



Review

Anthropogenic underwater noise: A review on physiological and molecular responses of marine biota

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ABSTRACT

The detrimental effects of anthropogenic underwater noise on marine organisms have garnered significant attention among scientists. This review delves into the research concerning the repercussions of underwater noise on marine species, with specific emphasis on the physiological and molecular responses of marine biota. This review investigates the sensory mechanisms, hearing sensitivity, and reaction thresholds of diverse marine organisms, shedding light on their susceptibility to underwater noise disturbances. The physiological and molecular effects of anthropogenic underwater noise on marine biota include oxidative stress, energy homeostasis, metabolism, immune function, and respiration. Additionally, changes in the gene expression profile associated with oxidative stress, metabolism, and immunological response are among the responses reported for marine biota. These effects pose a threat to animal fitness and potentially affect their survival as individuals and populations.

1. Introduction

Adverse effects of anthropogenic underwater noise on the marine environment have raised increasing interest among scientists since the latter part of the 20th century (Terhune, 1975; Malme et al., 1983, 1986). Over the past few decades, however, there have been increasing concerns on man-made underwater noise, especially of shipping and leisure boats that increased the ocean ambient noise in some regions by 12 dB re 1 μ Pa (Andrew et al., 2002; McDonald et al., 2006; Frisk, 2012). The underwater acoustic soundscape consists of natural and anthropogenic sounds (Dekeling et al., 2014; Verfuß et al., 2015), and all anthropogenic sounds are not necessarily harmful to aquatic species (Harding and Cousins, 2022). Underwater sounds refer to pressure fluctuations in water that have or do not have a distinguishable source, whereas underwater noise is often defined as a subset of sound that has the potential to cause negative impacts on marine life (Hildebrand, 2009).

Reid et al. (2019) classified man-made underwater noise among the “Emerging threats and persistent conservation challenges for freshwater biodiversity”. Underwater sound vibration can be emitted by various anthropogenic activities such as trawling, dredging, military exercises, oil and gas exploration (pre-construction surveys, construction and extraction phases), commercial shipping, recreational boats, windfarms

preconstruction (seismic survey), construction (pile driving) and post-construction (sounds emitted by operational turbines and maintenance vessels) (Carroll et al., 2017; Roberts and Elliott, 2017; Popper et al., 2022). Most aquatic vertebrates and many invertebrates use sound as their main communication tool. Animals use sound vibrations to learn more about their environment, predators, prey, potential mates, and competitors. Therefore, anything that interferes with the animal's ability to detect sounds, cues, or signals, potentially affects their survival as individuals and populations. Anthropogenic noise might mask biologically important cues or signals which might cause detrimental consequences such as the inability to find shelter or the right migratory route, finding food (prey), or even detecting a predator (Slabbekoorn et al., 2018). Marine mammals have highly developed hearing mechanisms with ears that have adapted to hearing in underwater environments (Verfuß et al., 2015). Seals can perceive and interpret sounds that are critical for survival, as it aids in navigation, communication, and prey detect.

Behavioural disturbance to bottlenose dolphins has been reported at distances up to tens of kilometres from underwater pile-driving for wind turbines (Bailey et al., 2010). Harbour porpoises may be affected by pile-driving noise from 10 to 15 km away (Tougaard et al., 2003, 2005). Research has shown that harbour porpoises (*P. phocoena*) have a remarkable ability to detect and discriminate sounds, especially in the

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higher frequency range, which is well-suited for their coastal habitat. They rely on echolocation, emitting clicks and listening to the echoes to perceive their surroundings. (Tougaard et al., 2015). Their well-adapted hearing capabilities contribute significantly to their ecological niche and overall survival in their marine habitats (Mooney et al., 2012). Similarly, fishes and crustacean larvae hear sounds and orient themselves toward reef sound settlement cues at a range of kilometres rather than hundreds of metres (Montgomery et al., 2006; Vermeij et al., 2010). Fish could vocalise together, forming a chorus and can follow circadian rhythm rising to as much as 20 dB above the background noise without the chorus (Zhang and Katsnelson, 2021). Sound is also important for crustaceans. For example, the ambient underwater sounds play a major role in influencing the spatial patterns of settlement behaviour for the larvae of several crab species that navigate and swim toward ambient underwater sound originating from coastal settlement habitats (Stanley et al., 2010, 2011).

There is extensive and emerging research highlighting the harmful effects of man-made noise on marine biota. These effects range from immediate death due to overexposure to extremely intense sounds to permanent or temporary injury. Exposure to intense sound can produce acute changes in hearing sensitivity that recover over time i.e. temporary threshold shifts (TTS), or a loss that does not recover to pre-exposure levels i.e. permanent noise-induced threshold shifts (PTS) (Ryan et al., 2016). Anthropogenic noise also causes behavioural changes that interrupt animal activities or displace them from their natural habitats (Kight and Swaddle, 2011). In addition to the behavioural responses caused by man-made underwater noise, various species also showed physiological or biochemistry-related changes associated with oxidative stress, metabolism, and immune response (Wale et al., 2019). Auditory and behavioural effects of underwater noise have been thoroughly covered by previous studies (Hawkins and Popper, 2017; Thomsen et al., 2021). However, effects of underwater noise on transcriptome and associated biological markers in marine biota have received less attention.

The purpose of this study is to review the existing literature and scientific studies on anthropogenic underwater noise and its physiological and molecular impacts on marine species. More specifically, the review aims to identify sensory mechanisms, hearing sensitivity, reaction thresholds, as well as physiological and genetic responses of various marine and brackish water organisms to improve the knowledge base for adverse biological effects of underwater noise.

2. Acoustic sensory mechanisms of aquatic species

2.1. Molluscs

Cephalopods can sense water-borne vibrations (both linear and rotational motion). Cephalopods contain ciliated sensory cells that resemble mechanoreceptors have been found in epidermal lines on the head and arms of squids (Packard et al., 1990). They also contain more sophisticated particle motion detection organ, the statocyst (Zhang et al., 2015). Those organs contain dense calcareous statoliths and are thus suitable for the detection of linear accelerations, particularly gravity with a sensitivity to vibrations within the range 10–200 Hz (Packard et al., 1990). Both particle motion and pressure components are involved with sound waves in air and water phases. In general, aquatic invertebrates and fish detect sound using particle motion, whereas sound pressure is detected by mammals and fish species that have a swim bladder connected to the inner ear (e.g. Nedelec et al., 2016). In suitable conditions, it is possible to calculate particle motion from sound pressure data. Most underwater noise campaigns, e.g. the Marine Strategy Framework Directive MSFD-based underwater noise monitoring in the Baltic Sea, rely on use of sound-pressure-detecting hydrophones.

In bivalve molluscs, a highly sensitive mechanosensory receptor called the abdominal sense organ (ASO) was shown to have a role in

directional sensitivity to water-borne vibrations at the upper threshold of 140 Hz (Zhadan, 2005). Clams and mussels sense vibrations through sensory systems of mechanoreceptors and chemoreceptors in the mantle, collar, and foot and also within the anterior byssus retractor muscle of blue mussels (*Mytilus edulis*) (Olivo, 1970; LaCourse, 1977). *M. edulis* responded to sinusoidal vibratory signals in the frequency range of 5 to 410 Hz with valve closure used as the behavioural indicator of reception and response (Roberts et al., 2015). Furthermore, *Mytilus* spp. mussels have been found to respond to underwater noise exposure of approximately 141 to 143 dB re 1 μ Pa at 200 and 350 Hz by altering their valve gape behaviour (Hubert et al., 2022).

2.2. Crustaceans

Crustaceans are unlikely to detect the pressure of sound since they are not equipped with air-filled cavities and compressible tissue, which are required to detect pressure in water. However, they are responsive to particle motion. Decapods have three types of hydrodynamic and acoustic receptors i.e., specialised sensory hairs on the body surface, mechanoreceptors sensing the deformation of the antennal flagella, and internal statocyst receptor systems (Bush and Laverack, 1982). Behavioural thresholds in crustaceans in response to vibrations were reported to have a range of 0.04–0.81 $\text{m}\cdot\text{s}^{-1}$ in the range of 30–400 Hz (Roberts and Elliott, 2017). Crayfish (*Astacidea*) have different receptor systems and show the highest sensitivity at frequencies below 150 Hz (Breithaupt and Tautz, 1990). Norway Lobster (*Nephrops Norvegicus*) were found to be displacement sensitive rather than pressure sensitive with a response threshold of 0.888 $\mu\text{m}\cdot\text{s}^{-1}$ which was independent of frequency within the range 20–200 Hz (Goodall et al., 1990). Heinisch and Wiese (1987) also reported that the sensitivity of the Brown shrimp (*Crangon crangon*) to the vibration of water, sand, and the buried animal itself is maximal at 170 Hz when the amplitude of particle displacement in the surrounding sand and water was 0.7 μm . This close relationship between mechanosensory pathways in crayfish and shrimp makes shrimp useful research model for behavioural tests on the sensory capacities of crustaceans.

2.3. Fish

In terms of auditory mechanisms, fishes can be roughly divided into species that either have or do not have a swim bladder (Wiernicki et al., 2020). Fishes without a swim bladder, or which have a swim bladder that is not connected to the inner ear, can mainly sense acoustic pressure through particle motion at frequencies approximately up to 200 Hz (Blaxter, 1981; Karlsen et al., 2004). On the other hand, fishes with gas-filled cavities and a swim bladder connected to the inner ear can detect variations in sound pressure and are also more sensitive to higher frequencies (Ramcharitar et al., 2006). Additionally, fish that possess a swim bladder can detect the pressure of sound through pressure-to-motion conversion via the air-filled cavity of the swim bladder (Campbell et al., 2019). Therefore, studies into the effects of man-made noise on aquatic animals should investigate both 1) particle motion measurements and 2) how and to what degree the animals detect and respond (Popper et al., 2022).

Atlantic herring (*Clupea harengus*) is an important fish species in the open sea waters of the northern Baltic Sea, due to its importance in Baltic sea's food web functioning, importance as source of food for predatory fish (Ojaveer et al., 2010) and main catch of commercial fishing (National Resources Institute Finland). Shallower and less saline coastal and archipelago areas offer favourable conditions to a wider range of fishes, such as cyprinids, perch (*Perca fluviatilis*), pikeperch (*Perca fluviatilis*), and more recently also three-spined sticklebacks (*Gasterosteus aculeatus*) (Olin et al., 2022). Atlantic herring (*C. harengus*) has a swim bladder that extends to the head and is directly connected to the inner ear (Blaxter, 1981). Hearing sensitivity of Atlantic herring has been measured by Enger (1967), and these measurements indicate that sounds of

approximately 80 dB re 1 μ Pa are audible to herring at frequencies up to 1200 Hz, whereas hearing sensitivity of *C. harengus* decreases steeply in 3000–4000 Hz and higher frequencies (Enger, 1967; HELCOM, 2019). Mann et al. (2007) conducted experiments with ninespine sticklebacks (*Pungitius pungitius*) that belong to the same family as their three-spined relatives (three-spined stickleback, *G. aculeatus*) and measured their hearing sensitivity. The auditory system was most sensitive at 100–200 Hz (approximately 90 to 100 dB re 1 μ Pa) and decreased at 400 Hz and above to >113 dB re 1 μ Pa. The audiogram of pike (*Esox lucius*) was relatively similar to ninespine sticklebacks (*P. pungitius*) in terms of frequencies and magnitude thresholds.

2.4. Mammals

The exterior ear structures of seals have been reduced to small apertures to ensure that sound is not distorted in water. Internally, their middle ear has an involuted tympanic bone, which improves sound transmission and sensitivity. Seals have a well-developed cochlea, the sensory organ responsible for turning sound vibrations into nerve signals, suggesting they possess sensitive hearing ability (Kastelein et al., 2012). Research on seals' hearing has revealed insights into their frequency range detection, sound localization, and communication capacities. Ringed seals (*Pusa hispida*) have hearing capacities comparable to spotted seals (*Phoca largha*) and harbour seals (*Phoca vitulina*), and are significantly better than previously reported for harp seals (*Pagophilus groenlandicus*). In water, the best sensitivity was 49 dB re 1 μ Pa (12.8 kHz), while in air, the best sensitivity was 12 dB re 20 μ Pa (4.5 kHz), rivalling the sensitive hearing capacities of some wholly aquatic and terrestrial animals in their respective environments. Studies have shown that critical ratios range from 14 dB at 0.1 kHz to 31 dB at 25.6 kHz (Sills et al., 2015), indicating that ringed seals, like other true seals, can extract signals from background noise over a wide frequency range.

Cetacea lack external pinnae, but vestigial pinnal rings can be observed imbedded in the subcutaneous fat around the external meatus in some individuals (Ketten, 1992). The harbour porpoise (*Phocoena phocoena*) possesses highly developed auditory systems that enable them to navigate, communicate, and locate prey in the underwater environment. Their hearing range spans from approximately 200 Hz to 180 kHz and sound exposure levels for pure tones that produce TTS are very stable at about 100 dB re 1 μ Pa over the hearing threshold (Kastelein et al., 2002). Sound pressure thresholds for avoidance reflexes are in the 40–50 dB re 1 μ Pa range which is above the hearing threshold (Tougaard et al., 2015). Bottlenose dolphin (*Tursiops truncatus*) minimal intensity discrimination was 1 dB, whereas frequency discrimination between 1 and 140 kHz; best values are found between 5 and 60 kHz (Au and Simmons, 2007). *T. truncatus* also produces sonar signals in its nasal system for echolocation to perceive object features (Harley et al., 2003). Most dolphins typically emit whistle signals and brief broadband and echolocation clicks with a sound pressure level ranges between 210 and 225 db (Au, 2000). Beluga whales (*Delphinapterus leucas*) have sophisticated hearing and echolocation abilities. Studies revealed a broad range of sensitive hearing from 22 to 110 kHz, with minimum detection levels near 50 dB. Overall detection ranges were discovered to be between 4 and 150 kHz (Castellote et al., 2014).

3. Physiological and molecular effects of anthropogenic noise on marine animals

3.1. Gene expression changes and DNA integrity

Anthropogenic noise has created a significant threat that affects the transcriptomes of aquatic species. For instance, in intertidal molluscs (a sea slug, *Onchidium reevesii*), acute low-frequency noise caused dysregulation in genes associated with cytokine receptor interaction, the Forkhead box O (FoxO) signalling pathway, natural killer cell-mediated cytotoxicity, apoptosis, and immune-related pathways. The

differentially expressed genes were also associated with energy metabolic pathways such as glycolysis, the tricarboxylic acid (TCA) cycle, and glycerophospholipid metabolism, as well as neurological pathways such as gamma-aminobutyric acid (GABA)ergic synapses, and the synaptic vesicle cycle (Tu et al., 2021). FoxO that was down regulated in noise-induced sea slugs, is a growth factor and stress-regulated transcription factor (Dos Santos et al., 2020). Its down-regulation will inhibit vital physiological processes such as apoptosis, cell proliferation, DNA repair, and resistance to oxidative stress (Farhan et al., 2017). Up-regulation of immune related-pathways (NF- κ B pathway and the MAPK pathway) under the stress of low-frequency noise will increase the inflammation and immune response (Sun and Andersson, 2002; Rao, 2001). TCA cycle, glucose metabolism and lipid metabolic pathways were significantly down-regulated, indicating that low-frequency noise have induced metabolic and oxidative stress, and inflammation that may also cause damage to the CNS in sea slug (Williams and O'Neill, 2018; Tu et al., 2021). Oxidative stress was also reported to alter key neurological pathways (Butterfield and Boyd-Kimball, 2018), this would explain the down-regulation of 4 neurologically related pathways such as gamma-GABAergic synapses, and the synaptic vesicle cycle in low-frequency noise induced sea slugs.

Similarly, acute noise exposure of 140 dB re 1 μ Pa caused significant transcriptomic changes related to metabolism, reproduction, and social behaviour in the hypothalamus of the African cichlid fish (*Astatotilapia burtoni*) (Butler and Maruska, 2021). The transcriptome of the head of the noise-exposed larvae had 66 differentially expressed genes that are involved in immune function or inflammatory responses, growth and development of muscles, connective tissues, bone, and the nervous system (Butler and Maruska, 2021). More importantly, the authors reported the up-regulation of galanin and ghrelin, neuropeptide Y receptors (NPYR), and the down-regulation of leptin receptor, cocaine and amphetamine-related transcript (CART), prolactin and vasotocin. Galanin, ghrelin, and NPYR are orexigenic neuropeptides that stimulate food intake whereas CART and leptin receptors are anorexigenic factors (Volkoff et al., 2005). Prolactin and vasotocin are the hormones of paternity and play a significant role in maternal care (Schradin and Anzenberger, 1999; Schulte and Summers, 2017). This would explain the cannibalism and decreased parental care observed in noise-exposed groups.

Furthermore, Peng et al. (2016) reported that anthropogenic underwater noise caused significant changes in the gene expression profile of razor clam (*Sinonovacula constricta*). The expression of genes involved in the glycolysis pathway, fatty acid biosynthesis, tryptophan metabolism and TCA cycle was significantly decreased in clams exposed to ~100 dB re 1 μ Pa of sound compared to controls showing lower metabolic activity. On the other hand, the mRNA expression of these genes was significantly higher with more active feeding behaviour when the clams were exposed to more natural ambient sound levels (~80 dB re 1 μ Pa). Also, the mRNA expression of hepatic antioxidant-related genes in response to simulated sounds from windfarms was investigated in black porgy fish (*Acanthopagrus schlegelii*) (Chang et al., 2018). The authors reported that the reactive oxygen species (ROS) levels increased, and the gene expression of superoxide dismutase (SOD) remained unchanged, however, the mRNA levels of glutathione peroxidase (GPx) and catalase (CAT) were up-regulated and down-regulated, respectively. ROS are generated in the biological systems and play an important role in a variety of physiological and pathological processes and signalling cascades including immune, thyroid, and cognitive functions and in modulation of nutrient sensors and ageing (Niess et al., 1999; Brieger et al., 2012). GPx is a key antioxidant enzyme in the glutathione redox cycle, and CAT, a scavenger of ROS (H₂O₂), efficiently decomposes H₂O₂ to water and O₂ (Zhao et al., 2019). Chronic ROS production might deplete and saturate the hepatic antioxidant system which can increase the risk of cancer, infectious diseases, chronic inflammation, and diseases including cardiovascular and neurological disorders (Brieger et al., 2012).

Table 1

List of the differentially expressed genes in various marine species in response to underwater noise, the canonical pathways associated with their direction of activation, and the sound level tested.

Gene	Change in Activation	Canonical pathway/ Function	Species	Intensity of the sound (re 1 μ Pa)	Reference
-PFK	Down-regulated	Glycolysis pathway	Razor clam	~100 dB	(Peng et al., 2016)
-PK	Down-regulated		(<i>Sinonovacula constricta</i>)		
-Prolactin	Down-regulated	Maternal care behaviours	African cichlid fish	~140 dB	(Butler and Maruska, 2021)
-Vasotocin	Down-regulated		(<i>Astatotilapia burtoni</i>)		
-AChAC	Down-regulated	Fatty acid biosynthesis	Razor clam (<i>S. constricta</i>)	~100 dB	(Peng et al., 2016)
- Afmid	Down-regulated	Tryptophan metabolism	Razor clam (<i>S. constricta</i>)	~100 dB	(Peng et al., 2016)
-CS	Down-regulated	Tricarboxylic acid (Krebs) cycle	Razor clam (<i>S. constricta</i>)/	~100 dB/ Co-exposure of Cd	(Peng et al., 2016, Charifi et al., 2018)
-NAD+	Down-regulated		Pacific oyster	and 150 dB	
-NADP+	Down-regulated		(<i>Magallana gigas</i>)		
-OGDC	Down-regulated				
-DHPST E2	Down-regulated				
-DHPST E3	Down-regulated				
-IDH3a	Down-regulated				
-MDH	Up-regulated				
-mfp-1	Down-regulated	Mussel byssal threads	Thick-shell mussels	~70 dB	(Zhao et al., 2021)
-mfp-2	Down-regulated		(<i>M. coruscus</i>)	or	
-mfp-3	Down-regulated			~100 dB	
-mfp-6	Down-regulated				
-preCOL-P	Down-regulated	Stiffness and extensibility property	Thick-shell mussels (<i>M.</i>)	~70 dB	(Zhao et al., 2021)
-preCOL-NG	Down-regulated			or	
-preCOL-D	Down-regulated			~100 dB	
-CAT	Down-regulated	Hepatic antioxidant system (oxidative stress response)	Black Porgy	138 dB/	(Chang et al., 2018, Charifi et al., 2018)
-GPx	Up-regulated		(<i>Acanthopagrus schlegelii</i>)/	Co-exposure of Cd and 150 dB	
-SOD	Up-regulated		Pacific oyster		
			(<i>Magallana gigas</i>)		
-AChE	Down-regulated	Neurotransmitter modulatory enzymes	Bood clam	Co-exposure of Cd and 100 dB	(Shi et al., 2019)
-AChR	Down-regulated		(<i>Tegillarca granosa</i>)		
-MAO	Down-regulated				
-Clec 1	Down-regulated	Lectin synthesis (growth/metabolism)	Pacific oyster (<i>M. gigas</i>)	Co-exposure of Cd and 150 dB	(Charifi et al., 2018)
-CS	Down-regulated	ATP synthesis	Blood clam (<i>T. granosa</i>)	Co-exposure of Cd and 100 dB	(Shi et al., 2019)
-SucA	Down-regulated				
-DLD	Down-regulated				
-Galanin	Up-regulated	Satiety, regulate energy balance	African cichlid fish	~140 dB	(Butler and Maruska, 2021)
-Ghrelin	Up-regulated		(<i>A. burtoni</i>)		
-NPYR	Down-regulated				
-LR	Down-regulated				

2-oxoglutarate dehydrogenase (SucA), 6-phosphofructokinase (PFK), Acetylcholine esterase (AChE), -Acetyl-CoA Carboxylase (AChAC), Acetylcholine receptor (AChR), Arylformamidase (Afmid), Catalase (CAT), Citrate synthase (CS), C-type lectin domain family 1 (clec1), Dihydroliipoamide dehydrogenase (DLD), Dihydroliipoamide succinyltransferase (DHPST), Glutathione peroxidase (GPx), Isocitrate dehydrogenase [NAD] subunit alpha, mitochondrial (IDH3a) Leptin receptor (LR), Monoamine oxidase (MAO), Mussel foot proteins (mpf), Nicotinamide adenine dinucleotide (NAD+), Nicotinamide adenine dinucleotide phosphate (NADP+), Neuropeptide Y receptor (NPYR), Oxoglutarate dehydrogenase (OGDC), Precursor collagen protein (2odelli-P), Pyruvate kinase (PK), Superoxide dismutase (SOD).

Protein expression was also characterized in Mediterranean mussels (*Mytilus galloprovincialis*) exposed to noise (150 dB rms re 1 μ Pa, 30 mins) (Vazzana et al., 2016). Densitometric analysis revealed a significant increase in the expression of Hsp70 protein in the gills of mussels treated with low-frequency noise. Hsp70 are cellular response proteins and were shown to be induced by a wide variety of stressors such as heat, xenobiotics, heavy metals, free radicals, and UV light (Mukhopadhyay et al., 2003). Hamer et al. (2004) investigated the levels of Hsp70 in the gills of *M. galloprovincialis* and discussed their usefulness as biomarkers of environmental pollution (Hamer et al., 2004). Moreover, 10 days playbacks of pile driving noise of 70 or 100 dB re 1 μ Pa significantly down-regulated mRNA levels of genes encoding structural proteins of byssal threads, including four mussel foot proteins (mfp-1, mfp-2, mfp-3, and mfp-6) and three precursor collagen proteins (preCOL-P, preCOL-NG, and preCOL-D) leading into weakened byssal attachment (Zhao et al., 2021). Strong byssal attachment is vital for mussel survival, movement, self-defense, reproduction and their ecological functions (Bandara et al., 2013; Carrington, 2002; Zhao et al., 2021).

Interestingly, ship noise playback (150–155 dB re 1 μ Pa) affected the DNA integrity (six-fold higher DNA single-strand breaks in haemocytes and gill epithelial cells) and oxidative stress (significant increase in thiobarbituric acid reactive substances in gill cells) of blue mussel (*M. edulis*) (Wale et al., 2019). Marine bivalves such as brown mussels (*Perna perna*) that were under a series of environmental adverse conditions

showed increased levels of ROS that increased lipid peroxidation, DNA strand breaks, and DNA oxidative damage (De Almeida et al., 2007). ROS excess generation contributes to oxidative stress that is one of the key toxicity mechanisms of environmental stress on aquatic organisms that in turn attributes to DNA damage (Zhang et al., 2020; Alarifi et al., 2013). DNA damage may activate both membrane death receptors and the endogenous mitochondrial damage pathway leading to cell death via apoptosis (Kaina, 2003). The full list of the genes differentially expressed in various marine species exposed to different levels of sound intensity is shown in Table 1.

3.2. Anthropogenic underwater noise aggravated cadmium toxicity

Anthropogenic underwater noise aggravated Cadmium (Cd) mutagenicity, neurotoxicity and its adverse impacts on metabolic processes, representing a previously unrecognised significant risk of heavily contaminated and busy coastal areas. Interestingly, 10 days of anthropogenic noise and Cd had synergistic effects on feeding activity, metabolism, and ATP synthesis in blood clam (*T. granosa*) (Shi et al., 2019). The author reported that both the noise and Cd augmented ammonia excretion rate, but on the other hand, significantly decreased the ATP content, 6-phosphofructokinase, pyruvate kinase, and AChE activity, and the clearance, respiration, and O:N ratio rate. Furthermore, the author also reported that the co-exposure of Cd and playback noise (100

dB) in blood clam (*T. granosa*) significantly down-regulated genes involved in neurotransmitter modulatory enzymes such as monoamine oxygenase, acetylcholinesterase, acetylcholine receptor and down-regulated genes in ATP synthesis such as citrate synthase, Dihydrolipoamide dehydrogenase, and 2-oxoglutarate dehydrogenase. This reduced metabolism caused by anthropogenic underwater noise, is an adaptive mechanism adopted by marine organisms in response to different environmental stressors (Pörtner, 2012). Similarly, the co-exposure of noise playback of cargo ship noise and Cd in the gills caused modification of expression genes such as C-Type Lectin-Like Receptor-1 (*cllec1*), isocitrate dehydrogenase 3 (*idh3a*), malate dehydrogenase (*mdh*), *sod2*, *cat*, metallothionein 2 (*mt2*), and acetyl-coenzyme A carboxylase (*acac*) that are associated with oxidative stress, a lower feeding activity, a decrease of fatty acid synthesis, lipogenesis, and lectin synthesis (Charifi et al., 2018). SOD and CAT up-regulation is a clear indication of oxidative stress as mentioned earlier. The *cllec1* gene, that was remarkably up-regulated; is a sensor of cell damage and a regulator of immune response (Thebault et al., 2009; Drouin et al., 2022). The *mt2* gene activation, which is a hallmark of Cd contamination, was also significantly up-regulated in the presence of cargo ship noise and Cd. The *acac* gene was significantly down-regulated in noise + Cd exposure compared to only Cd exposure that was up-regulated. The *acac* gene is key player in fatty acid metabolism and its down-regulation can cause a cascade of events in the etiology of the metabolic syndrome. Fatty acids are a vital energy source and important elements of membrane lipids, and they serve as cellular signalling molecules (Wakil and Abu-Elheiga, 2009). The effects of the anthropogenic sound (pile driving sound playbacks) and waterborne cadmium were reported in Norway lobster, (*N. norvegicus*) with clear dose-dependent interaction between cadmium and pile-driving playbacks (Stenton et al., 2022). Larval mortality increased synergistically with the combination of pile driving playbacks (170 dB re 1 μ Pa) and cadmium at concentrations $>9.62 \mu\text{g}[\text{Cd}] \text{L}^{-1}$. Furthermore, the authors reported that the coexposure treatments compared to Cd only treatment showed significant delays in larval development and significant differences in the swimming behaviour of the first juvenile stage. Biomarker analysis revealed significant increase in GPx, Glutathione (GSH), SOD, CAT and Thiobarbituric acid reactive substances (TBARS). GSH and GPx play significant role in the degradation of reactive oxygen and nitrogen species (Jefferies et al., 2003). TBARS is a biomarker of lipid peroxidation (Fraga et al., 1988), and its increase indicates that Cd and noise coexposure aggravated free radicals production causing lipid peroxidation and activating antioxidant defense system (i.e., GPx, SOD, and CAT).

3.3. Changes in physiology and biomarkers

Anthropogenic noise induced physiological changes affecting mechanisms underlying individual activity or processes such as oxidative stress, energy homeostasis, metabolism, immune function, and respiration in various marine species. Physiological changes were reported in sessile invertebrates such as bivalves and ascidians. Blue mussels (*M. edulis*) exposed to ship noise playback (150–155 dB re 1 μ Pa) showed 12 % reduced oxygen consumption, a 60 % increase in valve gape, and an 84 % reduced filtration rate (Wale et al., 2019). Also, the exposure to sound vibration within the ranges off 5 to 410 Hz caused a closure of the valves (Roberts et al., 2015). This behaviour is undoubtedly costly, in terms of energy, respiratory and heart rate disruption, and impaired excretion ability. Nonetheless, blue mussels showed habituation to repeated sound exposures, where the response strength decayed with repeated exposure. Ascidians such as *Styela plicata* have shown increased frequency and longevity of syphon closure in response to anthropogenic stimuli (White et al., 2021). Underwater noise (~ 80 dB re 1 μ Pa and ~ 100 dB re 1 μ Pa) exerted significant effects on the activity of $\text{Ca}^{2+}/\text{Mg}^{2+}$ -ATPase and the atomic ratio of oxygen to nitrogen (O:N) in clams (Peng et al., 2016). The increased the activity of $\text{Ca}^{2+}/\text{Mg}^{2+}$ -ATPase, and Ca^{2+} transport pump play key role in muscle

contraction, hence enabling active movement (Mandel et al., 1982; Chiesi and Wen, 1983; Haynes, 1983). When thick shell mussels (*M. coruscus*) were exposed to playbacks of (70 or 100 dB re 1 μ Pa) pile driving noise for 10 days, the secretion of byssal threads (e.g., diameter and volume) was reduced and their mechanical performance (e.g., strength, extensibility, breaking stress, toughness, and failure location) were weakened, leading to decrease in mussel byssal attachment strength (Zhao et al., 2021). Playbacks of recordings of ship noise led to faster yolk consumption despite also reducing growth rates and body width-length ratios in larval Atlantic cod (*Gadus morhua*) (Nedelec et al., 2015).

Anthropogenic noise could also affect the reproductive fitness in of marine species. For instance, mouthbrooding African cichlid fish (*Astatotilapia burtoni*) exposed to a 3 h period of playback noise (~ 140 dB re 1 μ Pa) cannibalised or pre-maturely released their brood and the surviving juveniles showed startle response, changes in swimming behaviour, and delayed onset of adult-typical colouration and behaviours (Butler and Maruska, 2021). The effects of anthropogenic noise on reproductive fitness were also seen in crustaceans, such as the brown shrimp (*Crangon crangon*) larvae. Low frequency (25 to 400 Hz) noise with a sound level of 30 dB re 1 μ Pa not only resulted in a significant reduction in growth, food uptake and reproduction rates, but also increased cannibalism and mortality rate of the shrimp (Lagardère, 1982).

Moreover, Buscaino et al. (2010) reported significant changes in haematological responses (increase in lactate and haematocrit levels and decrease of glucose) in European sea bass (*D. labrax*) and gilthead sea bream (*S. aurata*) in response to playback sounds mainly produced by ships. The authors also reported that when fish were exposed to noise, a linear correlation was found between blood parameters and motility (Buscaino et al., 2010). Lactate increase is an indicator of physical stress response since lactate is utilised by most vertebrates and its production increases during vigorous exercise when the demand for ATP and oxygen exceeds supply (Rabinowitz and Enerbäck, 2020). In fish, lactate is retained intramuscularly, and it is used for in situ glycogen replenishment (Gleeson, 1996). Interestingly, cortisol levels were reported to significantly increase in goldfish (*C. auratus*) when exposed to 160–170 dB re 1 μ Pa for 10 mins (Smith et al., 2004) or in carp (*Cyprinus carpio*), the gudgeon (*Gobio gobio*), and European perch (*P. fluviatilis*) when exposed to ship playback (153 dB re 1 μ Pa) for 30 min (Wysocki et al., 2006). Cortisol is a metabolic hormone, important regulator of obesity and inflammation and allostatic load biomarker of chronic stress (Lee et al., 2015). Similarly, Chang et al. (2018) reported that the long-term (2 weeks) physiological effects of simulated windfarms noise (138 dB re 1 μ Pa / 125.4 Hz; near the turbine) on black porgies (*Acanthopagrus schlegelii*) caused a significant increase in cortisol and ROS in these fish. Santulli et al. (1999) also evaluated the effects of seismic surveys by an air gun (low frequencies >100 Hz) on the biochemical markers in European sea bass (*D. labrax*) planted in different cages 5000 m apart. The authors reported that the cortisol serum levels increased as well in muscle and liver in which glucose, lactate, cortisol, and Cyclic-AMP serum levels significantly increased, alternatively, AMP, ADP and ATP serum levels significantly decreased. Cyclic-AMP plays a significant role in metabolism, heart function, reproduction, growth, hormone secretion and muscle relaxation in vertebrates. Likewise, c-AMP signalling plays a vital role in “catch response”, glucose metabolism, induction of spawning, regulation of mantle and syphon movement and cardiac contraction in bivalves (for reviews, see Fabbri and Capuzzo, 2010). These stress conditions created for instance by pile driving, have forced blue mussels (*M. edulis*) to increase the clearance rate and move from a physiological maintenance state to active metabolism (Spiga et al., 2016).

Vazzana et al. (2016, 2020) reported changes in haematological parameters in Mediterranean mussels (*M. galloprovincialis*) exposed to 30 min (Vazzana et al., 2016) or 3 h (Vazzana et al., 2020) of noise at very high frequency (100–200 kHz)

with a sound pressure level range between 145 and 160 dB re 1 Pa. The author demonstrated that the total haemocyte (THC) levels increased, nevertheless, glucose levels, cytotoxic activity, alkaline phosphatase (ALP), esterase, and peroxidase activity were significantly lower in noise-exposed mussels. However, glucose levels, osmolarity values, THC, and AchE activity in the mantle and the gills were significantly higher in the animals treated with low-frequency bands (Vazzana et al., 2016). Similarly, 30 min sound exposure of low-frequency vessel noise and mid-frequency sonar augmented haemolymph glucose signals of blue crabs (*Callinectes sapidus*) and American lobsters (*Homarus americanus*) for seven days (Hudson et al., 2022). Haemocytes of invertebrates play a key role in immunity, especially in immobilising or destroying invasive microorganisms, and the dramatic drop in THC may increase the risk of infection and even death (Söderhäll et al., 2003). Cytotoxic activity is one of the hallmarks of immune response and it is considered a marker of mussel health status (Malagoli and Ottaviani, 2005). Bivalve molluscs serve as bioindicators, especially for metal and organic contaminant pollution, and the decrease in glucose levels is among the main stress responses under hypoxic conditions (Rajalekshmi and Mohandas, 1993; Satyapameshwar et al., 2006). Alkaline phosphatase and esterase have been proposed as good biomarkers in ecotoxicology in response to chemical pollutants. Peroxidase is an antioxidant enzyme that provides efficient protection against oxidative damage and free radicals and its activity increased significantly in copper-exposed mussels (Regoli and Principato, 1995).

Turja et al. (2014) assessed the impact of chronic exposure to anthropogenic environmental pollutants in caged blue mussels (*Mytilus trossulus*) in the Baltic Sea. The author suggested a multi-biomarker approach such as the immune, enzymatic, biomarker, geno- and cytotoxicity responses, lysosomal membrane stability and heart rate recovery to be implemented as a tool to diagnose the anthropogenic stressors (Turja et al., 2014), an approach that can be also adopted to study the physiological effects of anthropogenic underwater noise on marine animals.

4. Conclusions

This review identifies sensory mechanisms, hearing sensitivity and reaction thresholds of various marine organisms shedding light on their susceptibility to underwater noise disturbances. It also summarizes the transcriptomic and physiological changes in marine biota in response to anthropogenic underwater noise. The responses include changes in the gene expression profile in genes related to oxidative stress, metabolism, and immune response which is something that is also seen in the biomarker analysis. Physiological responses include oxidative stress, glucose levels, and haematological, metabolic, and neurological responses. Anthropogenic underwater noise synergistically increased the toxicity of Cadmium and its adverse impacts on metabolic processes, providing new insight into the significant risk of heavily contaminated and busy coastal areas.

Future research efforts concerning underwater noise exposure studies should focus on testing the impacts of underwater noise at relatively low frequencies (approximately up to 1000–2000 Hz), as sound pressure at these frequencies affects various species groups in the sea. One must keep in mind that the survival rate of animals in controlled laboratory conditions and fixed sound exposures does not necessarily reflect the natural environment. Many of the laboratory sound exposure experiments reported behavioural and physiological responses where the animal needed time to recover, and the food was easily accessible. This recovery time is usually not obtainable in the wild where the risk of predation and the competition for food is high which drastically lowers the fitness of the animal in the wild. Finally, there is an urgent need to expand underwater acoustic monitoring tools to examine recovery rates of marine species and to complement the current methodologies for assessing the status of ecosystems disturbed by anthropogenic noise.

CRedit authorship contribution statement

Rami El-Dairi: Writing – review & editing, Writing – original draft, Visualization. **Okko Outinen:** Writing – original draft. **Harri Kankaanpää:** Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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