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A trait-based framework to identify North Sea fauna vulnerable to underwater noise

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ABSTRACT

In the absence of an internationally coordinated management strategy, continued exploitation of the North Sea is expected to exacerbate underwater radiated noise (URN), heightening risks of adverse impacts on marine life. Identifying indicator species and their habitats is a fundamental step in the EU framework for setting a scientifically grounded underwater noise limit value (UNLV). While past research has primarily emphasized marine mammals, there is an increasing effort to highlight that the impacts of URN extend to fishes and invertebrates. To support indicator species selection in the North Sea for URN risk assessment, a trait-based vulnerability scoring system for marine mammals, fishes and invertebrates was developed. Each scoring system evaluates multiple attributes related to a species' capacity to detect and produce sound, as well as the documented impacts from both impulsive and continuous anthropogenic noise, and highlights species of particular concern and socio-ecological significance. Five potential indicator species were identified from each of the three taxonomic groups (marine mammals, fishes and invertebrates) for URN risk assessment. The proposed vulnerability scoring system serves as an adaptive framework, open to iterative refinement as bioacoustics knowledge advances. Although data gaps persist, the establishment of regional UNLV to safeguard vulnerable species should not be delayed. By linking URN exposure with key habitats of identified indicator species, this approach facilitates an ecosystem-based management of URN in the North Sea and provides a transferable framework for other regions.

1. Introduction

Over the past century, the North Sea has been under escalating anthropogenic pressures. The region/basin has been identified as one of the most impacted regions of human developments globally (Halpern et al., 2008; Emeis et al., 2015). A newly recognised pollutant associated with anthropogenic activities is underwater radiated noise (URN; European Commission, 2008). The North Sea is one of the busiest shipping areas in the world, and numerous recreational boats operate in coastal, shallow, sensitive areas with high biodiversity and important ecosystem goods and services. Furthermore, a large-scale expansion of offshore wind farms is foreseen in the region to meet the EU's carbon emission reduction targets (European Commission, 2020). These activities all contribute to increasing ambient underwater sound levels, highlighting the further urbanisation of the North Sea (Van Mil and Rutte, 2021). In the absence of regulatory measures, URN is expected to intensify in the North Sea, with growing risks of detrimental impacts on marine life.

Anthropogenic noise is typically categorised as “impulsive” or

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"continuous". In the context of the EU's Marine Strategy Framework Directive (MSFD), the definitions applied in this paper are those of the EU expert group Technical Group on underwater noise (TG Noise). According to the SATURN terminology standard, adopted by TG Noise (Borsani et al., 2023; p47), impulsive sound is characterised by one or more brief bursts of sound pressure, while continuous sound is sound for which the mean square sound pressure is approximately constant for a specified range of averaging times, within a specified time window (Ainslie et al., 2024). Common sources of impulsive sound include explosions, seismic surveys and pile driving (Hildebrand, 2009), often associated with the construction or repair of bridges, docks, offshore wind farms and other infrastructures (Popper and Hastings, 2009). While explosions produce single or few signals per event, seismic airguns, ultrasonic antifouling devices and pile driving generate series of impulsive sounds. In contrast, tonal or broadband continuous sounds generally have a lower source level compared to impulsive sounds but persist over longer periods. Typical sources of continuous noise include vessel traffic, drilling and the operation of turbines. Although seismic surveys and pile driving are impulsive near the source, their sounds may resemble continuous noise at greater distances (Erbe et al., 2016).

Masking of biologically important sounds, behavioural changes, physiological stress, hearing impairment and mortality are some of the consequences of URN to aquatic animals (Slabbekoorn et al., 2010; Erbe et al., 2016; Southall et al., 2019; Solé et al., 2023). Although much attention has been focused on marine mammals in the past, there is an increasing effort to highlight that the impacts of URN extend to fishes, and more recently, to invertebrates. Similar to its impacts on marine mammals, URN has been demonstrated to disrupt critical biological processes—including navigation, communication, foraging, predator avoidance, settlement, reproduction, growth and development in fishes and invertebrates (Simpson et al., 2016; De Jong et al., 2020; Rising et al., 2022; Solé et al., 2023). These disruptions may have implications for survival and fitness, and can cascade to population-level impacts, potentially altering the structure and functioning of ecosystems. Animal sensitivity to URN generally depends on whether the sound overlaps in frequency with the hearing ability of the animal and whether the noise reaches levels above the animal's hearing threshold at a certain distance (Slabbekoorn et al., 2010; Duarte et al., 2021). Both impulsive and continuous noise may overlap with the hearing range of a wide range of taxa, including marine mammals, fishes and invertebrates (Popper and Hastings, 2009; Erbe et al., 2019; Popper and Hawkins, 2019; Duarte et al., 2021; Solé et al., 2023; Vereide and Kühn, 2023). The hearing abilities of marine mammals vary considerably across species, particularly regarding the frequency ranges to which species are most sensitive, spanning from 7 Hz up to 165 kHz (Southall et al., 2019; National Marine Fisheries Service, 2024). Based on direct behavioural and electrophysiological measurements, as well as indirect predictions derived from inner ear morphology, modelling, behaviour, vocalizations and taxonomy, marine mammals are typically classified into functional hearing groups. These include low-frequency cetaceans (including all Mysticetes), high-frequency cetaceans (including most delphinid species, beaked whales, sperm whales and killer whales), very high-frequency cetaceans (including true porpoises, most river dolphin species, pygmy and dwarf sperm whales, and certain oceanic dolphins), otariid pinnipeds (including sea lions and fur seals) and phocid pinnipeds (including all true seals). However, not all species within a group are sensitive across the entire frequency range attributed to that group (Southall et al., 2019; National Marine Fisheries Service, 2024).

Fishes are a diverse group of animals, with a wide range of hearing abilities. Some fish species perceive sound pressure, whereas all fish, and, based on present knowledge, all invertebrates, are sensitive to particle motion, or the displacement of particles within the medium through which kinetic energy manifests itself during the passage of a sound wave (Popper et al., 2014; Popper and Hawkins, 2018; Veith et al., 2024). Despite the widely acknowledged importance of particle motion in studying the sensitivity of fishes and invertebrates to sound, there still has been limited research in quantifying its impacts, mainly due to the difficulty of quantifying the relationship between pressure and particle motion, especially close to boundaries, e.g. in shallow waters (Parvulescu, 1964; Nedelec et al., 2016; Popper and Hawkins, 2018).

As for fish exposure to sound, criteria and guidelines have been set based on the different morphologies of their auditory apparatus, which mainly concern whether the fish possesses a swim bladder, and whether this swim bladder is in proximity of or connected to the ear (otolith) through special hearing adaptations (Popper et al., 2014; Popper and Hawkins, 2019). Lucke et al. (2024) described sound pressure sensitive and acceleration sensitive hearing groups. The sound pressure sensitive groups comprise fish with a swim bladder involved in hearing and are categorised into bladdered fish without adaptation to ears (such as Atlantic cod *Gadus morhua*), fish with anatomical structures that link the bladder to the ear (such as the Atlantic herring *Clupea harengus*; Fritzsch, 2000), and bladdered fish with ultrasonic adaptation (such as shads *Alosa alosa* and *Alosa fallax*). Fishes that either lack a swim bladder (including cartilaginous fishes and flatfish) or with a swim bladder not involved in hearing are acceleration sensitive hearing groups and are primarily particle motion-sensing fish (Popper and Hawkins, 2018).

Relatively little is known of how marine invertebrates detect sound, and the capacity to produce sounds is only known in crustaceans, bivalves and echinoderms, with crustaceans being the only ones known to actively produce sounds used for communication (Radford and Stanley, 2023). However, different taxa possess a great variety of sensory organs and mechano/hydrodynamic receptors to detect acoustic or vibratory stimuli and water movement, including hair-like superficial receptors, crustacean chordotonal organs and internal statocysts analogous to fish otoliths (Popper et al., 2001; Breithaupt, 2002; Radford and Stanley, 2023; Solé et al., 2023). Benthic species also possibly detect substrate-born vibrations via the seabed (Roberts and Breithaupt, 2016; Radford and Stanley, 2023). A few audiogram studies have shown that cephalopods (Mooney et al., 2010) and decapod crustaceans like crabs, prawns and lobsters (Lovell et al., 2005; Hughes et al., 2014; Dinh and Radford, 2021; Jezequel et al., 2021b; Radford et al., 2022) mainly detect frequencies below 1000 Hz (up to 3000 Hz in crabs and prawn), with highest sensitivity below or around 100–200 Hz. Behavioural experiments show similar sound detection ranges in scallops and oysters (Zhadan, 2005; Charifi et al., 2017), and even jellyfish have been described to possess sensitivity to low frequency sound (Solé et al., 2016). However, the vulnerability of species to noise does not necessarily depend only on the hearing ability, and animals may react to and be affected by noise outside their best hearing frequency range.

Under the EU's MSFD, North Sea countries are required to develop and implement programmes of measures to manage noise pollution and its impacts on biodiversity to achieve or maintain Good Environmental Status (GES). To support this, TG Noise introduced the Level of Onset of Biologically adverse Effects (LOBE), defined as the "noise level at which individual animals start to have adverse effects that could affect their fitness" (Borsani et al., 2023). However, this definition leaves substantial room for interpretation and is therefore difficult to translate into a value that can be directly used for management, as discussed in SATURN Deliverable 2.3 (Ainslie et al., 2024). To facilitate implementation in a regulatory context, Underwater Noise Limit Value (UNLV) has been proposed as a management-oriented concept. UNLV is defined as a specified value of an underwater noise metric, set by an appropriate authority, above which management action is considered necessary. The MSFD requires the definition of regional threshold values (European Commission, 2017). Defining indicator species and their habitats is a fundamental step in the assessment framework for setting the limit value as described by TG Noise (Borsani et al., 2023).

Indicator species are generally selected for the purpose of evaluating ecological integrity, the environmental state or change (Carignan and Villard, 2002), and therefore characterised by high sensitivity to either short-term stress events or long-term changes in the environment

(Siddig et al., 2016). While no single species can fully reflect complex ecological changes (Lindenmayer and Likens, 2011), indicator species are usually selected based on previous research, local abundance, ecological significance and/or conservation status (Siddig et al., 2016). Hitherto, important taxa (e.g. marine invertebrates, pelagic fish, etc.) have largely been overlooked in environmental risk assessments of noise pollution, despite their abundance and great importance to ecosystem structure and function. Moreover, target species are typically defined a priori for case-study-specific reasons; however, for a large-scale URN impact assessment intended to inform policy, a broad, transparent and systematic approach to evaluate multiple species (Hare et al., 2016) is lacking. Evaluating multiple species across different animal taxa to define indicator species is therefore crucial for a comprehensive and ecosystem-based evaluation of the effects of URN.

To identify potential indicator species in the North Sea for URN risk assessment, a trait-based vulnerability scoring system for marine mammals, fishes and invertebrates was developed and applied as part of the Interreg North Sea project DEMASK (Development and evaluation of noise management strategies to keep the North Sea healthy; https://www.interregnorthsea.eu/demask). The scoring system estimates the relative vulnerability between species to URN, serving as a framework to select suitable indicator species for the assessment of URN impacts. Trait-based approaches are widely applied in ecological risk assessments because they link species' intrinsic characteristics to sensitivity and resilience in response to stressors, even when empirical effect data are limited (Baird et al., 2008). Compared to conventional impact assessments that focus primarily on exposure and direct effects, this approach integrates life-history, physiological and demographic attributes, enabling biologically meaningful comparisons of relative species vulnerability (Butt et al., 2022).

This cross-taxa, multi-criteria approach, which incorporates a broad range of attributes influencing species' vulnerability to URN, allows for a more ecologically relevant assessment of how URN affects the North Sea ecosystem. It aims to capture the complexity of vulnerability, shaped not only by hearing sensitivity but also by individual- and population-level aggravating factors (Calonge et al., in press). Additionally, the scoring system highlights gaps in our knowledge by identifying species that may potentially be vulnerable to URN but are currently not suitable as representative indicator species for risk assessments due to lack of available data.

2. Methods

A trait-based vulnerability scoring system was designed for marine

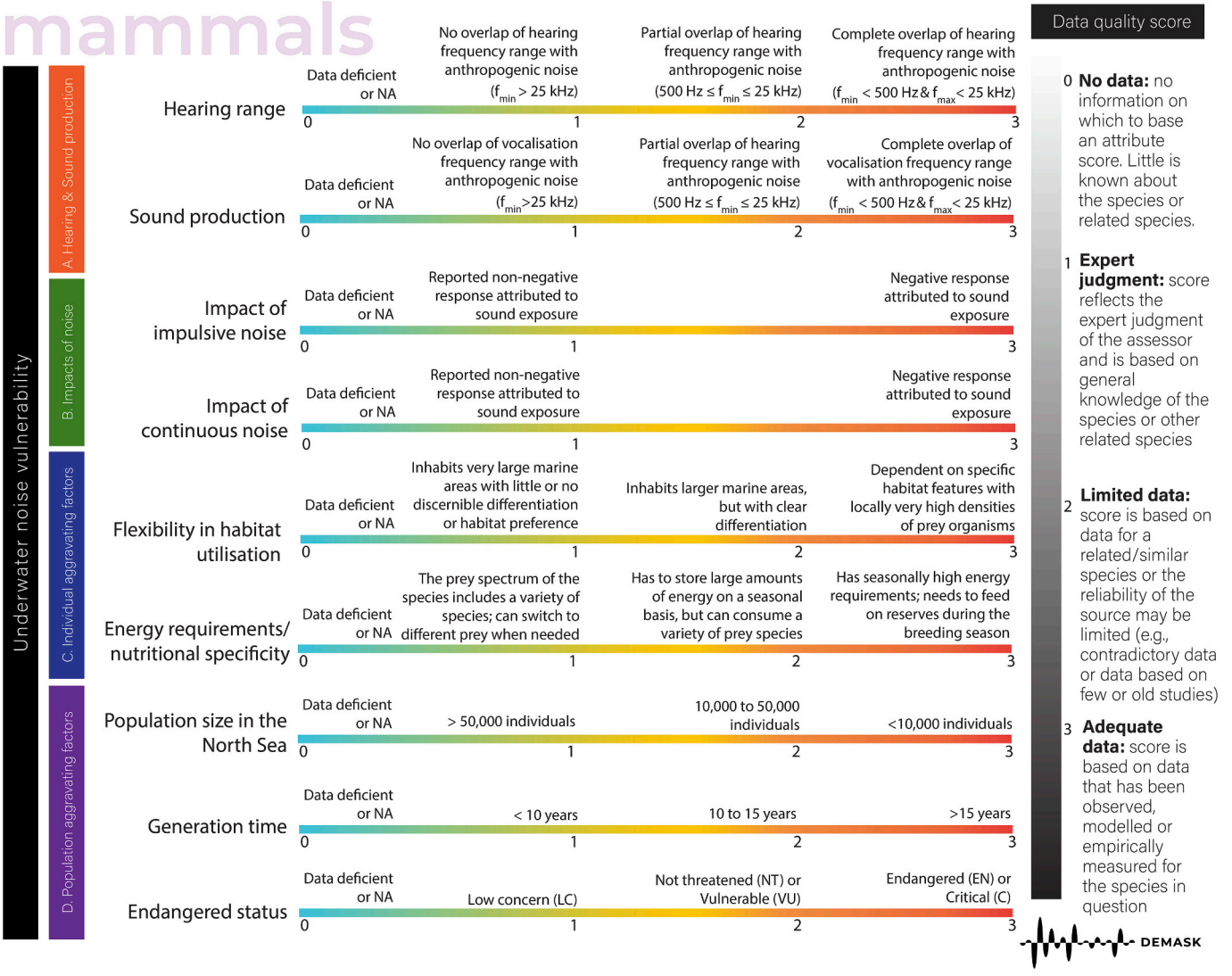

Fig. 1. Vulnerability scoring system developed for marine mammals. This involves four attribute categories: hearing and sound production (A), impacts of noise (B), individual aggravating factors (C) and population aggravating factors (D). Each category includes several vulnerability-defining attributes which can be scored from 0 to 3. The data quality of each attribute is also scored from 0 to 3.

mammals (Fig. 1), fishes (Fig. 2) and invertebrates (Fig. 3). Each scoring system evaluates multiple attributes related to a species' capacity to detect and produce sound, as well as documented impacts from both impulsive and continuous anthropogenic noise (Calonge et al., in press), and highlights species of particular concern and socio-ecological significance. For each evaluated attribute, species received a score from low to high vulnerability (1 to 3) and a data quality score to account for the type, quality and reliability of data used to assess each attribute, ranging from low (1) to adequate (3) data quality. Due to the difficulty of assessing the severity of different types of documented URN impacts, a high vulnerability score of 3 was given if there exists any reported effect on individuals or populations, and a low vulnerability score of 1 if studies indicated no negative response attributed to the sound exposure. When no information was available, the species received a score of 0 for both vulnerability and data quality scores. Equal weighting was employed for all attributes, as there is presently insufficient evidence to justify differential weighting. However, the scoring system should be seen as a framework and an alternative weighting could potentially be incorporated in future assessments as evidence base grows, making this judgement possible.

Eight priority marine mammals were pre-selected based on their importance and abundance in the North Sea ecosystem. However, applying the same approach to fishes and invertebrates was impractical given the region's biodiversity—hundreds of fish and thousands of invertebrate species (e.g. ~6000 marine invertebrate species documented in Southern Scandinavia alone; Hansson, 1994). Instead, we included all fish and invertebrate species for which data were available on at least one attribute related to hearing ability, sound production or documented noise impacts. For each of the selected marine mammal, fish and invertebrate species, an extensive literature review was undertaken to gather information on noise sensitivity, exposure to and impacts caused by URN, but also their socio-ecological status and general life history, habitat use or other relevant traits. The references included mainly peer-reviewed journals, but also conference papers and technical reports.

Additionally, an online expert consultation survey was personally sent to selected experts in the field of bioacoustics, mostly from the North Sea region, to fill the gaps in the literature of species' sensitivity and vulnerability to URN. The experts were allowed to score a maximum of six species from the animal group of their expertise. Where expert responses were sparse, scores were solely based on evidence from the literature. All data processing and analyses were performed in R version

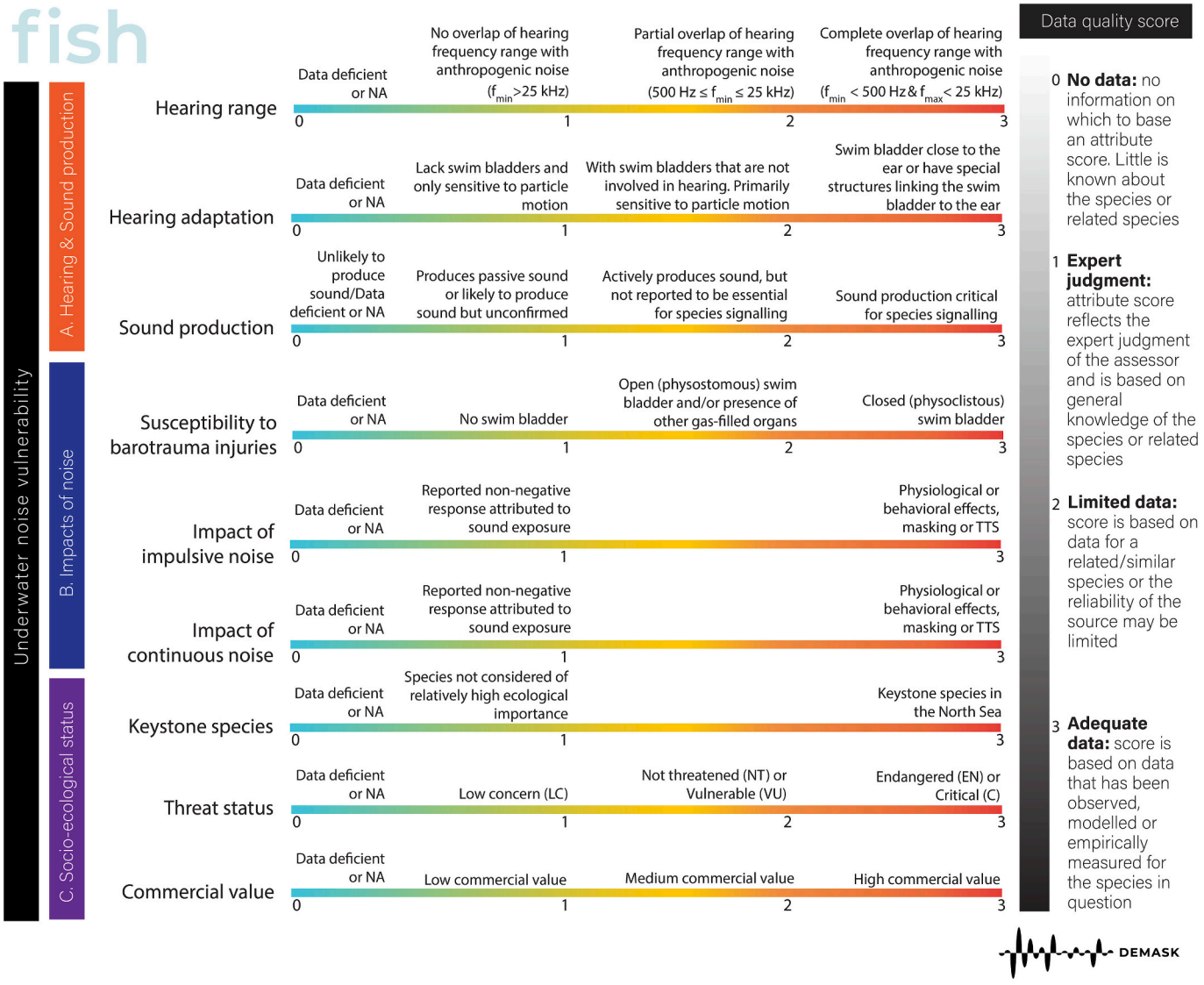

Fig. 2. Vulnerability scoring system developed for fish. This involves three attribute categories: hearing and sound production (A), impacts of noise (B) and socio-ecological status (C). Each category includes several vulnerability-defining attributes which can be scored from 0 to 3. The data quality of attributes related to hearing, sound production and impacts of noise (A&B) is also scored from 0 to 3.

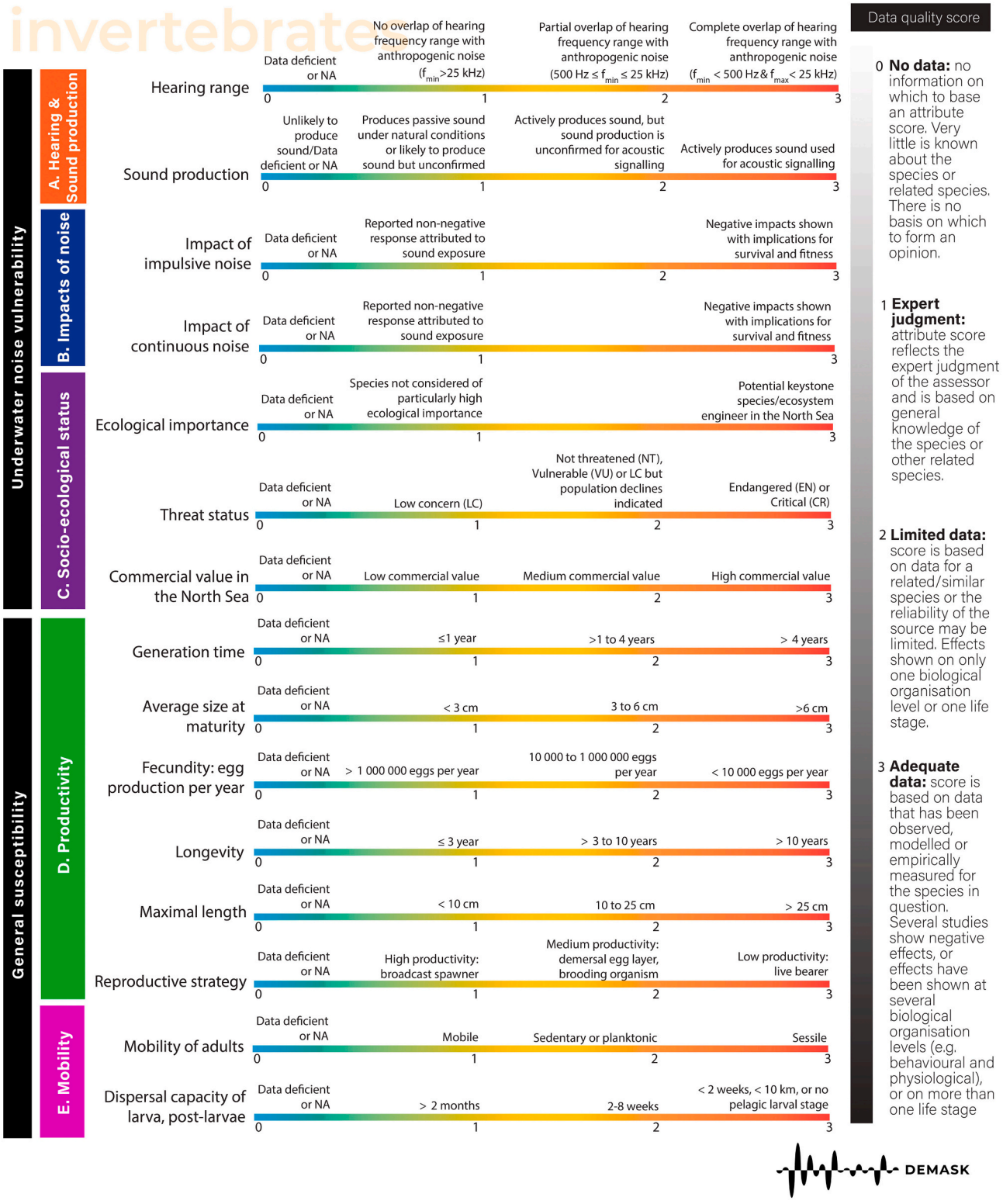

Fig. 3. Vulnerability scoring system developed for invertebrates. This involves three attribute categories related to underwater noise vulnerability: hearing and sound production (A), impacts of noise (B) and socio-ecological status (C). An additional set of basic life-history traits related to productivity (D) and mobility (E) was scored to estimate general susceptibility. Each attribute or trait can be scored from 0 to 3. The data quality of attributes related to hearing, sound production and impacts of noise is also scored from 0 to 3.

4.5.1 (R Core Team, 2025).

2.1. Vulnerability of marine mammals

The vulnerability of each marine mammal species to URN was assessed by integrating four groups of attributes (Fig. 1): sensitivity

based on hearing and sound production (A), vulnerability based on reported impacts of noise (B), aggravating factors at individual level (C) and aggravating factors at population level (D).

2.1.1. Sensitivity based on hearing and sound production

Sensitivity based on hearing and sound production was evaluated by determining the overlap between the species' hearing or vocalization frequency range and the frequency range of anthropogenic underwater noise (Tables S1, S4). Marine mammals possess highly specialized anatomical structures for detecting sound and exhibit acute underwater hearing abilities. As noted above, they are typically grouped into functional hearing categories based on their detectable frequency ranges. Anthropogenic noise is most dominant at low frequencies (< 500 Hz), but certain noise sources also contribute substantially to the mid-frequencies (500 Hz – 25 kHz; Hildebrand, 2009). Complete overlap was assigned when the hearing/vocalization frequency range lay entirely below 25 kHz and included frequencies below 500 Hz. Partial overlap was assigned when the range overlapped with frequencies below 25 kHz but did not meet the criteria for complete overlap (i.e. because it did not include frequencies below 500 Hz and/or extended above 25 kHz). No overlap was assigned when the hearing/vocalization frequency range lay entirely above 25 kHz. For both hearing range and sound production, species with no frequency overlap received a low vulnerability score, partial overlap resulted in a moderate score and complete overlap in a high score.

2.1.2. Vulnerability based on reported impacts of noise

Vulnerability based on reported impacts of noise considered both the impacts of impulsive and continuous noise sources. Marine mammals can exhibit a range of responses to noise, such as avoidance behaviour and disruption of foraging behaviour, which can result in indirect effects on the affected species and ultimately on the population, making the severity and long-term consequences of the impact difficult to quantify. Therefore, no severity scale was applied in this category. Species with documented non-negative responses to sound exposure, such as an absence of observable reaction, the demonstration of investigative behaviour or attraction towards the source, were assigned a low vulnerability score, while species with reported negative responses received a high score.

2.1.3. Aggravating factors at individual level

Aggravating factors at individual level included flexibility in habitat utilisation (home range) and energy requirements/nutritional specificity. Marine mammals may be displaced from suitable habitats due to noise-induced avoidance behaviour. Species with specific habitat requirements, such as access to adequate prey in terms of quantity, size and quality, or to seal haul-out sites, face greater costs than species with greater flexibility in habitat utilisation. Species inhabiting large marine areas without clear habitat preference were assigned a low vulnerability score. A moderate score was given to species occupying broad marine areas with some habitat differentiation, while species dependent on specific habitat features received a high score. Regarding energy requirements, species may differ in their sensitivity to displacement from foraging areas or to disturbances that can reduce foraging time, due to physiological or dietary differences. Generalist feeders with a broad prey spectrum received a low vulnerability score. A moderate score was assigned to generalist feeders that require high-energy food and depend on seasonal energy storage. Specialist feeders with a strong preference for single prey species, combined with high seasonal energy demands and reliance on stored reserves during the breeding season, received a high vulnerability score.

2.1.4. Aggravating factors at population level

Aggravating factors at population level included population size in the North Sea area, generation time and extinction risk status based on the International Union for Conservation of Nature's (IUCN) Red List of Threatened Species at the European level. Large populations are generally more resilient to anthropogenic disturbances than smaller populations. Therefore, species with fewer than 10,000 individuals in the North Sea were given a high vulnerability score, those with a population of 10,001 to 50,000 individuals a moderate score, and populations exceeding 50,000 individuals a low score. Generation time, defined as the average age of reproducing individuals of the current population, reflects the turnover rate in a population. Anthropogenic impacts such as injury, disturbance or habitat degradation can affect individual fitness and adversely affect the population through increased mortality and/or lower reproductive success, with a subsequent impact on population composition. Species with a generation time of under 10 years were scored as low, with 10 to 15 years as moderate, and with more than 15 years as highly vulnerable. For species that are already at risk from other pressures, exposure to underwater noise can act as an additional factor that leads to their decline. Vulnerable or threatened populations are generally more susceptible to anthropogenic stressors than non-threatened populations (Berry et al., 2013), partly explained by reduced genetic diversity, which limits adaptive potential and decreases the capacity of populations to evolve in response to rapid environmental change (Frankham, 2005; Willi et al., 2006). Therefore, species classified as “Least Concern” according to the IUCN Red List status received a low vulnerability score, those listed as “Near Threatened” or “Vulnerable” a moderate score, and “Endangered” or “Critically Endangered” species a high vulnerability score.

For the marine mammals, the results of the literature review (Supplementary Table S1) were assigned a weight equivalent to one expert assessment when calculating the final vulnerability and data quality scores. These final scores, derived from the combined input of all expert assessments and the literature review, were then used to identify indicator species. Indicator species were selected in a way that ensured representation of each functional hearing group, with the highest-scoring species within each group designated as indicator species.

A Principal Components Analysis (PCA) was conducted to explore the relationship between data quality scores of attributes directly related to sound (hearing sensitivity, sound production, impact of impulsive noise, impact of continuous noise) and data quality scores of individual and population aggravating factors (energy requirements, home range, population size and generation time). The PCA positioned the species relative to the variances explained by the different attributes.

2.2. Fishes

To assess the vulnerability of fish species to URN, key attributes were grouped into three major categories (Fig. 2): sensitivity based on hearing and sound production capabilities (A), vulnerability based on reported impacts of noise (B), and lastly, based on the socio-ecological status of the species (C). This allows for a comprehensive scoring system that covers the physiological aspects of the fish, as well as highlighting species of particular concern and ecological significance.

2.2.1. Sensitivity based on hearing and sound production capabilities

Sensitivity based on hearing and sound production factored in the overlap of the hearing frequency range of the fish with URN, the potential for masking of its relevant acoustic cues, and whether it has a swim bladder involved in hearing or a special structure that links the swim bladder to the ear, making it more sensitive to sound pressure. Overlap categories were defined using the same frequency boundaries as for marine mammals (2.1.1.). Acceleration sensitive groups, or those that are primarily or only sensitive to particle motion, such as species that lack a swim bladder and species with swim bladders not involved in hearing, were given lower vulnerability scores.

2.2.2. Vulnerability based on reported impacts of noise

The impact of noise considered the susceptibility of the fish to barotrauma injuries depending on the type of its swim bladder (open or

closed), and whether the fish displayed a negative physiological or behavioural response attributed to continuous or impulsive sound exposure. Physoclistous fish, or those with closed swim bladders, do not have a gut connection and are therefore only able to adjust the volume of gas in their swim bladder through a slower process of gas diffusion (Halvorsen et al., 2012; Casper et al., 2013). Physoclistous fish, being most susceptible to barotrauma injuries, were given higher vulnerability scores.

2.2.3. Socio-ecological status

For the socio-ecological status of the fish, we considered whether the fish was a keystone species, its extinction risk status according to the IUCN Red List of Threatened Species (similar scoring to the mammals) and its commercial value, which can exert additional anthropogenic pressure on populations. As there was no readily available list of marine keystone species from the North Sea, we decided to use the list of potential marine keystone species in the North Sea from Lai et al. (2022). Keystone species were defined by calculating spatial robustness–representing the geographical impact of a species on another species, and spatial vulnerability–indicating how a species is influenced by other species (Lai et al., 2022). To assess the commercial value of fish species, we used the most recent data available on value of landings. For EU countries, we relied on the 2024 Annual Economic Report on the EU Fishing Fleet published by the European Commission's Scientific, Technical and Economic Committee for Fisheries (STECF; Prezello et al., 2024). For the United Kingdom and Norway, we sourced information from national reports, including the UK Sea Fisheries Annual Statistics (Marine Management Organisation, 2024) and export records from the Norwegian Seafood Council (2024). These resources enabled us to identify the species of highest commercial value for the countries bordering the North Sea. Species that were more prominent in national commercial fisheries were considered to have a medium commercial value, while those that were more significant in recreational fishing were assigned with a low commercial value.

We assessed 55 fish species, for which information was available on at least one of the factors based on hearing and sound production or on the reported impacts of noise (Supplementary Table S2). One subclass, Elasmobranchs, was assessed collectively as a single group since available literature on hearing sensitivities and impacts from reported noise were sparse for any species. To facilitate a more representative selection of indicator species, fishes were further classified as demersal or pelagic, and categorised based on their migratory behaviour. As for the expert-based scores, these were compared and verified with the information gathered from the literature. When there was no available information for an attribute for a species, the expert score was used and given a low data quality score of 1. Species with scores from the 90th percentile of both vulnerability and data quality scores were identified as potential indicator species.

A PCA was conducted to explore the relationship of the data quality of URN-related attributes (hearing sensitivity, sound production, hearing adaptation and impacts of impulsive and continuous noise) to the socio-ecological status of the fish (commercial value and ecological importance) and the species' susceptibility to barotrauma injuries. The PCA positioned the species relative to the variances explained by the different attributes.

2.3. Invertebrates

Attributes used to assess the vulnerability of invertebrate species to URN were grouped into the same three major categories (A–C) as for the fish (Fig. 3). For ecological importance, it was considered whether the species functions as keystone species (e.g. as dominant prey/food sources or as important predators) or as an ecosystem engineer that modulates resource availability to other species, including infaunal organisms that bioturbate, bioirrigate and thus oxygenate seabeds, efficient filter feeders that reduce the nutrient load, or species that create habitats for other organisms (e.g. bivalve beds). For threat status, the IUCN Red List of Threatened Species at the European level and at Swedish level (SLU Artdatabanken, 2020) were considered, but also major population declines indicated from the literature. Finally, highly commercial species in the North Sea were identified using the most recent data available on value of landings (Prezello et al., 2024) and were differentiated from those with a medium commercial value and species more prominent in local commercial or recreational fisheries but with high price, while species of low price and/or more significant in recreational fishing were assigned with a low commercial value.

The literature review (Supplementary Table S3) identified altogether 20 invertebrate species from the North Sea region, for which data was available for at least one of the attributes based on hearing ability, sound production or reported impacts of URN. To facilitate a more representative selection of indicator species, invertebrates were further classified as benthic or pelagic.

To estimate the species' general susceptibility to environmental stressors, they were further scored for a set of basic life-history traits related to productivity (D) and mobility (E) (Fig. 3).

2.3.1. Productivity

For productivity (D), generation time, size at maturity, fecundity, longevity, maximal length and reproductive strategy are traits which in combination describe the timing and magnitude of the species' reproduction, growth and survival. For reproductive strategy, broadcast spawners are considered to have high productivity, demersal egg layers and brooding species were classified as medium productivity, while live bearers are considered to have low productivity (no live bearer species in our study). One extra point was assigned to hermaphroditism since this has been shown to increase vulnerability (Roberts and Hawkins, 1999), however, each species could only receive a maximum score of 3 for reproductive strategy.

2.3.2. Mobility

Mobility (E) considered adults' possibility to escape and move to quieter areas if disturbed or stressed by noise, as well as dispersal capability of larvae and post-larvae in terms of duration, i.e. time from hatching to settlement for benthic species or yolk sac re-adsorption for pelagic species or estimated dispersal range in kilometres.

Collectively, these life-history traits were used to estimate how resilient a species would likely be to anthropogenic stressors such as noise pollution. For example, a species with delayed reproduction, low fecundity, long life-span and low mobility is expected to have a lower resilience to stress induced by environmental stressors (Denney et al., 2002; Mace et al., 2008; Bush et al., 2016).

Life history data was based on IUCN Red List of Threatened Species, the Swedish IUCN Red List of Threatened Species (SLU Artdatabanken, 2020), SeaLifeBase, The Marine Life Information Network (MarLIN), World Register of Marine Species (WoRMS) and FAO FishFinder. Where data were lacking, an additional literature review and expert consultation were conducted. When life-history estimates varied across sources, region-specific and conservative estimates that correspond to lower productivity were used (i.e. higher estimates for maximum age, size, age at maturity, size at maturity and lower estimate for fecundity). Since several life-history traits vary with temperature and other environmental parameters, extreme values, most probably representing data from outside the North Sea region, were excluded. The cut-offs for low, medium and high susceptibility for each life history trait were determined by splitting species into three relatively equal sized bins based on the range the trait exhibited, following the procedure of Morgan et al. (2024), although considering the ecological relevance and biases due to the included taxa and species (e.g. all species with an average age at maturity of $\leq$1 year were assigned a low score, although constituting more than one third of the included species).

A combined average score was calculated for each of the three scoring categories assigned to the invertebrates: noise vulnerability,

data quality and general susceptibility (Fig. 3). Since each attribute for each scoring category was assigned a score from low to high (0 to 3), a maximum average score of 3 was possible for each of the scoring categories. The cut-offs for low-medium-high classification were set as follows: an average of <1 was classified as low, >1 but <2 was classified as medium, and an average score of ≥2 was classified as high, for all the three scoring categories.

A PCA was conducted to explore the relationship between attributes related to URN vulnerability (hearing range, sound production, impact of impulsive and continuous noise, ecological importance, threat status and commercial value). A separate PCA was conducted relating the noise vulnerability score to the scores of the different life-history traits considered to assess general susceptibility, positioning the species relative to the variances explained by these respective components.

3. Results

3.1. Marine mammals

The eight pre-selected marine mammal species assessed using the vulnerability scoring system for the North Sea were the harbour porpoise (*Phocoena phocoena*), common minke whale (*Balaenoptera a. acutorostrata*), bottlenose dolphin (*Tursiops truncatus*), white-beaked dolphin (*Lagenorhynchus albirostris*), killer whale (*Orcinus orca*), Atlantic white-sided dolphin (*Lagenorhynchus acutus*), Atlantic harbour seal (*Phoca vitulina vitulina*), and Atlantic grey seal (*Halichoerus grypus*) (Supplementary Table S1).

Expert evaluations were received from eight experts for six marine mammal species. The vulnerability scores derived from the expert evaluations closely aligned with those based on the literature review (Fig. 4A), particularly in terms of relative species ranking. Since the values for the attributes population size in the North Sea area, IUCN Red List status and generation time are fixed, these were taken directly from the literature and incorporated into the expert-based vulnerability scores to ensure comparability (Fig. 4A). Among the assessed species, the common minke whale received the highest vulnerability score, followed by the white-beaked dolphin and the Atlantic harbour seal, which were assigned comparable scores. Lower scores were assigned to the Atlantic grey seal and the harbour porpoise, with the bottlenose dolphin ranking lowest of all species assessed by experts. The Atlantic white-sided dolphin and killer whale, both of which received low scores in the literature-based vulnerability and data quality assessments, were not evaluated by any expert. In general, discrepancies in vulnerability scores between experts and the literature review primarily arose due to missing expert evaluations for specific attributes due to scoring uncertainty, resulting in lower overall scores (Fig. 4A).

Indicator species were selected based on the highest vulnerability and data quality scores within each functional hearing group. The harbour porpoise was selected for very high-frequency cetaceans, the white-beaked dolphin for high-frequency cetaceans, and the common minke whale for low-frequency cetaceans. Both the Atlantic harbour seal and Atlantic grey seal were included as indicator species for phocid pinnipeds due to their closely matched scores (Table 1; Fig. 5).

While some species received detailed comments from experts, others had individual attributes left unevaluated. Combined with a review of score ranges, several key patterns of uncertainty and consensus were revealed. For the harbour porpoise, uncertainty was expressed regarding energy requirements, while experts emphasized the species' high auditory sensitivity, including the potential for temporary hearing threshold shifts (TTS) and permanent threshold shifts (PTS). In contrast, no consensus emerged for the bottlenose dolphin, for which insufficient data on energy requirements, population size in the North Sea area and generation time contributed to a low overall vulnerability score. For the white-beaked dolphin, experts noted uncertainty regarding the impacts of impulsive noise and energy requirements. Despite this, the vulnerability scores showed high agreement across several attributes. Only two assessments were received for the common minke whale. One expert expressed uncertainty about the impacts of continuous noise, which contributed to the species' comparably low vulnerability score of 17 (Fig. 4A, bar with asterisk). For the Atlantic harbour seal and Atlantic grey seal, experts expressed uncertainty regarding the impact of continuous noise in the comments. Despite these uncertainties, there

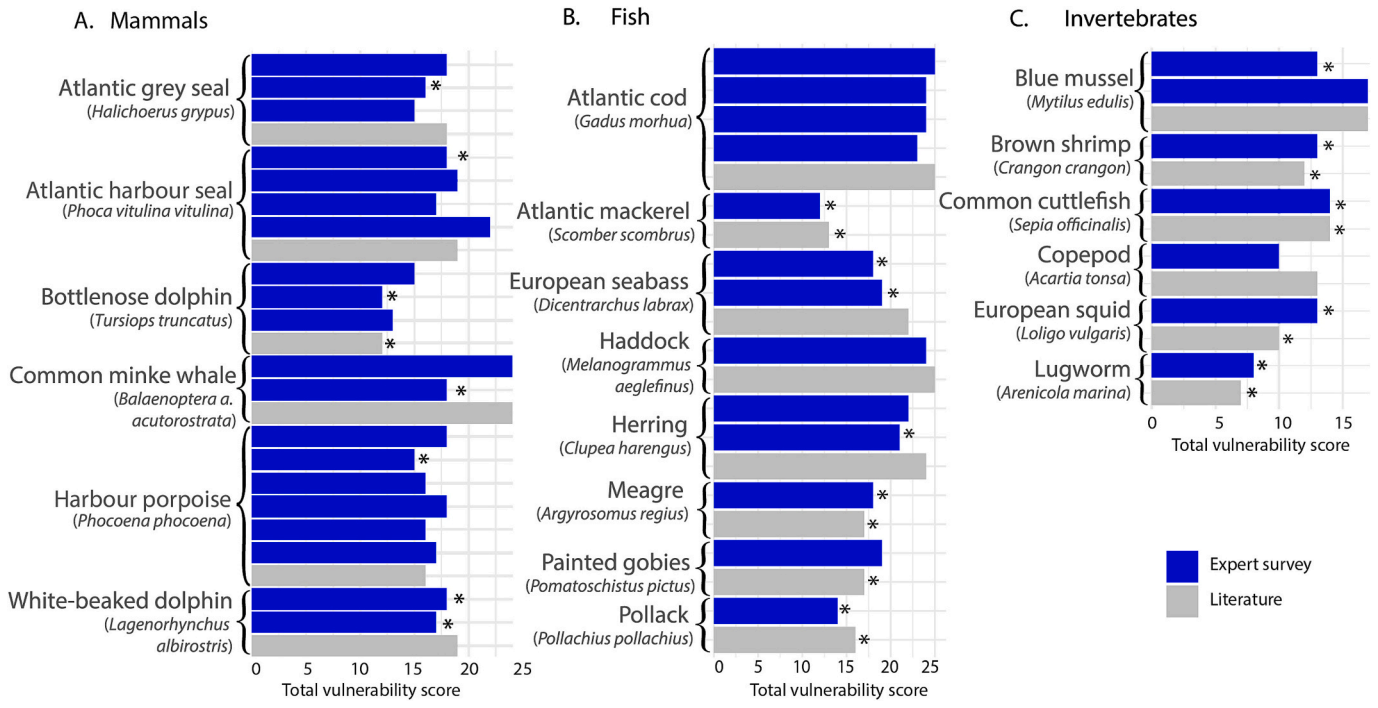

Fig. 4. Scores from the expert survey (blue bars) compared to the literature-based scoring (grey). Each blue bar represents one scoring from one expert. The asterisks at the end of the bars indicate that for at least one attribute, either the experts responded 'Unsure' or no information could be gathered from the literature. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1
Literature-based scoring of marine mammals that received the highest total vulnerability and data scores per functional hearing group. Each scored attribute is detailed, with references cited below the table. The orange columns are the vulnerability scores, while the blue columns are the data quality scores of each attribute.

Attribute	Harbour porpoise			White-beaked dolphin			Common minke whale			Atlantic harbour seal			Atlantic grey seal		
Hearing range	4-150 kHz[1,2,3] (VHF*)	2	3	16–181 kHz [4] (HF*)	2	3	30 Hz-90 kHz [5,6] (LF*)	2	1	0.5-40 kHz[7] (PW*)	2	1	4 - 20 kHz[8] (PW*)	2	1
Sound production	~130 kHz[9,10]	1	3	Up to 35 kHz[11]	2	1	50 Hz – 9.4 kHz[12]	3	1	Up to 4 kHz [13]	3	1	A few Hz up to 3 kHz [14]	3	1
Impact of impulsive noise	Behavioural[15], hearing impairment[16] & physiological[17]	3	3	Behavioural[18]	3	1	Behavioural[19]	3	1	Behavioural[20] & hearing impairment[21]	3	1	Behavioural[22]	3	1
Impact of continuous noise	Behavioural[23], masking[24] & hearing impairment[25]	3	3	Behavioural[26]	3	1	Behavioural[27] & masking[28]	3	1	Behavioural[29] & hearing impairment[30]	3	1	Behavioural[31]	3	1
Flexibility in habitat utilisation	Large areas, but depending on prey[32]	2	3	Large areas[33]	1	0	Specific habitat features[34]	3	2	Large areas, but depending on prey[35]	2	3	Large areas, but depending on prey[36]	2	3
Energy requirements/ nutritional specificity	Generalist feeder with requirement for high energy food[37]	2	3	Generalist feeder with requirement for high energy food[38]	2	0	Specialist feeder[39]	3	2	Generalist feeder[40]	1	3	Generalist feeder[41]	1	3
Population size in the North Sea	339,000 (CV=0.17)[42]	1	3	46,300 (CV=0.42)[43]	2	2	7,856 (CV=0.28)[44]	3	2	~100,000 - 125,000 mature individuals[45]	2	3	119,519[46]	1	3
Generation time	7,5[47]	1	3	18[48]	3	3	22[49]	3	3	14.8[50]	2	3	14[51]	2	3
Threat status	Least Concern (LC)[52]	1		Least Concern (LC)[53]	1		Least Concern (LC)[54]	1		Least Concern (LC)[55]	1		Least Concern (LC)[56]	1	
Total score		16	24		19	11		24	13		19	16		18	16

*Corresponding hearing groups as determined by National Marine Fisheries Service, 2024.
[1]Andersen, 1970, [2]Kastelein et al., 2002, [3]Kastelein et al., 2010, [4]Nachtigall et al., 2008, [5]Tubelli et al., 2012, [6]Houser et al., 2024, [7]Kastelein et al., 2009, [8]Ruser et al., 2014, [9]Møhl and Andersen, 1973, [10]Teilmann et al., 2002, [11]Rasmussen and Miller, 2002, [12]Gedamke et al., 2001, [13]Hanggi and Schusterman, 1994, [14]Asselin et al., 1993, [15]Brandt et al., 2018, [16]Lucke et al., 2009, [17]Siebert et al., 2022, [18]Rasmussen et al., 2016, [19]Kvadsheim et al., 2017, [20]Russell et al., 2016, [21]Hastie et al., 2015, [22]Aarts et al., 2018, [23]Wisniewska et al., 2018, [24]Hermannsen et al., 2025, [25]Kastelein et al., 2013, [26]Stone et al., 2017, [27]Boisseau et al., 2021, [28]Cholewiak et al., 2018, [29]Mikkelsen et al., 2019, [30]Kastak et al., 2008, [31]Mikkelsen et al., 2019, [32-36]Jefferson et al., 1993, [37]Andreasen et al., 2017, [38]Jefferson et al., 1993, [39]Olsen and Holst, 2001, [40,41]Jefferson et al., 1993, [42-44]Gilles et al., 2023, [45]IUCN, 2025, [46]OSPAR Commission, 2023, [47]ICES, 2014, [48,49]Taylor et al., 2007, [50]IUCN, 2025, [51]HELCOM, 2013, [52]Sharpe and Berggren, 2023a, 2023b, [53]Sharpe and Berggren, 2023a, 2023b, [54]Sharpe and Berggren, 2023a, 2023b, [55]Russell, 2025, [56]Bowen, 2025

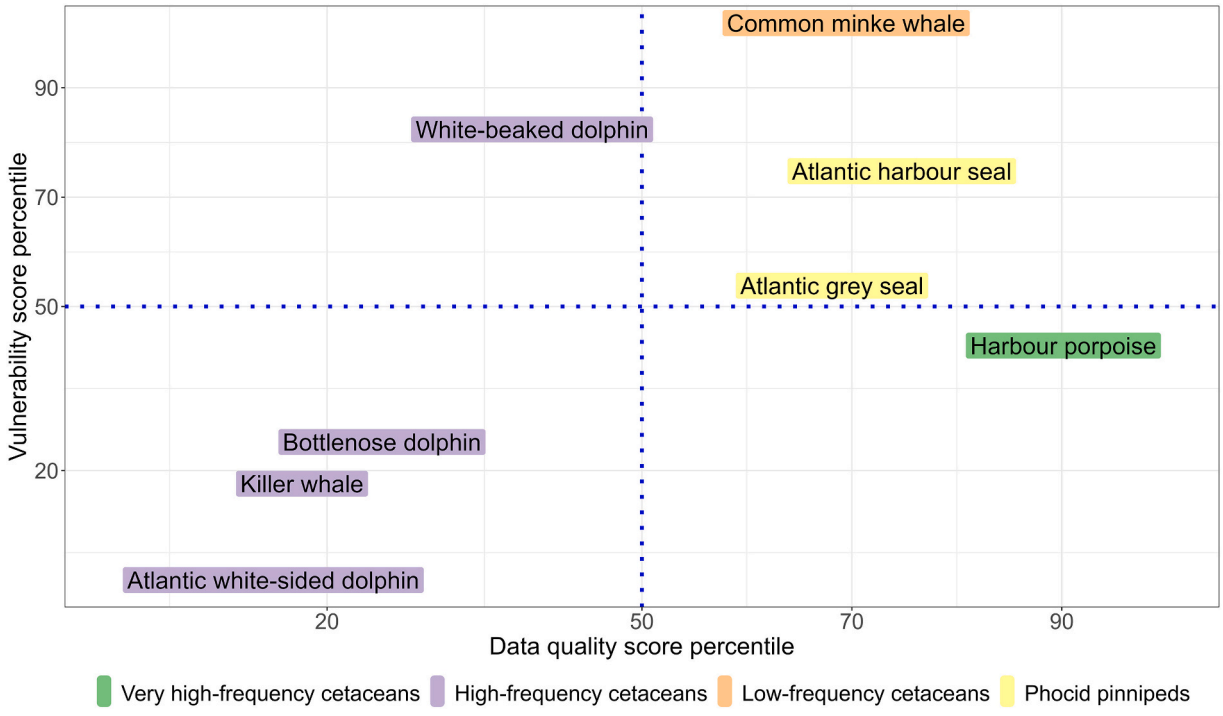

Fig. 5. Vulnerability and data quality score percentiles of the eight pre-selected marine mammals. Each species is coloured by the functional hearing group they belong to as determined by National Marine Fisheries Service, 2024.

was strong agreement on a presumed high vulnerability of both species regarding that attribute (score = 3). One expert highlighted the limited data available on the hearing of grey seals and behavioural responses to sound compared to harbour seals.

A positive correlation was found between data availability and vulnerability scores (r = 0.731), suggesting that species with more

comprehensive data coverage tend to receive higher vulnerability scores. Notable data gaps were identified for the Atlantic white-sided dolphin, killer whale (data quality score = 0 and 1, respectively) and for the bottlenose dolphin (data quality score = 6). Impacts from both impulsive and continuous noise were major contributors to the final vulnerability scores among species with higher vulnerability ratings. Additionally, population-level aggravating factors accounted for a substantial portion of these high scores.

The PCA revealed that hearing sensitivity contributed most strongly to the principal components (Supplementary Fig. S1). Attributes directly associated with sound (hearing sensitivity, sound production, impacts of impulsive noise and impacts of continuous noise) clustered closely, indicating strong positive correlations among these variables, as were the individual and population level aggravating factors energy requirements, home range, population size in the North Sea area and generation time. The PCA revealed substantial differences in data availability among species. The Atlantic white-sided dolphin and killer whale were positioned opposite to the direction of the vectors, indicating limited data coverage, whereas the position of the harbour porpoise reflects high data availability. The Atlantic harbour seal, Atlantic grey seal and common minke whale showed good coverage of individual and population-level attributes but lacked sound-related data, while the white-beaked dolphin and bottlenose dolphin showed the opposite pattern.

3.2. Fishes

Among the 55 North Sea fish species assessed (including elasmobranchs as a group), those with the highest literature-based vulnerability scores, i.e. falling within the 90th percentile, were Atlantic cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), Atlantic herring, ling (*Molva molva*), European seabass (*Dicentrarchus labrax*), European eel (*Anguilla anguilla*) and European sea sturgeon (*Acipenser sturio*) (Supplementary Table S2).

Additional vulnerability scores were obtained from seven experts through the expert consultation survey for eight fish species: Atlantic cod, Atlantic mackerel (*Scomber scombrus*), European seabass, haddock, Atlantic herring, meagre (*Argyrosomus regius*), painted gobies (*Pomatoschistus pictus*) and pollack (*Pollachius pollachius*) (Fig. 4B). Experts assigned the highest vulnerability scores to Atlantic cod, haddock and herring, aligning closely with our literature-based scoring. There were slight discrepancies between the expert survey and literature scores for most species, except for Atlantic mackerel and haddock, which received the same scores (Fig. 4B).

Despite cod being the most well-studied species for impacts of URN, differences arose between our literature-based scoring and the expert survey. Some experts assigned a score of 2 for cod's hearing range, hearing adaptation and commercial value. Based on our literature search, cod was given a high vulnerability score of 3 for these attributes due to the full overlap of cod's hearing range with URN (hearing sensitivity = 3), its swim bladder anterior extensions that enhances its sensitivity (hearing adaptation = 3) and commercial significance (commercial value = 3) in the North Sea fisheries (Table 2). The rest of the differences between the literature-based scoring and the expert survey were due to experts responding 'uncertain' to some of the factors such as sound production, ecological significance and commercial value of species.

For the European seabass, some experts expressed uncertainty regarding sound production and whether the species functions as a keystone species. For the herring, experts expressed uncertainty regarding the species' sound production. Acoustic communication in herring and seabass appeared likely, because they produce sounds in groups (Wilson et al., 2004; Rice et al., 2022), but the function of these sounds has not been verified through further research. Similarly,

Table 2
Literature-based scoring of fishes with the highest total vulnerability scores (90th percentile). Each scored attribute is detailed, with references cited below the table. The orange columns are the vulnerability scores, while the blue columns are the data quality scores of each attribute.

	Atlantic cod			Haddock			Herring			European seabass			Ling			European eel			European sea sturgeon		
Hearing range	30 to 470 Hz[1] (P1*)	3	3	30 - 500 Hz[2] (P1*)	3	3	< 4 kHz[3] (P2-3*)	3	3	< 1 kHz[4] (P1*)	3	3	30 - 500 Hz[2] (P1*)	3	3	10 - 300 Hz[5] (A4*)	3	3	100-500 Hz[6] (A4*)	3	1
Hearing adaptation	Swim bladder anterior extensions[7]	3	3	Swim bladder involved in hearing[8]	3	3	Specialized connection[9]	3	3	Swim bladder involved in hearing[8]	3	2	Swim bladder likely involved in hearing[8]	3	2	Swim bladder distant from the ear[5]	2	3	Swim bladder not involved in hearing[10]	2	3
Sound production	30 - 250 Hz, courtship & spawning[11]	3	3	30-600 Hz, spawning[12,13]	3	3	1.7 - 2.2 kHz, social mediation appears likely[14]	3	1	Likely but unconfirmed[15]	1	1	Likely but unconfirmed[12]	1	1	10 - 200 Hz, courtship and spawning[16]	3	1	Active sound[17]	2	3
Susceptibility to barotrauma injuries	Physoclistous[18]	3	3	Physoclistous[19]	3	3	Physostomous[20]	2	3	Physoclistous as adults[21]	3	3	Physoclistous[22]	3	3	Physoclistous as adults[23]	3	3	Physostomous[24]	2	3
Impact of impulsive noise	Physiological & behavioral[25]	3	3	Behavioral[26]	3	2	Physiological[27] & behavioural[28]	3	2	Physiological & Behavioral[29,30]	3	3	Behavioral[26]	3	3	No studies available	0	0	Physiological[31]	3	1
Impact of continuous noise	Physiological[32] & behavioral[33]	3	3	Behavioral[33]	3	3	Behavioral[34]	3	3	Behavioral[29]	3	3	Behavioral[2]	3	3	Physiological & behavioral[35]	3	3	Behavioral[36]	3	1
Threat status	Least concern (LC)	1		Least concern (LC)	1		Least concern (LC)	1		Near threatened (NT)	2		Least concern (LC)	1		Critically endangered (CR)	3		Critically endangered (CR)	3	
Commercial value in Europe	Highly commercial	3		Highly commercial	3		Highly commercial	3		Highly commercial	3		Medium commercial	2		Highly commercial	3		Medium commercial	2	
Keystone species	Yes	3		Yes	3		Yes	3		No	1		Yes	3		No	1		No	1	
Total score		25	18		25	17		24	15		22	15		22	15		21	13		21	12

*Corresponding hearing groups from Lucke et al., 2024 as interpreted by the present authors.
[1]Chapman and Hawkins, 1973, [2]Chapman, 1973, [3]Enger, 1967, [4]Lovell, 2003, Jerko et al., 1989, Lovell et al., 2005, [7]Hawkins and Popper, 2020, [8]Lucke et al., 2024, [9]Allen et al., 1976, [10]Popper and Calfee, 2023, [11]Rowe and Hutchings, 2006, [12]Hawkins and Picciulin, 2019, [13]Hawkins, 2022, [13]Tolstoganova, 2001, [14]Wilson et al., 2004, [15]Rice et al., 2022, [16]Lagardère and Ernande, 2004, [17]Tolstoganova, 2001, [18]Sand and Hawkins, 1973, [19]Rommens, 1997, [20]Ganias et al., 2015, [21]Bolle, 2014, [22]Morrison et al., 1993, [23]Zwerger et al., 2002, [24]Williot et al., 2011, [25]Davidsen et al., 2019, [26]Løkkeborg et al., 2012, [27]Engell-Sørensen and Skyt, 2002, [28]Slotte et al., 2004, [29]Spiga et al., 2017, [30]Santulli et al., 1999, [31]Halvorsen et al., 2017, [32]Sierra-Flores et al., 2015, [33]Stanley et al., 2017, [34]Doksæter et al., 2012, [35]Simpson et al., 2015, [36]Higgs and Beach, 2021

discrepancies in the scoring of commercial value and potential keystone status were noted for meagre and pollack between the expert survey and literature search. For painted gobies, the only difference was that the expert considered it as a keystone species whereas literature did not support this designation for the North Sea population.

Species within the top 90th percentile of both vulnerability and data quality scores include the Atlantic cod, haddock, Atlantic herring, European seabass and ling (Fig. 6). These species were therefore identified as potential fish indicator species for URN in the North Sea. The European eel and the European sturgeon, although within the 90th percentile of vulnerability scores, could not be chosen as indicator species due to low data quality scores particularly with regards to impacts of URN. Additionally, Atlantic salmon (*Salmo salar*), sand goby and plaice were among the species within the 90th percentile of data quality scores but fell below the 90th percentile of vulnerability scores.

The vulnerability and data quality scores resulted in a high positive correlation value of $r = 0.782$. Species with high vulnerability scores tend to be those with high data quality scores. Only nine species had information available for all attributes defined in the scoring system (Fig. 6). These species were the Atlantic cod, haddock, Atlantic herring, ling, Atlantic salmon, European sea sturgeon, European seabass, gilt-head bream and plaice. The remaining species had incomplete data for certain attributes outlined in the scoring framework, which limited the ability to conduct a consistent and equitable assessment.

The PCA (Supplementary Fig. S2) found attributes with the highest contributions to the principal components to be data scores of impulsive noise, hearing sensitivity, continuous noise and sound production. Impulsive noise data scores were most correlated to the high commercial status of a fish, while hearing sensitivity data scores were correlated to high data scores of continuous noise and sound production. Species positioned in the first quadrant, opposite the direction of the arrows, such as the long spined sea-scorpion (*Taurulus bubalis*), short-snouted seahorse (*Hippocampus hippocampus*), sand sole (*Pegusa lascaris*) and tusk (*Brosme brosme*), had very low data scores, indicating insufficient information for objective assessment. Cod, haddock, seabass, salmon, ling, plaice and herring, were well-studied for their hearing sensitivity and impacts of continuous and impulsive noise when compared to the literature available for the rest of the species.

3.3. Invertebrates

Among the 20 invertebrate species from the North Sea region included in our analysis (comprising 3 cephalopods, 10 crustaceans, 4 bivalves, 1 Ascidia, 1 Annelida and 1 Echinodermata; Supplementary Table S3), the blue mussel (*Mytilus edulis*), European lobster (*Homarus gammarus*) and Norway lobster (*Nephrops norvegicus*) received the highest noise vulnerability scores and data quality scores, thus identified as invertebrate species most vulnerable to URN based on the knowledge and data available today (Fig. 7; Table 3). Generally, species with high noise vulnerability scores also had high data quality scores, with a high positive correlation value of $r = 0.82$. The three species also received high scores for general susceptibility (i.e. life-history traits related to productivity and mobility), indicating that they can be regarded as susceptible to environmental stressors like noise pollution based on intrinsic factors uncoupled to the specific literature currently available for the noise vulnerability assessment. Other species that scored high for all three assessment categories (noise vulnerability, data quality and general susceptibility), were the great scallop (*Pecten maximus*) and common cuttlefish (*Sepia officinalis*) (Table 4). Thus, our literature-based scoring method identified five top candidate species as indicator species for URN risk assessments. It should be noted that all five species are benthic or primarily benthic. Among the few pelagic invertebrates assessed, the copepod *Acartia tonsa* received the highest noise vulnerability and data quality scores, although with only medium scores for all scoring categories, including general susceptibility.

For several species, limited data precluded a comprehensive assessment due to a lack of studies on noise impacts and hearing abilities. The flat oyster (*Ostrea edulis*) received a high noise vulnerability score and both flat oyster and the invasive Pacific oyster (*Magallana gigas*) were identified as potentially highly susceptible to environmental stressors (general susceptibility scores ≥ 2), but a lower data quality score highlights the need for more research and better-quality data on noise

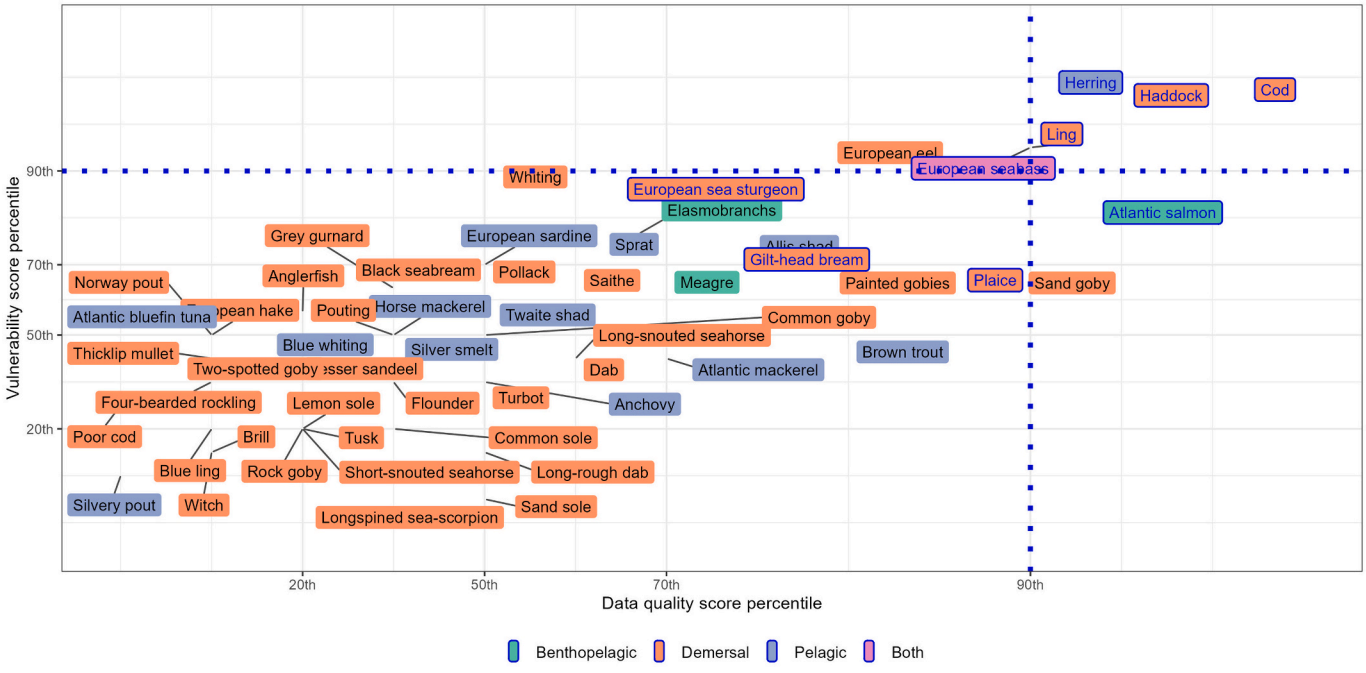

Fig. 6. Vulnerability and data quality score percentiles of the 55 North Sea fish species (and elasmobranchs as a group). Each species is coloured by their habitat. Among the fish species scored based on their vulnerability to underwater noise and data quality, only those highlighted with a blue border had sufficient information for all defined factors of underwater noise vulnerability in this study. The blue dashed lines indicate the 90th percentile. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

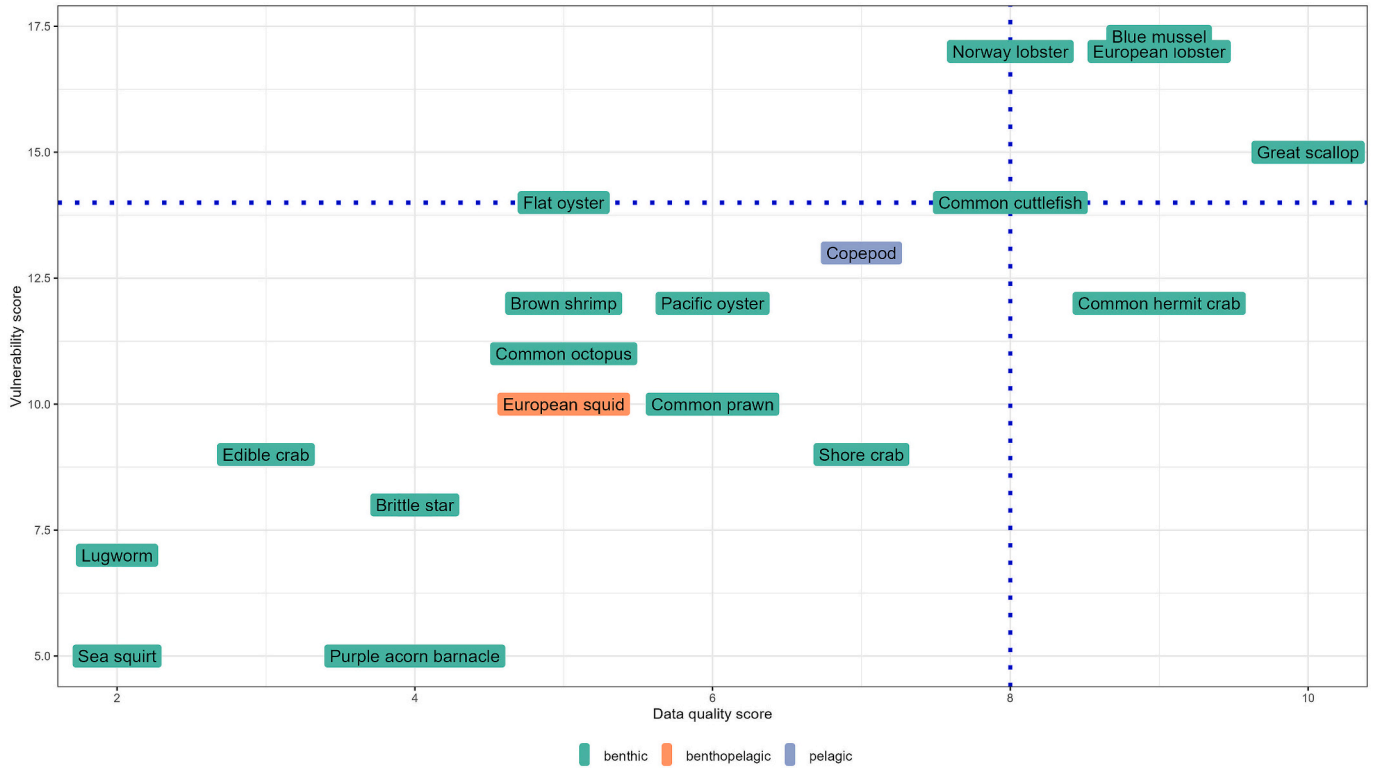

Fig. 7. Invertebrate species scored based on their vulnerability to underwater noise and the quality of the available data used for the vulnerability scoring. The blue dashed lines indicate the cut-offs for a high score on the total scale in both axes (equivalent to an average score of ≥2 in Table 4). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 3
Literature-based scoring of the invertebrate species that scored the highest for vulnerability and data quality assessment and the copepod *Acartia tonsa* selected to represent pelagic species. The orange columns give the vulnerability scores, while blue columns give data quality scores of each attribute. References for attribute details cited given below the table (when referring to closely related species, the species is indicated in parentheses).

Attribute	European lobster			Norway lobster			Blue mussel			Great scallop			Common cuttlefish			Copepod *Acartia tonsa*		
Hearing range	80 to 250 Hz[1]	3	2	20-180 Hz[2]	3	2	5 - 410 Hz[3]	3	2	20 - 1000 Hz[4]	3	2	<400 Hz[5]	3	2	40-1000 Hz[6]	3	1
Sound production	55-180 Hz, agonistic behaviour[7]	3	2	Likely but unconfirmed	1	1	Likely but unconfirmed	1	1	20–27 kHz, valve movements[8]	2	2	No studies available	0	0	Likely but unconfirmed[9]	1	1
Impact of impulsive noise	Physiological[10,11]	3	2	Behavioural[12,13] & larval development[12]	3	3	Physiological[14-17], behavioural[18,19]	3	3	Larval development[20, 21]	3	3	Acoustic trauma[22-25], behavioural[26] & egg and larval development[25]	3	3	Mortality[27,28] & physiological[28]	3	3
Impact of continuous noise	Masking[29] & behavioral[30]	3	3	Behavioural[13]	3	2	Physiologial[31] & behavioural[31-33]	3	3	Physiological[34] & larval development[20,34]	3	3	Acoustic trauma[25], behavioural[35] & egg and larval development[25]	3	3	Physiological/Behavioural[36]	3	2
Ecological importance	Less	1		High; ecosystem engineer	3		High; ecosystem engineer	3		Less	1		Less	1		High; essential food source	3	
Threat status	Least concern (LC), but high fishing pressure and depleted popuations[37-39]	2		Least concern (LC)	1		Least concern (LC), but declining populations, on OSPAR lists of threatened/declining habitats[40-42]	2		Least concern (LC)	1		Least concern (LC)	1		Unknown (NE)	0	
Commercial value	Medium; mainly recreational fishing, very high price	2		High	3		Medium; cultured commercially	2		Medium; locally fished and cultured, high price	2		High	3		Negligible/Not applicable	0	
Total score		17	9		17	8		17	9		15	10		14	8		13	7

[1]Jezequel et al., 2021a, 2021b, [2]Goodall et al., 1990, [3]Roberts et al., 2015, [4]Zhadan, 2005 (*Mizuhopecten yessoensis, Chlamys swifti*), [5]Packard et al., 1990, [6]Yen et al., 1992 (*Acartia fossae*), [7]Jezequel et al., 2020, [8]Di Iorio et al., 2012, [9]Kühn et al., 2023a, 2023b (*Meganyctiphanes norvegica*, *Calanus* spp.), [10]Hudson et al., 2022 (*H. americanus*), [11]Payne et al., 2007 (*H. americanus*), [12]Stenton et al., 2022, [13]Solan et al., 2016, [14]Spiga et al., 2016, [15]Zhao et al., 2021 (*Mytilus coruscus*), [16]Vazzana et al., 2016 (*Mytilus galloprovincialis*), [17]Vazzana et al., 2020 (*M. galloprovincialis*), [18]Hubert et al., 2020, [19]Hubert et al., 2023, [20]Gigot et al., 2023, [21]Aguilar de Soto et al., 2013 (*Pecten novaezelandiae*), [22]André et al., 2011; [23]Solé et al., 2013; [24]Solé et al., 2018, [25]Solé et al., 2022, [26]Samson et al., 2014, [27]McCauley et al., 2017, [28]Vereide et al., 2023, [29]Jezequel et al., 2021a, 2021b, [30]Leiva et al., 2021, [31]Wale et al., 2019, [32]Jolivet et al., 2016, [33]Hubert et al., 2023, [34]Olivier et al., 2023, [35]Kunc et al., 2014, [36]Kühn et al., 2023a, 2023b, [37]Agnalt et al., 1999, [38]Sundelöf et al., 2013, [39]Ellis et al., 2015, [40]OSPAR Commission, 2015, [41]SLU Artdatabanken, 2020, [42]Baden et al., 2021

vulnerability. Similarly, the edible crab (*Cancer pagurus*) and the polychaetae lugworm (*Arenicola marina*) were identified as generally susceptible, potentially vulnerable to noise, but where data limitation hinders noise vulnerability assessment at this point. On the contrary,

Table 4
Average scores (out of maximum 3) for all three scoring categories assigned to each invertebrate species. Green indicates an average score of <1, classified as low; yellow indicates an average score of ≥1 to <2, classified as medium; red indicates an average score of ≥2, classified as high. Species in bold scored high for all three scoring categories.

Species group	Species	pelagic or benthic (adults)	Average Noise Vulnerability Score	Average Data Quality Score	Average General Susceptibility Score
Cephalopoda	**Common cuttlefish (*Sepia officinalis*)**	benthic	2.00	2.00	2.25
	Common octopus (*Octopus vulgaris*)	benthic	1.57	1.25	1.88
	European squid (*Loligo vulgaris*)	benthopelagic	1.43	1.25	1.75
Crustacea	**European lobster (*Homarus gammarus*)**	benthic	2.43	2.25	2.50
	Norway lobster (*Nephrops norvegicus*)	benthic	2.43	2.00	2.50
	Edible crab (*Cancer pagurus*)	benthic	1.29	0.75	2.13
	Shore crab (*Carcinus maenas*)	benthic	1.29	1.75	1.63
	Common prawn (*Palaemon serratus*)	benthic	1.43	2.00	1.13
	Common hermit crab (*Pagurus bernhardus*)	benthic	1.71	2.25	1.63
	Brown shrimp (*Crangon crangon*)	benthic	1.71	1.50	1.88
	Copepod (*Acartia tonsa*)	pelagic	1.86	1.75	1.25
	Krill (*Euphausia* spp.)	pelagic	1.14	1.00	1.38
	Purple acorn barnacle (*Amphibalanus amphitrite*)	benthic	0.71	0.75	1.75
Bivalvia	**Blue mussel (*Mytilus edulis*)**	benthic	2.43	2.25	2.00
	Pacific oyster (*Magallana gigas*)	benthic	1.71	1.50	2.13
	Flat oyster (*Ostrea edulis*)	benthic	2.00	1.25	2.25
	Great scallop (*Pecten maximus*)	benthic	2.14	2.50	2.00
Ascidia	Sea squirt (*Ciona intestinalis*)	benthic	0.71	0.50	1.88
Annelida	Lugworm (*Arenicola marina*)	benthic	1.00	0.50	2.13
Echinodermata	Brittle star (*Amphiura filiformis*)	benthic	1.14	1.00	1.63

relatively high-quality data was available for the common hermit crab (*Pagurus bernhardus*), but the species still only received medium noise vulnerability and general susceptibility scores and was therefore not considered a priority species.

Vulnerability scores were obtained for seven invertebrate species from four experts through the expert consultation survey: common cuttlefish, blue mussel, lugworm, copepod *A. tonsa*, European squid (*Loligo vulgaris*) and brown shrimp (*Crangon crangon*). In general, the expert assessments aligned with the literature-based scoring (Fig. 4C). Blue mussel, common cuttlefish and European squid were assigned the highest vulnerability scores by the experts; however, no expert scores were received for the European lobster, Norway lobster or great scallop. A notable difference between the expert survey and literature scores was that all experts rated their species as of high ecological importance, while our literature-based scoring was more conservative and did not rate the two cephalopod species and *C. crangon* as keystone species, although being important as predators and prey. The vulnerability score for blue mussel was rated similarly to our literature-based assessment by one expert but lower by another expert that expressed uncertainty regarding the species hearing ability, while sound detection ability was identified from the literature survey (Roberts et al., 2015; Hubert et al., 2022, 2023). Similarly, *A. tonsa* was scored 0 for hearing range and sound production by the expert, while the literature review found indicative support of sound production and detection from other copepod species (Yen et al., 1992; Kühn et al., 2023b). While the expert expressed uncertainty regarding impacts of continuous noise in cephalopods, the literature survey identified acoustic trauma, behavioural effects and reduced hatching success and survival of larvae in *S. officinalis* after exposure to playback drilling and vessel noise (Kunc et al., 2014; Solé et al., 2022). Conversely, brown shrimp was scored medium for sound production by the expert, indicating that the species actively produces sound, while we only found indicative support, e.g. of incidental sound production during feeding from other shrimp and prawns (Radford and Stanley, 2023). Furthermore, lugworm was scored medium for hearing ability by the expert, indicating that their hearing frequency range partially overlaps with anthropogenic noise, while no references regarding the species' hearing ability were found from the literature. Direct consultation with the experts later confirmed our scoring.

The PCA found attributes with the highest contributions to the principal components to be impacts of impulsive noise, commercial value and hearing sensitivity, while impacts of continuous noise, sound production, ecological importance and threat status had less influence (Supplementary Fig. S3A). Hearing sensitivity scores were strongly correlated with commercial status, indicating that hearing sensitivity studies have primarily focused on commercially important species such as the cephalopods and lobsters. A separate PCA, relating noise vulnerability scores to the scores of the different life-history traits considered to assess the general susceptibility, shows that noise vulnerability foremost correlates with larval dispersal ability and with high age and large size at maturity, but also with longevity and maximum length (Supplementary Fig. S3B). Noise vulnerability does not, however, appear to be correlated with fecundity, reproductive strategy or mobility of the adults. Most species that received the highest noise vulnerability scores, i.e. European lobster, Norway lobster, blue mussel, great scallop and flat oyster, cluster in the left, lower-mid part of

the PCA plot, indicating that larger, long-lived species with high age at maturity are more vulnerable to noise impacts. The Pacific oyster and the edible crab cluster in the same region, again highlighting these species as potentially vulnerable to URN, although currently lacking crucial information to be fairly assessed.

4. Discussion

4.1. Documented vulnerable species to anthropogenic noise

The vulnerability scoring system enabled the identification of species with demonstrated vulnerabilities to URN across diverse taxa in the North Sea, highlighting their suitability as indicator species for URN impact assessment (Table 5).

The common minke whale was rated as the most vulnerable marine mammal species in the North Sea with respect to anthropogenic URN. Minke whales produce low-frequency vocalizations, typically centred around 100 Hz and extending up to a few kHz, which are used for communication and orientation (Edds-Walton, 2000). This frequency range substantially overlaps with dominant anthropogenic noise sources such as shipping and seismic exploration (Ainslie et al., 2009). However, the high vulnerability score is also driven by the species' small population size in the North Sea, its dependence on specific habitat features and its long generation time. Although empirical data on noise-related impacts remain limited, the minke whale received the highest overall vulnerability score based on our scoring system. This highlights the importance of considering a broader set of biological traits, beyond hearing sensitivity, when assessing species vulnerability to URN.

In contrast, the harbour porpoise, which achieved the highest data quality score among marine mammals, was rated as least vulnerable to anthropogenic URN among the indicator species, despite well-documented impacts from both impulsive and continuous noise exposure. This lower score can be attributed to low vulnerability in population-level aggravating factors, i.e. population size and generation time. The comparison between the common minke whale and the harbour porpoise illustrates a central insight from the vulnerability scoring system: sensitivity to noise does not necessarily equate to high overall vulnerability towards URN. Instead, vulnerability emerges from the combined effects of acoustic sensitivity with species-specific ecological, demographic and life-history traits, supporting the need for multi-criteria approaches in evaluating URN risks across taxa.

Atlantic cod, haddock and herring garnered the highest vulnerability scores among fish species, which could be attributed to the broad amount of evidence regarding their sensitivity to noise and the behavioural connotations of their sound production, their high commercial value and ecological importance. Given cod and herring's substantial economic, ecological and cultural relevance (Link et al., 2009), and their histories of pronounced stock collapses in the North Sea (Engelhard et al., 2014), they have become among the most extensively studied marine species. The well-documented acoustic sensitivities of cod and herring have likely contributed to the relatively comprehensive body of research examining their behavioural and physiological responses to URN. Reduced egg production and fertilization rates (Sierra-Flores et al., 2015), short-term lowered heart rate and changed swimming direction (Davidsen et al., 2019) and changed swimming depth (McQueen et al., 2023, 2024) were some of the reported responses of cod when exposed to URN. As for herring, vertical displacements were observed upon exposure to engine sounds (Doksæter et al., 2012) and seismic airguns (Slotte et al., 2004). Juvenile herring mortality has been reported following sonar exposure at sound pressure levels of 180–190 dB re 1 μPa (Jørgensen et al., 2005). Both cod and herring have relatively high auditory sensitivities to URN. Although cod does not have accessory hearing organs, its swim bladder has anterior extensions in proximity to the ears, making it sensitive to both particle motion and sound pressure (Hawkins and Popper, 2020). The Atlantic herring is one of the few fish species in the North Sea, alongside sprat (*Sprattus sprattus*), possessing a direct physical connection between the swim bladder and the air-filled otic bullae in proximity to its inner ear (Allen et al., 1976). Due to this anatomic specialization, the herring has an enhanced auditory sensitivity up to 4 kHz (Enger, 1967).

Unlike the cod and herring, haddock did not go through dramatic fish stock collapses in the past in the North Sea. It also does not possess any specialised connection between its bladder and ear. However, reduced catch rates explained by increased swimming activity and negatively affected foraging behaviour were reported for haddock when exposed to air-gun sound emissions (Løkkeborg et al., 2012). Anthropogenic noise may interfere with vocal communication in both cod and haddock, potentially compromising the effectiveness of their acoustic signalling (Stanley et al., 2017). Cod's vocalizations were related to courtship and spawning (<1 kHz; Rowe and Hutchings, 2006) and territorial and aggressive interactions (Hawkins and Picciulin, 2019; Hawkins and Popper, 2020), while haddock's acoustic repertoire serves a significant proven role in male-female reproductive behaviour synchronization (Hawkins and Amorim, 2000). The masking of these biologically important cues could impair reproductive success and, by extension, population viability (Rowe and Hutchings, 2006). In contrast, the functional significance of herring vocalizations remains poorly understood, and thus the potential impacts of acoustic masking on this species are still uncertain (Wilson et al., 2004).

The European seabass and ling received comparatively lower vulnerability scores than cod, haddock and herring (Table 2). Although both seabass and ling are physoclistous species, their capacity for sound production remains unconfirmed. For the European seabass, its IUCN classification as *Near Threatened* in Europe coupled with its high commercial value contributed to its vulnerability score. Ling, despite its moderate commercial value and IUCN classification as *Least Concern*, is regarded as a keystone species in the North Sea. Together, the European seabass (semi-pelagic) and the ling (deep demersal species), alongside cod (demersal), haddock (demersal) and herring (pelagic), enrich the diverse assemblage of potential indicator species identified for the region.

Impact studies of impulsive noise have mostly been conducted on commercially valued fish species (Nedwell et al., 2006; Mueller-Blenkle et al., 2010; Radford et al., 2016), while hearing sensitivities and sound production of fish were usually studied in parallel to impacts of continuous noise (Supplementary Fig. S2; Wahlberg and Westerberg, 2005; Stanley et al., 2017; Vieira et al., 2021). Several species, including poor cod (*Trisopterus minutus*), brill (*Scophthalmus rhombus*), witch flounder (*Glyptocephalus cynoglossus*), Norway pout (*Trisopterus esmarkii*) and horse mackerel (*Trachurus trachurus*), were identified as potential keystone species in the North Sea (Lai et al., 2022). However, due to the lack of available studies on noise impacts, these species could not be considered as representative (indicator) fish species based on literature

Table 5
Selected potential indicator species for the assessment of underwater noise (URN) in the North Sea, based on a multi-taxa and multi-criteria vulnerability scoring system.

Potential URN indicator species for the North Sea		
Marine mammals	Fish	Invertebrates
Harbour porpoise (*Phocoena phocoena*)	Atlantic cod (*Gadus morhua*)	Common cuttlefish (*Sepia officinalis*)
White-beaked dolphin (*Lagenorhynchus albirostris*)	Haddock (*Melanogrammus aeglefinus*)	European lobster (*Homarus gammarus*)
Common minke whale (*Balaenoptera acutorostrata*)	Atlantic herring (*Clupea harengus*)	Norway lobster (*Nephrops norvegicus*)
Atlantic harbour seal (*Phoca vitulina vitulina*)	Ling (*Molva molva*)	Blue mussel (*Mytilus edulis*)
Atlantic grey seal (*Halichoerus grypus*)	European seabass (*Dicentrarchus labrax*)	Great scallop (*Pecten maximus*)

available.

The invertebrate species rated as most vulnerable to URN based on our scoring system were the common cuttlefish, the European and Norway lobsters and the bivalves blue mussel and great scallop. This could be accredited to all species having at least indicated hearing ranges that overlap in frequency with anthropogenic noise, their medium to high commercial value, and a broad amount of evidence of demonstrated impacts of both impulsive and continuous noise at different biological organisation levels, and in some cases, on different life stages (Table 3 and references therein): All five species have demonstrated behavioural effects such as impaired feeding activity, antipredator responses, burrowing or settlement, as well as induction of a range of physiological and cellular stress responses. Disrupted early-life development, such as reduced egg hatching, larval development and survival, has been shown in the Norway lobster, great scallop and cuttlefish, and both adult and juvenile cuttlefish have demonstrated clear signs of physical damage to the auditory system at high noise exposure to pile driving, drilling and sinusoidal wave sweeps (André et al., 2011; Solé et al., 2013, 2018, 2022).

The European lobster is the only invertebrate species from the North Sea region where there was evidence of masking of sounds used for communication, implied by an increased number of agonistic, low-frequency buzzing sounds produced by males in areas with high levels of vessel noise (Jezequel et al., 2021a). Moreover, the Norway lobster and blue mussel are regarded as ecosystem engineers of particular ecological importance: the infaunal lobster bioturbates and thus oxygenates soft seabeds; and the blue mussel is an efficient filtrator, reducing the nutrient load in coastal areas, and forms banks that offer important habitats for other organisms. Although not classified as threatened according to IUCN Red Lists, the European lobster and blue mussel were assigned medium vulnerability score for threat status. The recreational fishing pressure of European lobster is high and populations are considered severely depleted in several areas, and insufficient data hinder comprehensive assessment (Agnalt et al., 1999; Sundelöf et al., 2013; Ellis et al., 2015). For the blue mussel, the lack of quantitative monitoring of population or distribution of mussel banks hinder assessment of reported and observed declining mussel banks and populations, and in certain areas like the Wadden Sea, it is on OSPAR lists of threatened and/or declining habitats (OSPAR Commission, 2015; SLU Artdatabanken, 2020; Baden et al., 2021; Laugen et al., 2023). In contrast, although Norway lobster stocks were close to collapse in some parts of its range (particularly NE England), stocks have recovered after fishing pressure was cut and the species is not considered threatened according to global and Swedish IUCN Red Lists (last assessed 2009 and 2020, respectively).

By relating noise vulnerability to general susceptibility based on intrinsic life-history traits, it was found that several species that received high noise vulnerability scores, i.e. European lobster, Norway lobster, great scallop and flat oyster, are larger, long-lived species with high age at maturity (Supplementary Fig. S3B). For example, the European lobster can live for over 50 years and grow over 60 or even 100 cm long, with sexual maturity reached after 5–8 years. Similar life-history traits are seen for the Pacific oyster and the edible crab, highlighting them as potentially vulnerable to URN. However, crucial data are currently lacking for these species to be fairly assessed. In contrast, the common cuttlefish received high vulnerability scores despite being mobile and having a short lifespan of 1–2 years. Still, it is a relatively large species, males reaching up to 49 cm and females 29 cm (mantle length), and has relatively low fecundity and benthic hatchlings with little dispersal potential.

Among the few pelagic invertebrates assessed, the copepod *A. tonsa* received the highest noise vulnerability scores, although with only medium scores for all scoring categories (Table 4). While sensitivity to low-frequency vibrations and sound production have only been indicated through other copepod species (Yen et al., 1992; Kühn et al., 2023b), exposure to seismic airguns may decrease growth and increase mortality in *A. tonsa* with impacts extending >1 km (McCauley et al., 2017; Vereide et al., 2023), and decreased feeding has been demonstrated at exposure to harbour traffic noise (Kühn et al., 2023a). Even if data availability is currently poor, we suggest including *A. tonsa* as an indicator species, to cover the group of planktonic invertebrates, not least considering copepods' role as keystone species of exceptional importance to the marine ecosystem as important food source to a range of species and a linkage between primary production and higher trophic levels.

4.2. Ecosystem-based approach to URN management

In contrast to a predominantly pressure-based approach taken in the past that emphasises quantifying environmental sound pressure, a new ecosystem-oriented, risk-based framework for URN management was proposed to assess the extent to which species' fitness and survival could be adversely affected by the stressor (Sigray et al., 2025). The selection of indicator species is a fundamental step in this approach, enabling the establishment of UNLV that links URN to habitat loss and its consequent impacts on populations. The vulnerability scoring system presented here, a multi-criteria and multi-taxa approach for determining the most vulnerable species, enables a holistic and ecosystem-based URN assessment.

The trait-based vulnerability scoring system and the subsequent selection of species follow strictly two of the five principles in the selection of indicator species, as reported by TG Noise (2016): first, there must be evidence for impact from sound on that species and second, the species must be relevant for the ecosystem. The third and fourth principles, which state that information on the species' distribution must be available and that species should be widely distributed, are not key rules in the proposed species selection but are rather taken into consideration in the following distribution mapping stage of the potential indicator species.

The fifth principle states that "the species should not be impacted by many other strong pressures, in order to distinguish the impact of sound from other pressures." However, most species are exposed to multiple other anthropogenic stressors from e.g. bycatch, climate change, (chemical) pollution and habitat degradation or loss, and not least, several fish and invertebrate species are commercially exploited and subject to great fishing pressures (Dethlefsen and Tiews, 1985; OSPAR Commission, 2023). Based on the range of anthropogenic pressures that marine species are facing in the North Sea, strict adherence to this fifth principle is not feasible. Consequently, the scoring system and selection of indicator species inevitably involve taxa that are affected by multiple pressures. However, this does not invalidate the need for a URN vulnerability assessment. In a multi-stressor environment, establishing a transparent baseline of quantifiable URN-related vulnerability is a necessary step to support the selection of indicator species as a basis for attributing potential effects to noise. By including population-level attributes such as population size and conservation status, the vulnerability scoring system also acknowledges reduced resilience as a consequence of other pressures. In this sense, the framework captures baseline vulnerability under real-world conditions, shaped by multiple stressors, while maintaining a clear focus on URN-specific vulnerability. The outputs of this framework can subsequently be integrated into population-level approaches such as Population Consequences of Disturbance frameworks, which link short-term disturbances to changes in vital rates and population-level effects under realistic multi-stressor conditions, thereby enabling the assessment of cumulative impacts and stressor-stressor interactions (e.g. additive or synergistic effects; Pirotta et al., 2018, 2022).

Following common risk frameworks, where risk equates to the interaction of hazard, exposure and vulnerability, we treat exposure as a distinct component in this method, rather than a trait (Fig. 8). This assessment quantifies intrinsic vulnerability (sensitivity/susceptibility and socio-ecological significance) and provides a set of multi-taxa

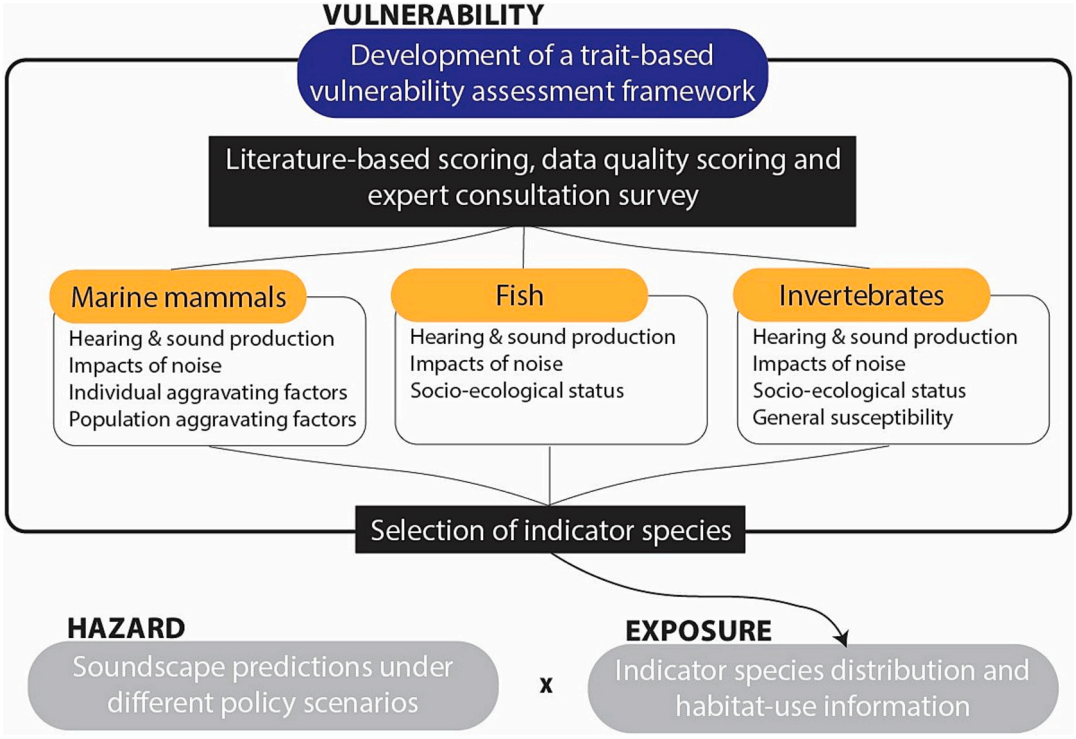

Fig. 8. A conceptual framework relating the trait-based vulnerability assessment framework (blue) developed in this study within the larger risk framework including the hazard and exposure component (grey), which are both outside of the scope of this study. The vulnerability component highlights the assessment workflow employed in this study, including a literature-based scoring, data quality scoring and expert consultation survey to select multi-taxa indicator species. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

indicator species for which exposure (i.e. spatiotemporal overlap with noise sources) will be modelled in a subsequent step. Seasonal distribution maps of vulnerable species, including key habitats such as spawning grounds and migration corridors, will be developed (or compiled where existing) and combined with the sound level maps, generated under current and future policy scenarios, for the assessment of spatiotemporal overlap.

The general risk framework (Fig. 8), which uses trait-based vulnerability as a central input to support decision-making, provides full transparency on the implications of selecting different regulatory UNLVs by reporting the proportion of vulnerable species' habitat exposed to URN over space and time. This information is essential for marine spatial planning and for the implementation of MSFD Descriptor 11.

4.3. *Limitations of the scoring system linked to data gaps*

The species selected as indicator species for the North Sea region are the most data-supported candidates. However, especially for fish and invertebrates, data gaps are substantial, and the species only represent a small fraction of all species and taxa possibly vulnerable to underwater noise in the region. Ideally, a wider range of taxa should be included, with species representing a variety of life forms and habitats.

The scoring method estimates the relative vulnerability to URN between species, with the objective to identify species at high risk and prioritise among species, while also considering the quality of the data used for the vulnerability assessment. The scoring system's reliance on the availability of quality underlying data is a key limitation. Across all three animal groups, species with high vulnerability scores tend to be those most well-studied, generating high data quality scores. Data limitations related to the effects of sound are widely acknowledged in literature. Notably for fishes and invertebrates, the high correlation between data availability and vulnerability scores was expected as most of the species could not be fully assessed, or given a score for all attributes defined, due to the lack of noise impact studies or available information regarding their hearing mechanisms and sound production (Tables S2, S3). Only 55 fishes and 20 invertebrate species from the North Sea region had data available on at least one of the attributes related to hearing ability, sound production or documented noise impacts, and could be included in our analysis. Several of these species were scored with limited evidence based on a few studies.

For marine mammals, data limitations highlighted in the literature include the restricted number of species for which data are available, the limited number of individuals studied within each species, and the narrow range of sound sources tested (Southall et al., 2019; National Marine Fisheries Service, 2024). Knowledge gaps persist, even in relatively well-studied regions like the North Sea (Supplementary Table S1). This is clearly illustrated by the scoring of the bottlenose dolphin, which received a rather low vulnerability score that reflects the lack of available data rather than a genuinely low vulnerability to URN. This highlights the risk of underestimating the vulnerability of data-poor species and underscores the importance of interpreting vulnerability scores in conjunction with data quality scores. Nonetheless, by making such data gaps visible and linking them to specific species, the scoring system provides a valuable framework not only for identifying suitable indicator species but also for prioritising future research initiatives to improve the robustness of URN vulnerability assessments.

As studies progress in future assessments, greater emphasis may be applied on literature involving particular methodologies, exposure levels or endpoints. Vulnerability assessments will benefit from further studies on species' hearing sensitivity, the relationship between sound pressure and particle motion, which intrinsic factors are more important to determine organisms' susceptibility to noise exposure, and the mechanisms behind demonstrated noise impacts and their consequences for populations. An alternative weighting for specific attributes may also be relevant when employing the scoring system in other regions. Consequently, species rankings and the resulting set of indicator species

should be revisited.

Although data gaps persist, the establishment of regional UNLV to safeguard vulnerable species should not be delayed. Considering indicator species from different taxa, habitats and trophic levels, including invertebrates that more or less have been neglected in risk assessments until now, will be a great step forward to achieve a more comprehensive and ecosystem-based risk assessment of URN. By linking URN exposure (and regional UNLV) with key habitats of identified indicator species, this approach facilitates an ecosystem-based management of URN in the North Sea and provides a transferable framework for other regions.

5. Conclusions

The developed vulnerability scoring system described here enabled the identification of potential indicator species across marine mammals, fishes and invertebrates in the North Sea—a critical primary step in implementing an ecosystem-based management of URN. Although data gaps persist, the establishment of regional underwater noise limits to safeguard vulnerable species should not be deferred. Given that bioacoustics is an emerging discipline, the vulnerability scoring system proposed here should be regarded as a framework for iterative and adaptive refinement of indicator species selection. As research advances, this approach is expected to highlight additional species of relevance. Standardisation of data metrics is essential to adequately evaluate the impacts of diverse URN sources on sensitive taxa, as was identified during the literature review of this study. Integrating URN exposure with spatial distributions of key habitats facilitates an ecosystem-based and adaptive URN management by quantifying the proportion of critical habitats affected under present and projected noise levels.

CRediT authorship contribution statement

Arienne Calonge: Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Helena Eicher:** Writing – review & editing, Writing – original draft, Validation, Methodology, Investigation, Formal analysis, Data curation. **Anna-Sara Krång:** Writing – review & editing, Writing – original draft, Validation, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Elisabeth Debusschere:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Funding acquisition, Conceptualization. **Karen de Jong:** Writing – review & editing, Validation, Supervision, Project administration, Methodology, Investigation, Conceptualization. **Kate McQueen:** Writing – review & editing, Validation, Investigation. **Michael A. Ainslie:** Writing – review & editing, Writing – original draft, Validation, Supervision, Investigation. **Merel E. den Held:** Writing – review & editing, Project administration. **Bob Rumes:** Writing – review & editing, Supervision. **Joseph G. Schnitzler:** Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization.

Declaration of Generative AI and AI-assisted technologies in the writing process

During the preparation of this work the authors used ChatGPT 5.2 in order to improve the language and readability. After using this tool/service, the authors reviewed and edited the content as needed and take full responsibility for the content of the published article.

Declaration of competing interest

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

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marpolbul.2026.119406.

Data availability

All data used were cited within the manuscript or supplementary file.

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Glossary

Aggravating factors: Biological, ecological or life-history characteristics that increase the susceptibility of an organism or population to stressors (here underwater radiated noise, URN) by reducing resilience, recovery potential, or adaptive capacity.
Exposure: Coincidence of an organism, species or habitat with a stressor (here URN) in terms of frequency, intensity, duration, time and space.
Hazard: Stressor that creates the likelihood of injury or other negative impact. For URN, it is characterised by its source type, frequency, magnitude and spatio-temporal extent.
Hearing adaptation: Here related to the presence of anatomical or physiological structures that enhance fishes' sensitivity to sound pressure, such as Weberian ossicles, auditory bullae or swim bladder-ear specializations (Hawkins and Popper, 2017).
Level of Onset of Biologically Adverse Effects (LOBE): Noise level at which individual animals start to have adverse effects that could affect their fitness (TG Noise, 2023).
Risk assessment: Systematic assessment of the likelihood and severity of potential negative impacts of a stressor, which equates to the interaction of hazard, exposure and vulnerability.
Sensitivity: Refers here to auditory sensitivity, i.e. the capacity of an organism or species to detect and/or respond to acoustic stimuli.
Socio-ecological status: Species' commercial value, extinction risk status and ecological importance.
Susceptibility: Vulnerability of individuals to URN or other environmental stressors, related to life-history traits and other intrinsic factors (behaviour and physical, physiological and developmental state) that collectively make individuals more resilient or prone to adverse outcomes of a given exposure.
Threshold value: For URN management, defined as the maximum permitted percentage area affected by URN, which is currently up to 20% of a given marine area (EC Directorate-General for Environment, 2022).
Trait-based vulnerability assessment: Assessment of species' vulnerability to threats or stressors involving the analysis of multiple attributes rather than extensive empirical data or models, to identify species that are of most risk.
Underwater Noise Limit Value (UNLV): Value of a specified underwater noise metric, as determined by an appropriate authority, above which management action is considered (Ainslie et al., 2024).
Vocalization frequency range: Frequency interval, expressed in hertz (Hz), within which a species produces acoustic signals, bounded by the minimum and maximum frequencies of its vocalizations as documented from empirical recordings.
Vulnerability: Degree to which a species is affected by a stressor (here URN) (IPCC, 2007).