

1 Managing Aquaculture Noise: Impacts on Fish Hearing, Welfare, and Mitigation Strategies

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30 Abstract

31 As intensive aquaculture continues to develop, substantial investments have been made in
32 equipment to sustain high-density farming. However, this has resulted in elevated noise levels
33 within these aquaculture environments, particularly below 2000 Hz, matching the hearing range
34 of most cultured species. Fish under noise conditions may experience hearing loss and
35 physiological stress, which can negatively affect their growth, foraging efficiency, reproductive
36 success, and increase their susceptibility to diseases. These adverse effects compromise the
37 welfare of farmed fish, potentially decreasing production quality and increasing mortality rates.
38 Despite these notable effects, the understanding and management of noise conditions in
39 aquaculture systems lag behind other environmental parameters in terms of recognition and
40 control.

41 In this review, we cover the fundamentals of fish auditory systems, the hearing range of key
42 farmed fish species, and the most common noise sources and levels prevalent in current
43 intensive aquaculture systems. Additionally, we examine recent discoveries on the effects of
44 anthropogenic noise on fish hearing, physiological responses and behavior. Finally, we provide
45 strategies for noise monitoring and management in aquaculture industry, while also highlighting
46 open questions for future research. Our goal is to assist researchers and practitioners in
47 comprehending underwater noise and its effects on cultured organisms, providing a valuable
48 resource for promoting healthy and sustainable development of intensive aquaculture.

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50 **Keywords:** Fish welfare, Aquaculture, Underwater noise, Auditory sensitivity, Noise control

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1. Introduction

The United Nations predicts that by the year 2100, the global population will reach at least 11 billion. Therefore, any industry capable of producing sustainable food will need to expand and become more efficient than ever to meet the growing human demand for food and nutrients ¹. The Food and Agriculture Organization of the United Nations (FAO) reported that in 2020, the total production of both fisheries and aquaculture sectors reached a record of 185 million tons, with per capita consumption standing at 20.7 kg (excluding algae), more than double the consumption rate of 9.9 kg per capita observed 50 years ago ¹. Currently, nearly 90% of wild caught species are facing overfishing, and the global capture from marine fisheries is no longer sufficient to meet demand growth sustainably ^{2,3}. FAO reports that in 2022, the total amount of aquaculture in the world exceeded the production of capture fisheries for the first time. Populations will increasingly depend on aquatic products from aquaculture, which continues to grow at a rate of 7.8% annually, surpassing pork, dairy, beef, and cereals. This highlights the importance of aquaculture in enhancing the resilience of the global food system ⁴. In the face of pressing challenges such as rapid population growth, resource constraints, eutrophication and climate change, aquaculture must adapt to foster healthy, diverse, and highly productive practices ^{5,6}. In recent times, various aquaculture models have rapidly emerged, with intensive aquaculture farms demonstrating extensive potential owing to their controlled environment, enhanced efficiency, and reduced energy consumption. Intensive aquaculture requires advanced instrumentation and management techniques to achieve high-density cultivation, substantial product yields, and significant economic benefits. Currently, notable methods within this category include the recirculating aquaculture systems (RAS), deep-sea cage system, and in-pond raceway systems (IPRS). However, the aquaculture industry still faces considerable challenges related to spatial constraints, fish diseases, food safety, environmental pollution, and consumer acceptance ⁷⁻⁹. To achieve sustainable production and cope with the growing consumer demand, it is crucial to prioritize animal welfare and ethical aquaculture practices ¹⁰. In intensive aquaculture systems, such as RAS models, several potential stressors related to water quality and noise conditions are difficult to manage due to the pursuit of high

yields. These stressors are often exacerbated in high-density farming, as fish have limited space to escape from their impact within the tank, resulting in compromised fish welfare and affecting economic profitability¹¹. While current studies on stressors in intensive aquaculture systems primarily focus on parameters like culture density, lighting, and water quality, there is comparatively less attention given to noise conditions.

In intensive aquaculture, equipment like pumps, aerators, and filtration systems are necessary to maintain high-density aquaculture environments, inevitably generating low frequency underwater noise¹²⁻²². Most fish and invertebrates, including those used in aquaculture industry, show best hearing sensitivity and sound production with this frequency range²³⁻²⁵.

Extended exposure to elevated noise levels imposes a persistent burden on organisms. This ultimately results in the deterioration of various bodily functions, compromising growth and even survival^{14,25-27}. Multiple studies have demonstrated that long-term exposure to anthropogenic noise can impact fish hearing, physiological responses, growth, reproduction, and behavior²⁸⁻³².

Notably, close to the noise source, where noise levels are highest, a variety of significant and permanent effects can occur simultaneously. In contrast, at greater distances from the noise source, fewer physiological impacts are observed, and no permanent damage is detected (Figure 1). Understanding such negative consequences from chronic noise exposure and how they impact fish well-being at the species level is crucial for developing effective soundscape management and noise mitigation strategies.

This review provides a comprehensive overview of the fish auditory system, including its structure and sensitivity across major cultured species. It highlights the importance of the hearing sense for these animals and discusses the audiometry methods for measuring auditory thresholds and detecting hearing impairments in future research. Besides, it also covers non-auditory effects of noise exposure, ranging from general physiological effects to behavioral changes and impact on reproduction.

Finally, this review proposes strategies for effectively regulating noise within aquaculture settings. The ultimate goal is to inform aquaculture scientists and farmers with theoretical guidance for creating more sustainable and healthier aquaculture systems for intensive farming.

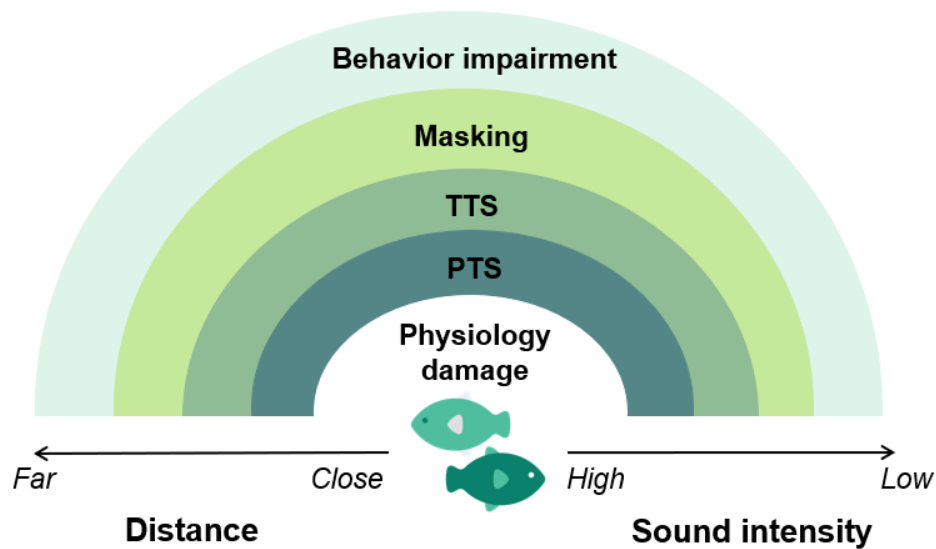


Fig.1 Multiple effects of anthropogenic noise on fishes considering their distance to the noise source. Simultaneous effects including physical damage and mortality occur closer to the noise source, whilst mild or temporary effects are typically found at greater distances. (TTS, Temporary auditory Threshold Shifts; PTS, Permanent auditory Threshold Shifts).

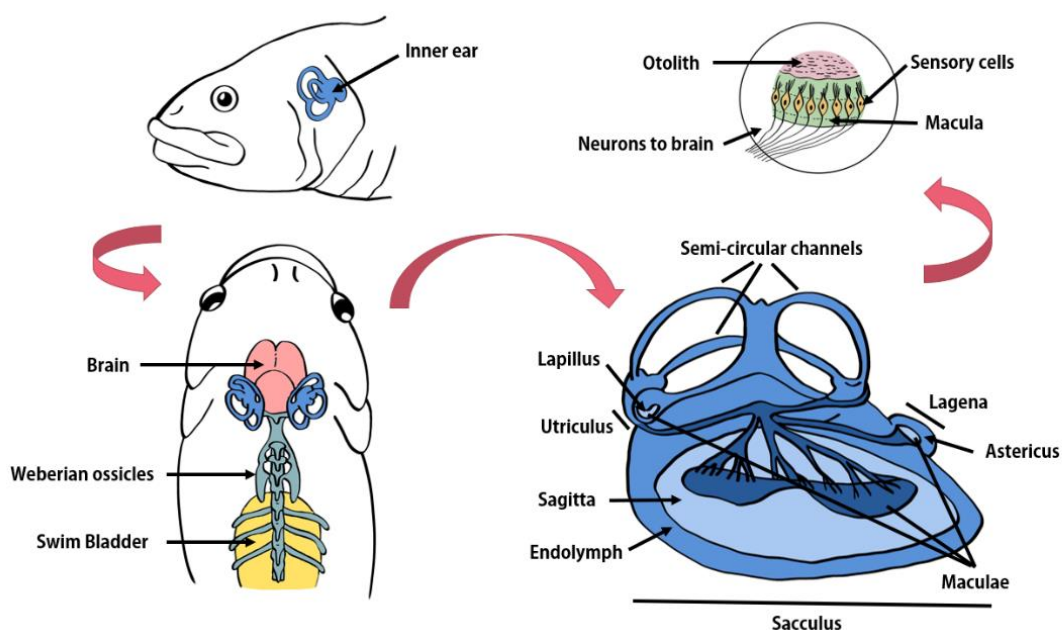
2. Fish Sensing: Detecting Sound and Vibrations

Fish species have undergone adaptive evolutionary processes to develop a wide range of sensory structures specifically for detecting underwater sound and vibrations. These specialized adaptations enable fish to effectively navigate and interact within their aquatic environment. The peripheral auditory organs of fish include the inner ears and, in some species, accessory morphological hearing structures to enhance their auditory sensitivity and expand their sensitive frequency range. Besides, most fish species possess a lateral line system for detecting vibrations and water movement, which aids in spatial orientation and playing a critical role in behaviors such as schooling.

2.1. The auditory system

Ray-finned fishes (Actinopterygii), representing over half of extant vertebrates, exhibit remarkable diversity in hearing structures and sound-producing mechanisms. These adaptations serve orientation and communication within their highly diverse and acoustically rich environments³³. Considerable variation exists in the shape and size of the inner ears across the over existing 30,000 fish species. This diversity likely results in differences in their sensitive ranges, auditory thresholds, and directional hearing³⁴.

The inner ear comprises of three perpendicular semicircular canals that respond primarily to body movement and postural changes, and three otolithic endorgans - utricle, saccule, and lagena, each containing a single dense calcium carbonate otolith^{35,36} – see Fig. 2. Each endorgan contains a sensory epithelium populated with auditory receptors called hair cells, which are covered by a gelatinous membrane and mechanically linked to the calcareous otolith. Movement of these hair cells triggers the opening of transduction channels, generating a receptor potential and stimulating afferent fibers along the axis of movement. The differential inertia between the sensory macula and the attached otolith enables these endorgans to function as biological accelerometers, encoding linear acceleration and particle motion³⁷.



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150 Fig. 2 Position and structure of the fish inner ears and their relative distance to the swimbladder
151 and connecting Weberian ossicles (left). Detail of the inner ear showing the three otolithic
152 endorgans – sacculus, utricle and lagena. Each otolithic endorgan contains a macula with
153 auditory sensory hair cells that detect acoustic stimuli through stereocilia bending caused by
154 otolith vibrations (right). Adapted from illustrations by Carlyn Iverson and Antoni Lombarte.

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156 At the top of each sensory hair cell, there is a bundle of cilia, and the arrangement of cilia is
157 related to the polarization of each hair cells. When the stereocilia bend towards the kinocilium
158 cause depolarization or excitation of the sensory cell, while bending to the opposite direction
159 causes hyperpolarization. Fish rely on these polarity-related responses to discriminate sound
160 features including directionality^{38,39}. Sensory hair cells communicate with the auditory nerve (VIII
161 cranial nerve) and information is then transmitted to the central nervous system for further
162 auditory processing³⁷.

163 Sound waves in the water environment have both a pressure and a particle motion component. A
164 sound wave propagates because particles next to a vibrating source move back and forth in the
165 same location but transmitting their oscillatory motion to their neighboring particles. The
166 particles oscillate along the direction of sound propagation and are followed by waves of
167 compression and rarefaction corresponding to increase and decrease in pressure, respectively.
168 This phenomenon is termed sound pressure. Particle motion, on the other hand, can be specified
169 in terms of particle displacement, velocity, or acceleration^{24,40}.

170 Particle oscillations in the water can either be detected directly by hair cells present along the
171 fish lateral line or by the inner ear hair cells due to the relative motion (impedance difference)
172 between the fish body and the denser otoliths³⁷.

173 Most aquatic animals, including fish and invertebrates primarily sense sound using particle
174 motion⁴¹⁻⁴⁴. However, several fish species exhibit higher auditory sensitivity and/or an extended
175 frequency bandwidth, due to accessory structures that enhance hearing by acoustically coupling
176 air-filled cavities to the inner ear, converting sound pressure into movements that can be
177 detected by otoliths⁴⁵. Examples include the Weberian apparatus in Ostariophysi, enhancing

hearing in fish like carp (*Cyprinus carpio*) and goldfish (*Carassius auratus*), and adaptations like the air-breathing organ in Anabantoidei. The inner ear's connection to the swim bladder varies, influencing hearing sensitivity. These connections can be direct or proximate, such as in Herringiformes and Stenopterygians, or absent, as in cod and salmon, resulting in lower auditory sensitivities.

2.2. The lateral line system

In addition to their auditory system, fish also possess a specialized sensory system known as the lateral line, which detects water motion and pressure gradients, and mediates capabilities such as predators and prey detection, hydrodynamic imaging and various behaviors such as rheotaxis, schooling, and courtship displays⁴⁶⁻⁵⁰. The lateral lines are linear structures running along both sides of the fish's body, comprising numerous canal neuromasts that open to the environment through multiple pores. These neuromasts, also distributed across the head, trunk, and tail fin, are sensory structures consisting of hair cell epithelia and a cupula connecting the ciliary bundles of the hair cells with the surrounding water^{51,52}.

Neuromasts exist in various configurations and integumental positions, typically categorized into superficial neuromasts, which are located on the surface of the epidermis, and canal neuromasts, situated in subdermal canals that form through invagination of the epidermis³⁷. While surface neuromasts have cupulas that extend beyond the boundary layer and move proportionally to water velocity, canal neuromasts align with the canal axis and their cupulas move in response to fluid velocity within the canal, which is determined by pressure differences between canal pores. Thus, neuromasts detect both fluid velocity and acceleration, providing the central nervous system with a three-dimensional pattern of fluid flow across the body surface^{49,53,54}.

The oscillations perceived by the lateral line receptors are in the low-frequency range, typically from 1-5 to 100-200 Hz^{51,52}. The maximum sensitivity differs between canal neuromasts, which are most sensitive at 20-30 to 100 Hz, and superficial neuromasts, which are most sensitive at 2-5 to 10-15 Hz⁵⁵. For example, In the sculpin *Cottus bairdi*, canal neuromasts are most sensitive at

50 Hz, while free neuromasts show maximum sensitivity at 10 Hz ⁵⁶. The trunk lateral line of the plainfin midshipman fish, *Porichthys notatus*, only has superficial neuromasts, which responded maximally to frequencies of 20-50 Hz ⁵⁷. The spectral sensitivity ranges of the inner ear and lateral line system partially overlap, but their peak sensitivities differ significantly. The primary distinction is that the lateral line system's receptors respond to displacement waves, whereas the inner ear's receptors respond to pressure waves. The lateral line cannot detect sound oscillations because the fish body, neuromast cupulae, and surrounding water oscillate simultaneously. However, the inner ear receptors are stimulated by the inertia of the otolith, which is nearly three times denser than the fish body ⁵¹.

2.3. Acoustic and vibrational sensitivity

The auditory capabilities of most fish species have been reported between 50 to 1000 Hz, with some species demonstrating the capacity to perceive sounds exceeding 3 kHz. Remarkably, only a very small fraction of species exhibit the ability to detect sounds above 100 kHz ⁵⁸. The hearing ranges of most well-known farming fish are detailed in Table 1.

Table 1: Auditory Sensitivity of Key Farmed Fish Species for Human Consumption and Ornamental Purposes. All data were obtained using the Auditory Evoked Potential recording technique and thresholds given in dB re 1 μ Pa, unless otherwise stated.

Order	Species	Frequency range (Hz)	Best Response Frequency (Hz)	Minimum Threshold (dB re 1 µPa)	Reference
Perciformes	Pacific bluefin tuna (<i>Thunnus orientalis</i>)	325 ~ 800	500	83	Poper et al. ⁵⁹
	Large yellow croaker (<i>Larimichthys crocea</i>)	600 ~ 800	600		Liu et al. ⁶⁰
	Red drum (<i>Sciaenops ocellatus</i>)	100 ~ 1k	400	95	Horokvskv et al. ⁶¹
	Jack mackerel (<i>Trachurus japonicus</i>)	200 ~ 800			Babaran et al. ⁶²
	Red sea bream (<i>Pagrus major</i>)	100 ~ 2k	300	80	Kojima at al. ⁶³
Cypriniformes	Silver carp (<i>Hypophthalmichthys molitrix</i>)	300 ~ 2k	750 ~ 1.5k	104.2	Lovell et al. ⁶⁴
	Bighead carp (<i>Aristichthys nobilis</i>)	300 ~ 2k	750 ~ 1.5k	105.7	
	Common carp (<i>Cyprinus carpio</i>)	100 ~ 500	100 ~ 505	70	Kojima et al. ⁶⁵
		1000 (by ECG)	100 (by ECG)	75 (by ECG)	
	Crucian carp (<i>Carassius auratus</i>)	300 ~ 1k	800	70	Wang et al. ⁶⁶
Clupeiformes	Pacific herring (<i>Clupea pallasii</i>)	200 ~ 5k			Mann et al. ⁶⁷
	Scaled Sardine (<i>Harengula jaguana</i>)	100 ~ 2k		120 – 130	
	Round sardinella (<i>Sardinella aurita</i>)	100 ~ 1k			
Salmoniformes	Chinook salmon (<i>Oncorhynchus tshawytscha</i>)	100 ~ 1k	250	105	Oxman et al. ⁶⁸
Siluriformes	Bullhead catfish (<i>Ictalurus nebulosis</i>)	100 ~ 5k	700	35 (dB below 1 dyn/cm ²)	Weiss et al. ⁶⁹

Gadiformes	Walleye pollock (<i>Theragra chalcogramma</i>)	40 ~ 450	100 ~ 200	75	Mann et al. ⁶⁹ 223
Pleuronectiformes	Olive flounder (<i>Paralichthys olivaceus</i>)	60 ~ 700	100	94.1	Xing et al. ⁷⁰ 224
Acipenseriformes	Yangtze sturgeon (<i>Acipenser dabryanus</i>)	100 ~ 500	300	133	Xiang et al. ⁷¹

For decades, researchers used to classify fish into two distinct categories based on their auditory abilities – “hearing generalists” (or “non-specialists”) and “hearing specialists”. The former group, including salmonids and tunas, typically exhibited a narrower frequency detection range or bandwidth and poor sensitivity (high auditory thresholds). On the other hand, the latter group, comprised of *Ostariophysi* and *Clupeiformes*, as well as some members of *Holocentridae* and *Sciaenidae*^{45,72}. This divergence in hearing abilities is attributed to the presence of specialized morphological structures, such as the Weber apparatus, in the latter group, that facilitate sound transmission from the swim bladder to the inner ear to increase hearing sensitivity. Nevertheless, further research on fish hearing has revealed that the aforementioned classifications fail to encompass all fish species and lack clarity and evolutionary support^{73,74}. More recently, Popper et al. proposed another strategy of using the terms specialist and non-specialist together with information on the specific structure of function that is considered a specialization⁷³.

It is equally important to understand that although we know that all fish and many invertebrates are sensitive to the particle motion components of sound⁷⁵, and only some fish can detect sound pressure, we know very little about the sensitivity of aquatic animals to the vibrations produced inside and near substrates^{76,77}. At present, research on the vibration sensitivity of aquatic animals mostly focuses on invertebrates and crustaceans, while research on fish only involves some benthic fish. Berghahn et al. investigated the vibrational sensitivity of plaice (*Pleuronectes platessa*), sole (*Solea solea*), and lemon sole (*Microstomus kitt*), exposed the fishes to between 40 and 300 Hz. The gill ventilation, eye movement and burial behavior demonstrated that the sensitivity of the fishes was greatest between 100 and 200 Hz, with sole being the most sensitive at 170Hz (10 cm s⁻² at 20–170 Hz)⁷⁸. As for invertebrates, there is evidence to suggest that mussels (*Mytilus edulis*) and hermit crabs, are sensitive to physical vibrations at frequencies of 5-410 Hz^{77,79,80}. The North Sea shrimp (*Crangon Crangon*) is sensitive to vibrations from water, sand, and buried animals themselves, reaching its maximum at 170 Hz.

2.4. Importance of the underwater Soundscape and Vibroscape

Sensory channels like vision, olfaction, and touch have limitations in aquatic environments, especially when providing rapid, long-distance, and three-dimensional information. As a result, sound becomes an exceptionally effective vehicle for transmitting information among aquatic organisms, particularly in waters with low visibility ²⁴.

Sound is crucial for the survival of marine organisms, and research has shown that aquatic acoustic signals between 50 Hz and 10 kHz play a vital role in fish communication, orientation, foraging, and defense ⁸¹. Furthermore, the auditory structures of most fish species are fully developed within a few days post-hatching, highlighting the importance of sound detection in their life history ⁸².

The aquatic soundscape can be defined as a combination of sound sources known as geophony, biophony, and anthrophony ^{83,84}. Geophony, known for its intensity and variability, includes sounds such as those generated by wind, rain, hydraulic turbulence or sediment transport with frequencies spanning up to 25 kHz ⁸⁵⁻⁸⁹. Biophony, on the other hand, is produced by a wide range of taxa, from large cetaceans producing loud, long-travelling calls and fish choruses to small invertebrates, such as snapping shrimps ^{90,91}.

Over 989 fish species spanning 175 families have been found to actively produce sounds so far ^{33,92}. Fish primarily produce sound in two ways: by vibrating their swim bladder using sonic muscles ⁹³, and by using modified pectoral fins and pectoral girdles for sound production ⁹⁴. They produce sounds for various purposes, including communication, courtship, territorial defense, and group coordination. For example, some fish produce sounds during courtship rituals to attract mates or establish dominance within their territory. These self-generated sounds can vary in frequency, duration, and intensity depending on the species and the specific behavior being exhibited ^{95,96}. Additionally, the ability to differentiate between the sounds of prey, predators, and conspecifics aids fish in finding food and avoiding threats ^{58,97,98}.

Altogether, the acoustic environment can be extremely rich in information for fish species, offering essential cues for orientation and habitat identification ⁹⁹⁻¹⁰³. For instance, coral reef fishes rely on these cues after spawning, when fertilized eggs drift away with the current.

Juveniles' survival depends on their ability to navigate back to the reef, guided by acoustic signals generated by fish and invertebrate populations ¹⁰⁴⁻¹⁰⁷. The vibrational component of aquatic environments, termed vibroscape, plays a crucial role in addition to soundscapes ⁷⁷. Growing evidence shows that vibrational signals are produced and detected by several benthic and demersal species, including salmonids and sculpins ¹⁰⁸. On the seabed, there is evidence to suggest that deep-sea shrimp use vibration to detect falling prey ¹⁰⁹, flatfish (such as *Pleuronectes platessa* and *Solea spp.*) may use vibration to detect predators ⁷⁸. Even though there is limited knowledge in this field, studies, particularly on invertebrates, suggest that vibrational stimuli induce physiological and behavioral responses. Roberts et al. exposed blue mussels (*Mytilus edulis*) and marine hermit crab (*Pagurus bernhardus*) in cages to a pile driver. The sound and vibration during the pile driving process were quantified using water-borne particle motion sensor, hydrophones, and tri-axial geophone. Animals exposed showed changes in oxygen consumption (*M. edulis*) and behavior, such as environmental sampling and anti-predator responses (both species) ⁷⁷. Vibrations may be crucial to communication and environmental sensing, providing an additional sensory channel when other modalities are less effective. The vibroscape is thus an essential part of the sensory world of fish, overlapping with the soundscape. With various anthropogenic activities altering the acoustic and vibrational features of underwater environments - crucial for fish sensory adaptation, communication, and orientation - it is vital to fully understand the stimuli fish respond to. This requires considering substrate vibration alongside sound pressure and particle motion when characterizing a sensory environment. ¹⁰⁸.

3 Noise in the aquaculture environment

The modern aquaculture industry comprises various large-scale artificial rearing systems, such as Recirculating Aquaculture Systems (RAS), Deep-sea Cage System, In-Pond Raceway System (IPRS). In contrast to natural habitats, these environments require extensive equipment, including air compressors, aerators, ventilation devices, water pumps, filtration equipment, and other

maintenance equipment, to maintain in high-density cultures. The operation of this equipment generates substantial noise within these rearing systems ^{15,110}. Consequently, it is essential to characterize the acoustic and vibrational aquaculture settings to understand the potential impact of noise as a stressor on cultured species ¹¹¹.

3.1 Noise sources in aquaculture

The impact of underwater sound in aquaculture facilities is influenced by both the species being farmed and the specific design and location of the facility. Different fish farms may have different machinery and equipment based on their production needs, influencing sound generation and propagation, and creating a unique soundscape and vibroscape for each facility. Despite its recognized importance, the acoustic features of most aquaculture environments remain insufficiently understood.

In RAS, high-frequency noise generally arises from electric equipment such as filters, oxygenators, air compressors and pumps, as well as from collapsing air bubbles. On the other hand, low-frequency noise typically originates from water currents and vibration of ground and tank walls ^{15,110}.

To increase aquaculture density, it becomes crucial to elevate dissolved oxygen levels to inhibit anaerobic bacteria and improve water quality. This requires aeration and oxygenation systems, which typically include a Roots blower, an aeration pipeline, and gas stones. The vibration and acoustic radiation of the Roots blower is commonly the main source of underwater noise in RAS ^{112,113}. Although modern systems often locate the Roots blower outside the facility or in a separate isolated room, vibrations from the blower can still propagate into the farm through the aeration pipeline. Moreover, the high-speed gas flow within the pipeline generates noise due to fluctuations in flow rate or pressure, and interactions between gas and the pipe wall ¹⁵.

Pumps are also a major source of underwater noise in aquaculture. Tanks are typically placed directly on concrete surfaces with pumps located near at the bottom and adjacent to the same concrete slab. This design allows pump noise to propagate directly through the water and from the air-water interface, while also allowing vibrations to travel through the underlying concrete slab ¹⁵.

When the blower is turned off, the primary background noise comes from the water flow and aeration process. In flow-through or RAS, continuous water flow generates considerable noise, especially when large volumes create air gaps under the inflow pipe. Gutscher et al. found that water flowing above the surface produces high-frequency noise, with external filters contributing more noise than submerged ones, suggesting that more air entering the water raises sound pressure levels (SPLs) ¹⁶. Craven et al. and Yin et al. identified that high-frequency noise (>1000 Hz) mainly comes from surface bubbles and aeration stones, with finer stones producing smaller bubbles and thus higher-frequency noise and SPLs ^{15,114}.

It is important to note that activities by facility staff, though not yet empirically proven, may significantly impact fish. Unlike the consistent noise from machinery, these sounds are usually brief, occurring during daylight hours - such as the use of specific tools or impacts on tank walls. Fish cannot anticipate these unpredictable noises, which may trigger fear or flight responses ¹¹⁵.

While RAS systems are a markedly louder environment for species otherwise held in earthen ponds, the deep-sea cage environment clearly represents the most variable and loudest aquaculture system, reaching noise levels capable of eliciting a measurable physiological response in many species and revealing a likely source of chronic stress ¹¹¹. The pronounced variability exhibited by deep-sea cage systems can be ascribed to the inherent openness of the system itself, the site-specific and external sound sources originating from the surrounding environment, as well as the aquaculture production system itself. These sources of sound encompass abiotic, biotic, and anthropogenic factors. Abiotic or physical sources encompass elements such as wind, rain, and water turbulence. Additionally, anthropogenic sources included access vessels, an associated feed barge, oxygen storage, compressed air automated feeder and a temporary handling facility linked to the site contribute to the overall soundscape. Among the more notable impacts observed, the effects stemming from vessel noise generated by service vessels or other transiting ships have been identified as particularly significant ¹¹¹.

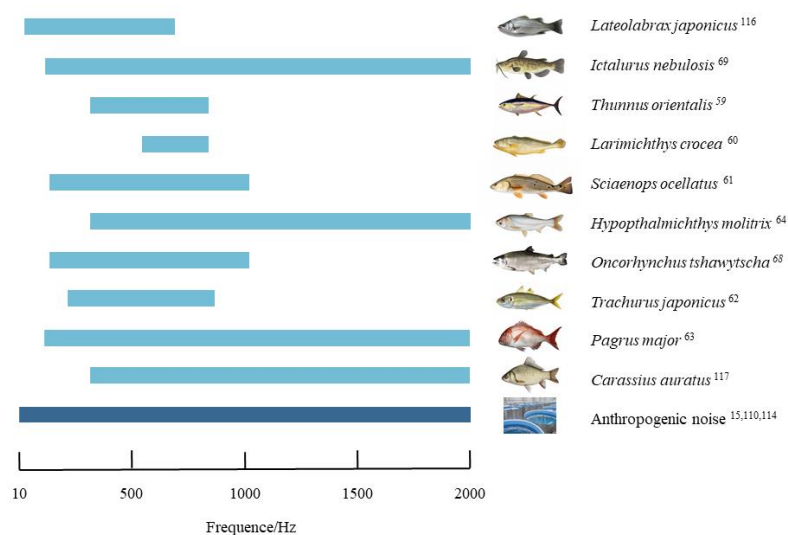
Pond aquaculture systems are characterized by the lowest noise levels among all aquaculture systems, primarily due to their limited utilization of mechanical equipment ¹¹¹. Nevertheless, in outdoor pond systems, motorized paddlewheel aerators have been identified as a significant

364 contributor to noise levels ¹¹¹.

365

366 3.2 Relevant noise frequencies and sound pressure levels

367 Researchers have conducted studies to monitor the frequency range and sound pressure levels of
368 noise generated by aquaculture systems or associated activities. In intensive aquaculture
369 systems, the average broadband sound pressure levels can vary significantly. For example, in
370 pond without aerators, the average sound pressure level is around 70 dB, while in circular
371 fiberglass tanks, it can reach up to 130 dB re 1 μ Pa ¹¹⁰. These noises exist in all aquaculture water
372 bodies, and their frequencies match the hearing sensitivity range of most aquaculture fish
373 species (10-2000Hz) (Fig. 3). The main acoustic environment of the aquaculture system is the
374 comprehensive product of the acoustic contribution of each component. By measuring the
375 acoustic properties of individual components, it is possible to separate which components
376 dominate and quantify the acoustic recognition of each component. This is important because it
377 can directly compare the acoustic characteristics of individual device components with the
378 hearing ability of fish.



379

380 Fig. 3 The auditory frequency range of major farmed fish species and the overlap with the noise
381 conditions in the farmed environment (Data based on Huang et al. ¹¹⁶; Weiss et al. ⁶⁹; Poper et al.
382 ⁵⁹; Liu et al. ⁶⁰; Horokvskv et al. ⁶¹; Lovell et al. ⁶⁴; Oxman et al. ⁶⁸; Babaran et al. ⁶²; Kojima at al. ⁶³;

Van et al.¹¹⁷; Bart et al.¹¹⁰; Craven et al.¹⁵; Yin et al.¹¹⁴).

Yin et al. conducted a study to record the aquaculture environmental noise in open fiberglass tanks, and their findings indicated that the SPLs of aquaculture environmental noise were around 87.48 – 90.65 dB. This noise was a combination of low-frequency resonance noise generated by aquaculture working equipment and the inner walls of the tanks, with the main frequency peak at 100 Hz, bubble noise from the surface water body at 1,250 Hz, and working noise from aeration stones, aerators, and air compressors at 1,600 to 2,500 Hz¹¹⁴. This result is same as Bart et al., high-frequency noise (1~2 kHz) from electric equipment such as motors, oxygenators, and air compressors, as well as low-frequency noise (25~100 Hz) from water flow, ground vibration, and pool wall vibration. Yao et al. found that the maximum SPLs corresponded to a frequency of 125 Hz at Chinese sturgeon nursery workshop, which is a low-frequency noise (≤ 200 Hz)¹¹². Low-frequency noise has the characteristics of long wavelengths, making it easy to cross obstacles, propagate over long distances, and attenuate slowly. The low-frequency noise generated by working equipment can easily propagate through the integrated pipe gutter in the breeding area to the roof, where it reflects and produces a very long reverberation. The superposition of direct and reverberant acoustic energy enhances indoor low-frequency noise, making it crucial to control low-frequency noise¹¹².

Previous research has highlighted the significant influence of structural design and distance between tanks and mechanical equipment on the SPLs of underwater noise in land-based aquaculture systems. Lara et al. conducted a study on zebrafish housing homes and found that the SPLs ranged from 122 to 143 dB, predominantly at frequencies below 1000 Hz. The SPLs were notably affected by the proximity of pumps and filters, with fish experiencing higher noise levels as these units moved closer together. Comparison of the soundscape spectral curves with the zebrafish hearing sensitivity revealed significant overlap within the zebrafish hearing range of 100 to 8000 Hz, which was 22.4 dB above the hearing threshold²¹. Barnes et al. reported an ambient noise level of 50 dB in a salmonid hatchery breeding room. When water flowed into the two mentioned rooms, the noise level increased to 73 dB¹⁸. In the tanks investigated by Craven et al., the main contributor to the peak at 187.5 Hz was the sound generated by the pumps. Aeration

sounds ranged from >7600 Hz up to 22 kHz, and the maximum sound pressure level produced by coarse air stones was 119 dB, with larger and stronger bubbles generated below 8 kHz¹⁵. Yao et al. conducted a study on the indoor and outdoor noise of a Chinese sturgeon nursery workshop. The average sound pressure level in the outdoor unit area reached 94-98 dB, and the unit noise transmitted to the outer wall of the breeding area was 77 dB. The average indoor noise in the breeding area was 83 dB¹¹².

The cleaning of rearing ponds and filtration systems has been found to significantly increase underwater noise levels. Voorhees et al. found that the noise level during the cleaning of the tank in the salmon hatchery was as high as 77dB, compared to 68dB under normal water flow conditions. Noise levels in the rearing pavilion were highest in the proximity of the power washer, reaching upwards of 83 dB²⁰. Similarly, Stone et al. found that noise SPLs could increase up to 80 dB during the cleaning of the filtration system¹¹⁸. Heise et al. monitored noise levels in the Vancouver Aquarium rearing tanks and found that the average SPLs across all frequencies were 91.9 dB (range 87.0-104.5 dB). They also discovered that the highest sustained pressure levels were observed during cleaning activities, increase of approximately 25 dB¹⁹.

In aquaculture systems, the SPLs and frequency of underwater noise vary depending on the depth. Craven et al. investigated the soundscape in RAS tank. The highest SPLs were found to be 124 dB at the bottom of the tank and 115 dB at the shallowest level. The soundscape in the tank was stratified and positively correlated with depth¹⁵. However, the effects of noise on cultured species in aquaculture systems vary considerably due to differences in their physiological ability to perceive sound, as well as their behavior. For instance, shrimp and flounder tend to stay the bottom and walls of tanks, which exposes them to different acoustic environments and may result in more significant noise effects from vibrations in the tank itself compared to upper fish⁷⁷.

Nevertheless, the correlation between water depth and noise level is not always absolute. Yin et al. and Craven et al. observed different results with the main peak of background noise at 187.5 Hz at different depths, and there was no change in the noise frequency with increasing water depth^{15,114}. The reason is that Craven used closed, covered tanks, while Yin used open tanks. The transmission and attenuation of sound in a closed body of water are significantly different from those in open conditions. In closed tanks, the SPLs of the background noise gradually decrease

from the bottom to the surface, but there is no change in the frequency of the main peak. However, in open tanks, the transmission of equipment noise from the air to the water is attenuated, and the SPLs of high-frequency noise in the surface layer are relatively high, while the low-frequency resonance of the bottom layer of equipment with the inner wall of the tank is the highest, and high-frequency noise is relatively low. An alternative explanation for the vertical stratification of sound is that the propagation of sound through the water is also affected by bubbles rising from the aeration stone, an effect similar to that of bubble curtains used to reduce the propagation of sound from pile driving ¹¹⁹.

The combination of materials and structural design of tanks indeed plays a significant role in determining the acoustic conditions within them. Terhu et al. discovered that noise levels in fiberglass tanks were, on average, 4 to 16 dB higher than those in concrete tanks ¹⁴. Bart et al. found that fiberglass tanks being noisier than concrete tanks ¹¹⁰. Craven et al. investigated an aquaculture facility with concrete rearing tanks, where mean peak spectral levels ranged from 105 to 117 dB, and the peak frequency remained at 187.5 Hz ¹⁵. Davidson et al. characterized the acoustic environment of fiberglass tanks and reported a sound pressure range of 105 to 130 dB for the highest spectral levels below 100 Hz ⁷⁷. Bart et al. discovered that SPLs reached 120 dB in concrete raceways and 130 dB in fiberglass tanks. Overall, concrete tanks were found to be the least noisy, while fiberglass tanks exhibited the highest sound pressure levels ¹¹⁰.

In a study conducted by Radford et al. showed that sound levels in cage farms were consistently higher, ranging from 107 to 112 dB, and exhibited more variability compared to RAS, while ponds were found to be the quietest ¹¹¹. In modern aquaculture, where aquatic animals may transition between different aquatic systems during their life cycle, it is important to understand how these species adapt to sudden changes in the perceived environmental sound. For example, when juveniles reared in RAS are transferred to cage, it is not yet known how they might respond to the altered soundscape. All cage cultured fish, including salmon, seabass, and snapper, are typically raised in cage after being bred in land-based tanks and RAS. However, the relatively loud sounds of RAS may cause stress in more sensitive species or early life stages. These animals may experience significant stress due to inappropriate soundscapes, which can potentially affect their health and growth rates ⁷⁷.

471 **4. Effects of environmental noise on fish in aquaculture**

472 In the natural environment, fish obtain a large amount of information by listening to the sounds
473 of their surroundings. In aquaculture environments, sustained noise may lead to shielding,
474 increased stress levels, and changes in fish behavior. Generally speaking, aquaculture noise does
475 not cause fish death, but long-term noise may reduce the growth rate, immunity, survival rate,
476 and spawning and reproduction rate of fish, ultimately affecting the welfare of aquaculture
477 animals ^{26,106,120-122}.

478 At present, people mainly use hydrophones to monitor the noise in aquaculture environments.
479 After detailed analysis of the noise, it is compared with the sensitive threshold of aquaculture
480 species. At present, the main research work on the impact of noise on fish is focused on
481 laboratory conditions. The collected aquaculture noise is replayed through underwater speakers,
482 and short-term or long-term noise exposure experiments are conducted on fish to study the
483 effects of noise on their hearing, behavior, physiology, and other aspects (Fig. 4). It should be
484 noted that the research mentioned in this review focuses on the impact of human noise on
485 rearing species, and does not pay too much attention to other wild species.

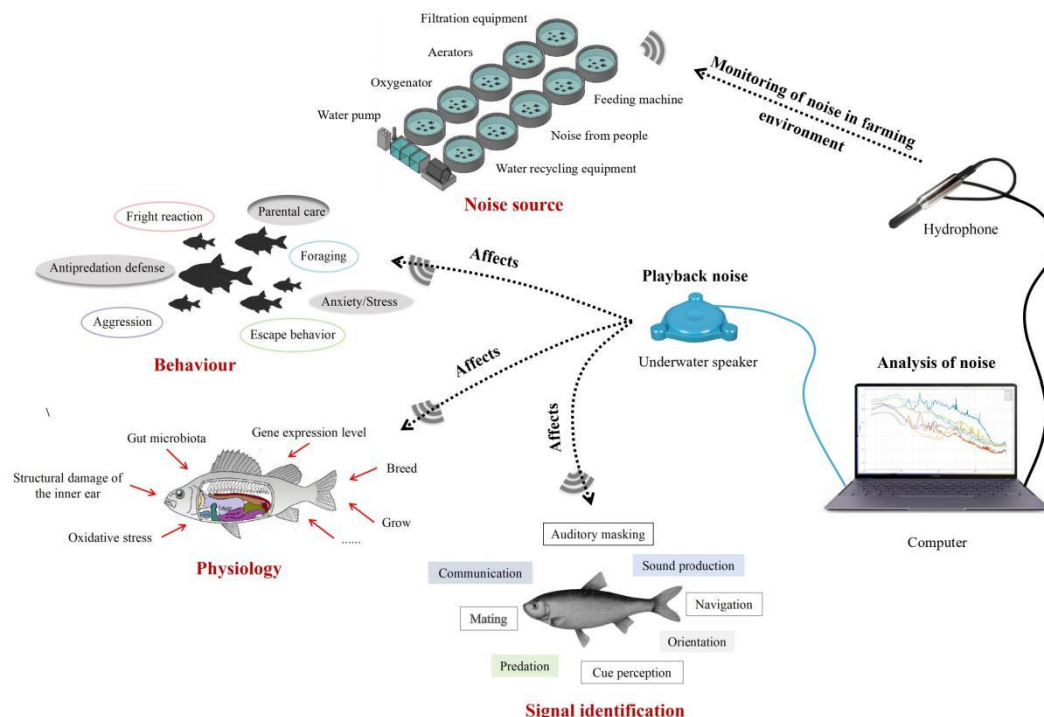


Fig. 4 Experimental method for the impact of aquaculture noise on fish. Aquaculture noise is collected by hydrophones, processed by computers, and replayed on fish, focusing on the impact of noise on fish behavior, physiology, individual recognition, and other aspects.

4.1 Effects on hearing and communication

The impact of noise on fish hearing can be categorized into two types: PTS and TTS¹²³. Fish exposed to low-intensity noise over an extended period or high-intensity noise for a brief period may encounter temporary auditory threshold displacement¹²⁴. If the hearing loss is not fully restored prior to subsequent noise stimulation, a portion of the loss may become permanent, resulting in a condition known as PTS. The PTS is irreversible and accompanies the death of auditory HCs and the loss of synaptic connections within the inner ear of fish¹²⁵⁻¹²⁷.

In current studies on the impact of noise on fish hearing, various noise sources are utilized. These include single-frequency sounds, white noise^{128,129}, and the playback of anthropogenic noise recordings¹³⁰. Oscar fish (*Astronotus ocellatus*) exposed to a continuous tone of 180 dB re 1μPa for one hour exhibited impairment in HCs function²⁸. Goldfish (*Carassius auratus*) demonstrated

susceptibility to aquarium filtered noise, with a maximum threshold change of 15 to 19 dB in hearing at 100 and 300 Hz ¹⁶. Exposed common roach (*Rutilus rutilus*) and sand goby (*Pomatoschistus minutus*) to continuous broadband noise, the TTS in common roach at 250 Hz and 1000 Hz (11.9 and 13.4 dB, respectively), while sand goby exhibited a non-significant shift of 6.6 dB at 125 Hz ¹³¹. Breitzler et al. subjected adult zebrafish to white noise at varying SPLs (130, 140, and 150 dB) for 24 hours, results indicated TTS up to 33 dB along with increased response latency. Fish exposed to 130 and 140 dB noise levels experienced restored hearing function within 7 days, whereas those exposed to 150 dB noise levels required 14 days for their auditory thresholds to return to baseline. HCs loss was only observed significantly in the 150 dB noise treatment, and sensory tissue (number of hair cell receptors) fully regenerated within 7 days ¹³². Andrew et al. assessed the auditory thresholds of silver (*Hypophthalmichthys molitrix*) and bighead (*H. nobilis*) carp before and after exposure to high-intensity (155 dB) broadband sound, revealing TTS in both species ¹³³. Caiger et al. exposed snappers to low-intensity noise of 120 dB for a duration of 2 weeks, resulting in increased auditory thresholds at 100, 200, and 400 Hz ¹³⁴. Amoser et al. subjected goldfish (*Carassius auratus*) to white noise of 158 dB, yielding a significant decrease in sensitivity of 26 dB ¹³⁵. Smith et al. raised goldfish under white noise conditions ranging from 160-170 dB. Even after a mere 10 minutes of noise exposure, goldfish exhibited significant changes in their hearing thresholds, which linearly increased to approximately 28 dB after 24 hours of continuous exposure. Subsequent noise exposure did not lead to further threshold shifts. After 21 days of noise exposure, it took goldfish 14 days to fully recover to normal hearing levels ¹³⁶. Gutscher et al. explored the repercussions of filter noise (110-114 dB) in aquaculture systems on goldfish, resulting in masking of hearing thresholds by up to 20 dB (0.1 kHz) and up to 24 dB (0.5 kHz) ¹⁶.

4.2 Masking effects on signal recognition

One potential barrier to acoustic communication is increasing levels of background noise, which reduces the ability of fish to detect important signals related to the environment and other animals ^[15,128]. Artificial noise is different from natural environmental sounds and cannot provide useful survival information for fish. The frequency of artificial noise is partially consistent with the

aquatic organism vocalizations and may disrupt their communication. When reducing the presence of other sound waves, the ability of fish to detect related sound waves is significantly affected, forcing the auditory threshold of fish to increase. This phenomenon is called masking¹³⁷. Usually, only noise within a critical frequency band around the signal frequency can effectively mask the signal. Generally speaking, within the sensitive frequency range, the sound pressure of the signal is 15-30dB higher than the environmental noise sound pressure, so that fish can distinguish the signal sound¹³⁷.

Lara et al. recorded higher SPLs (122-143 dB), predominantly below 1000 Hz, with more spectral peaks in noise recordings from zebrafish housing systems, indicating a potential for significant auditory masking effects²¹. Radford et al. found that noise generated by both RAS and cage culture systems exceeded the auditory thresholds of common carp, Atlantic salmon, and European perch at 100 Hz. Zhang et al. discovered that underwater noise from wind turbines overlapped with the auditory sensitivity and vocalization of zebrafish, suggesting a potential masking effect on their acoustic communication¹³⁸.

4.3 Impact on Physiology

Fish are often stimulated by various stressors in their living environment, leading to acute or chronic stress^{139,140}. External (environmental) and internal (disease, metabolic imbalance) stressors can significantly alter certain biochemical parameters, which may reveal poor animal welfare conditions. Stress stimuli induce major neuroendocrine responses in fish, manifested as an increase in corticosteroids (especially cortisol) and catecholamines. As a direct consequence of its high levels in the circulatory system, extensive secondary stress responses can be observed, such as elevated blood sugar levels from tissue glycogen reserves. In addition, in adaptive stress response, the hematopoietic activity of the spleen increases, as well as other related parameters such as hematocrit value and hemoglobin content. Even in the medium or long term, the tertiary stress response can have destructive effects on fish by inhibiting growth rate and interfering with reproductive processes. Noise has always been considered a stressor, and its impact on fish may be as severe or more severe as hearing or behavior.

Ship noise has been shown to cause a significant increase in cortisol stress in various freshwater

558 fish species (*Cyprinus carpio*, *Gobio gobio*, and *Perca fluviatilis*)¹⁴¹. Carp (*Carassius auratus*,
559 Linnaeus, 1758) and goldfish (*Carassius auratus*, Linnaeus, 1758) showed a brief peak in plasma
560 cortisol levels after 24 hours of noise exposure¹³⁶. The plasma cortisol levels of milkfish (*Chanos*
561 *chanos*) exposed to offshore wind farm noise were higher during the first 24 hours¹⁴². Exposure
562 to continuous ship noise also amplified plasma cortisol levels in large yellow croakers
563 (*Pseudosciaena crocea*) and Japanese sea bass (*Lateolabrax japonicus*) for up to 6 days¹⁴³.
564 Filiciotto et al. observed that fish exposed to noise from land-based aquaculture systems had
565 higher levels of serum cortisol, glucose, red blood cell count, red blood cell pressure, and
566 hemoglobin content, while lower levels of white blood cells¹⁴⁴.
567 Prolonged exposure to offshore wind farm noise (138 dB) resulted in heightened levels of ROS in
568 the plasma of black porgy (*Acanthopagrus schlegelii*)¹⁴⁵. Zhang et al. revealed that artificial
569 acoustic landscapes (RAS: 107 dB, IPRS: 115 dB) had deleterious effects on the immune,
570 antioxidant, and digestive enzymes of largemouth bass (*Micropterus salmoides*)¹⁴⁶. Hang et al.
571 discovered that environmental noise from RAS (115 dB) adversely affected the antioxidant and
572 immune systems of largemouth bass (*Micropterus salmoides*)¹²². Wysocki et al. demonstrated
573 that aquaculture noise can induce long-term stress in rainbow trout (*Oncorhynchus mykiss*).
574 Following 8 months of exposure to noise (115 dB, 130 dB, and 150 dB), plasma chloride and
575 sodium ion concentrations decreased, while glucose concentrations increased¹². Filiciotto et al.
576 examined the impact of offshore aquaculture systems' environmental noise on gilthead sea
577 bream (*Sparus aurata*) juveniles. The results showed that the total oxidation state, lysozyme
578 activity, anti-protease activity, and white blood cell levels of the fish significantly increased, while
579 the albumin/globulin ratio significantly decreased¹⁴⁷. Short-term exposure to 150 dB of noise
580 significantly increased the levels of lactate and red blood cell accumulation in gilthead sea bream
581 (*Sparus aurata*, Linnaeus 1758) and European sea bass (*Dicentrarchus labrax*, Linnaeus 1758),
582 while glucose levels in the gilthead sea bream significantly decreased¹⁴⁸. Hang et al. observed
583 that the liver tissue of largemouth bass (*Micropterus salmoides*) showed elevated levels of
584 oxidative stress after exposure to underwater noise¹²². Trabulo et al. exposed Meagre
585 (*Argyrosomus regius*) larvae to ship noise and observed an increase in lipid droplet consumption,
586 a decrease in body depth, a slight decrease in superoxide dismutase (SOD) activity, and no

change in DNA damage or electron transfer system (ETS) activity in the 2dph larvae ¹⁴⁹. Lara et al. studied the effects of continuous exposure to 130 and 150 dB of continuous white noise on zebrafish juveniles (*Danio rerio*). At 3 and 5 days after fertilization, heart rate, yolk sac consumption, and cortisol levels significantly increased with rising noise levels ²⁶. After 10 days of exposure to ship noise (123-136 dB), the ACTH, cortisol, glucose, lactate, hematocrit, Hsp70, cholesterol, triglycerides, and osmotic pressure values of the gillhead sea bream (*Sparus aurata*, Linnaeus 1758) significantly increased, indicating the primary and secondary stress responses of fish to ship noise ¹⁵⁰.

Furthermore, several scholars have delved into the impact of noise on the inner ear, gut microbiota, and other factors. Wong et al. conducted an exposure experiment on zebrafish subjected to 150 dB white noise, observing a significant decrease in presynaptic Ribeye b protein in the inner ear ¹⁵¹. Peled (*Coregonus peled*) exposed to a 300 Hz noise ranging from 176 to 186 dB for 18 days, acoustic exposure resulted in ultrastructure changes to otoliths, morphological damage to sensory hair cells of the macula sacculi, and a gradual decrease in the number of functionally active mitochondria in the red blood cells but no changes to telomeres¹⁵². Following short-term noise stimulation at 120 dB, *Larimichthys crocea* and *Nibeia albiflora* displayed a sharp increase in physiological indicators. Conversely, after prolonged stimulation, growth and immune indicators exhibited significant decreases. The proportion of intestinal microbiota became severely imbalanced, with *Vibrio* and *Pseudomonas* dominating, while the abundance of other genera was notably low, particularly some common intestinal probiotics ¹⁵³.

The employment of histological techniques enables the systematic exploration of diverse responses and regulatory pathways in organisms under stress, providing a comprehensive understanding of intricate biological phenomena ¹⁵⁴. Transcriptomics has played a pivotal role in illuminating the comprehensive landscape of gene expression and its interconnections ¹⁵⁵. In the case of small yellow croakers (*Larimichthys polyactives*) exposed to 120 dB ship noise, there is an upregulation observed in synaptic membranes, receptor-mediated endocytosis, and neurotransmitter secretion processes in brain tissue. This phenomenon is particularly noteworthy in the context of impaired extracellular matrix (ECM) composition ¹⁵⁶. Wei et al. noted elevated plasma cortisol levels in milkfish (*Chanos chanos*) exposed to wind farm noise

within the first 24 hours. Additionally, the mRNA levels of head kidney star (steroidogenic acid regulation) and hsd11b2 (11-b-hydroxysteroid dihydrogenase 2) showed significant increases ¹⁴². Continuous exposure to wind farm noise (138dB) resulted in changes in the mRNA levels of antioxidant related genes (sod1, cat, and gpx) in the liver of Black Porgy (*Acanthopagrus schlegelii*) (downregulation of cat and upregulation of gpx) ¹⁴⁵. Andrew et al. conducted a comprehensive study on the gene expression levels of Atlantic salt (*Salmo salt*) before and after noise exposure, and found transcriptional expression differences related to cell energy, cell respiration, oxygen transport, glycolytic pathways, TCA cycle (tricarboxylic acid cycle), and electron transport chains ¹⁵⁷. Shuck et al. found that after noise exposure, there were significant differences in the biological functions regulated by the inner ear of zebrafish, including cancer, cell growth and proliferation, and inflammation. The neuroendocrine system responded to physiological environmental pressure to restore the homeostasis of the entire body organs and cells¹⁵⁸. Under noise stress, hybrid sturgeon liver tissue cell apoptosis and cell movement are enhanced, DNA replication, RNA transcription and translation, protein synthesis are inhibited, and lipid metabolism, nucleotide metabolism, and vitamin D3 metabolism pathways are also inhibited. However, the initiation of some immune responses ensures their normal immune ability¹⁵⁹.

4.4 Effects on growth and reproduction

As the development of the auditory vesicle occurs in fish during the embryonic period, the impact of noise on fish can manifest as early as the embryonic stage, influencing embryos and larvae through direct (albeit potentially silent) acoustic activity. This, in turn, affects the growth and development of the adult fish. Increased mortality of eggs and embryos has been noted in environments where the ambient noise level is only 15 dB higher than the natural environment. However, in surviving fry, excessive noise can also result in slower growth rates ²⁷. For longnose killifish (*Fundulus similis*) and sheepshead minnow (*Cyprinodon variegates*), reductions in egg viability and growth rate occurred when the sound level in the aquarium was approximately 20 dB higher than that in the control aquarium ²⁷. Terhune et al. found that the growth rate of

Atlantic salmon (*Salmo salar*, Linnaeus 1758) was diminished in high-noise environments ¹⁴. Wysocki et al. observed a reduction in feeding and a slight slowing of growth in rainbow trout at the onset of noise exposure ¹⁶⁰. Kusku et al. discovered that urban noise adversely affects the growth and feed efficiency of Koi fish (*Cyprinus carpio*) ¹⁶¹. The mean body weight of largemouth bass (*Micropterus salmoides*) was significantly lower than that of the control group under the influence of IPRS (115.1 dB) noise ¹⁴⁶. Hang et al. also reported that RAS noise significantly reduced the weight gain rate of larval largemouth bass (*Micropterus salmoides*) ¹²².

Nonetheless, some studies have indicated that noise may not exert a significant impact on the growth of certain fish species, or that fish can gradually adapt to noisy environments. Wysocki et al. conducted an exposure experience on rainbow trout (*Oncorhynchus mykiss*), subjecting them to long-term exposure to varying decibel levels of farm noise. The findings revealed that the noise did not exacerbate rainbow trout's susceptibility to pathogens, and it had no discernible effects on growth or hearing. The authors suggested that this lack of impact might be linked to genetic variations among different populations of rainbow trout and the absence of a hearing sensitivity advantage relative to carp and catfish ¹⁶⁰. Lara et al. found no significant effects of continuous exposure to 130 and 150 dB continuous white noise on the development and hatching of larval zebrafish (*Danio rerio*) ²⁶. Intensive culture noise (149 dB) negatively affected the growth of rainbow trout (*Oncorhynchus mykiss*) in the first month, resulting in lower mean body weights, lengths, specific growth rates, condition factors, feed factors, and survival rates. However, after five months of exposure, no significant differences in growth parameters were observed between the noise-exposed and control groups ¹³. Larval Atlantic cod (*Gadus morhua*) exhibited lower growth rates and higher yolk sac depletion than controls after two days of noise disturbance from intensive culture. Cod larvae subjected to 16 days of noise disturbance had a lower body length, impacting their survival rate. However, as the duration of noise disturbance increased, the fish's growth performance gradually returned to normal, indicating long-term adaptation to noise ¹⁶².

Sound plays a crucial role in the reproductive success of fish, as acoustic signals often convey information about characteristics such as male size and condition, influencing female spawning behavior and, consequently, mating success. Consequently, fish reproduction relying on acoustic

communication may be particularly vulnerable to anthropogenic noise. Butler et al. found that under the influence of pure tones in the range of 100 to 2000 Hz, male African cichlid fish (*Astatotilapia burtoni*) altered the location of their courtship behavior, resulting in a decreased likelihood of females detecting them ¹⁶³. Jong et al. tested the impact of continuous noise on the courtship behavior of the painted goby (*Pomatoschistus pictus*) in an aquarium, and the results indicated a lower likelihood of female painted goby yielding under noise conditions. This suggests that reproductive success may be sensitive to noise pollution, potentially reducing adaptability ¹⁶⁴. Blom et al. found that continuous noise exposure increased nest guarding and egg-laying latency in female common goby (*Pomatoschistus microps*) and decreased the probability of egg-laying Crovo et al. found that growling signals facilitated the onset of spawning behavior in female blacktail shiner (*Cyprinella venusta*), and this response might be inhibited by anthropogenic noise pollution ¹⁶⁵.

4.5 Effects on behavior

Noise serves as a distraction for fish, diverting their limited attention from their primary tasks towards the environmental noise stimuli. Anthropogenic noise not only induces physiological damage to fish but also exerts profound effects on their behavior. Fish perceive noise as a threat, leading to the development of avoidance behaviors, instigating fear responses, and causing a loss of control over their normal behavior. Moreover, noise has the potential to mask communication signals among animals, hindering effective communication within and between groups. This disruption in communication may alter the way individuals interact within a group, potentially impacting the group dynamics or even the entire ecosystem.

Engås et al. discovered that fish exhibited a fleeing response from noise sound sources, impacting their normal feeding and mating behaviors ¹⁶⁶. Codarin et al.'s study also revealed that ship noise affected the auditory sensitivity of various fish species, subsequently influencing mate searching, foraging, and individual communication behaviors in these fish ¹⁶⁷. Short-term exposure to 150 dB noise significantly increased the locomotor performance of gilthead sea bream (*Sparus aurata*, Linnaeus 1758) and European sea bass (*Dicentrarchus labrax*, Linnaeus 1758) ¹⁴⁸.

Moderate sound levels (112 dB) can affect zebrafish swimming behavior by altering school cohesion, swimming speed, and swimming height, while artificial noise of 120-140 dB elicited a startle response and caused many individuals to dive to the bottom¹⁶⁸. Exposure of zebrafish to white noise of 150 dB significantly induced anxiety and stress¹⁵¹. Different temporally structured sounds (both continuous and intermittent at 165 dB) increased startle response, swimming speed, group cohesion, and submarine diving in European seabass (*Dicentrarchus labrax*)¹⁶⁹. Sabet et al. exposed adult zebrafish to noise conditions around 122 dB and found significant increases in startle response, swimming speed, and foraging ability, especially with intermittent treatments¹⁷⁰. Lavral zebrafish (*Danio rerio*) consistently exposed to continuous white noise at 130 and 150 dB / 1 μ Pa showed enhanced dark avoidance and impaired spontaneous alternation behavior in an anxiety-related dark/light preference test²⁶.

Due to the ability of fish to perceive various sound stimuli through the inner ear and lateral line, resulting in various behavioral responses such as phonotaxis, fish's phonotaxis is divided into positive phonotaxis and negative phonotaxis. Positive phonotaxis is manifested by the tendency to move toward the sound source under external acoustic stimulation. For example, in recent years, the emergence of "sound-induced fisheries" and "ocean ranching" is based on the positive phonotaxis of fish. Sound-induced fishing technology is a novel fishing technique that applies acoustic principles to lure fish. It involves playing back recorded biological sounds of fish (such as feeding, mating, schooling, etc.) underwater using specific instruments. This method clusters fish and induces them to enter a predetermined fishing area, thereby achieving the purpose of fishing. Michael et al. used audio frequencies in the range of 50 to 400 Hz to train mahi-mahi and rainbow trout, intending to control the aggregation of fish in net cages and attract escaped fish back to the cages through acoustic training. The study showed that when the audio frequency was adjusted to 250 Hz, both mahi-mahi and rainbow trout could be simultaneously controlled to feed on bait. The trained fish could be gathered and maintained long-term memory¹⁷¹. Negative phonotaxis is manifested by fish swimming away from the direction of the sound source under sound stimulation. Researchers often use this negative phonotaxis of fish to deter and drive them using sound. Hawkins experimentally demonstrated that fish exhibit different behavioral responses to different frequencies of sound. Nestler et al. studied the response of herring to

sound frequency and intensity. When the sound intensity was in the range of 160 to 175 dB and the frequency was in the range of 100 to 1000 Hz, the startled response of herring was short. When the sound intensity was in the range of 187 to 200 dB and the frequency was in the range of 124.6 to 130.9 kHz, the herring fled from the sound source to a distance of 60 meters, lasting for 1 hour ¹⁷².

In recent years, numerous scholars have delved into the behavioral repercussions on fish induced by the playback of ship or land-based culture system noise under captive conditions. Price et al. observed that ship noise reduced the reaction latency and duration of grouper and black sparrow, while aquaculture noise had a mitigating effect on the reaction speed of black sparrow. Interestingly, ship noise exhibited a more pronounced impact on anti-predator behavior compared to aquaculture noise ¹⁷³. Vessel noise has been found to decrease swimming behavior in spottail shiner (*Notropis hudsonius*) and bluegill sunfish (*Lepomis macrochirus*). However, spottail shiner demonstrated true avoidance behavior, indicating a more extreme response in species with refined auditory abilities ¹⁷⁴. Small yellow croaker (*Larimichthys polyactis*) exposed to 120 dB of vessel noise exhibited escape behavior from the noise source. By the end of the exposure, *L. polyactis* was motionless on the water's surface, losing the ability to maintain balance ¹⁵⁶. Zhang et al. observed more discrete polarity and cohesion in fish under the influence of RAS (107.7 dB) and IPRS (115.1 dB) compared to controls ¹⁴⁶. Hang et al. assessed the effects of commercial industrial RAS noise on the swimming behavior of larval largemouth bass (*Micropterus salmoides*) and found that the mean angle and distance between the focal fish of the noise group and its nearest neighbor fish were greater than those of the ambient group. This indicates a more dispersed and less cohesive population ¹²². Hasan et al. placed fathead minnows (*Pimephales promelas*) into airstones and filter noise and found that exposure to novel filter noise resulted in decreased boldness, with a return to bolder behavior when placed back into the original noisy environment ¹⁷⁵. Sabat et al. discovered that under captive conditions, noise induced significant startle response behavior in zebrafish (*Danio rerio*), increased swimming speed, caused Lake Victoria cichlids (*Haplochromis piceatus*) to move downward, and stay longer at the bottom of the tank ¹⁷⁶.

758 **5 The impact of noise on other aquatic species**

759 In recent years, numerous scholars have investigated the multifaceted impacts of noise on the

760 growth, development, behavioral response, and physiological aspects of other aquatic species.

761 The summary of the impact of human noise on other aquatic species in recent years is presented

762 in Table 2.

763 Table2 The impact of human noise on other aquatic species.

Species	Noise level	Influence	Reference
Brown shrimp (<i>Crangon crangon</i>)	25 - 400Hz 30 dB $\mu V^{-1} \mu bar^{-1}$ above habitat	significant reduction in growth and reproduction rates, increase aggression (cannibalism) and mortality rate and to decrease food uptake	Lagardère et al. ¹⁷⁷
	average increase 30 dB $\mu bar^{-1} Hz^{-1}$	22% increase of the ammonia excretion rate, 15% of increase of the O ₂ consumption rate	Regnault et al. ¹⁷⁸
Sea hare (<i>Stylocheilus striatus</i>)		reduced successful development of embryos by 21% and increased mortality of recently hatched larvae by 22%	Nedelec et al. ¹⁷⁹
Cephalopods (<i>Loligo vulgaris</i> , <i>Sepia officinalis</i> , <i>Octopus vulgaris</i> , <i>Illex coindetii</i>)	50 - 400Hz	permanent and substantial alterations of the sensory hair cells of the statocysts	André et al. ¹⁸⁰
Cuttlefish (<i>Sepia officinalis</i>)	315 - 400Hz 139 - 142 dB re 1 μPa^2	injuries in statocysts, the damage degree increases with the decrease of distance from the sound source and the increase of time	Solé et al. ¹⁸¹
	80 – 300 Hz 140 dB re. 1 μPa rms	escape responses (inking, jetting), body patterning changes and fin movements	Samson et al. ¹⁸²

	particle accelerations of 0.01 m s^{-2}		
Razor clams (<i>Sinonovacula stricta</i>)	80 - 100 dB re $1 \mu\text{Pa}$	alteration in the O:N ratios and the expression of ten metabolism-related genes from the glycolysis, fatty acid biosynthesis, tryptophan metabolism, and Tricarboxylic Acid Cycle (TCA cycle) pathways, induced avoidance response	Peng et al. ¹⁸³
Longfin squid (<i>Doryteuthis pealeii</i>)	80 – 100 Hz	a range of behavioral responses to sound include fleeing, deimatic and protean behaviors	Mooney et al. ¹⁸⁴
Blue mussel (<i>Mytilus edulis</i>)	140- 155 dB re $1 \mu\text{Pa}^2\text{Hz}^{-1}$ Particle acceleration peaked at 160–175 dB re $1 (\mu\text{ms}^{-2})^2 \text{Hz}^{-1}$	changes in DNA integrity (six-fold higher DNA single strand-breaks in haemocytes and gill epithelial cells) and oxidative stress (68% increased TBARS in gill cells), physiological and behavioral changes (12% reduced oxygen consumption, 60% increase in valve gape, 84% reduced filtration rate)	Wale et al. ¹⁸⁵
European spiny lobster (<i>Palinurus elephas</i> , Fabricius, 1787)	$125 \pm 5 \text{ dB re } 1 \mu\text{Pa/V re } 1$	Total haemocyte count (THC) and haemolymphatic protein concentration, phenoloxidase (PO) activity decreased significantly, whereas total protein and heat shock protein 27 (Hsp27) expression increased significantly	Ceill et al. ¹²⁰
Mediterranean spiny lobster		increased significantly locomotor activities and	Filiciotto et al. ¹⁸⁶

<i>(Palinurus elephas)</i>		haemolymphatic bioindicator of stressful conditions such as glucose, total proteins, Hsp70 expression and THC	
Red swamp crayfish (<i>Procambarus clarkii</i>)	148 dB _{rms} re	behavioral pattern changes, altered blood immune parameters	Ceil et al. ¹⁸⁷
Linear seahorse (<i>Hippocampus erectus</i>)	137.3 ± 0.7 dB re: 1 µPa	significant increases in immune indicators, sharp decreases in body weight (Δ Wt), Fulton condition factor (Δ K), liver body index, and sex gland index	Anderson et al. ¹²¹
Shore crabs (<i>Carcinus maenas</i>)		consumed more oxygen, indicating a higher metabolic rate and potentially greater stress	Wale et al. ¹⁸⁸

765

766 **6 Noise control**

767 There are two main measures for noise control in intensive aquaculture systems: sound source
768 control and propagation control. Sound source control should consider using special devices from
769 the beginning of the design of the breeding workshop or facility to reduce noise at the source. If
770 the cost of sound control is relatively high for breeding facilities that have already been put into
771 use, it is possible to consider using isolation and sound absorption measures to control noise
772 transmission. The "quality law" of sound insulation states that the density of sound insulation
773 materials is directly proportional to the amount of sound insulation, meaning that the higher the
774 quality of the material, the better the sound insulation effect. The "resonance principle" of sound
775 absorption indicates that when the frequency of the incident noise sound wave is consistent with
776 the natural frequency of the sound absorbing material, the sound absorbing material will
777 undergo resonance phenomenon, which can efficiently reduce sound energy ¹¹².
778 In section 3.1, it is highlighted that machinery, particularly electric motors and air compressors,
779 stands as prevalent and highly impactful noise sources within aquaculture facilities. When
780 designing aquaculture systems, thoughtful consideration must be given to the scientific
781 utilization and arrangement of aquaculture equipment with the aim of minimizing noise
782 disruptions in fish farming operations. Lara et al. conducted a study revealing that aquaculture
783 tanks linked to autonomous water treatment units exhibit significantly lower noise levels
784 compared to tanks integrated with water treatment systems ²¹. Consequently, in the strategic
785 planning of indoor aquaculture sites, it is advisable to position aquaculture tanks away from
786 noise-prone zones, such as those housing water treatment units. Presently, most RAS position
787 blowers outside the breeding workshop sans any sound insulation measures, resulting in
788 elevated sound pressure levels when transmitted indoors ¹¹². For established RAS setups, outdoor
789 blowers should be outfitted with a composite structure incorporating sound insulation and
790 absorption, complemented by the installation of exhaust silencers in the workshop's ventilation
791 openings. The application of sound insulation and absorption materials on indoor ceilings and

walls is also recommended. In the case of newly planned RAS, due consideration should be given to isolating blowers through elastic brackets and enclosing them within insulated spaces.

Moreover, it is imperative to ensure that doors leading to rooms housing such equipment remain consistently closed¹¹⁸. Other types of aquaculture environments, such as outdoor ponds, etc., can be equipped with noise reduction devices outside of electric equipment.

The combination of materials and structural design in aquaculture ponds plays a significant role in determining the acoustic conditions inside the pond. As stated in section 3.2, the noise level of fiberglass tanks is significantly higher than that of tanks made of other materials. Therefore, if conditions permit, indoor aquaculture systems should choose tanks with lower noise levels such as concrete tanks.

Most machinery will transmit low-frequency noise to the breeding pond through various pipelines. Therefore, in addition to isolating the breeding pond from these mechanical equipment, soundproofing materials can also be installed on the pipelines or brackets can be set up under the noisy equipment. According to Lawrence and Mason, in order to minimize noise sources in zebrafish housing systems, dampers should be included on supports for pumps or other vibration and noise equipment¹⁸⁹. Davidson et al.¹⁹⁰, Craven et al.¹⁵, and Gutscher et al.¹⁶ provided some strategies to modify the design of the water tank and pipeline system to reduce noise, including avoiding physical contact between the inlet and outlet pipes and the water tank, insulating the connecting pipes with foam fillers, and directly connecting the water tank and the support to prevent neoprene isolation pads to raise the water tank above the floor. Yin et al. suggested that the following measures can be taken for fiberglass aquaculture tanks: (1) the inlet pipe should avoid contact with the inner wall of the tank; (2) Separate the outlet pipe from the main drainage pipe; (3) The water outlet pipe under the sink should avoid contact with the wall; (4) The sink should be fixed on shock-absorbing material¹¹⁴.

After turning off the blower, the background noise in the breeding workshop is mainly generated by the interaction between the aquaculture water and the pool water, as well as the interaction between the aeration airflow and the pool water. According to the sound energy formula, the sound energy of water droplet impact is directly proportional to the radius of the water droplet and the water droplet falling velocity. Due to the limitation of aquaculture scale, reducing the

flow rate is not advisable. Reducing the radius of water droplets contributes significantly to reducing water splashing noise and does not affect the total water consumption. Therefore, a flexible porous noise reduction net can be added before the aquaculture water impacts the pool. After passing through the noise reduction net, the radius of the aquaculture water decreases, which not only reduces noise, but also allows water droplets to disperse and fall into the pool, bringing in more air ¹¹⁴. Gutscher et al. suggested that (1) the outlet of the inlet pipe of the sink should be placed near or below the water surface; (2) The water flow should not enter the water surface vertically (should be angled); (3) The external filter should not come into contact with the table or bracket where the sink is located¹⁶

The aeration tube directly enters the water, and the airflow generates bubbles. The bubbles rise to the water surface and burst, producing noise. Craven et al. suggested using open top water tanks and fine air stones (instead of coarse air stones) in aquariums to reduce environmental noise ¹⁵. To reduce noise and sound energy, multiple rows of porous aeration grilles can be connected at the outlet of the aeration pipe. From the perspective of energy conservation, the friction between the airflow and the small holes in the gas grid will result in energy consumption and a reduction in sound energy. Moreover, after the airflow passes through the small hole, the volume and quantity of bubbles decrease, increasing the contact area between water and air, which is beneficial for dissolved oxygen ¹¹². Alternatively, Radford et al. suggest that oxygenation can be carried out in cone systems separate (and distant) from holding tanks ¹¹¹.

7. Conclusion and prospect

So far, the impact of chronic noise on the welfare of fish farming is still an emerging research topic. More and more evidence suggest that the impact of underwater noise on fish has become a serious ecological problem. With the gradual increase in underwater noise levels, it is necessary to fully recognize and manage noise before it causes irreversible damage to the welfare of farmed aquatic organism and the underwater ecosystem. This article provides a comprehensive overview of the auditory organs and mechanisms of fish, as well as their growth, physiology, and behavioral responses to noise. It also elaborates on the noise control strategies for aquaculture

environments in existing literature, providing strategies for regulating anthropogenic noise in intensive aquaculture.

Although significant progress has been made in the impact of anthropogenic noise on aquatic animals such as fish in the past few decades, there is currently a relative lack of research on the effects of noise on fish in artificial aquaculture environments, and the following problems still exist:

1. The underwater soundscape in intensive aquaculture system remains uncertain. Although many studies have shown that noise in intensive aquaculture systems do not have adverse effects on the hearing sensitivity, growth, survival, and disease susceptibility of farmed fish. It is important to note that these results cannot be universally applied to all farmed fish, given the species-specific variations in auditory sensitivity and tolerance to potential stressors.

2. While low-intensity noise in intensive aquaculture environments may have a relatively modest short-term impact on the welfare of farmed fish, its long-term effects cannot be ignored. Striking a balance between aquaculture density, mechanical operations, and noise reduction is a crucial direction that warrants exploration.

3. Considering the increasing number of intensive aquaculture systems being applied, meeting the natural biological needs of farmed fish becomes increasingly challenging. It is important not only to determine the characteristics of individual fish species, but also to choose the most appropriate combination of technologies and methods. Therefore, given that the environmental requirements of each fish species are unique and vary according to their biological age, it must be emphasized that their health level at any time is the result of the interaction of many biological and environmental factors.

4. The characteristics of noise in artificial aquaculture environments are low intensity and long-term, and it is difficult to visually observe the damage to farmed fish through behavior and organizational observation alone, especially the potential and long-term effects caused by noise exposure. With the development and widespread and low-cost application of molecular biology, molecular biology methods can be fully utilized to more accurately assess and comprehensively analyze the impact of noise exposure on fish.

5. Detecting the movement of particles in water to determine the direction of the sound source

is indispensable for the hearing of all fish. Popper pointed out that the main challenges in investigating the impact of particle movement on fish are the difficulty in measuring particle movement, modeling particle movement, and the lack of experimental data on the potential adverse effects of particle movement on fish ⁷⁵. Calibrated sensors should be used to measure particle movement in different water environments, model particle movement, better understand the mechanical and physiological mechanisms of fish in detecting particle movement, and explore the adverse effects of high particle movement levels on fish. In the context of increasingly tight environmental policies and shrinking aquaculture space, environmentally friendly intensive aquaculture systems have become one of the important ways to solve the contradiction between fishery development and environmental protection. The increase in intensive production and the demand for scientific and precise aquaculture will further stimulate the research and application process of welfare based aquaculture noise and environmental regulation for fish farming.

AUTHOR CONTRIBUTIONS

Shanshan Duan: Investigation; validation; data curation; original – draft. Raquel O. Vasconcelos: Investigation; formal analysis; writing – review & editing. Lele Wu: Investigation; original – draft. Xin Li: Data curation; visualization. Wen Sun: Investigation; visualization. Xian Li: Conceptualization; supervision; writing – review & editing.

CONFLICT OF INTEREST STATEMENT

The authors declare that there are no conflicts of interest.

DATA AVAILABILITY STATEMENT

Since this is a review paper, there is no data available. All information can be found in the cited references.

905 Reference

- 906 1. FAO. The State of World Fisheries and Aquaculture 2024. Blue Transformation in action.
907 <https://digitallibrary.un.org/record/4050926?v=pdf>
- 908 2. Dulvy NK, Pacoureau N, Rigby CL, et al. Overfishing drives over one-third of all sharks and rays
909 toward a global extinction crisis. *Curr Biol*. 2021;31(21):4773-4787.e8.
- 910 3. McCauley DJ, Pinsky ML, Palumbi SR, Estes JA, Joyce FH, Warner RR. Marine defaunation: Animal
911 loss in the global ocean. *Science*. 2015;347(6219):1255641.
- 912 4. Troella M, Naylor RL, Metian M, et al. Does aquaculture add resilience to the global food system?
913 *PNAS*. 2014;111(37):13257-13263.
- 914 5. Poore J, Nemecek T. Reducing food's environmental impacts through producers and consumers.
915 *Science*. 2018;360(6392):987-992.
- 916 6. Golden CD, Koehn JZ, Shepon A, et al. Aquatic foods to nourish nations. *Nature*. 2021;598:315-320.
- 917 7. Ha TTP, Dijk Hv, Bosma R, Sinh LX. Livelihood Capabilities and Pathways of Shrimp Farmers in the
918 Mekong Delta, Vietnam. *Aquacult Econ Manag*. 2013;17(1):1-30.
- 919 8. Little DC, MacKenzie S. Grand challenges for global aquaculture. *Front Aquac*. 2023;2:1232936.
- 920 9. Cherdsak V. The Current Challenges of Sustainable Aquaculture in the Asia-Pacific Region and the
921 Measures Recommended. *Asia Pac J Rural Dev*. 2022;32(2)
- 922 10. Ashley PJ. Fish welfare: Current issues in aquaculture. *Appl Anim Behav*. 2006;104(3):199-235.
- 923 11. Olesen I, Alfnes F, Røra MB, Kolstad K. Eliciting Consumers' Willingness to Pay for Organic and
924 Welfare-labelled Salmon in a Non-hypothetical Choice Experiment. *Livest Sci*. 2010;127(2-3):218-226.
- 925 12. Wysocki LE, Davidson JW, Smith ME, et al. Effects of aquaculture production noise on hearing,
926 growth, and disease resistance of rainbow trout *Oncorhynchus mykiss*. *Aquaculture*. 2007;272(1-
927 4):687-697.
- 928 13. Davidson J, Bebak J, Mazik P. The effects of aquaculture production noise on the growth, condition
929 factor, feed conversion, and survival of rainbow trout, *Oncorhynchus mykiss*. *Aquaculture*. 2009;288(3-
930 4):337-343.
- 931 14. Terhune JM, Friars GW, Bailey JK, O'Flynn FM. Noise levels may influence Atlantic salmon smolting
932 rates in tanks. *J Fish Biol*. 1990;37(1):185-187.
- 933 15. Craven A, Carton AG, McPherson CR, McPherson G. Determining and quantifying components of
934 an aquaculture soundscape. *Aquacult Eng*. 2009;41(3):158-165.
- 935 16. Gutscher M, Wysocki LE, Ladich F. Effects of aquarium and pond noise on hearing sensitivity in an
936 otophysine fish. *Bioacoustics*. 2011;20(2):117-136.
- 937 17. Anderson PA. Acoustic characterization of seahorse tank environments in public aquaria: A citizen
938 science project. *Aquacult Eng*. 2013;54:72-77.
- 939 18. Barnes ME, Hewitt CR, Parker TM. Fish Hatchery Noise Levels and Noise Reduction Techniques *J*
940 *Agric Saf Health*. 2015;21(3):187-195.
- 941 19. Kathy H, Harald Y, Chad N, Lance B-L. A Permanent Soundscape Monitoring System for the Care of
942 Animals in Aquaria. *Adv Exp Med Biol*. 2016;875:455-459.
- 943 20. Voorhees J, Barnes ME. Occupational Noise Levels in Two Fish Rearing Buildings at an Aquaculture
944 Facility. *Occup Environ Med*. 2017;5(02):58-66.
- 945 21. Lara RA, Vasconcelos RO. Characterization of the Natural Soundscape of Zebrafish and Comparison
946 with the Captive Noise Conditions. *Zebrafish*. 2018;16(2):152-164.

947 22. Radford C, Slater M. Soundscapes in aquaculture systems. *Aquacult Env Interac*. 2019;11:53-62.

948 23. Radford AN, Kerridge E, Simpson SD. Acoustic communication in a noisy world: can fish compete
949 with anthropogenic noise? . *Behav Ecol*. 2014;25(5):1022-1030.

950 24. Popper AN, Hawkins AD. Fish hearing and how it is best determined. *ICES J Mar Sci*. 2021;78(7)

951 25. Davis LE, Schreck CB. The Energetic Response to Handling Stress in Juvenile Coho Salmon. *Trans*
952 *AM Fish Soc*. 1997;126(2):248-258.

953 26. Lara RA, Vasconcelos RO. Impact of noise on development, physiological stress and behavioural
954 patterns in larval zebrafish. *Sci Rep*. 2021;11(1):6615.

955 27. Banner A, Hyatt M. Effects of Noise on Eggs and Larvae of Two Estuarine Fishes. *Trans Am Fish Soc*.
956 1973;102(1):134-136.

957 28. Mardi HC, Popper AN, Finneran JJ, Lanford PJ. Effects of low-frequency underwater sound on hair
958 cells of the inner ear and lateral line of the teleost fish *Astronotus ocellatus*. *J Acoust Soc Am*.
959 1996;99(3):1759-1766.

960 29. McCauley RD, Fewtrell J, Popper AN. High intensity anthropogenic sound damages fish ears. *J*
961 *Acoust Soc Am*. 2003;113(1):638-642.

962 30. Santulli A, Modica A, Messina C, et al. Biochemical Responses of European Sea Bass (*Dicentrarchus*
963 *labrax* L.) to the Stress Induced by Off Shore Experimental Seismic Prospecting. *Mar Pollut Bull*.
964 1999;38(12):1105-1114.

965 31. Sverdrup A, Kjellsby E, Krüger PG, et al. Effects of experimental seismic shock on vasoactivity of
966 arteries, integrity of the vascular endothelium and on primary stress hormones of the Atlantic salmon.
967 *J Fish Biol*. 2010;45(6):909-1135.

968 32. Kunc HP, McLaughlin KE, Schmidt R. Aquatic noise pollution: implications for individuals,
969 populations, and ecosystems. *Proc Biol Sci*. 2016;283(1836):20160839.

970 33. Rice AN, Farina SC, Makowski AJ, et al. Evolutionary patterns in sound production across fishes.
971 *Ichthyol Herptol*. 2022;110(1):1-12.

972 34. Ladich F, Schulz-Mirbach T. Diversity in Fish Auditory Systems: One of the Riddles of Sensory Biology.
973 *Front Ecol Evol*. 2016;4(28):1-26.

974 35. Carlstrom D. A crystallographic study of vertebrate otoliths. *Biol Bull*. 1963;125:441-463.

975 36. Lovell JM, Findlay MM, Harper G, Moate RM, Pilgrim DA. The polarisation of hair cells from the ear
976 of the European bass (*Dicentrarchus labrax*). *Comp Biochem Phys A*. 2005;141(1):116-121.

977 37. Vasconcelos RO, Alderks PW, Sisneros JA. Development of Structure and Sensitivity of the Fish
978 Inner Ear. *Adv Exp Med Biol*. 2016;877:291-318.

979 38. Masui Y, Wang P. Cell cycle transition in early embryonic development of *Xenopus laevis*. *Biol Cell*.
980 2012;90(8):537-548.

981 39. Lindström E, Chen D, Norlén P, Andersson K, Håkanson R. Control of gastric acid secretion:the
982 gastrin-ECL cell-parietal cell axis. *Comp Biochem Phys A*. 2001;128(3):503-511.

983 40. Nedelec SL, Campbell J, Radford AN, Simpson SD, Merchant ND. Particle motion: the missing link
984 in underwater acoustic ecology. *Methods Ecol Evol*. 2016;7(7):836-842.

985 41. Popper AN, Salmon M, Horch KW. Acoustic detection and communication by decapod crustaceans.
986 *J Comp Physiol A*. 2001;187(2):83-89.

987 42. Bleckmann H. 3-D-orientation with the octavolateralis system. *J Physiol - Paris*. 2004;98(1-3):53-
988 65.

989 43. Kaifu K, Akamatsu T, Segawa S. Underwater sound detection by cephalopod statocyst. *Fish Sci.*
990 2008;74(4):781-786.

991 44. Hawkins AD, Hazelwood RA, Popper AN, Macey PC. Substrate vibrations and their potential effects
992 upon fishes and invertebrates. *J Acoust Soc Am.* 2021;149(4):2782-2790.

993 45. Ladich F. Acoustic communication and the evolution of hearing in fishes. *Philos Trans R Soc Lond B*
994 *Biol Sci.* 2000;355(1401):1285-8.

995 46. Montgomery JC, Baker CF, Carton AG. The Lateral Line Can Mediate Rheotaxis in Fish. *Nature.*
996 1997;389(6654):960-963.

997 47. Satou M, Takeuchi HA, Takei K, Hasegawa T, Okumoto N. Characterization of vibrational and visual
998 signals which elicit spawning behavior in the male hime salmon (landlocked red salmon, *Oncorhynchus*
999 *nerka*). *Comp Physiol A.* 1994;174(5):527-537.

1000 48. Satou M, Takeuchi HA, Nishii J, et al. Behavioral and electrophysiological evidences that the lateral
1001 line is involved in the inter-sexual vibrational communication of the himé salmon (landlocked red
1002 salmon, *Oncorhynchus nerka*). *J Comp Physiol A.* 1994;174(5):539-549.

1003 49. Coombs S, Finneran JJ, Conley RA. Hydrodynamic image formation by the peripheral lateral line
1004 system of the Lake Michigan mottled sculpin, *Cottus bairdi*. *Philos Trans R Soc Lond B Biol Sci.*
1005 2000;355(1401):1111-4.

1006 50. Campenhausen Cv, Riess I, Weissert R. Detection of stationary objects by the blind Cave
1007 Fish *Anoptichthys jordani* (Characidae). *J Comp Physiol.* 1981;143(3):369-374.

1008 51. Kasumyan AO. The Lateral Line in Fish: Structure, Function, and Role in Behavior. *J Ichthyol*
1009 2003;43(Supplement 2):S175–S213.

1010 52. Bleckmann H, Zelick R. The Lateral Line System of Fish. *Integr Zool.* 2009;4:13-25.

1011 53. Yoshizawa M, Jeffery WR, Netten SMv, McHenry MJ. The sensitivity of lateral line receptors and
1012 their role in the behavior of Mexican blind cavefish (*Astyanax mexicanus*). *J Exp Biol.* 2014;217(6):886-
1013 895.

1014 54. Chicoli A, Butail S, Lun Y, Bak-Coleman J, Coombs S, Paley DA. The effects of flow on schooling
1015 *Devario aequipinnatus*: school structure, startle response and information transmission. *J Fish Biol.*
1016 2014;84(5):1401-21.

1017 55. Montgomery J, Coombs S, Janssen J. Form and Function Relationships in Lateral Line Systems:
1018 Comparative Data from Six Species of Antarctic Notothenioid Fish. *Brain Behav Evol.* 2008;44(6):299-
1019 306.

1020 56. Coombs S, Janssen J. Behavioral and neurophysiological assessment of lateral line sensitivity in the
1021 mottled sculpin, *Cottus bairdi*. *J Comp Physiol A.* 1990;167(4):557-567.

1022 57. Weeg MS, Bass AH. Frequency response properties of lateral line superficial neuromasts in a vocal
1023 fish, with evidence for acoustic sensitivity. *J Neurophysiol.* 2002;88(3):1252-62.

1024 58. Mann DA, Lu Z, Hastings MC, Popper AN. Detection of ultrasonic tones and simulated dolphin
1025 echolocation clicks by a teleost fish, the American shad (*Alosa sapidissima*). *The Journal of the Acoustical*
1026 *Society of America.* 1998;104(1):562-568.

1027 59. Popper A, Dale J, Gray MD, Keith W, Block B, Rogers PH. Threshold of hearing for swimming Bluefin
1028 tuna (*Thunnus orientalis*). *J Acous Soc Am.* 2013;19(1):01005.

1029 60. ZhenWen L, XiaoMei U, ErHui H, YanMing Y. Study on behavior of sound stimulation for large yellow
1030 croaker (*Pseudosciaena crocea*). *J Appl Oceang.* 2014;33(01):105-110.

61. Horodysky AZ, Brill RW, Fine ML, Musick JA, Latour RJ. Acoustic pressure and particle motion thresholds in six sciaenid fishes. *J Exp Biol.* 2009;211(9):1504-1511.
62. Babaran RP, Anraku K, Ishizaki M, Watanabe K, Matsuoka T, Shirai H. Sound generated by a payao and comparison with auditory sensitivity of jack mackerel *Trachurus japonicus*. *Fish Sci.* 2008;74(6):1207-1214.
63. Kojima T, Suga T, Kusano A, et al. Acoustic pressure sensitivities and effects of particle motion in red sea bream *Pagrus major*. *Fish Sci.* 2010;76(1):13-20.
64. Lovell JM, Findla MM, Nedwell JR, Pegg MA. The hearing abilities of the silver carp (*Hypophthalmichthys molitrix*) and bighead carp (*Aristichthys nobilis*). *Com Biochem Physiology A Mol Integr Physiol.* 2006;143(3):286-291.
65. Kojima T, Ito H, Komada T, Taniuchi T, Akamatsu T. Measurements of auditory sensitivity in common carp *Cyprinus carpio* by the auditory brainstem response technique and cardiac conditioning method. *Fish Sci.* 2005;71(1):95-100.
66. Yining W, Jiangnan Y, Xin Z, et al. Auditory sensitivity in crucian carp *Carassius auratus* Linnaeus. *J Dalian Oce Uni.* 2018;33(6):775-781.
67. Mann DA, Higgs DM, Tavalga WN, M. J. Souza, Popper AN. Ultrasound detection by clupeiform fishes. *The Journal of the Acoustical Society of America.* 2001;109(6):3048-3054.
68. Oxman DS, Barnett-Johnson R, Smith ME, et al. The effect of vaterite deposition on sound reception, otolith morphology, and inner ear sensory epithelia in hatchery-reared Chinook salmon (*Oncorhynchus tshawytscha*). *Can J Fish Aquat Sci.* 2007;64(11):1469-1478.
69. Weiss BA, Hartig GM, Strother WF. Hearing in the Bullhead Catfish (*Ictalurus nebulosus*). *J Acoust Soc Am.* 1969;46(114)
70. Binbin X, Zhenyu W, Guosheng Z, et al. Study on hearing capacities of *Paralichthys olivaceus* using an ECG method. *J Fish Sci China.* 2018;25(3):467-474.
71. Jie X, Qiaolin Z, Hao D, Chengyou W, Qiwei W. Threshold of the juvenile *Acipenser dabryanus* Dumeril. *Acta Hydrobiol Sin.* 2022;46(10):1563-1568.
72. Mann DA, Higgs DM, Tavalga WN, Popper AN. Ultrasound detection by clupeiform fishes. *J Acoust Soc Am.* 2001;109(6):3048-3054.
73. Popper AN, Sisneros ADHA. Fish hearing "specialization" - a re-valuation. *Hear Res.* 2022;425:108393.
74. Popper AN, Fay RR. Rethinking sound detection by fishes. *Hear Res.* 2011;273(1):25-36.
75. Popper AN, Hawkins AD. The importance of particle motion to fishes and invertebrates. *J Acoust Soc Am.* 2018;143(1):470-488.
76. Roberts L, Cheesman S, Elliott M, Breithaupt T. Sensitivity of *Pagrus bernhardus* (L.) to substrate-borne vibration and anthropogenic noise. *J Exp Mar Biol Ecol.* 2016;474:185-194.
77. Roberts L, Elliott M. Good or bad vibrations? Impacts of anthropogenic vibration on the marine epibenthos. *Sci Total Environ.* 2017;595:255-268.
78. Berghahn R, Wiese K, Lfidemann K. Physical and physiological aspects of gear efficiency in North Sea brown shrimp fisheries *Helgol Mar Res.* 1995;49:507-518.
79. Roberts L, Cheesman S, Breithaupt T, Elliott M. Sensitivity of the mussel *Mytilus edulis* to substrate-borne vibration in relation to anthropogenically generated noise. *Mar Ecol Prog Ser.* 2015;538:185-195.
80. Roberts L, Laidre ME. Finding a home in the noise: Crossmodal impact of anthropogenic vibration on animal search behaviour. *Biol Open.* 2019;8(7):bio041988.

1074 81. Chahouri A, Elouahmani N, Ouchene H. Recent progress in marine noise pollution: A thorough
1075 review. *Chemosphere*. 2021;291:132983.

1076 82. Leis JM, Siebeck U, Dixon DL. How Nemo Finds Home: The Neuroecology of Dispersal and of
1077 Population Connectivity in Larvae of Marine Fishes. *Integr Comp Biol*. 2011;51(5):826-843.

1078 83. Staatterman E, Rice AN, Mann DA, Paris CB. Soundscapes from a Tropical Eastern Pacific reef and a
1079 Caribbean Sea reef. *Coral Reefs*. 2013;32(2):553-557.

1080 84. Pijanowski BC, Villanueva-Rivera LJ, Dumyahn SL, et al. Soundscape Ecology: The Science of Sound
1081 in the Landscape. *BioScience*. 2011;61(3):203-216.

1082 85. Cato DH, Tavener S. Ambient sea noise dependence on local, regional and geostrophic wind speeds:
1083 Implications for forecasting noise. *Appl Acoust*. 1997;51(3):317-338.

1084 86. Curtis KR, Howe BM, Mercer JA. Low-frequency ambient sound in the North Pacific: Long time
1085 series observations. *J Acoust Soc Am*. 1999;106:3189-3200.

1086 87. Ma BB, Nystuen JA, Lien R-C. Prediction of underwater sound levels from rain and wind. *J Acoust*
1087 *Soc Am*. 2005;117(6):3555-3565.

1088 88. Haxel JH, Dziak RP, Matsumoto H. Observations of shallow water marine ambient sound: The low
1089 frequency underwater soundscape of the central Oregon coast. *J Acoust Soc Am*. 2013;133(5):2586-
1090 2596.

1091 89. Tonolla D, Lorang MS, Heutschi K, Gotschalk CC, Tockner K. Characterization of spatial
1092 heterogeneity in underwater soundscapes at the river segment scale. *Limnol Oceanogr*.
1093 2011;56(6):2319-2333.

1094 90. Hildebrand JA. Anthropogenic and natural sources of ambient noise in the ocean. *Mar Ecol Prog*
1095 *Ser*. 2009;395:5-20.

1096 91. Bittencourt L, Barbosa M, Fernandes M, Bisi TL, José Lailson-Brito J, Azevedo AF. Fish chorus
1097 variation in a tropical estuarine environment. *J Acoust Soc Am*. 2023;154:3158-3167.

1098 92. Looby A, Cox K, Bravo S, et al. A quantitative inventory of global soniferous fish diversity. *Rev Fish*
1099 *Biol Fish*. 2022;32:581-595.

1100 93. Bass AH, Ladich F. Vocal–Acoustic Communication: From Neurons to Behavior. *Fish Bioacoust*.
1101 Springer; 2008:253-278.

1102 94. Eric P, Orphal C, David L. New insights into sound production in *Carapus moulani* (Carapidae). *Bull*
1103 *Mar Sci*. 2016;92(3):335-342.

1104 95. Ladich F. Diversity of sound production and hearing in fishes: Exploring the riddles of
1105 communication and sensory biology. *J Acoust Soc Am*. 2024;155:218-228.

1106 96. Amorim MCP. Diversity of sound production in fish. *Commun Fish*. 2006;1:71-105.

1107 97. Mann DA, Lobel PS. Propagation of damselfish (Pomacentridae) courtship sounds. *J Acoust Soc Am*.
1108 1997;101(6):3783-3791.

1109 98. Myrberg AA. Underwater sound: Its relevance to behavioral functions among fishes and marine
1110 mammals. *Mar Freshw Behav Phy*. 1997;29(1):3-21.

1111 99. Lagardère JP, Bégout ML, Lafaye JY, Villotte JP. Influence of Wind-produced Noise on Orientation in
1112 the Sole (*Solea solea*). *Can J Fish Aquat Sci*. 1994;51(6):1258-1264.

1113 100. Tavolga WN. Sound Production and Detection. *Fish Phy*. 1971;5(5):135-205.

1114 101. Montgomery JC, Jeffs A, Simpson SD, Meekan M, Tindle C. Sound as an Orientation Cue for the
1115 Pelagic Larvae of Reef Fishes and Decapod Crustaceans. *Adv Mar Biol*. 2006;51:143-196.

1116 102. Simpson SD, Meekan MG, Jeffs A, Montgomery JC, McCauley RD. Settlement-stage coral reef fish
1117 prefer the higher-frequency invertebrate-generated audible component of reef noise. *Anim Behav.*
1118 2007;75(6):1861-1868.

1119 103. Radford CA, Stanley JA, Simpson SD, Jeffs AG. Juvenile coral reef fish use sound to locate habitats
1120 *Coral Reefs.* 2011;30(2):295-305.

1121 104. Cato DH. Marine biological choruses observed in tropical waters near Australia. *J Acoust Soc Am.*
1122 1998;64(3):736-743.

1123 105. Leis J, Carson-Ewart B, Cato D. Sound detection in situ by the larvae of a coral-reef damselfish
1124 (Pomacentridae). *Mar Ecol Prog Ser.* 2002;232(1):259-268.

1125 106. Tolimieri N, Haine O, Montgomery JC, Jeffs A. Ambient sound as a navigational cue for larval reef
1126 fish. *Bioacoustics.* 2012;12(2-3):214-217.

1127 107. Leis JM, Carson-Ewart BM. Orientation of pelagic larvae of coral-reef fishes in the ocean. *Mar Ecol*
1128 *Prog Ser.* 2003;252(1):239-253.

1129 108. Louise R, Rice AN. Vibrational and acoustic communication in fishes: The overlooked overlap
1130 between the underwater vibroscape and soundscape. *J Acoust Soc Am.* 2023;154(4):2708-2720.

1131 109. Klages M, Muyakshin S, Soltwedel T, Arntz WE. Mechanoreception, a possible mechanism for food
1132 fall detection in deep-sea scavengers. *Deep-Sea Res Pt I.* 2002;49(1):143-155.

1133 110. Bart AN, Clark J, Young J, Zohar Y. Underwater ambient noise measurements in aquaculture
1134 systems: a survey. *Aquacult Eng.* 2001;25(2):99-110.

1135 111. Radford CA, Slater MJ. Soundscapes in aquaculture systems. *Aquacult Env Interac.* 2018;11:53-62.

1136 112. Yao J, Cao J. Analysis of Noise Spectrum Characteristics and Application of Denoise Processing in
1137 Chinese Sturgeon Conserving and Breeding Workshop. *Noi Vib Contr.* 2022;42(3):192-195,214.

1138 113. Andrew W, David L, James Y, et al. Scoping a Public Health Impact Assessment of Aquaculture with
1139 Particular Reference to Tilapia in the UK. *ISRN Publ Health.* 2012;2

1140 114. Leiming Y, Xuezhong C, Xuguang Z, Lingzhi L, Hongliang H. Measurement and analysis of the
1141 aquaculture noise for *Larimichthys crocea* in the fiberglass fish tank. *Mar Fish.* 2017;39(3):314-321.

1142 115. Violet M, Franck V. Analysis of Group of Fish Response to Startle Reaction. *J Nonlinear Sci.*
1143 2022;32(6)

1144 116. Yulin H. Response to the acoustic stimulation of common sea bass (*Lateolabrax Japonicus*). *Journal*
1145 *of Oceanography in Taiwan Strait.* 1983;02:119-125.

1146 117. Van HY, Fine ML, Hom NS, Colon WE. Variability in the role of the gasbladder in fish audition. *J*
1147 *Comp Physiol A.* 2000;186(5):435-445.

1148 118. Stone JK, Moro L. Occupational noise exposure in Canada's salmonid aquaculture industry.
1149 *Aquaculture.* 2022;550:737831.

1150 119. WuÈrsig B, C.R. Greene J, Jefferson TA. Development of an air bubble curtain to reduce underwater
1151 noise of percussive piling. *Mar Environ.* 2000;49(1):79-93.

1152 120. Celi M, Filiciotto F, Vazzana M, et al. Shipping noise affecting immune responses of European spiny
1153 lobster (*Palinurus elephas*). *Can J Zool.* 2015;93(2):113-121.

1154 121. Anderson PA, Berzins IK, Fogarty F, Hamlin HJ, Jr. LJG. Sound, stress, and seahorses: The
1155 consequences of a noisy environment to animal health. *Aquaculture.* 2011;311(1-4):129-138.

1156 122. Hang S, Zhao J, Ji B, et al. Impact of underwater noise on the growth, physiology and behavior of
1157 *Micropterus salmoides* in industrial recirculating aquaculture systems. *Environ Pollut.* 2021;291:118152.

123. Dooling RJ, Leek MR, Popper AN. Effects of noise on fishes: What we can learn from humans and birds. *Integr Zool.* 2015;10(1):29-37.
124. Lonsbury-Martin BL, Martin GK, Bohne BA. Repeated TTS exposures in monkeys: alterations in hearing, cochlear structure, and single-unit thresholds. *J Acoust Soc Am.* 1987;81(5):1507-1518.
125. Hamernik RP, Patterson JH, Turrentine GA, Ahroon WA. The quantitative relation between sensory cell loss and hearing thresholds. *Hear Res.* 1989;38(3):199-211.
126. Johnsson LG, Jr JEH. Sensory and neural degeneration with aging, as seen in microdissections of the human inner ear. *Ann Otol Rhinol Laryngol.* 1972;81(2):179-193.
127. Kujawa SG, Liberman MC. Adding Insult to Injury: Cochlear Nerve Degeneration after "Temporary" Noise-Induced Hearing Loss. *J Neurosci.* 2009;29(45):14077-14085.
128. Scholik AR, Yan HY. Effects of underwater noise on auditory sensitivity of a cyprinid fish. *J Acoust Soc Am.* 2000;107(5):2786-2786.
129. Scholik AR, Yan HY. The effects of noise on the auditory sensitivity of the bluegill sunfish, *Lepomis macrochirus*. *Comp Biochem Physiol A Mol Integr Physiol.* 2002;133(1):43-52.
130. Scholik AR, Yan HY. Effects of Boat Engine Noise on the Auditory Sensitivity of the Fathead Minnow, *Pimephales promelas*. *Environ Biol Fish.* 2002;63(2):203-209.
131. Maurer N, Baltzer J, Schaffeld T, Ruser A, Schnitzler JG, Siebert U. Effects of amplitude and duration of noise exposure on the hearing and anti-predator behaviour of common roach (*Rutilus rutilus*) and sand goby (*Pomatoschistus minutus*). *J Acoust Soc Am.* 2023;154:671-681.
132. Breitzler L, Lau IH, Fonseca PJ, Vasconcelos RO. Noise-induced hearing loss in zebrafish: investigating structural and functional inner ear damage and recovery. *Hear Res.* 2020;391:107952.
133. Nissen AC, Vetter B, Rogers L, Mensinger AF. Impacts of broadband sound on silver (*Hypophthalmichthys molitrix*) and bighead (*H. nobilis*) carp hearing thresholds determined using auditory evoked potential audiometry. *Fish Physiol Biochem.* 2019;45(4):1683-1695.
134. Caiger P, Montgomery J, Radford C. Chronic low-intensity noise exposure affects the hearing thresholds of juvenile snapper. *Mar Ecol Prog Ser.* 2012;466:225-232.
135. Amoser S, Ladich F. Diversity in noise-induced temporary hearing loss in otophysine fishes. *J Acoust Soc Am.* 2003;113(4):2170-2179.
136. Smith ME, Kane AS, Popper AN. Noise-induced stress response and hearing loss in goldfish (*Carassius auratus*). *J Exp Biol.* 2004;207(3):427-435.
137. Clark CW, Ellison WT, Hatch BoL, Parijs SMV, Frankel A, Ponirakis D. Acoustic masking in marine ecosystems: intuitions, analysis, and implication. *Mar Ecol Prog Ser.* 2009;395:201-222.
138. Zhang X, Guo H, Chen J, et al. Potential effects of underwater noise from wind turbines on the marbled rockfish (*Sebasticus marmoratus*) *J Appl Ichthyol.* 2021;37:514-522.
139. Pottinger T, Yeomans W, Carrick T. Plasma cortisol and 17 β -oestradiol levels in roach exposed to acute and chronic stress. *J Fish Biol.* 2010;54(3):525-532.
140. Montero D, Tort LL, Izquierdo MS, et al. Hematological recovery in *Sparus aurata* after bleeding. A time course study. *Rev Esp Fisiol.* 1995;51(4):219-226.
141. Wysocki LE, Dittami JP, Ladich F. Ship noise and cortisol secretion in European freshwater fishes. *Biol Conserv.* 2006;128(4):501-508.
142. Wei CA, Lin TH, Chen RD, Tseng YC, Shao YT. The effects of continuously acoustical stress on cortisol in milkfish (*Chanos chanos*). *Gen Comp Endocr.* 2018;257:227-234.

143. Huixiong S, Haifeng J, Zhongjie Y, Yajun W, Songhai LI, Jilin XU. The effect of ship noise on the secretion of cortisol in *Lateolabrax japonicus* and *Pseudosciaena crocea*. *Acta Ecologica Sinica*. 2010;30(14):3760-3765.
144. Filiciotto F, Giacalone VM, Fazio F, et al. Effect of acoustic environment on gilthead sea bream (*Sparus aurata*): Sea and onshore aquaculture background noise. *Aquaculture*. 2013;414:36-45.
145. Chang H-Y, Lin T-H, Anraku K, Shao YT. The Effects of Continuous Acoustic Stress on ROS Levels and Antioxidant-related Gene Expression in the Black Porgy (*Acanthopagrus schlegelii*). *Zool Stud*. 2018;57:e59.
146. Zhang Y, Shitu A, Hang S, et al. Assessing the Impacts of Aquaculture Soundscapes on the Growth, Physiology and Behavior of *Micropterus salmoides*. *Fishes*. 2023;8:377.
147. Filiciotto F, Cecchini S, Buscaino G, Maccarrone V, Piccione G, Fazio F. Impact of aquatic acoustic noise on oxidative status and some immune parameters in gilthead sea bream *Sparus aurata* (Linnaeus, 1758) juveniles. *Aquac Res*. 2017;48(4):1895-1903.
148. Buscaino G, Filiciotto F, Buffa G, et al. Impact of an acoustic stimulus on the motility and blood parameters of European sea bass (*Dicentrarchus labrax* L.) and gilthead sea bream (*Sparus aurata* L.). *Mar Environ*. 2010;69:136-142.
149. Rita T, Amorim MCP, Fonseca PJ, et al. Impact of anthropogenic noise on the survival and development of meagre (*Argyrosomus regius*) early life stages. *Mar Environ*. 2023;185
150. Monica C, Francesco F, Giulia M, et al. Vessel noise pollution as a human threat to fish: assessment of the stress response in gilthead sea bream (*Sparus aurata*, Linnaeus 1758). *Fish Physiol Biochem*. 2016;42(2):631-641.
151. Wong MI, Lau IH, Gordillo-Martinez F, Vasconcelos RO. The effect of time regime in noise exposure on the auditory system and behavioural stress in the zebrafish. *Sci Rep*. 2022;12:15353.
152. Sapozhnikova YP, Koroleva AG, Yakhnenko VM, et al. Molecular and cellular responses to long-term sound exposure in peled (*Coregonus peled*). *J Acoust Soc Am*. 2020;148(2):895-907.
153. Lin T, Wang C, Liu X, Zhang D. Impacts of ship noise on the growth and immunophysiological response in the juveniles of two Sciaenidae species, *Larimichthys crocea* and *Nibea albiflora*. *J Appl Ichthyol*. 2019;35(6):1234-1241.
154. Alcaraz AJG, Baraniuk S, Mikulášek K, et al. Comparative analysis of transcriptomic points-of-departure (tPODs) and apical responses in embryo-larval fathead minnows exposed to fluoxetine. *Environ Pollut*. 2022;295:118667.
155. Velculescu VE, Zhang L, Zhou W, et al. Characterization of the Yeast Transcriptome. *Cell*. 1997;88:243-251.
156. Xuguang Z, Jun Z, Wengang X, Wei Z, Huafeng Z, Jun L. Transcriptomic and Behavioral Studies of Small Yellow Croaker (*Larimichthys polyactis*) in Response to Noise Exposure *Animals*. 2022;12(16):2061.
157. Andrews CD, Payne JF, Rise ML. Identification of a gene set to evaluate the potential effects of loud sounds from seismic surveys on the ears of fishes: a study with *Salmo salar*. *J Fish Biol*. 2014;84:1793-1819.
158. Schuck JB, Sun H, Penberthy WT, Cooper NGF, Li X, Smith ME. Transcriptomic analysis of the zebrafish inner ear points to growth hormone mediated regeneration following acoustic trauma. *BMC Neurosci*. 2011;12:88.
159. Yong Z, Chunhua L, Jiehao L, et al. Multi-omics reveals response mechanism of liver metabolism of hybrid sturgeon under ship noise stress. *Sci Total Environ*. 2022;851:158348.

1243 160. Wysocki LE, Davidson JW, Smith ME, et al. The effects of aquaculture production noise on hearing,
1244 growth, and disease resistance of rainbow trout, *Oncorhynchus mykiss*. *Aquaculture*. 2007;272(1-
1245 4):687-697.

1246 161. Kuskü H, Ergün S, Yılmaz S, Güroy B, Yigit M. Impacts of Urban Noise and Musical Stimuli on Growth
1247 Performance and Feed Utilization of Koi fish (*Cyprinus carpio*) in Recirculating Water Conditions. *Türk*
1248 *J Fish Aquat Sc*. 2019;19(6):513-523.

1249 162. Nedelec SL, Simpson SD, Morley EL, Nedelec B, Radford AN. Impacts of regular and random noise
1250 on the behaviour, growth and development of larval Atlantic cod (*Gadus morhua*). *Proc R Soc B*.
1251 2015;282:20151943.

1252 163. Butler JM, Maruska KP. Underwater noise impairs social communication during aggressive and
1253 reproductive encounters. *Anim Behav*. 2020;164:9-23.

1254 164. Jong Kd, Amorim MCP, Fonseca PJ, Fox CJ, Heubel KU. Noise can affect acoustic communication
1255 and subsequent spawning success in fish. *Environ Pollut*. 2018;237:814-823.

1256 165. Crovo JA, Mendonça MT, Johnston CE. Acoustic modulation of reproductive hormones in the
1257 blacktail shiner, *Cyprinella venusta*, a soniferous cyprinid. *Anim Behav*. 2022;186:101-106.

1258 166. Engås A, Løkkeborg S. Effects of seismic shooting and vessel-generated noise on fish behaviour and
1259 catch rates. *Bioacoustics*. 2002;12(2-23):313-316.

1260 167. Codarin A, Wysocki LE, Ladich F, Picciulin M. Effects of ambient and boat noise on hearing and
1261 communication in three fish species living in a marine protected area (Miramare, Italy). *Mar Pollut Bull*.
1262 2009;58(12):1880-1887.

1263 168. Neo YY, Parie L, Bakker F, et al. Behavioral changes in response to sound exposure and no spatial
1264 avoidance of noisy conditions in captive zebrafish. *Front Behav Neurosci*. 2015;9:28.

1265 169. Neo YY, Seitz J, Kastelein RA, Winter HV, Cate Ct, Slabbekoorn H. Temporal structure of sound
1266 affects behavioural recovery from noise impact in European seabass. *Biol Conserv*. 2014;178:65-73.

1267 170. Sabet SS, Neo YY, Slabbekoorn H. The effect of temporal variation in sound exposure on swimming
1268 and foraging behaviour of captive zebrafish. *Anim Behav*. 2015;107:49-60.

1269 171. Tlustý MF, Andrew J, Baldwin K, Bradley TM. Acoustic conditioning for recall/recapture of escaped
1270 Atlantic salmon and rainbow trout. *Aquaculture*. 2008;274(1):57-64.

1271 172. Nestler JM, Ploskey GR, Pickens J, Menezes J, Schilt C. Responses of blueback herring to high-
1272 frequency sound and implications for reducing entrainment at hydropower dams. *North American*
1273 *Journal of Fisheries Management*. 1992;12(4):667-683.

1274 173. Price NW, Liu Y, Chen K-S, et al. Acute noise is harmful on the anti-predator behaviour of
1275 commercially important juvenile coral reef fishes. *Behav Process*. 2023;210:104908.

1276 174. Stasso JJ, Pieniazek RH, Higgs DM. Interspecific variation in the response of fish to anthropogenic
1277 noise. *Freshwater Biol*. 2022;68:25-32.

1278 175. Hasan MR, Crane AL, Poulin NP, Ferrari MCO, Chivers DP. Altered acoustic environments influence
1279 boldness in minnows. *Appl Anim Behav*. 2018;209(109-113)

1280 176. Sabet SS, Wesdorp K, Campbell J, Snelderwaard P, Slabbekoorn H. Behavioural responses to sound
1281 exposure in captivity by two fish species with different hearing ability. *Anim Behav*. 2016;116:1-11.

1282 177. Lagardère JP. Effects of noise on growth and reproduction of *Crangon crangon* in rearing tanks.
1283 *Mar Biol*. 1982;71(2):177-185.

1284 178. Regnault M, Lagardère J-P. Effects of ambient noise on the metabolic level of *Crangon*
1285 *crangon*(Decapoda, Natantia). *Mar Ecol Prog Ser*. 1983;11:71-78.

- 1286 179. Nedelec SL, Radford AN, Simpson SD, Nedelec B, Lecchini D, Mills SC. Anthropogenic noise playback
1287 impairs embryonic development and increases mortality in a marine invertebrate. *Sci Rep.* 2014;4(1):1-
1288 4.
- 1289 180. André M, Solé M, Lenoir M, et al. Low-frequency sounds induce acoustic trauma in cephalopods.
1290 *Front Ecol Environ.* 2011;9(9):489-493.
- 1291 181. Solé M, Sigray P, Lenoir M, Schaar Mvd, Lalander E, André M. Offshore exposure experiments on
1292 cuttlefish indicate received sound pressure and particle motion levels associated with acoustic trauma.
1293 *Sci Rep.* 2017;7(1):1-13.
- 1294 182. Samson JE, Mooney TA, Gussekloo SWS, Hanlon RT. Graded behavioral responses and habituation
1295 to sound in the common cuttlefish *Sepia officinalis*. *J Exp Biol.* 2014;217(24):4347-4355.
- 1296 183. Peng C, Zhao X, Liu S, et al. Effects of anthropogenic sound on digging behavior, metabolism,
1297 $\text{Ca}^{2+}/\text{Mg}^{2+}$ ATPase activity, and metabolism-related gene expression of the bivalve *Sinonovacula*
1298 *constricta*. *Sci Rep.* 2016;6(1):1-12.
- 1299 184. Mooney TA, Samson JE, Schlunk AD, Zacarias S. Loudness-dependent behavioral responses and
1300 habituation to sound by the longfin squid (*Doryteuthis pealeii*). *J Comp Physiol A.* 2016;202(7):489-501.
- 1301 185. Wale MA, Briers RA, Hartl MGJ, Bryson D, Diele K. From DNA to ecological performance: Effects of
1302 anthropogenic noise on a reef-building mussel. *Sci Total Environ.* 2019;689:126-132.
- 1303 186. Filiciotto F, Vazzana M, Celi M, et al. Behavioural and biochemical stress responses of *Palinurus*
1304 *elephas* after exposure to boat noise pollution in tank. *Mar Pollut Bull.* 2014;84(1-2):104-114.
- 1305 187. Celi M, Filiciotto F, Parrinello D, et al. Physiological and agonistic behavioural response of
1306 *Procambarus clarkii* to an acoustic stimulus. *J Exp Biol.* 2012;216(4):709-718.
- 1307 188. Wale MA, Simpson SD, Radford AN. Size-dependent physiological responses of shore crabs to
1308 single and repeated playback of ship noise. *Biol Lett.* 2013;9(2):20121194.
- 1309 189. Christian L, Timothy M. Zebrafish housing systems: a review of basic operating principles and
1310 considerations for design and functionality. *ILAR J.* 2012;53(2):179-191.
- 1311 190. Davidson J, Frankel AS, Ellison WT, et al. Minimizing noise in fiberglass aquaculture tanks: Noise
1312 reduction potential of various retrofits. *Aquacult Eng.* 2007;37(2):125-131.

1313