crabs are sensitive to both substrate-borne and airborne sounds and, fiddler crabs responds to substrate-born vibrations.

2.2.3 Acoustic sensitivity in molluscs and crustaceans

Using a broad definition – the reception of vibratory stimuli of any kind and nature, provided that the sound source is not in direct contact with the animal's body (Budelmann, 1992b) – hearing is widespread among invertebrates. Although the research on invertebrate acoustic sensitivity is scarce, some studies on bivalves, cephalopods and crustaceans have determined some important aspects about the invertebrate threshold sensitivities.

Early studies on sound detection by **bivalves** reported induced burrowing behaviour in clam species (Mosher, 1972; Ellers, 1995). Recent work has quantified sensitivity of marine bivalves to substrate-borne vibration (Zhadan, 2005; Kastelein, 2008; Roberts et al., 2015). By exposure to vibration under controlled conditions using valve closure as the behavioural indicator of reception and response

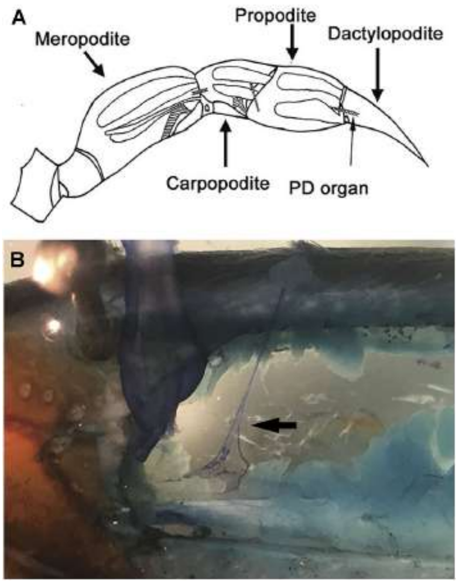

FIGURE 7
Crab chordotonal organ. **(A)**: Drawing of the first walking leg of a crab showing the anatomical location of chordotonal organs (hatched regions). PD organ spans the most distal joint in the limb between the propodite and dactylopodite. **(B)**: Innervation of chordotonal organs. Image of a dissected first walking leg of a blue crab (*Callinectes sapidus*). PD nerve dissected away from the main leg nerve (arrow). The individual neurons stained with methylene blue are visible. (PD: Propodite-dactylopodite chordotonal organ) (Image courtesy of Dr. Robin L. Cooper**)**.

(Roberts et al., 2015), the thresholds were shown to be within the range of vibrations measured in the vicinity of anthropogenic operations such as pile-driving and blasting. Using pure-tone exposures and an accelerometer fixed to the shell to detect valve closure, Japanese oysters (*Crassostrea gigas*) were shown to have maximum sensitivity from 10 to 200 Hz (Charifi et al., 2017). The **bivalve abdominal sense organ (ASO)** is highly sensitive to water-born vibration in the range 20–1500 Hz (Zhadan and Semen'kov, 1984; Zhadan et al., 2004).

While there is uncertainty regarding the biological importance of particle motion sensitivity versus acoustic pressure, recent behavioural (including changes in ventilation rhythm) and electrophysiological studies confirmed **cepaholopd** sensitivity to frequencies under 400 Hz (*Sepia officinalis*, (Packard et al., 1990); *Sepioteuthis lessoniana*, (Hu et al., 2009); *Octopus vulgaris* (Packard et al., 1990; Kaifu et al., 2007; Kaifu et al., 2008; Hu et al., 2009; Kaifu et al., 2011), *Loligo vulgaris*, (Packard et al., 1990), *Loligo pealeii*, (Mooney et al., 2010). Whole body vibrations due to particle motion were detected in cuttlefish *Sepia officinalis* (André et al., 2016) through an experimental set-up based on laser Doppler vibrometer techniques (frequencies 60, 120 and 320 Hz). This work confirmed the hypothesis that particle motion can encompass the whole body of cephalopods and cause it to move with a similar phase and amplitude. Mantle movement (lengthened ventilation or jetting) has been used as an indicator of the sound perception to understand the perceptionmechanism (Kaifu et al., 2007; 2008 Packard et al., 1990) or to understand the biological significance of their acoustical perception (Wilson et al., 2007; Samson et al., 2014; Mooney et al., 2016; Jones et al., 2021). In most cases, unconditioned animals were used to observe their baseline behavior. Mantle muscle movements were recorded using an electromyograph (Kaifu et al., 2007; Kaifu et al., 2008) or measurement of the changes of mantle muscle thickness based on impedance between two electrodes inside and outside the mantle (Packard et al., 1990). Cephalopod behavioural responses were then categorized to response type (e.g., inking, jetting, startle, colour change, fin movement, no response).

Among **crustaceans**, Lovell and colleagues studied the mechanism of the reception of sound and hearing abilities of the prawn *Palaemon serratus* using a combination of anatomical techniques, electron microscopy and electrophysiology (Lovell et al., 2005). They concluded that *P. serratus* is sensitive to sounds with frequencies ranging between 100 and 3000 Hz. The same authors (Lovell et al., 2006) demonstrated that all *P. serratus* individuals were able to hear sound with a frequency of 500 Hz, regardless of their size. Although data are not available on frequency-specific hearing/particle motion detection capability, preliminary experiments demonstrated *Nephrops norvegicus* postural responses to water vibrations (Goodall et al., 1990). The hermit crab (*Pagurus berhnardus*) showed antenna/maxilliped movement and forward locomotion in response to particle motion (Roberts et al., 2016). Auditory evoked potential (AEP) analyses of *Panopeus* sp. crabs evidenced their sensitivity to particle motion (Hughes et al., 2014). This response range overlaps with peak frequencies associated with airgun, pile-driving, sonar activities and biologically sources of underwater noise (Jeffs et al., 2003; Radford et al., 2007). Marine crustaceans present sensory hairs covering their bodies, which, when stimulated by water or substrate-borne vibrations associated with changes in acceleration hydrodynamic flow or sound, help animals sense nearby biological movements (Tautz and Sandeman, 1980; Radford et al., 2016). The American lobster *Homarus americanus* shows sensory hairs sensitives to low frequency (Derby, 1982) and ontogenic variations in AEP response up to 5 kHz (Pye and Watson, 2004; Jezequel et al., 2021). **Crustacean chordotonal organs** are stimulated by vibrations. One specialised organ, present on fiddler and ghost crabs, Barth's myochordotonal organ (Barth's MCO), is sensitive to frequencies above 300 Hz. All walking legs contain the sensory organ and if an individual loses a walking leg, it would still be able to detect vibrations through its other walking legs (Derby, 1982). Pelagic crab larva with capacity to detect specific underwater sounds/vibrations are able to use sound as an orientation cue to settle (Montgomery et al., 2006; Stanley et al., 2010; Stanley et al., 2012) (Jeffs et al., 2003; Radford et al., 2007).

Relevant studies on marine invertebrate acoustic sensitivity are detailed in Table 2.

2.3 Production of sound

Marine invertebrates can produce and use sounds to reveal their presence and for a broad variety of behaviours. They can generate the sound unintentionally during moving or feeding (Radford et al., 2008; Di Iorio et al., 2012) or deliberately for communication (Salmon, 1984; Popper et al., 2001; Chitre et al., 2012) (e.g. reproduction (Lucrezi and Schlacher, 2014) or defence (Patek, 2001; Buscaino et al., 2011). The capacity to produce sounds is known in only three groups of marine invertebrates: bivalves, echinoderms and crustaceans.

Many mussels (**bivalves**) produce snapping sound by stretching and breaking byssal threads, which the animals use to attach themselves to hard substrates. In addition, mussels can produce sound with the valve movements (Ubirajara Gonçalves et al., 2020).When expelling water and faeces from their central inner cavity, scallops "cough" by the contraction of the two valves of their shell. In this process, scallops produce a sharp "crack" followed by a long puffing noise as the two valves close (Di Iorio et al., 2012).

Among **Echinodermata**, there are some examples of sound producers. The long-spined sea urchin (*Diadema antillarum*) produces, during movement, crackling sounds by stridulation of its stiff spines and with a special feeding structure, the Aristotle's lantern. This animal uses the five teeth of the lantern to scrape kelp or invertebrates from the substrate. In addition, sea urchin have a calcified test that act as a resonator. The sound originated by the feeding noises of sea urchins, which frequencies are in the range of 800 to 2800 Hz, are amplified by the ovoid calcareous skeleton of urchins acting as a Helmholtz resonator (Radford et al., 2008). There is noise associated with *Kina* (a sea urchin from New Zeland*)* caused by feeding apparatus and spines and by the fluid inside the Aristotle's lantern that produces sound by resonance. Sounds associated with grazing *Kina* urchins contribute to the surrounding soundscape, increasing ambient sounds level 20– 30 dB during the sunrise/sunset periods (Radford et al., 2010).

Crustaceans are the only marine invertebrates in which communication *via* acoustic signals is well known (Aicher and Tautz, 1990; Budelmann, 1992a; Schmitz, 2002; Buscaino et al., 2011; Staaterman et al., 2011; Edmonds et al., 2016). In marine crustacea, the production of sound has been described only in two

TABLE 2 Relevant studies on marine invertebrate acoustic sensitivity.

Species	Common name	Acoustic Perception	Method	Study
Bivalves				
Donax variabilis	coquina	Sounds below 4096 Hz	Burrowing behaviour responses to sound	(Ellers, 1995)
Macoma balthica	Baltic clam		Digging movements after vibratory stimulation	(Mosher, 1972)
Mytilus edulis	blue mussel	Vibration stimulus (Sinusoidal excitation -tonal signals (5–410 Hz). Thresholds 0.06–0.55 m/s^2 (RMS)	Behavioural changes (valve closure)	(Roberts et al., 2015)
Crassostrea gigas	Japanese oyster	10–200 Hz pure tones	Valve closure (accelerometer oyster shell)	(Charifi et al., 2017)
Mizuhopecten yessoensis	Japanese scallop	30–1000 Hz	Behavioural (shell oscillations) directional sensitivity of ASO to water-borne vibrations.	(Zhadan, 2005)
Chlamys swifti	swifti scallop	30–1000 Hz	Behavioural (shell oscillations) directional sensitivity of ASO to water-borne vibrations.	(Zhadan, 2005)
Patinopecten yessoensis	Ezo giant scallop	ASO Fibres I: 20–1000 Hz (max 250–300 Hz) ASO Fibres II: 20–340 Hz	Electrophysiological study ASO	(Zhadan and Semen'kov, 1984)
Cephalopods				
Sepia officinalis	European common cuttlefish	Particle motion (acceleration) $<4x\ 10^{-3}$ m/s^2	Behavioural changes in breathing and jetting activity	(Packard et al., 1990
Sepia officinalis	European common cuttlefish	Fit the frequency dependence of particle motion sensitivity model	Physical model of the sensory system	(Kaifu et al., 2011)
Sepia officinalis	European common cuttlefish	PM encompass the whole body of cephalopods and cause it to move with same phase and amplitude	Experimental set based on laser Doppler vibrometer techniques	(André et al., 2016)
Sepioteuthis lessoniana	oval squid	400–1500 Hz	Auditory brainstem response (ABR) approach	(Hu et al., 2009)
Octopus vulgaris	common octopus	400–1000 Hz	Auditory brainstem response (ABR) approach	(Hu et al., 2009)
Octopus vulgaris	common octopus	Fit the frequency dependence of particle motion sensitivity model	Physical model of the sensory system	(Kaifu et al., 2011)
Octopus vulgaris	common octopus	Particle motion (acceleration) $<4x\ 10^{-3}$ m/s^2	Behavioural changes in breathing and jetting activity	(Packard et al., 1990)
Amphioctopus fangsiao/ Octopus ocellatus[1]	*webfoot octopus*	50–150 Hz	Behavioural changes (respiratory activities)	(Kaifu et al., 2007)
Amphioctopus fangsiao/ Octopus ocellatus[1]	*webfoot octopus*	141 Hz particle motion at particle accelerations below 1.3 × 10 -3 m/s^2	Behavioural changes (respiratory activities)	(Kaifu et al., 2008)
Amphioctopus fangsiao/ Octopus ocellatus[1]	*webfoot octopus*	Fit the frequency dependence of particle motion sensitivity model	Physical model of the sensory system	(Kaifu et al., 2011)
Loligo vulgaris	European squid	Particle motion (acceleration) $<4x\ 10^{-3}$ m/s^2	Behavioural changes in breathing and jetting activity	(Packard et al., 1990)

(Continued)

TABLE 2 Continued

Species	Common name	Acoustic Perception	Method	Study
Loligo pealeii	longfin squid	30–500 Hz (lowest thresholds between 100–200 Hz)	Auditory evoked potentials (AEPs) with electrodes placed near the statocysts	(Mooney et al., 2010)
Crustaceans				
Palaemon serratus	*common* prawn	100–3000 Hz	Anatomical techniques, electron microscopy and electrophysiology	(Lovell et al., 2005) (Lovell et al., 2006)
Nephrops norvegicus	*Norway lobster*	20–180 Hz	Behaviour responses to water vibrations	(Goodall et al., 1990)
Pagur Panopeus sp.*us berhnardus*	hermit crab	[5–400 Hz at particle velocities of 0.03–0.044 m/s^2 (RMS)]	Behavioural responses to particle motion	(Roberts et al., 2016)
Panopeus sp.	mud crabs	predatory fish sounds (or vibrations) 90–200 Hz, (vibrations <0.01 m/s^2)	Electrophysiological, auditory evoked potential (AEP)	(Hughes et al., 2014)
Cherax destructor	Australian freshwater crayfish	150–300 Hz	Electrophysiological recordings (Sensory hairs located on the claws)	(Tautz & Sandeman, 1980)
Ovalipes catharus	paddle crabs	100–200 Hz	Medical imaging technology, microCT, and auditory evoked potentials (AEP)	(Radford et al., 2016)
Homarus americanus	American lobster	20–300 Hz	Electrophysiological recordings (Sensory hairs, cuticular sensilla)	(Derby, 1982)
Uca sp. *Ocypode* sp.	fiddler crab ghost crab	≥300 Hz	Barth's myochordotonal organs (Barth's MCO)	(Popper et al., 2001)
Alpheus richardsoni	snapping shrimp	≥1500 Hz. (more sensitive: 80–100 Hz)	Electrophysiological, auditory evoked potential (AEP) in response to only particle motion and to both particle motion and sound pressure.	(Dinh & Radford, 2021)

([1]*Octopus ocellatus* has been accounted as a junior synonym of *Amphioctopus fangsiao* (Norman and Hochberg, 2005).

groups – barnacles (*Cirripeda*) and decapods (*Decapoda*) – but the detection of sound is widespread. In barnacles, the sound is produced incidentally when the chitinous appendages scrape on its shells during feeding (Fish, 1967). This movement produces rhythmic crackling (Budelmann, 1992a). In decapods, stridulatory movements during which several body parts are scratched against each other produce creaky sounds on spiny lobster, crayfish, shrimps and crabs (Budelmann, 1992a). These sounds may serve to scare off potential predators (Takemura, 1971; Patek, 2002). Patek showed the slip-stick mechanism (similar to bowing a violin) in the spiny lobsters (Patek, 2001). This was the first description of this mechanism in the animal kingdom, which is similar to the system underlying pectoral spine stridulation in blue catfish (Mohajer et al., 2015).

There is scarce knowledge about which sounds are incidentally produced or used for intra/extra-species communication. Snapping shrimp produce explosive clicks (Au and Banks, 1998; Versluis et al., 2000; Kim et al., 2009). These clicks have a fundamental role in the territorial behaviour of the shrimp and are used to stun prey or interspecific opponents (Au and Banks, 1998). Crustaceans produce acoustic signals that span a wide range of frequencies (Edmonds et al., 2016). Stomatopod mantis shrimp (*Hemisquilla californiensis*) and American lobsters *(Homarus americanus)* produce low-frequency rumblings. European spiny lobsters *(Palinurus elephas*) emit ultrasonic signals (Patek and Caldwell, 2006; Staaterman et al., 2011). *P. elephas* use a stridulating organ (plectrum) and rigid file to produce audible rasps associated with anti-predator responses (Buscaino et al., 2011). Jézérel experimentally investigated the propagation features of the sounds from various sizes of European spiny lobsters (*Palinurus elephas*) in natural conditions (Jézéquel et al., 2020a). The sound propagation and its attenuation with the distance on European spiny lobsters varied significantly with the body size. California spiny lobsters (*Palinurus interruptus*) produce pulsatile rasps using frictional structures located at the base of each antenna when interacting with potential predators (Patek et al., 2009). American lobsters produce carapace vibrations (Henninger and Watson, 2005), by simultaneously contracting the antagonistic remotor and promotor muscles located at the base of the second antenna. These sounds may serve in addition as a territorial or courtship role (Stocker, 2002). Red swamp crayfish (*Procambarus clarkii*) produce sound signals related to a territorial role (Buscaino et al., 2012). The sound-producing and acoustic behaviour of 11 large crustacean species of North East Atlantic such as moving, feeding, mandible rubbing, swimming, species-specific behaviour were analysed (Coquereau et al., 2016a; Coquereau et al., 2016b). The male of European lobsters (*Homarus gammarus*) use buzzingsounds for intraspecific communication during agonistic interactions (Jézéquel et al., 2018; 2020b).

Relevant studies on sound production are detailed in Table 3.

3 Effects of anthropogenic noise in marine invertebrates

Acoustic impact generally refers to activities of anthropogenic origin that generate sounds with frequencies that overlap those of the auditory range of marine organisms (Richardson et al., 1995). The underwater sounds that can affect marine biota can be differentiated between acute and chronic effects. Acute effects are those that cause immediate hearing damage or body injuries due to intense sound sources. Chronic effects are produced by prolonged exposure to moderate pressure level sounds. In addition, sounds can be differentiated between intentional (produced by seismic surveys, navy sonar, etc.) and unintentional (associated to pile-driving, shipping, harbour construction, etc.) sources whose potential effects range from behaviour changes, immediate hearing damage, body injuries or physiological trauma due to intense sound sources, to habitat degradation or expulsion from preferred habitats for prolonged periods. Much of the damage comes from the vibration of the invertebrate body created by the particle motion travelling through the water or the substrate (André et al., 2016). These impacts can affect individuals, populations or even entire ecosystems to unpredictable levels.

Relevant studies on invertebrate effects of noise are detailed in Tables 4–7.

3.1 Early life stages

There are few scientific studies which have directly investigated the effects of low-frequency sound on larvae and other early life stages of invertebrates. Acoustic impacts can be expressed throughout the life cycle of marine invertebrates, 2/3 of whose species have a bentho-planktonic life cycle (Thorson, 1964), i.e., they have a pelagic larval stage of variable duration. This section focuses on the larval, paralarval and juvenile stages, which can exhibit developmental impact (body malformations, higher hatchlings mortality, lower hatch rate and immature hatchlings and slower growth rate) after sound exposure.

Anthropogenic sound exposure resulted in delayed hatching and development of crustaceans eggs, and impaired embryonic development or significantly increase larvae abnormality and mortality rates in crustaceans, bivalve and gastropod (Christian et al., 2003; Courtenay et al., 2009; Stanley et al., 2010; Aguilar et al., 2013; Nedelec et al., 2014). Nedelec et al. (2014) showed negative effects on sea hare *Stylocheilus striatus* larvae of exposure to boat noise, whilst Aguilar de Soto, 2013 found a negative impact of exposure to high levels of seismic air gun noise on *Pecten novaezelandiae* larvae.

Two more general studies focused on the impacts of anthropogenic noise on zooplankton or some of its permanent components (copepods, krill) as invertebrate larvae are temporarily found there (meroplankton). Fields et al. conducted an *in situ* experiment on seismic air gun impacts on *Calanus* spp. showing low mortality (Fields et al., 2019). McCauley et al. through an *in situ* sampling strategy estimated major impacts on zooplankton (copepods, cladocera in particular; mass mortality for krill larvae) after seismic surveys (McCauley et al., 2017). Although the results of these two works could seem contradictory, the opposite results can be explained by the size of the plankton species. McCauley et al. (2017) showed that seismic mostly affected small copepod species, while *Calanus finmarchicus*, the species assessed by Fields et al. (2019) is a very large species. This reinforces the idea that the effects on one species is not applicable on taxonomically near species.

A recent study suggests a critical period of increased sensitivity to acoustic trauma in three species of cephalopod hatchlings *(Sepia officinalis, Loligo vulgaris* and *Illex coindetii*) after sound exposure (Solé et al., 2018). This is the first analysis of noise damaged sensory epithelia in the statocyst and lateral line system on cephalopod hatchlings.

For decades, barnacles have been a study model of choice for research in larval ecology, particularly because of their major role in the ‘fouling’ of ship hulls. More than three decades ago, Branscomb and Rittschof (1984) demonstrated that the primary settlement of young cypris stages of *Amphibalanus amphitrite* fails when exposed to low-frequency noise (Branscomb & Rittschof, 1984). Testing the impact of continuous ultrasound on their larvae collected from plankton there were delays in metamorphosis, which highly reduces primary settlement of cypris larvae (Guo et al., 2012; Choi et al., 2013). This last study further reveals that the other classical components of sessile epibiosis (polychaetes, bryozoans, ascidians and algae) are not affected by these low-frequency, low intensity ultrasound. Mussel larvae could use low-frequency sounds to select the natural habitat of mussel adults in a high-energy coastal area as suggested after exposure of *Mytilus edulis* to boat sounds (Jolivet et al., 2016).

Many other benthic invertebrates have a free-swimming larval stage and use biotic sounds for orientation, habitat selection and settlement (Jeffs et al., 2003; Montgomery et al., 2006; Lillis et al., 2013). Anthropogenic can lead to developmental delays during the metamorphosis and settlement stages after tidal and wind turbines sound exposure (Pine et al., 2016). In this study, the times to metamorphosis of megalope larvae of the crabs *Austrohelice crassa* and *Hemigrapsus crenulatus* decreased in ambient sound recorded in a natural estuarine environment and tidal and wind turbine sounds treatments. This reduction classically corresponds to a positive effect in larval ecology but the authors also suggest that spectral composition rather than sound level is more relevant to explain the observed results.

Whiteleg shrimp *Litopenaeus vannamei* exposed to aquaculture production system soundscapes (sound recordings of a commercial recirculating aquaculture system, RAS) showed no effects on early stages of this species probably due to a rapid habituation or higher

TABLE 3 Relevant studies on sound production on marine invertebrates.

Species	Common Name	Sound Type	Sound Origin	Study
Bivalbes				
Perna perna	brown mussel	Impulsive activities: 4–6 kHz band with a max SPL between 43 to 105 dB re 1µPa	Valve movements	(Ubirajara Gonçalves et al., 2020)
Pecten maximus	great scallop	Coughing sounds: 20–27 kHz	Valve movements	(Di Iorio et al., 2012)
Echinoderms				
Diadema antillarum	long-spined sea urchin	Crackling sounds	Stridulation of its stiff spines and Aristotle's lantern (calcified test act as a resonator)	(Radford et al., 2008)
Evechinus chloroticus	Kina	Grazing sounds (800 Hz–28 kHz)	Feeding apparatus and spines Fluid inside the Aristotle's lantern (produces sound by resonance)	(Radford et al., 2010)
Crustaceans				
Cirripeda	*barnacle*	1–3 ms pulses peak amplitude 70 dB (measured at 50 cm of distance)	Chitionous appendages scrape on its shell during feeding	(Fish, 1967)
Linuparus trigonus	spear lobster (spiny lobster)	2 type series of pulses: *A* type; slow repetition rate (10–80 times/sec) - weak at the low frequency range below 3 kHz; *B* type sound, powerful at low frequency. Repetition rate very high	Creaky sounds by rubbing the protuberance of the antennal coxa against the white tubercle in front of its optic stalk	(Takemura, 1971)
Palunirus argus *Palinurus elephas*	spiny lobsters	Stick-and-slip' sounds	Rubbing the base of each antenna against the antennular plate	(Patek, 2002)
Synalpheus paraneomeris	snapping shrimp	Explosive clicks, source levels between~175–220 dB re 1 µPa (peak–peak) @ 1 m; frequency spectrum 2-200 kHz with (peak energy at 2 kHz))	Forceful closing of the chela (in addition to a strong jet of water)	(Au and Banks, 1998) (Kim et al., 2009) (Versluis et al., 2000)
Hemisquilla californiensis	mantis shrimp	Low frequency rumblings (20–60 Hz)	Vibrating their posterior mandibular remoter muscles	(Edmonds et al., 2016)
Palinurus elephas	European spiny lobster	Ultrasonic signals (20–55 kHz)	Stridulating organ (plectrum) and rigid file	(Patek & Caldwell, 2006) (Staaterman et al., 2011)
Palinurus elephas	European spiny lobster	Audible rasps in the 2–75 kHz range (15 kHz peak frequency)	Stridulating organ (plectrum) and rigid file	(Buscaino et al., 2011)
Panulirus interruptus	California spiny lobster	Pulsatile rasps (150.4+/-2.0 dB re 1 microPa) at distances from 0.9 to 1.4 m.	Frictional structures located at the base of each antenna	(Patek, 2002)
Homarus americanus	American lobster	Mean frequency of 183.1·Hz (range 87–261·Hz), range in duration from 68 to 1720·ms (mean 277.1·ms) and lead to waterborne acoustic signals	Produce carapace vibrations, by simultaneously contracting the antagonistic remotor and promotor muscles located at the base of the second antenna	(Henninger & Watson, 2005)
Procambarus clarkii	red swamp crayfish	Sound signals [multi-pulsed, 0.4 ms duration, 128 dB re 1 µPa (zero-peak), mean bandwidth 20 kHz]		(Buscaino et al., 2012)
Cancer pagurus *Carcinus maenas* *Necora puber* *Pachygrapsus marmoratus*	11 large crustacean species of NE Atlantic	Single pulse and pulse train signals distributed across a peak frequency of 3 to 45 kHz with received levels	34 sounds were associated with behaviours such as moving, feeding, mandible rubbing, swimming, species-specific	(Coquereau et al., 2016b)

(Continued)

TABLE 3 Continued

Species	Common Name	Sound Type	Sound Origin	Study
Galathea squamifera *Lophozozymus incisus*		between 93 and 142 dB re 1 µPa (peak to peak)	behaviour and other unidentified behaviours	
Alpheus heterochaelis *Alpheus angulosus* *Alpheus* sp.	Snapping shrimp	Snaps	collapse of a cavitation bubble upon the rapid closure of their specialized snapping claw	(Lillis et al., 2017) (Lillis & Mooney, 2018)
Homarus gammarus	European lobster	"Rattles"	*Rattles when feeding*	(Jézéquel et al., 2018)
Homarus gammarus	European lobster	Buzzing sounds	When stressed vibrated its carapace, producing a low-frequency sound similar to 'buzzing' sound of the American lobster	(Jézéquel et al., 2020b)
Palinurus elephas	European spiny lobster	SL, at one meter from the animals, varied with size (largest SLup to 167 dB re 1 µPa2)		(Jézéquel et al., 2020a)

hearing thresholds of hatchery-produced individuals, (Slater et al., 2020).

3.2 Adults

Animals under exposure to low-frequency sounds may suffer physical damage such as changes in the hearing threshold or barotraumatic ruptures. Morphological or histological analysis allows detection of physical trauma (internal injuries, sensory cell damage of statocysts, epidermal sensory cells and neurons) that can lead to death. This trauma can affect structures involved in sound perception. Invertebrates can behaviourally respond to sound (increased aggressiveness, alarm responses, predator defence, orientation, habitat selection which could have consequences for reproduction and survival). Stress bioindicators such as hormones, immune responses, heat shock proteins, cardiac physiology and overall degraded body condition are the main physiological responses. Metabolic rate, which is the most direct indicator of stress, can be measured from respiration, oxygen consumption or feeding rate. In some cases, irreversible DNA damages has been reported.

3.2.1 Physical effects

In **bivalves**, field studies of airgun exposure found no evidence of increased mortality in adult scallops and clams (La Bella et al., 1996; Parry et al., 2002; Harrington et al., 2010). In another field study, a dose-dependent increase scallop mortality was found four months after exposure to an airgun (Day et al., 2016). In addition, scallops exhibited abnormal reflexes that may indicate damage to mechanosensory organs (Day et al., 2017). The opposite results of these works could be explained by the time of monitoring. Harrington et al. (2010) only monitored scallops for two months, whereas Day et al. (2016) showed that significantly higher mortality rates only occurred towards the end of the 4-month period. Parry and Gason (2006) also stated that to detect mortality in such studies, very significant mortality level would be needed.

Low-frequency noise exposure causes anatomical damage in **cephalopods**. After an increase in the frequency of strandings in North Spain (Guerra et al., 2004), recent findings showed that exposure to artificial noise had a direct consequence on the functionality and physiology of cephalopod statocysts, which are the sensory organs responsible for equilibrium and movements in the water column (André et al., 2011; Solé et al., 2013a; Solé et al., 2013b; Solé et al., 2017). Exposure to noise was challenging the life of exposed individuals in laboratory and offshore conditions (feeding and mating cancellation and irregular swimming). Lesions present on the exposed animals were consistent with a manifestation of a massive acoustic trauma observed in vertebrate species.

Cnidarians and **ctenophores**, both in the polyp and the medusa stage, possess sensory organs located in their tentacles, able to detect vibration in water associated to prey movement and changes in their surrounding environment. A study described morphological effects (severe damages to the statocyst sensory epithelia) after noise exposure on two species of Mediterranean Scyphozoan medusa, *Cotylorhiza tuberculata* and *Rhizostoma pulmo* (Solé et al., 2016).

Among **crustaceans**, blue crabs (*Callinectes sapidus*) suffer mortality as a result of underwater explosions (Moriyasu et al., 2004). Although no lethal effects of underwater noise have been described for *C. pagurus, Homarus gammarus* or *Nephrops norvegicus*, sub-lethal effects of continuous, low-frequency anthropogenic noise have been reported among the Decapoda (Edmonds et al., 2016).

Although no significant effects were detected in snow crabs after exposure (Christian et al., 2003), airgun exposure caused ultrastructural statocyst damages in rock lobsters up to a year later (Day et al., 2016). In a recent study, lobsters showed impaired righting and significant damage to the sensory hairs of the statocyst after exposure equivalent to a full-scale commercial assay passing within 100–500 m (Day et al., 2019). Reflex impairment and statocyst damage persisted over the course of the experiment – up to 365 days post-exposure – and did not improve following moulting.

3.2.2 Behavioural effects

Behavioural responses, not necessarily associated with startle responses, has been observed in **bivalves** (e.g., valve closure and

TABLE 4 Relevant studies on noise impact on bivalves.

Bivalves						
Species	Common name	Stage	Sound effects	Sound source	Received Levels	Reference
Pecten fumatus	Southern Australian scallop	Larva	**Impaired development** Significant under development Body malformations (D-veliger larva)	Seismic pulses playback	SEL pulse 165 dB re 1 Y/ µPa^2	(Aguilar et al., 2013)
Pecten fumatus	Southern Australian scallop	Larva	**High Mortality** Behaviour and reflex responses disruption Permanent Immunosuppression	Seismic airgun	Max SEL$_{cum}$ 198 dB re 1 µPa	(Day et al., 2017)
Perna canaliculus	New Zealand green-lipped mussel	Larva	**Behaviour** Faster settlement with decreased size of the settlers	Ship noise	126 and 100 dB re 1µParms	(Wilkens et al., 2012)
Mytilus edulis	blue mussel	Adult	**Physiology (stress)/Behaviour** Increased clearance rates/valve movement	Pile driving playback	SELss 153,47 dB re 1µPa	(Spiga et al., 2016)
Mytilus edulis	blue mussel	Adult	**Physiology (stress)** Higher breaks in the DNA Lower algal clearance rates, higher oxygen-consumption rates	Ship noise playbacks		(Wale et al., 2019)
Mytilus edulis	blue mussel	Adult	**Physiology (stress)** Changes in biochemical and immunological parameters in digestive gland	Playback	high frequency acoustic treatment (100–200 kHz)	(Vazzana et al., 2020a)
Mytilus edulis	blue mussel	Larva	Larva settlement increase	Low frequency vessel noises	127 ± 3 dB re 1 µ Pa between 100 and 1,000 Hz	(Jolivet et al., 2016)
Mytilus edulis	blue mussel	Adult	**Behaviour** Reduction responsiveness over sequential exposures Mostly respond to the onset of a pulse train.	single pulses and pulse trains (laboratory conditions)	150 and 300 Hz tones	(Hubert et al., 2021)
Mytilus galloprovincialis	Mediterranean mussel	Adult	**Physiology (stress)/Behaviour** No changes in behaviour Changes in plasma and tissue biochemical parameters (glucose, total proteins, total haemocyte number (THC), heat shock protein 70 (Hsp70) expression, and Acetylcholinesterase (AChE) activity)	Low frequency	linear chirp 0.1-5 kHz SPL 150 dB re 1µPa rms	(Vazzana et al., 2016)
Mytilus galloprovincialis	Mediterranean mussel	Adult	**Physiology (stress)** Changes in biochemical and immunological parameters in digestive gland	Linear chirp Playback	SPL 145-160 dB 1µPa rms high frequency acoustic treatment (100–200 kHz)	(Vazzana et al., 2020a)
Magallana gigas	Pacific oyster	Adult	**Physiology** Lower growth rate (2.6 time slower) **Behaviour** Decreased valve activity (lower metal contamination/ decreased grow)	Cargo ship noise (with trace metal contamination, Cd)	150 dBrms re 1µPa	(Charifi et al., 2018)
Ruditapes philippinarum	Manila clam	Adult	**Behaviour** Reduced maximum depth of sediment particle redistribution Reduced valve activity Effects on benthic ecosystem **Physiology** Tissue biochemistry effects due to perturbations in the delivery of oxygen to tissues	Continuous Broadband Noise (CBN) and Impulsive Broadband Noise (IBN) (similar offshore shipping and construction)	SEL 135-150 dB re 1 µPa	(Solan et al., 2016)
Sinonovacula solanconstricta	razor clam	Adult	**Behaviour** Avoidance response: deeper digging **Physiology (stress)** Changes in metabolic activity (O:N ratios) Altered expression of metabolic genes Affected activity of Ca2+/Mg2+-ATPase	White noise and sine wave	80 dB re 1 µPa (induced gens expression) 100 dB re 1 µPa (repressed gens expression)	(Peng et al., 2016)
Cardium edule	common cockle	Adult	**Behaviour** Cockles retracted their siphons and closed the shells	Seismic operations		(Kastelein, 2008)

(Continued)

TABLE 4 Continued

Bivalves						
Species	Common name	Stage	Sound effects	Sound source	Received Levels	Reference
Paphia aurea	golden carpet shell	Adult	**Physiology (stress)** Hydrocortisone, glucose and lactate Ievel increase	Seismic operations	210 dB re to 1μPa	(La Bella et al., 1996)
Crassostrea virginica	Eastern oyster	Larva	**Behaviour** Higher levels of oyster settlement in larval cultures	Acoustic signatures ambient reef sound	1.5–20 kHz	(Lillis et al., 2013)
Crassostrea gigas	Pacific oyster	Larva	**Behaviour** No response to sound on unfed larvae Increased swimming activity fed larvae	Natural and anthropogenic sound (laboratory conditions)		(Stocks et al., 2012)
Mytilus coruscus	Korean mussel	Adult	**Physiology** reduced byssal threads secretion mechanical performances (strength, extensibility, breaking stress, toughness and failure location) wakened	Ambient underwater condition	~50 dB re 1 μPa	(Zhao et al., 2021)
			Physiology reduced byssal threads secretion mechanical performances (strength, extensibility, breaking stress, toughness and failure location) wakened	Playbacks of pile-driving	~70 or ~100 dB re 1 μPa	
Placopecten magellanicus	giant scallop	Adult/ juveniles	**Behaviour** repeated valve closures (stronger effects for juveniles)	Pile driving sounds in field experiments	single strike levels: VH (near site = 136.60 ± 4.98 dB re (1 μm·s-^{2})^{2}s, far site = 116.20 ± 4.03 dB re (1 μm·s-^{2})^{2}s) IH (near site = 94.39 ± 1.34 dB re (1 μm·s-^{2})^{2}s, far site = 72.48 ± 2.51 dB re(1 μm·s-^{2})^{2}.s	(Jézéquel et al., 2022)
Limecola balthica	Baltic macoma Baltic clam	Adult	**Behaviour** Potential anti-burrowing stress response	"noise eggs"	low-frequency multi-tone ~ 100 Hz – 200 Hz	(Wang et al., 2022)
Pecten maximus	King scallop	Larva	**Mortality** <4% mortality rates without any noise influence **Physiology/Growth** Interactive impact on postlarval growth between trophic environment and noise level /spectra No change in fatty acid profiles	Pile Driving playback Drilling playback	*Pile driving (increasing levels P1, P2, P3)* SPLpp 147.6 (P1) up to 187.6 dB (P3)re 1 mPa s SEL24h 186.9 (P1) up to 215.8 dB (P3) re 1 mPa s *Drilling (increasing levels D1, D2, D3)* SPLrms 107.0 (D1) up to 175.4 dB (D3) re 1 mPa s SEL24h 153.4 (D1) up to 221.7 dB (D3) re 1 mPa s	(Olivier et al. 2023)

recessing reflex behaviour). These responses were used to establish thresholds of sound detection (Roberts et al., 2015). In addition to classic behavioural patterns (i.e., persistent alterations in recessing reflex behaviour), a novel flinching behaviour (a rapid retraction of the velum and then returned to position) was observed on commercial scallops (*Pecten fumatus*) after exposure to a seismic survey. This behaviour was observed before the acoustic wave reached the animal, suggesting that it was a response to the faster traveling ground roll wave (Day et al., 2016). Changes in scallop behaviour and reflex responses disruption were observed at least 120 days after seismic survey exposure (Day et al., 2017).

Among **cephalopods**, behavioural startling responses (jetting and inking) were observed in squids during seismic surveys (Fewtrell & McCauley, 2012) and in response to noise in laboratory conditionss (Samson et al., 2014). Squid show fewer alarm responses with subsequent exposure to noise from seismic surveys (Fewtrell & McCauley, 2012). This process of habituation has been observed in different species of cephalopods (McCauley et al., 2000; Samson et al., 2014; Mooney et al., 2016). While other studies also reported behavioural response to acoustic stimuli in a context of anti-predator defence (Hanlon and Budelmann, 1987; Kaifu et al., 2007); the capture of *Todarodes pacificus* reportedly increased in the presence of underwater sound (Maniwa, 1976). Feeding and foraging behaviour has been shown to be altered in response to different noise stimuli in cephalopods (Jones et al., 2021).

Decapod **crustaceans** exposed to seismic sound exhibited alarm behaviour (startle responses) when they were very near from the sound source (Goodall et al., 1990; Christian et al., 2003). *Carcinus*

TABLE 5 Relevant studies on noise impact on cephalopods.

Cephalopods						
Species	Common name	Stage	Sound effects	Sound source	Levels	Reference
Loligo vulgaris	European squid	Adult	**Damage to sensory systems** substantial, permanent, cellular damage to the statocysts and neurons	Sinusoidal wave sweeps	157 dB re 1 µPa (peak levels up to 175 dB re 1 µPa	(André et al., 2011) (Solé et al., 2013a)
Loligo vulgaris	European or common squid	Larva	**Damage to sensory systems** cellular damage to the statocysts and lateral line system	Sinusoidal wave sweeps	157 dB re 1 µPa (peak levels up to 175 dB re 1 µPa	(Solé et al., 2018)
Illex coindetii	Southern shortfin squid	Adult	**Damage to sensory systems** substantial, permanent, cellular damage to the statocysts and neurons	Sinusoidal wave sweeps	157 dB re 1 µPa (peak levels up to 175 dB re 1 µPa	(André et al., 2011) (Solé et al., 2013a)
Illex coindetii	southern shortfin squid	Larva	**Damage to sensory systems** cellular damage to the statocysts and lateral line system	Sinusoidal wave sweeps	157 dB re 1 µPa (peak levels up to 175 dB re 1 µPa	(Solé et al., 2018)
Sepioteuthis australis	southern reef squid	Adult	**Stress** Alarm responses Aggression jetting	Seismic airgun	168-173 dB re 1 µPa	(Fewtrell & McCauley, 2012)
Architeuthis dux	giant squid	Adult	**Mortality** **Damage to sensory systems** Nine strandings Extensive damage to internal muscle fibres, and organs including statocysts	Seismic airgun		(Guerra et al., 2004)
Sepia officinalis	common Mediterranean cuttlefish	Adult	**Damage to sensory systems** Substantial, permanent, cellular damage to the statocysts and neurons	Sinusoidal wave sweep	157 dB re 1 µPa (peak levels up to 175 dB re 1 µPa	(André et al., 2011) (Solé et al., 2013b)
Sepia officinalis	common Mediterranean cuttlefish	Adult	**Damage to sensory systems** Injuries to the statocysts the severity of the injuries was greater, the closer the distance to the sound source	Sinusoidal wave sweep	139-142 dB re 1 µPa2 at 1/3 octave bands centred at 315 Hz and 400 Hz (off-shore experiments)	(Solé et al., 2017)
Sepia officinalis	common Mediterranean cuttlefish	Larva	**Damage to sensory systems** Cellular damage to the statocysts and lateral line system	Sinusoidal wave sweep	157 dB re 1 µPa (peak levels up to 175 dB re 1 µPa	(Solé et al., 2018)
Sepia officinalis	common Mediterranean cuttlefish	Adult	**Physiology** Changes on the statocyst endolymph proteomic composition	Sinusoidal wave sweep	157 dB re 1 µPa (peak levels up to 175 dB re 1 µPa	(Solé et al., 2019)
Sepia officinalis	common Mediterranean cuttlefish	Adult	**Behaviour** Escape responses (inking, jetting) Body patterning changes and fin movements Sound habituation	Pure-tone pips	Pure-tone pips from 80 to 300 Hz (> 140 dB re. 1 µPa rms and 0.01 m s−2) and (Solé et al., 2022)Part. accel. of 0–17.1 m s−2 80 and 300 Hz 200Hz	(Samson et al., 2014)
Sepia officinalis	common Mediterranean cuttlefish	Adult/ Larva/ Eggs	**Damage to sensory systems** cellular damage to the statocysts and lateral line system (adult and larva) Decreased larva survival rate Decreased hatching success	Pile-driving playback Drilling playback	Max. 170 dB re 1 µPa2 Max: 167 dB re 1 µPa2,	(Solé et al., 2022)
Octopus vulgaris	common octopus	Adult	**Damage to sensory systems** Substantial, permanent, cellular damage to the statocysts and neurons	Sinusoidal wave sweeps	157 dB re 1 µPa (peak levels up to 175 dB re 1 µPa	(André et al., 2011) (Solé et al.2013a)

TABLE 6 Relevant studies on noise impact on crustaceans.

Crustaceans						
Species	Common name	Stage	Sound effects	Sound source	Levels	Reference
Daphnia magna	water flea	Adult	**Behaviour** No effects on swimming speed or depth	Ambient noise (continuous regular and irregular intermittent)	122 dB re 1 µ Pa	(Sabet et al., 2015)
Palaemon serratus	common prawn	Adult	**Behaviour** Change in locomotor patterns **Physiology (stress)** Change in haemolymph and brain total protein content, DNA fragmentation Change in brain protein (HSP 27, HSP 70) level expression	Boat noise (Laboratory experiments)	Power spectrum peaks up to 140 dB re 1µPa rms in the frequency band 0.1-3 kHz	(Filiciotto et al., 2016)
Litopenaeus schmitti *Farfantepenaeus subtilis* *Xyphopenaeus kroyeri*	southern white shrimp southern brown shrimp Atlantic Seabob	Larva/Adult	**Catch rate** No significant deleterious impact	Seismic survey	635 cu. 196 dB peak re 1 µ Pa	(Andriguetto-Filho et al., 2005)
Crangon crangon	southern brown shrimp	Adult	**Physiology (stress)** Significant growth and reproduction rates reduction Increased **Mortality** rate	High ambient sound-level in tanks	30 dB (25 to 400 Hz)	(Lagardère, 1982)
Crangon crangon	southern brown shrimp	Adult	**Behaviour** Increased cannibalism Increased food intake **Physiology (stress)** Increased ammonia excretion Increased O_2 consumption	High ambient sound-level in tanks	105 dB re 1 µPa	(Regnault & Lagardere, 1983)
Balanus amphirite	barnacle	Larva	**Impaired development** Larva metamorphosis and settling reduction	Low frequency sound (30Hz)		(Branscomb & Rittschof, 1984)
Jasus edwardsii	southern rock lobster	Larva	No effects on larva hatching and morphology	Airgun	>185 dB re 1 µPa^2.s	(Day et al., 2016)
Jasus edwardsii	southern rock lobster	Adult	**Physiology (stress)** Suppressed total haemocyte count 120 days post-exposure, but biochemical haematological homeostasis resilient to seismic signals after 365days Chronic impairment of nutritional condition	Air-gun seismic signals/ controlled field experiments	(2000-40000 cu.in.) 185 dB re 1 µPa^2.s at 20 m range	(Fitzgibbon et al., 2017)
Nephrops norvegicus	Norway lobster	Adult	**Physiology** Tissue biochemistry effects due to perturbations in the delivery of oxygen to tissues **Behaviour** Reduced maximum depth of sediment particle redistribution reduced burying and bioirrigation	Continuous Broadband Noise (CBN) and Impulsive Broadband Noise (IBN)	135-150 dB re 1 µPa	(Solan et al., 2016)
Nephrops norvegicus	Norway lobster	Adult	No effects on catch or size	Air-gun seismic operations	210 dB re to µPa/m.	(La Bella et al., 1996)
Homarus americanus	American lobster	Adult	**Behaviour** Increase in food intake **Physiology** Change in serum biochemistry **Mortality** No effect on delayed mortality No effects on catch	Airgun sounds	227 dB re 1 µPa (peak–peak) @ 1 m] at 144-169 dB re 1 µPa^2/Hz average peak energy density 187 re 1 µPa^2/Hz	(Payne et al., 2008)

(Continued)

TABLE 6 Continued

Crustaceans						
Species	**Common name**	**Stage**	**Sound effects**	**Sound source**	**Levels**	**Reference**
			No damage to equilibrium sensory systems **Physiology** Sub-lethal physical changes in serum biochemistry and hepatopancreatic cells **Behaviour** changes in feeding level	Airgun exposure on aquarium	[202 dB re 1 μPa] at 144-169 dB re 1 μPa^2/Hz	
			No effects	Vessel noise	< 1kHz	
			Physiology Increase haemolymph glucose	Mid-frequency sonar	1-s 1.67 kHz /2.5 to 4.0 kHz 1-s	
Palinurus elephas	European spiny lobster	Adult	**Physiology (stress)** Total haemocyte count (THC), henoloxidase (PO) activity in cell-free haemolymph activity decreased significantly, total protein and Hsp27 expression increased significantly	Ships noise (tank experiments)	Power spectrum peaks up to 120 dB below 10 kHz	(Celi et al., 2015)
Palinurus elephas	European spiny lobster	Adult	**Behaviour** Increased locomotion **Physiology** Increased levels of haemolymph stress bio indicators (glucose, total protein, heat-shock proteins (HP 70), and total haemocyte count)	Ship noise (tank experiment)	Power spectrum peaks up to 120 dB below 10 kHz	(Filiciotto et al., 2014)
Carcinus maenas	shore crab	Adult	**Physiology (stress)** Size-dependent response as oxygen consumption (higher metabolic rate and potentially greater stress) **Behaviour** Effects on feeding Behaviour (remaining immobile). Slower to retreat to shelter. Faster righting reflex	Ship noise playback	148–155 dB re 1 μPa Rms	(Wale et al., 2013a) (Wale et al., 2013b)
Carcinus maenas	shore crab	Adult	Reduced food aggregation in crabs and released competition for shrimp	Playback of a broadband artificial sound	129.5 to 142.0 dB re 1 μPa depending on the location	(Hubert et al., 2018)
Coenobita clypeatus	Caribbean hermit crab	Adult	**Behaviour** Delayed response to predator risk	Boat motor playback	98.1 dB SPL re 1 μPa at 1 m range	(Chan et al., 2010)
Pagurus bernhardus	common hermit crab	Adult	**Behaviour** Faster shell selection (critical for reproduction and survival)	Anthropogenic noise/ playback experiments	165 dB re 1 μPa	(Walsh et al., 2017)
Cancer magister	dungeness crab	Larva	**Mortality** For immediate and long-term survival and time to molting, the field experiment revealed no statistically significant effects	Air guns (controlled field experiments)	Mean sound pressure 231 dB re 1 μPa cumulative energy density up to 251 J/M^2	(Pearson et al., 1994)
Chionoecetes opilio	snow crab	Adult	**Catch rates** No change in catch (limited statistical power)	Airgun seismic array	Max 155–163 dB re 1 μPa at 1m	(Morris et al., 2018)
Jasus edwardsii	rock lobster	Adult	**Behaviour** Impaired righting reflex **Damage to sensory systems** Damaged statocyst	Airgun seismic array	109–125 dB re 1 μPa	(Day et al., 2019)
Callinectes sapidus	blue crab	Adult	**Mortality** **No effects**	Underwater explosions Vessel noise	< 1kHz	(Moriyasu et al., 2004)
Callinectes sapidus	blue crab	Adult	**Behaviour** Changes competitive behaviour	Mid-frequency sonar	1-s 1.67 kHz /2.5 to 4.0 kHz 1-s	(Hudson et al., 2022)

(Continued)

TABLE 6 Continued

Crustaceans						
Species	Common name	Stage	Sound effects	Sound source	Levels	Reference
			Physiology Increase haemolymph glucose			
Chionoecetes opilio	snow crab	Adult	**Physiology** No significant acute effects upon adult snow crabs (haemolymph, hepatopancreas, heart, and statocysts)	Seismic airgun	[broadband received levels 197–220 dB re 1 µPa (zero-peak)]	(Christian et al., 2003)
		Larva	Slower developmental rates and higher mortality or abnormality rates in larvae of crabs	Seismic airgun	[224–227 dB re 1 µPa (zero-peak) @ 1 m]. peak sound levels of 216 dB re 1 µPa every 10 s for 33 min	
Chionoecetes opilio	snow crab	Adult	**Physiology** Bruised hepatopancreas and ovaries on adult crabs resultant larvae of exposed eggs were smaller than controls	Seismic survey		(Christian et al., 2004)
Austrohelice crassa	tunnelling mud crab	Larva	**Physiology** Delayed due to interference with natural sound associated with mudflats which has been shown to mediate crab metamorphosis	Wind and tidal	125–245 dB re 1 µPa, up to 10 kHz	(Stanley et al., 2012)
Hemigrapsus crenulatus	hairy-handed crab or papaka huruhuru	Larva	**Physiology** Delayed due to interference with natural sound associated with mudflats which has been shown to mediate crab metamorphosis	Wind and tidal	125–245 dB re 1 µPa, up to 10 kHz	(Pine et al., 2012) (Pine et al., 2016)
Hemigrapsus sexdentatus *Cyclograpsus lavaux* *Macrophthalmus hirtipes* *Grapsidae*	hairy-handed crab smooth shore crab stalk-eyed mud crab	Larva	Reductions between 34–60% metamorphosis time	Exposure to underwater reef noise		(Stanley et al., 2010)
Amphibalanus amphitrite	Acorn barnacle	Larva	**Behaviour** Fails on primary settlement **Physiology** Delays in metamorphosis up to nearly 2 weeks	Exposure to low frequency noise	30 Hz but no specified level	(Branscomb & Rittschof, 1984)
Amphibalanus amphitrite	Acorn barnacle	Larva	**Behaviour** significantly reduced cyprid settlement	Exposure to ultrasound (antifouling treatment)	(ultrasound - continuous sound at 23 kHz) - discontinuous sound: 5 min at 20-25 kHz/20 min pause).	(Guo et al., 2012)
Amphibalanus Amphitrite *Elminius sp.*	Acorn barnacle	Larva	**Behaviour** significantly reduced fixation rates above 260 Hz	Exposure to low frequency sounds (fouling study)	70-445Hz	(Choi et al., 2013)
Carcinus maenas	Shore crab	Adult	**Behaviour** increase in activity and antennae beats (males higher activity than females) **Physiology** No effects on oxygen consumption	Geophones supported on a softly sprung frame to induce a seabed vibration	20 Hz	(Aimon et al., 2021)
Lepeophtheirus salmonis	Sea lice	Adult Larva (copepodids, chalimus and pre-adults)	**Damage to sensory systems** Damaged sensory setae of the first antenna Damaged cells involved in frontal filament production Damaged nervous system	Continuous acoustic signals (SEL at a level that induces sufficient lesions in the sensory organs to disrupt vital functions)	**Laboratory experiments**: Discrete frequencies 100Hz - 1kHz **Field experiments**: continuous exposure to individual 350 Hz and 500 Hz signals) during, respectively, a	(Solé et al., 2021b)

(Continued)

TABLE 6 Continued

Crustaceans						
Species	Common name	Stage	Sound effects	Sound source	Levels	Reference
					cumulative cycle of 2 h and 1 h, played back every 4 h	
Homarus gammarus	European lobster	Adult (young-of-year)	**Behaviour** Increased exploring time and decreased hiding time	"noise eggs"	low-frequency multi-tone ~ 100 Hz	(Leiva et al., 2021)
Nephrops norvegicus	Norway lobster	Larva/ Juvenile	**Mortality** Larval mortality, antagonistic to cadmium toxicity. **Physiology** Delays in larval development **Behaviour** differences in swimming behaviour juvenile stage.	combination of pile driving playbacks and cadmium combined synergistically at concentrations >9.62 µg [Cd] L^{-1}	170 dBpk-pk re 1 µPa	(Stenton et al., 2022)
Corophium volutator		Adult	**Behaviour** lower bioturbation rates and shallower luminophore burial depths	"noise eggs"	low-frequency multi-tone ~ 100 Hz – 200 Hz	(Wang et al., 2022)
Callinectes sapidus	Blue crab	Adult	**Behaviour** No impact on olfactory-mediated foraging No cross-modal effects	Natural sounds of predators and soundscape	Atlantic croaker (*Micropogonias undulates)* and red drum (*Sciaenops ocellatus)* and marine background sounds	(Solé et al., 2023)
			Behaviour No impact on olfactory-mediated foraging No cross-modal effects **Physiology** Righting reflex Damaged sensory statocyst epithelia No damaged antennule or eye sensory epithelia	Sinusoidal wave sweep	171 dB of 1 µPa^2 ; max 180 dB of 1 µPa^2	

maenas subjected to boat noise were more likely to suspend their search for food, although their ability to find food was not affected (Wale et al., 2013a). Crabs subjected to boat noise took longer to find refuge than when subjected to ambient noise (Wale et al., 2013a). Increased respiration, decreasing escape responses and reduction on foraging activity in the presence of sound from its predatory species suggests that crustaceans use sound as a sensory cue for the presence of fish (Regnault and Lagardere, 1983; Hughes et al., 2014). *Nephrops norvegicus* showed a reduced activity, bury less deeply and flush their burrows less regularly under impulsive anthropogenic noise (Solan et al., 2016). Anthropogenic noise can modify foraging interactions, reducing food aggregation in crabs (*C. maenas*) and thereby release competition for shrimps (*C. crangon*) (Hubert et al., 2018).

Variables related to locomotion such as distance travelled, linear and angular velocity, or single events such alarm responses, intraspecific aggressive encounters and sheltering behaviour were found in crustacean species exposed to underwater noise (Celi et al., 2013; Filiciotto et al., 2014; De Vincenzi et al., 2015). Lobsters and common prawn exposed to boat noises modified their locomotor activities (distance moved, velocity, proximity with conspecific) when exposed to ship noise (Filiciotto et al., 2014; Filiciotto et al., 2016). Roberts et al. showed modification on the hermit crab (*Pagurus bernardus*) antennae movement under sound exposure (Roberts et al., 2016). Righting reflex (time to right itself) of the rock lobster (*Jasus edwardsii*) was delayed after exposure to airguns (Day et al., 2016). Shrimp *Procrambarus clarkii* showed decreased agonistic behaviour under frequencies between 100 and 25,000 Hz (Celi et al., 2013).

Behavioural effects on movement of snow crabs (*Chionoecetes opilio*) after 2D seismic noise exposure, analysed by positioning telemetry, were similar to natural vibrations, and smaller than the responses of crabs to handling, temperature and time of day (Morris et al., 2020a). Habituation to vibrations in crabs has been shown and crabs maintained in captivity for short periods of time presented greatest sensitivity to particle motion (Roberts et al., 2016).

Hermit crabs (*Pagurus bernhardus* show interaction of ship noise exposure with predator presence reaction, shell size and the mean duration *to* accept or reject the optimal empty shell (Tidau and Briffa, 2019b). Ship noise, but not loud natural ambient noise, causes adverse effects on the shore crabs (*C.maenas*) capacity to change the carapace colour to improve camouflage and predator escape responses (Carter et al., 2019). Bioturbation may affect intra and inter-specific behaviour on lobster (*Nephrops* norvegicus) and after exposure to continuous and impulsive low-frequency noise (Solan et al., 2016).

3.2.3 Physiological effects

A few studies conducted on marine **bivalves** exposed to sound have highlighted its effects on physiological and molecular

TABLE 7 Relevant studies on noise impact on Gastropods, Bryozoa, Echinoderms, Cnidarians, Tunicates and zooplankton.

Other taxa							
Species	Taxa	Common name	Stage	Sound effects	Sound source	Levels	Reference
Stylocheilus striatus	Gastropod	sea hare	Larva	**Impaired development** Reduced embryos development Increased larva mortality	Boat noise playback (field experiment)		(Nedelec et al., 2014)
Bolinus brandaris	Gastropod	purple dye murex	Adult	**Behaviour** Reduction of Motility No mortality	Air-gun seismic operations	210 dB re 1 µPa/m.	(La Bella et al., 1996)
Bembicium nanum	Gastropod	striped-mouth conniwink	Larva	**Behaviour** Increased swimming activity	Natural and anthropogenic sound (laboratory conditions)		(Stocks et al., 2012)
Pomacea maculata	Gastropod	apple snail	Adult	**Damage to sensory systems** Cellular damage to the statocysts	Sinusoidal wave sweep	157 dB re 1 µPa (peak levels up to 175 dB re 1 µPa	(Solé et al., 2021a)
Ciona intestinalis	Tunicate	sea squirt	Larva	**Physiology** Increase rate of settlement, metamorphosis and survival	Vessel generator noise (biofouling study)	127.5-140.6 dB re 1 µ Pa	(McDonald et al., 2014)
Zooplankton (copepods, Cladocera, krill)	Multiple taxa		Larva/ Adult	**Mortality** Increase in dead zooplankton All immature krill (shrimp-like zooplankton) killed	Airgun	156 dB re 1 µ Pa2 s−1 sound exposure levels and 183 dB re 1 µ Pa peak-to-peak	(McCauley et al., 2017)
Zooplankton (*Calanus* sp.)	Multiple taxa		Larva/ Adult	**Mortality** Increase in dead zooplankton	Airgun	1363 kPa, yielding SEL 221 dB re 1 mPa2 s, and 25 kPa yielding SEL 183 dB re 1 mPa2 s	(Fields et al., 2019)
Bugula neritina	Bryozoan	brown bryozoan	Larva	**Behaviour** Decrease swim activities	Boat noise (laboratory conditions)		(Stocks et al., 2012)
Amphiura filiformis	Echinoderm	brittle star	Adult	**Physiology** Tissue biochemistry effects due to perturbations in the delivery of oxygen to tissues **Behaviour** Reduced maximum depth of sediment particle redistribution	Continuous Broadband Noise (CBN) and Impulsive Broadband Noise (IBN)	135-150 dB re 1 µPa	(Solan et al., 2016)
Heliocidaris erythrogramma	Echinoderm	Australian sea urchin		**Behaviour** No differences on swimming behaviour	Natural and anthropogenic sound (laboratory conditions)		(Stocks et al., 2012)
Arbacia lixula	Echinoderm	Black sea urchin	Adult	**Physiology** Changes in enzyme activity, expression of the HSP70 gene and protein	Laboratory condition, linear chirp 100-200 kHz	145-160 dB re 1 µPa rms	(Vazzana et al., 2020b)
Cotylorhiza tuberculate	Cnidarian	fried egg jellyfish	Adult	**Damage to sensory systems** Extruded or missing hair cells Bent, flaccid or missing kinocilia	Sinusoidal wave sweeps	157 dB re 1 µPa (peak levels up to 175 dB re 1 µPa	(Solé et al., 2016)
Rhizostoma pulmo	Cnidarian	barrel jellyfish	Adult	**Damage to sensory systems** Extruded or missing hair cells Bent, flaccid or missing kinocilia	Sinusoidal wave sweeps	157 dB re 1 µPa (peak levels up to 175 dB re 1 µPa	(Solé et al., 2016)
Styela plicata	Ascidian	pleated sea squirt	Adult	**Behaviour** increased the frequency and longevity of siphon closure events	3 separate stimuli: boat motor, song recording, water current to simulate turbulence.		(White et al., 2021)
Arenicola marina	Polychaete	lugworm sandworm	Adult	**Behaviour** Increased shallower particle burial depths	"noise eggs"	low-frequency multi-tone ~ 100 Hz – 200 Hz	(Wang et al., 2022)

mechanisms. Increased sound intensity result in an alteration in metabolism related genes (Peng et al., 2016) or increases in the levels of biochemical stress parameters measured in their plasma and tissues (La Bella et al., 1996; Vazzana et al., 2016; Vazzana et al., 2020a). The long-term capability of scallops to maintain homeostasis was reduced after airgun exposure (Day et al., 2016).

Among **cephalopods**, analysis of statocyst endolymph of the Mediterranean common cuttlefish (*Sepia officinalis*) showed changes in the protein content immediately and 24 h after sound exposure (Solé et al., 2019). The affected proteins were mostly related to stress and cytoskeletal structure. Hemocyanin isoforms, tubulin alpha chain and intermediate filament protein were down-regulated after exposure.

Among **crustaceans** sub-lethal physiological changes (serum biochemistry and hepatopancreatic cells) were observed in American lobsters (*H. americanus*) after one month of sound exposure (Payne et al., 2007). Permanent high-level exposure to sound caused a significant reduction in the rate of growth and reproduction, an increase in the level of aggressiveness (cannibalism) and the mortality rate, and a reduction in feed intake of shrimp *Crangon crangon* (Lagardère, 1982; Regnault and Lagardere, 1983). Reduced growth and reproductive rates are known tertiary effects of stress response (Barton, 2002). Some crustaceans show alterations on respiration (increase on metabolic rate) in high ambient noise conditions (Regnault and Lagardere, 1983; Wale et al., 2013b). European spiny lobsters are affected by noise in both cellular and biochemical parameters. Filiciotto et al. (Filiciotto et al., 2016) found in laboratory experiments that the common prawn *Palaemon serratus* exhibits stress responses to playback of boat noise. In particular, noise exposure produced alterations in total protein concentrations in the haemolymph and brain, in DNA integrity, in the expression protein levels of HSP 27 and 70 in brain tissues.

Respiratory responses to noise exposure are often species-specific with some animals, such as the shore crab *Carcinus maenas* (Wale et al., 2013b), displaying an increased oxygen consumption in response to noise exposure, whilst others, such as the blue mussel *Mytilus edulis* (Wale et al., 2019) and the blood clam *Tegillarca granosa* (Shi et al., 2019), showing decreased respiration during noise exposure. Among the echinoderms, brittle stars (*Amphiura filiformis*) showed signs of physiological stress after low-frequency noise exposure (Solan et al., 2016) and in the sea urchin *Arbacia lixula* significant change was found in enzyme activity and in gene and protein expression of the HSP70 (Vazzana et al., 2020b).

3.3 Effects on populations and ecosystems

Noise exposure could have an enormous impact on the regional population structure of a species because of the induced emigration, unbalanced prey–predator relation, and the effects on larva development that leads to a reduced recruitment (Peng et al., 2015). Physical, behavioural and physiological effects may result in a reduction of the population within a given area that leads to a decline in the fisheries catch. Some studies analysed the effects of seismic noise exposure on regional catch rates (snow crabs in Canada (Christian et al., 2004) and rock lobsters and scallops in Australia (Parry and Gason, 2006; Harrington et al., 2010). A recent study found no negative effects on catch rates of snow crab (*Chionoecetes opilio*) after 3D seismic noise exposure (Morris et al., 2020b). No statistical significance was found on catch rate of different marine invertebrate groups after seismic exposure (cephalopods (La Bella et al., 1996), bivalves (Parry et al., 2002; Harrington et al., 2010), gastropods (La Bella et al., 1996; Christian et al., 2003; Parry and Gason, 2006; Boudreu et al., 2009), and stomatopods (La Bella et al., 1996).

Acoustic noise pollution can disrupt the antagonistic behaviour, the communication, the social grouping and associations (including their dominance hierarchies and mating systems) and consequently their capacity to act collectively or mate normally by altering the medium through which signals are transmitted or directly altering physiology (Fisher et al., 2021).Changes in mating behaviour and grouping behaviour are shown in crustaceans (Ruiz-Ruiz et al., 2020; Tidau and Briffa, 2019a) demonstrating noise-induced changes in social interaction. Population level could be compromise due to changes in predator avoidance behaviours, if sound exposure induces behavioural changes in prey (i.e. recessing reflex, or decreasing the time of shell selection (Walsh et al., 2017) and consequently, the predation rates increase (Chan et al., 2010). Avoidance behaviours have a greater impact than startling responses on populations that migrate from the areas where seismic surveys are conducted. More research is needed to determine if marine invertebrates avoid other types of noise or can modify their sound characteristics (e.g. amplitude, frequency, and signal timing) in the presence of noise as in some terrestrial invertebrate species, which have shown the physical ability to adjust the frequencies of their courtship signals to avoid anthropogenic masking (Cator et al., 2009) limiting the effects on their population.

4 Gaps and perspectives: The responses to noise

This review provides the current information concerning marine invertebrate bioacoustics and effects of anthropogenic noise. This effort can assist scientists, natural resource managers, industries and policy-makers to predict potential consequences of noise exposure on marine ecosystems and may allow implementing mitigation measures and define a successful strategy for a complete marine noise risk management. On the basis of this review, we identified gaps in our current knowledge on the potential effects that noise exposure may trigger in marine invertebrates:

(1) The biological mechanisms of sound detection and production lack of descriptive data for most species.

(2) Some marine invertebrate groups are very poorly investigated (i.e., annelids and echinoderms). Expanding taxonomic sampling will provide tools to identify species that are especially vulnerable to noise, including those that play an important role in local ecosystems. Priority should be devoted to biological productivity, vulnerability and sensitivity to noise exposure in addition to legal protection aspects and commercially importance of target species.

(3) The physical and physiological variables related to stress, energy metabolism and hormones responses need to be

improved (including proteomic and metabolomics methods), especially how these changes may influence individual and population health.

(4) Sound impacts in populations, communities and ecosystems involves referring to sensory systems and auditory capabilities, social structure, life history, ecological role, and evolutionary adaptation. Gathering more information will help predicting noise responses of understudied species or species that could be presumably unaffected by noise because they survive in noisy habitats or possess lower hearing sensitivity to noise sources.

(5) There is a need to undertake and compare large-scale/long-term field and laboratory studies. Very few research studies have explored the effects of noise at large scales or over long periods of time (e.g. seasonal, yearly) due to the logistical and experimental challenges that they represent. Large-scale studies can provide interesting outputs on cumulative effects of noise exposure related to population persistence, ecological integrity, and evolutionary processes. In addition, it is necessary to increase the number of opportunities to investigate the effects of exposure to a gradient noise in contrast to the traditional research that compares quiet/noisy treatments. This would allow to determine the levels of noise at which a response is initiated and the changes in response when increasing noise levels. In laboratory studies, it is necessary to work in an acoustic environment that would be as close as possible as the invertebrate's natural environment, particularly to what concerns particle motion effects.

(6) Given the short life cycle of most invertebrates, adaptation and habituation to long-term noise exposure or a potential recovery from chronic noise exposure effects are not likely to occur but this has not been investigated.

(7) Current literature references mostly lack of detailed metrics to interpret results. A standardised protocol in future publications should always include duration, frequency range, weighting filters applied, reference pressure used, source and received levels, distance and duration of recordings, including data on the magnitude and direction of particle motion respect to the source.

(8) When performing field studies, particularly under Controlled Exposure Experiments, a previous characterisation of the local soundscapes should be provided to extract the contribution of noise exposure to potential effects.

(9) Changes in environmental factors do not usually occur independently from other stressors. Different changes can operate simultaneously and have antagonistic or synergistic effects (in addition to noise introduction, artificial light, habitat fragmentation, global warming, acidification, etc.). The interactions between these different stressors (multistressors) must be considered when describing noise effects.

(10) Dose-response data is necessary to provide regulators and decision-makers with proper information.

5 Conclusions

(1) We reported on the current scientific knowledge on marine invertebrate bioacoustics (detection and production of sound) and their responses (physical, physiological and behavioural effects) to anthropogenic noise at different life stages, population and ecosystem levels. Although the impact of noise pollution in marine invertebrates is understudied, an exhaustive and systematic revision of literature provided evidence that anthropogenic noise is detrimental not only to these species but also to the natural ecosystems they inhabit.

(2) Considering that the effects of noise can be elicited from cellular to ecosystems level, the understanding of noise impact requires an interdisciplinary expertise to embrace a holistic vision of the problem.

(3) Further research must include a detailed protocol that would ideally provide not only accurate acoustic metrics and methods, but also long-term experiments, cumulative effects, gradients of noise exposure, potential recovery from chronic noise in a variety of taxonomic groups and noise sources.

(4) Multiple stressors effects have to be considered when assessing potential impacts of noise exposure.

(5) This review represents a valuable reference to provides guidance to natural resource managers when evaluating anthropogenic noise effects and developing future operations at temporal and spatial scales that are relevant to oceanic ecosystems.

Author contributions

MS and MA wrote a first version of the manuscript that was completed and significantly improved with the expert input of all co-authors. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Glossary

GLOSSARY OF TERMS 1

Marine noise pollution: Noise produced by human activities which can potentially damage marine organisms by interfering with or masking biological relevant signals, causing physiological stress, physical damage on sensory systems or behavioural reactions

Vibration: Mechanical oscillation able to propagate in an elastic medium (air, water, etc.).

Impulsive sound: Sound of short duration and wide frequency bandwidth reaching a rapid maximum value followed by a fast decay. (e. g. explosions, military sonar, pile driving, airgun arrays, cetacean echolocation signals).

Continuous sound: Sound of a narrow frequency range that extends over long periods of time (e.g. dredging, drilling, wind turbines, tidal and wave energy devices, ships, etc.).

Sound Pressure: component of the underwater sound waves consisting on the pressure fluctuations of the local hydrostatic pressure in the medium (ISO/DIS, 2016) .

Particle motion: component of the underwater sound waves consisting on the back-and-forth motion of particles in the medium (ISO/DIS, 2016)

GLOSSARY OF TERMS 2

Statocyst: Invertebrates internal sensory receptor that act as an equilibrium and sound/vibration perceptor system.

Hydrodynamic receptor systems: Invertebrate epidermal sensory systems located all over external body surface that are used to detect movement and vibration.

Lateral line system: sensory organ (analogous to fish lateral line) used to detect movement and vibration in some invertebrate larvae. Usually they are ciliated cell lines running over the head and arms.

Chordotonal organs: proprioceptive organs associated with flexible articulations on the crustacean appendages that monitor joint movement, direction of movement, static position and sound perception.

Stridulation: Mechanism of sound-production where the vibrations are produced by rubbing two rigid structures against each other.

Dose–response: Relationship between the sound exposure level and the magnitude of the response.

Physical effects: damage produced after noise exposure consisting in barotraumatic ruptures, massive internal injuries, statocyst sensory cell ultrastructural damages, epidermal sensory cells and neurons that can lead to death.

Behavioural effects: changes produced in the species normal behaviour after noise exposure related to reproduction and survival, increased aggressiveness, alarm responses or predator defence.

Physiological effects: changes in physiological parameters after noise exposure. Stress bioindicators such as hormones, immune responses, heat shock proteins, cardiac physiology and metabolic rate are main physiological responses to noise exposure.

Cortisol (stress hormone): corticosteroid hormone or glucocorticoid involved in response to stress after sound exposure.

Masking: Situation where a biological signal occurs at the same time as noise, leading to an increase of the threshold for detection by the receiver.

Mitigation: Procedure to reduce harmful effects, in this case from exposure to underwater sound.