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Marine and Freshwater Sounds Impact Invertebrate Behavior and Physiology: A Meta-Analysis

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ABSTRACT

The diversity of biotic and abiotic sounds that fill underwater ecosystems has become polluted by anthropogenic noise in recent decades. Yet, there is still great uncertainty surrounding how different acoustic stimuli influence marine and freshwater (i.e., aquatic) communities. Despite capabilities to detect and produce sounds, aquatic invertebrates are among the most understudied taxa within the field of soundscape ecology. We conducted a meta-analysis to understand how sounds from various sources influence the behavior and physiology of aquatic invertebrates. We extracted 835 data points from 46 studies conducted in 15 countries. The resulting data included 50 species, a range of experimental conditions, and four sound categories: anthropogenic, environmental, synthetic, and music. We used meta-analytic multivariate mixed-effect models to determine how each sound category influenced aquatic invertebrates and if responses were homogeneous across taxa. Our analyses illustrate that anthropogenic noise and synthetic sounds have detrimental impacts on aquatic invertebrate behavior and physiology, and that environmental sounds have slightly beneficial effects on their behavior. Defence responses were the most impacted behaviors, while the most prominent physiological responses were related to biochemistry, genetics, and morphology. Additionally, arthropods and molluscs exhibited the most pronounced physiological responses to anthropogenic and synthetic noise. These findings support the conclusion that many invertebrate species are sensitive to changes in aquatic soundscapes, which can cause adverse or favorable consequences to individuals and populations, dependent on the sound source. This quantitative synthesis highlights the necessity of including marine and freshwater invertebrates in acoustic exposure studies, aquatic ecosystem assessments, and emerging noise pollution policies.

1 | Introduction

Sound is a critical sensory modality for invertebrates in marine, brackish, and freshwater environments (Kunc, McLaughlin, and Schmidt 2016; Solé et al. 2023). Underwater sound sources include biological sounds, abiotic natural sounds, and sounds generated by human activities, cumulatively creating soundscapes (Pijanowski et al. 2011). Invertebrates detect components of the soundscape through a variety of mechanisms to receive information about their surroundings (Solé

et al. 2023). While underwater sound is composed of both sound pressure and particle motion, many invertebrate species perceive sounds mainly through particle motion (i.e., oscillating particles in the medium), using various internal and epidermal sensory organs dependent on taxa (André et al. 2016; Popper, Salmon, and Horch 2001; Solé et al. 2023). Particle motion is especially useful for directional hearing and short-distance communication (Hawkins and Popper 2017); however, it remains an understudied aspect of acoustic ecology (Nedelec et al. 2016). Numerous invertebrate species, including crustaceans, cephalopods, and annelids, also use sounds for communication, such as in defensive or aggressive behaviors (Bouwma and Herrnkind 2009; Goto, Hirabayashi, and Palmer 2019; Guerra et al. 2007). The hearing and production of underwater sounds, their associated ecological functions, and the invertebrates themselves, however, may be disrupted by anthropogenic noise pollution (i.e., human-made sounds that negatively affect the health and well-being of organisms; Solé et al. 2023).

Global underwater soundscapes have become increasingly inundated by expanding ranges and intensities of anthropogenic noise, through activities such as shipping, resource exploration (e.g., seismic surveys), and infrastructure development (e.g., pile driving; Duarte et al. 2021; Kunc, McLaughlin, and Schmidt 2016; Slabbekoorn et al. 2010). Low-frequency ambient sound levels in open ocean environments have increased around 3 dB per decade between the 1950s and early 2000s (Frisk 2012; McDonald, Hildebrand, and Wiggins 2006). Anthropogenic sounds dominate these lower frequencies, overlapping with the hearing and acoustic communication ranges of many animals (Duarte et al. 2021; Merchant et al. 2020). Anthropogenic noise has become so pervasive that it has been recognized by the World Health Organization as a major global pollutant and hazardous contributor to environmental change (World Health Organization 2011). Since most human-made sounds contain little to no beneficial information, they are generally considered to be noise pollution (Kunc, McLaughlin, and Schmidt 2016; Pijanowski et al. 2011). Many aquatic (i.e., marine and freshwater) animals have adaptations that increase their abilities to detect and produce sounds, including marine mammals, fishes, and some aquatic invertebrates (Kasumyan 2008; Morley, Jones, and Radford 2013; Tyack 2008); however, these adaptations also make them very susceptible to the effects of noise pollution (Cox et al. 2018; Duarte et al. 2021). Studies investigating the potential impacts of noise pollution exposure on aquatic animals have found that it can cause both behavioral and physiological changes, such as movement from preferred habitats, impaired ability to detect predators or prey, modified stress levels, reduced fertility, permanent injury or death, and many others (Duarte et al. 2021; Kunc, McLaughlin, and Schmidt 2016).

While noise pollution is a critical concern in marine and freshwater ecosystems around the globe, other sources of underwater sounds are also of interest (Cox et al. 2018; Duarte et al. 2021). Synthetic sounds (e.g., linear sweeps, tones, and white noise) are used in aquatic environments and laboratory tank experiments to expose animals to specific frequency ranges and amplitudes of sounds, often mimicking anthropogenic noise sources (Hubert et al. 2022; Vazzana et al. 2020; Yağcılar and Yardımcı 2021).

These simulated sounds also have unique applications, including inhibition of barnacle settlement and reduced survival of invasive snails (Branscomb and Rittschof 1984; Solé et al. 2021). Aquatic animals are also exposed to a variety of environmental sounds, including biotic reef sounds (e.g., from fishes and crustaceans) and freshwater fish sounds (Looby et al. 2022; Rountree, Juanes, and Bolgan 2020; Vermeij et al. 2010), as well as species-specific acoustic cues (Hughes, Mann, and Kimbro 2014). Additionally, acoustic enrichment (e.g., classical music) can promote aquatic animal welfare and growth but has yet to be thoroughly studied for fishes and aquatic invertebrates (Arechavala-Lopez et al. 2022; Cox et al. 2018; Ren et al. 2021). While the impacts of most sound sources on marine mammals and fishes are relatively well-studied, an increasing amount of research is being conducted to investigate impacts on aquatic invertebrates (Carroll et al. 2017; Duarte et al. 2021; Wale, Briers, and Diele 2021).

To assess the importance of sounds in aquatic ecosystems, it is critical to consider invertebrate taxa, as many are highly valued economically and ecologically, including species that are important food resources, form the base of marine food webs, create habitat, and recycle nutrients (Anderson et al. 2011; Kunc, McLaughlin, and Schmidt 2016). There are over 170,000 known species of multi-cellular marine invertebrates, and they are increasingly being documented detecting and responding to acoustic cues (Weilgart 2018). Research on the effects of sounds has been conducted on a diversity of aquatic invertebrate taxa, including corals, jellyfishes, bivalves, cuttlefish, gastropod molluscs, squid, crabs, lobsters, shrimp, sea urchins, and various zooplankton (Lecchini et al. 2018; Solé et al. 2023; Tu et al. 2021). A variety of behavioral and physiological responses to sounds have also been recorded, ranging from impacts on acoustic emissions and recruitment, to oxygen levels and survival (Filiciotto et al. 2018; Lillis, Bohnenstiehl, and Eggleston 2015; Ren et al. 2021; Wale et al. 2019).

We conducted a meta-analysis to quantify the impacts of sounds on aquatic invertebrate behavior and physiology. Through our analysis, we reveal the main sound sources that invertebrates have been experimentally exposed to. We also examine how invertebrates respond to these sound sources, including bioacoustic behaviors, biochemical metrics, defence, development, foraging ability, genetics, morphology, movement, recruitment, and survival. Finally, we assess the extent to which responses to each sound source are homogeneous across the taxonomic groups represented in our study to identify taxa that may be more susceptible to acoustic stimuli. Taxa included arthropods (e.g., barnacles, copepods, and decapod crustaceans), bryozoans, cnidarians (i.e., corals and jellyfishes), echinoderms (i.e., sea urchins), and molluscs (e.g., bivalves, cuttlefish, sea slugs, snails, and squid). While syntheses of the effects of sounds on aquatic invertebrates have been conducted (e.g., Di Franco et al. 2020; Duarte et al. 2021; Solé et al. 2023), these studies are limited to review methodologies that do not quantify impacts to species, focus on limited sound sources or locations, or only briefly discuss invertebrates as part of wider taxonomic reviews. Meta-analyses allow for transparent and generalizable conclusions to be reached through data synthesized from many studies and are an effective method for evaluating ecological trends (Del

Re 2015). This research is the first quantitative, systematized review of how aquatic sounds influence invertebrate behavior and physiology, providing insight into the impacts of anthropogenic noise on understudied taxa, the importance of natural sounds for maintaining ecological processes, and the extent to which aquatic invertebrates will respond to experimentally manipulated or enriched soundscapes.

2 | Materials and Methods

2.1 | Literature Review

Web of Science was used to consolidate peer-reviewed literature on how sounds influence aquatic invertebrate behavior and physiology. The specific search terms used were "noise or sound or acoustic*", "marine or aquatic", and "invertebrate* or benthic or arthropod* or cephalopod* or cnidaria* or crustacean* or echinoderm* or mollus*", where asterisks indicate truncation wildcards and quotation marks enclose search phrases. The search initially considered studies published between 1900 and 2018 and returned 1095 potentially relevant peer-reviewed studies. An additional 10 studies were identified through other sources such as previous knowledge and reference searching (i.e., thoroughly reviewing bibliographies of relevant reviews; Murchy et al. 2020). The search was updated in March 2022 using the same string, identifying 611 potentially relevant peer-reviewed studies published from 2018 to 2022. To ensure sufficient coverage between the two searches, the year 2018 was included in both examinations. Following the second search, an additional 10 studies were identified from other sources. The titles and abstracts of the 1726 studies identified by both searches were reviewed to determine which papers addressed the effects of sound on aquatic invertebrate behavior or physiology (Figure 1). Articles that met these criteria ($n = 73$) were then further evaluated to identify those that met the following criteria: original

research, listed sound source, the inclusion of an experimental control, reported mean values with either standard deviation or standard error, and reported sample sizes.

In total, 46 studies from 15 countries met the search criteria (Figure 1; Table S1). The studies spanned the years 1982 to 2022, included four main types of sound exposures (i.e., anthropogenic, environmental, music, and synthetic), and investigated behavioral and physiological responses of 50 species from seven taxonomic groups (Figure 2). The mean, standard deviation, and sample size were extracted from the treatment and control groups of each relevant comparison within a selected study, and studies commonly included multiple relevant comparisons. Data were obtained from tables and text wherever possible, and the extraction software GraphClick (Arizona-Software 2008) and WebPlotDigitizer (Rohatgi 2022) were used to collect data from figures when necessary. A total of 835 data points (i.e., each mean response of a species to sound exposure within a reference) were collected from the 46 studies.

### 2.2 | Effect Size (ES) Calculation

ES and variance are standardized measures of the magnitude of the relationship between two variables and the associated precision of the ES estimate, respectively.

ES and variance were calculated for each response variable in RStudio using the metafor package (R Core Team 2023; Viechtbauer 2010). The standardized mean difference ES (Cohen's d), which compares the mean of a numerical response variable between two groups based on their sample sizes and standard deviations, was calculated using Equation (1) (Del Re 2015).

$$d = \frac{\bar{Y}_1 - \bar{Y}_2}{sd_{pooled}} \tag{1}$$
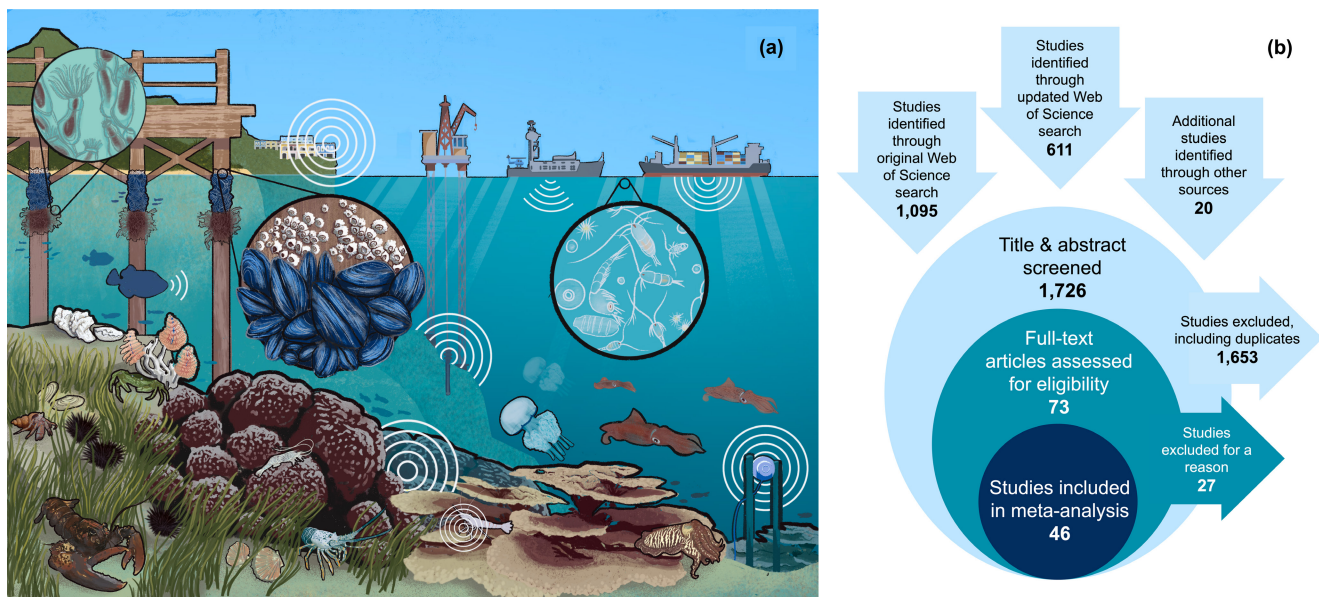
FIGURE 1 | Evaluating the changing acoustic conditions that aquatic invertebrates are exposed to using a meta-analytical approach. (a) A representative marine ecosystem depicting the invertebrate taxa and main sound sources (i.e., anthropogenic noise, environmental sounds, synthetic sounds, and music) included in the analysis and (b) a PRISMA diagram of each phase of the meta-analysis literature review.
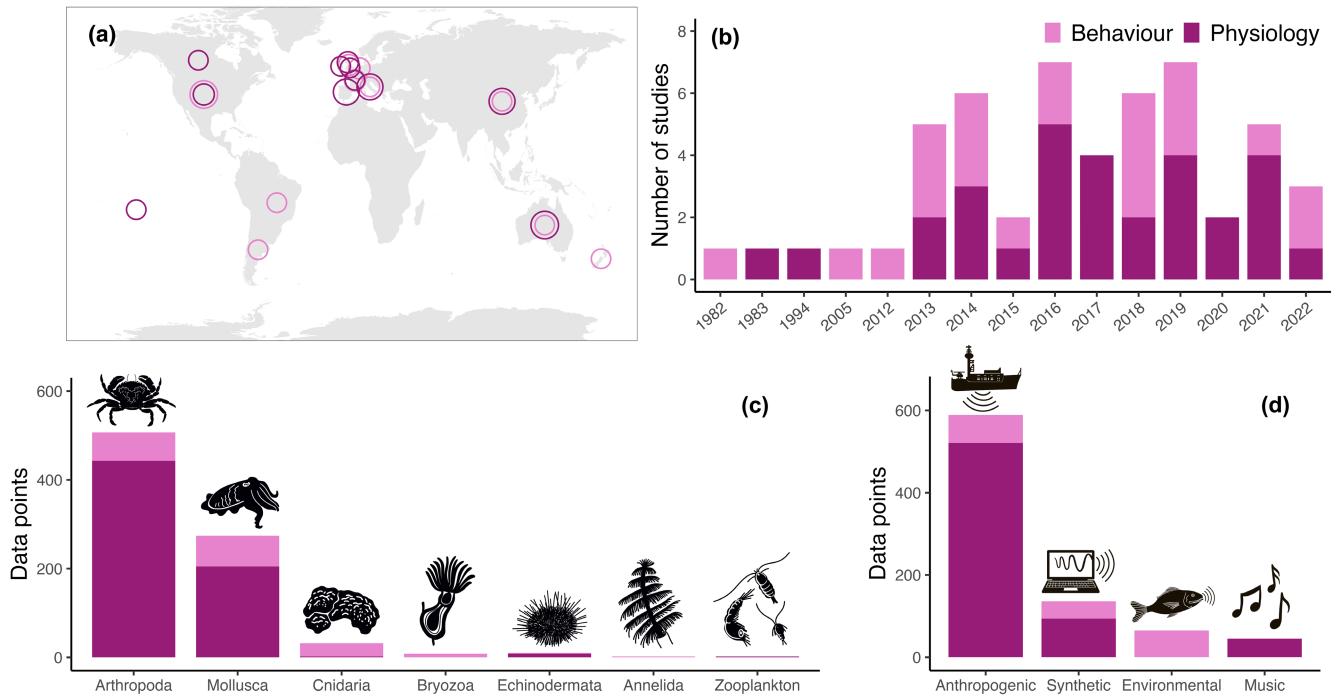
FIGURE 2 | The spatiotemporal coverage and data composition of the 46 studies included in the meta-analysis. Behavioral data are light pink, and physiological data are dark pink—in the five cases where single studies included both behavioral and physiological data, they were plotted as separate points. (a) The 15 countries where the research was conducted. Circle size is proportional to the density of studies (the number of studies in each country as follows: Argentina 1, Australia 7, Brazil 1, Canada 1, China 5, England 2, France 3, French Polynesia 2, Ireland 1, Italy 5, Netherlands 2, New Zealand 1, Spain 5, United Kingdom 3, and United States 7). (b) The number of studies published in each year (years with zero studies are not shown). (c) The number of data points corresponding to each invertebrate taxonomic group. (d) The number of data points included within each sound source category.

$\bar{Y}_1$ and $\bar{Y}_2$ are the mean values of the treatment and control group, respectively; sd_{pooled} is the pooled standard deviation of both group means, computed as in Equation (2) (Del Re 2015).

$$sd_{pooled} = \sqrt{\frac{(n_1 - 1)s_1^2 + (n_2 - 1)s_2^2}{n_1 + n_2 - 2}} \quad (2)$$

The sample sizes are indicated by n_1 and n_2 and standard deviations by s_1 and s_2. The variance of Cohen's d is given by Equation (3).

$$V_d = \frac{n_1 + n_2}{n_1 n_2} + \frac{d^2}{2(n_1 + n_2)} \quad (3)$$

The positive bias in Cohen's d was automatically corrected within the function, yielding Hedges' g (Viechtbauer 2010). The difference between the mean responses is weighted by the sd_{pooled}. The conversion of Cohen's d to Hedges' g was computed using the correction factor given by Equation 4 (Del Re 2015).

$$J = 1 - \frac{3}{4 \times df - 1} \quad (4)$$

The degrees of freedom (df) are the group size minus one. The correction factor J was used to compute unbiased estimators g and V_g as in Equations 5 and 6, respectively.

$$g = J \times d \quad (5)$$

$$V_g = J^2 \times V_d \quad (6)$$

Accounting for the diversity of response variables is a critical step in an ecological meta-analysis. The directionality of each response was determined to ensure that negative and positive ESs represented negative and positive responses, respectively. For example, we ensured that an increase in the survival rate would result in a positive ES since it is a beneficial response, while an increase in damaged hair cells would result in a negative ES since it is a detrimental response. Directionality was accounted for by multiplying the ES by a correction factor of 1 if the response direction was accurate and by a negative 1 if it was inaccurate, thereby ensuring that the various responses could be evaluated along the same axis (Cox et al. 2018; Vesterinen et al. 2014).

2.3 | Statistical Analyses

Data were separated into behavioral and physiological responses and were further divided into the four sound source categories: anthropogenic noise, environmental sounds, music, and synthetic sounds (Table S2). Within each sound source, behavioral response variables were categorized as bioacoustics, defence (i.e., anti-predator and aggressive behaviors), foraging, movement, or re-cruitment (i.e., larval settlement); physiological response variables were categorized as biochemistry, defence (i.e., color changes), development, genetics, morphology, or survival (Table S3).

All analyses were conducted in RStudio (R Core Team 2023). Data were organized and plotted using dplyr and ggplot2 packages (Wickham 2016; Wickham et al. 2022). Zero values present in the data were accounted for by approximating a small constant, 10^{-7} (Viechtbauer 2010). To determine the summary effect (i.e., weighted average of individual study ES) and confidence intervals (CIs) of each sound category, random-effects models with a restricted maximum-likelihood estimator were used to create forest plots using metafor and MAd packages (Figures S1 and S2; Del Re and Hoyt 2014; Viechtbauer 2010). Individual ESs were aggregated by study when generating forest plots to reduce bias in the estimates, using Borenstein's method within the MAd package (Del Re 2015; Del Re and Hoyt 2014). This model was selected to account for the varied methodologies and characteristics of the studies included in the meta-analysis, such as different invertebrate taxa, recorded sound pressure levels, experimental conditions (e.g., field and tanks), life stage of organisms (e.g., larvae, juvenile, and adult), and other factors. Since publication bias (i.e., the discrepancy between published studies and all studies on a topic) is a concern when conducting a meta-analysis, funnel plots of the random-effects models for each sound source category were created and visually examined for asymmetry and heterogeneity (Figures S3 and S4; Del Re and Hoyt 2014; Viechtbauer 2010).

Meta-analytic multivariate mixed-effect models for each sound source category were used to determine how the ESs of behavioral and physiological responses differed from a "zero" line of no effect, using the metafor package (Viechtbauer 2010). To allow the models to run, behavioral or physiological response variables with less than three data points were excluded, which occurred only once (Table S4). Histograms of the ES for each category were plotted and examined for normality with Shapiro–Wilk tests. The ESs were transformed into a normal shape using the Box–Cox method in the MASS package, and the transformed histograms were visually examined. Reduced models were constructed with response variables as a fixed effect and study as a random effect, while full models included response variables as a fixed effect and data point ID nested within study as a random effect (Table S4). The full models were consistently the best-fitted models after comparison through analysis of variance (ANOVA) tests and examination of the Akaike information criterion (AIC) values. When the sound category of interest contained a single study with multiple response types (i.e., physiological responses to music), the model included response as a fixed effect and data point ID as a random effect (Table S4). The resulting model estimates and 95% CIs were then plotted to visualize the effect of each sound source on the response variables, and 95% CIs that did not overlap with the zero-line indicated trends that were non-random (Table S5; Wickham 2016; Wilke 2020). The p-value ($\alpha = 0.05$) and z-value were reported for all model estimates, and both statistically significant and non-significant trends were explored.

The influence of each sound source on the taxonomic groups was determined following the same modelling process, with the only difference being the inclusion of phyla (e.g., Arthropoda and Mollusca) instead of behavioral or physiological response category (e.g., foraging and biochemistry). Briefly, meta-analytic multivariate mixed-effect models for each sound

source category were used to determine if the behavioral and physiological responses of each taxonomic group differed from a "zero" line of no effect, using the metafor package (Viechtbauer 2010). Reduced models were constructed with the taxonomic group as a fixed effect and study as a random effect, while full models included the taxonomic group as a fixed effect and data point ID nested within study as a random effect (Table S6). Six taxa with less than three data points were excluded from the models (Table S6). Model outputs were plotted to visualize the differences between the taxonomic groups (Table S7).

The validity of all models was assessed using several statistical tests. Model residuals were examined for normality using histograms and studentized quantile-quantile (Q-Q) plots, and variance components were visualized using profile likelihood plots (Figure S5a–c; Viechtbauer 2010). Influential case diagnostics using Cook's distances, DFBETAS values, and hat values ensured that outliers did not cause considerable changes to the fitted models (Figure S5d). Cook's distance estimates the influence of data points by excluding them from model fitting, DFBETAS evaluates the change in the standard deviation of the predicted values with and without each data point, and hat values determine the extent to which a predictor value differs from the other predictor values (i.e., leverage). Comparatively large Cook's distances, DFBETAS values above 2 divided by the square root of the sample size, and hat values approaching or exceeding 1 were examined as potential outliers (Viechtbauer 2010; Viechtbauer and Cheung 2010). This process identified three data points across three models that required examination and ultimately warranted removal. Excluding these data points had minimal influence on the insights drawn from these models, but improved model fit in all cases. The ability of all models to generate data that overlaps the data used to create the model was examined using the "ranef" function in the metafor package (Figure S5e; Viechtbauer 2010; Viechtbauer and Cheung 2010). The distribution of these predictions was compared to the raw data visually and using Student's t-tests. The data and code that support this meta-analysis are openly available in Borealis (Davies et al. 2024).

3 | Results

3.1 | Summary Effects

Forest plots showed that both behavioral and physiological responses varied strongly based on the sound source category (Figures 3, S1 and S2). Anthropogenic noise had a slight negative effect on invertebrate behavior and a significantly negative effect on physiology (Figure 3). Studies addressing behavioral responses had an overall ES of −0.37 with 95% CI of −0.98 and 0.24 (Figure S1a), while studies of physiological responses had an overall ES of −1.31 with 95% CI of −2.00 and −0.61 (Figure S2a). Environmental sounds had a variable, but overall, slightly positive effect on behavioral responses, with an ES of 0.10 (CI −0.00, 0.20; Figure 3, S1b), and we did not identify any studies that investigated the effects of environmental sounds on invertebrate physiology. No studies addressed the impact of music on invertebrate behavior. The single study that examined the effect of music on invertebrate physiology had a slight positive effect of
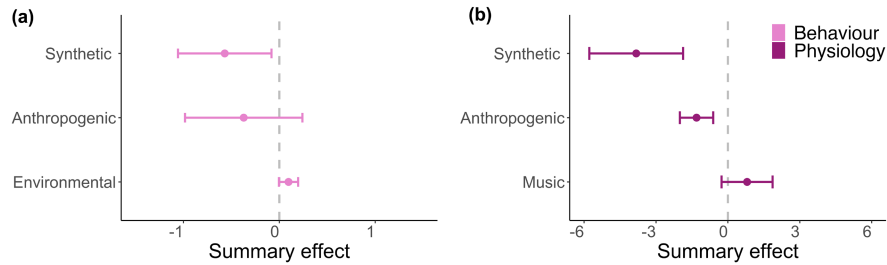
FIGURE 3 | Summary effects and 95% confidence intervals (CIs), derived from forest plots that examined each study within the meta-analysis (Table S1 and Figures S1 and S2), illustrating the influence of each broader sound category on aquatic invertebrate (a) behavior (light pink) and (b) physiology (dark pink). The vertical dotted line indicates an effect size of zero and non-overlapping 95% CIs are significant.
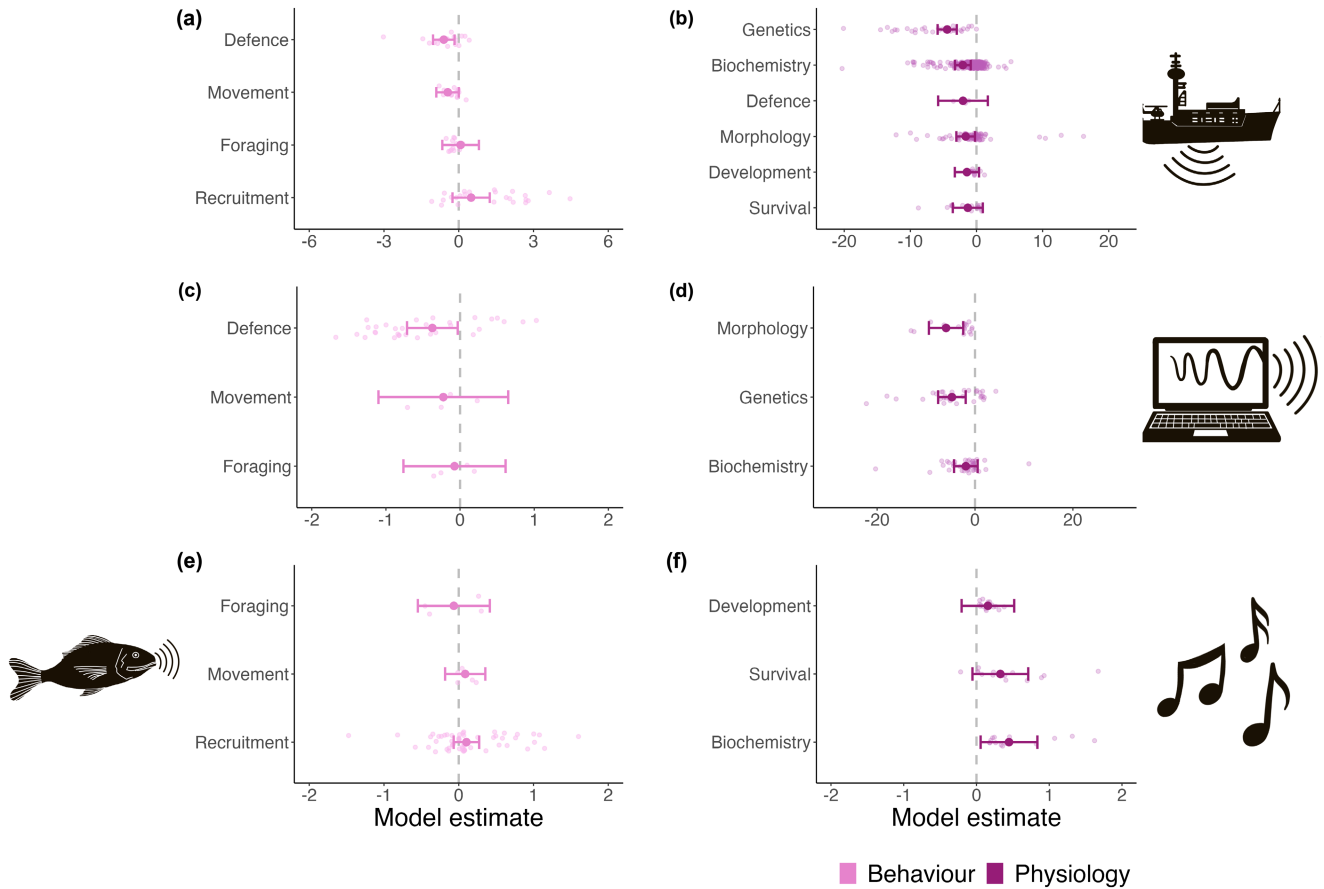
FIGURE 4 | Model estimates and 95% confidence intervals (CIs) of the behavioral (light pink) and physiological (dark pink) responses of aquatic invertebrates to sounds, derived from meta-analytic multivariate mixed-effect models which evaluated responses to (a) and (b) anthropogenic noise, (c) and (d) synthetic sounds, (e) environmental sounds, and (f) music. Points illustrate the transformed effect size data that were used in each model. The vertical dotted line indicates an effect size of zero and non-overlapping 95% CIs are significant.

0.80 (CI −0.26, 1.87; Figures 3 and S2b). Synthetic sounds had a significantly negative effect on both invertebrate behavior and physiology (Figure 3)—behavioral responses had an overall ES of −0.57 (CI –1.06, −0.00; Figure S1c), and physiological responses had a much more negative ES of −3.82 (CI –5.78, −1.87; Figure S2c).

Additionally, funnel plots did not indicate that there were major effects of publication bias within any of the behavioral response categories (Figure S3). Funnel plots examining physiological responses to anthropogenic noise and synthetic sounds indicated

minor asymmetry and increased variation associated with these studies (Figure S4).

3.2 | Effects of Sounds on Behavioral Responses

Anthropogenic noise had both detrimental (i.e., negative) and beneficial (i.e., positive) effects on behaviors (Figure 4a, Table S5a). Defence behaviors, including hiding time, raised arms, righting time, bivalve gape, and sheltering, were significantly and negatively affected (estimate = −0.60, $p = 0.007$,

$z = -2.72$). Movement-related behaviors, such as activity level, chemical cue attraction, and time swimming were slightly negatively impacted (estimate $= -0.44$, $p = 0.051$, $z = -1.95$). In contrast, anthropogenic noise marginally impacted foraging (estimate $= 0.08$, $p = 0.841$, $z = 0.20$) and slightly positively impacted recruitment (estimate $= 0.50$, $p = 0.192$, $z = 1.30$).

Synthetic sounds were detrimental to all the response categories examined (Figure 4c, Table S5a). Defence behaviors were significantly negatively impacted by the presence of synthetic sounds, including digging depth, bivalve gape, fights, and tail flips (estimate $= -0.37$, $p = 0.032$, $z = -2.15$). Movement responses (i.e., encounters and number moving) were slightly negatively affected (estimate $= -0.23$, $p = 0.613$, $z = -0.51$), and foraging behaviors (i.e., the number of individuals foraging or near a food source) were marginally impacted (estimate $= -0.07$, $p = 0.831$, $z = -0.21$).

Environmental sounds had variable effects on the response categories examined (Figure 4e, Table S5a). Foraging behaviors, measured by consumption, were marginally negatively impacted (estimate $= -0.07$, $p = 0.789$, $z = -0.27$). In contrast, movement (i.e., activity level) and recruitment behaviors were slightly positively impacted in the presence of environmental sounds (estimate $= 0.09$, $p = 0.529$, $z = 0.63$; estimate $= 0.10$, $p = 0.236$, $z = 1.19$).

3.3 | Effects of Sounds on Physiological Responses

Anthropogenic noise detrimentally impacted various physiological responses (Figure 4b, Table S5b). Genetic responses, including biomarkers of DNA health and gene expression, were significantly negatively impacted by anthropogenic noise (estimate $= -4.43$, $p < 0.0001$, $z = -5.99$). Biochemical metrics were also significantly negatively affected overall, such as adenosine triphosphate (ATP) content, heat shock proteins, respiration rate, and enzyme activity (estimate $= -2.06$, $p = 0.001$, $z = -3.38$). Non-behavioral defence responses, including color changes in crabs and cuttlefish, were slightly negatively impacted (estimate $= -2.04$, $p = 0.287$, $z = -1.06$). Invertebrate morphology was significantly negatively affected by anthropogenic noise, including reductions in body condition and byssal thread size and strength as well as increased hair cell damage and shell size (estimate $= -1.70$, $p = 0.022$, $z = -2.30$). A slight negative effect was detected for developmental parameters, such as developmental success, development time, and percent metamorphosis (estimate $= -1.63$, $p = 0.023$, $z = -2.28$). Finally, survival rates were also slightly negatively impacted by anthropogenic noise (estimate $= -1.31$, $p = 0.256$, $z = -1.14$).

Examinations of how invertebrate physiology was influenced by synthetic noise and music exhibited varied responses (Table S5b). Synthetic sounds had significantly negative impacts on morphology in the form of increased hair cell damage (estimate $= -5.91$, $p = 0.001$, $z = -3.30$) and genetics (i.e., gene expression; estimate $= -4.72$, $p = 0.001$, $z = -3.29$; Figure 4f). Biochemical parameters, such as enzyme activity, heat shock proteins, hemocyte count, and respiration rate, were slightly negatively affected (estimate $= -1.87$, $p = 0.128$, $z = -1.52$). One study on one species examined the effects of classical music

on three response types. Development time and survival rate slightly increased (estimate $= 0.16$, $p = 0.395$, $z = 0.85$; estimate $= 0.33$, $p = 0.094$, $z = 1.68$), while biochemical metrics (i.e., respiration rate) were significantly improved in music-enhanced conditions (estimate $= 0.45$, $p = 0.025$, $z = 2.25$; Figure 4g).

3.4 | Effects of Sounds on Taxa

The responses of different taxonomic groups to sound exposure varied according to the sound source and whether responses were behavioral or physiological (Table S7). The significantly negative physiological responses of arthropods and molluscs to anthropogenic noise (estimate $= -2.00$, $p = 0.005$, $z = -2.79$; estimate $= -2.08$, $p = 0.021$, $z = -2.31$; Figure 5b) and synthetic sounds (estimate $= -6.02$, $p = 0.024$, $z = -2.26$; estimate $= -4.96$, $p < 0.0001$, $z = -5.35$; Figure 5d) were the most pronounced. To a lesser extent, this trend was mirrored by the significantly negative behavioral responses of molluscs to synthetic sounds (estimate $= 0.48$, $p = 0.030$, $z = -2.17$). Behavioral responses of all other taxa included in this analysis were not significantly impacted (Figure 5a,c,e). Additionally, responses within each analysis (e.g., behavioral responses to anthropogenic noise) were relatively similar across taxa (Figure 5).

4 | Discussion

This study comprises the first quantitative global review addressing the effects of sounds on aquatic invertebrates. We synthesized 46 peer-reviewed studies across 15 countries and quantified impacts on invertebrate behavior and physiology. The studies consisted exclusively of marine taxa apart from two freshwater species (*Pomacea maculata* and *Procambarus clarkii*); however, many of the taxonomic groups studied are represented in both habitats (e.g., arthropods and crustaceans). Sound exposure occurred in highly varied field and laboratory environments, and models summarized trends across these studies from the 825 extracted data points. Our meta-analysis found that anthropogenic noise and synthetic sounds had overall negative effects on aquatic invertebrate behavior and physiology, and environmental sounds had slightly positive effects on behavior. Defence behaviors, genetics, biochemistry, and morphology were the most impacted response types. Additionally, the greatest impacts were on arthropods and molluscs exposed to anthropogenic noise and synthetic sounds.

Exposure to anthropogenic noise negatively affected invertebrate behavior and physiology. Behavioral responses including defence and movement were negatively impacted, similar to the negative behavioral effects of noise pollution on other taxa including fishes and marine mammals (Cox et al. 2018; Duarte et al. 2021; Southall et al. 2019). However, in some cases, invertebrate responses to anthropogenic noise were inconsistent. Effects of ambient tank noise and shipping on foraging responses were marginal, possibly due to limited data and higher levels of uncertainty interpreting these behaviors. Shipping noise had a positive effect on recruitment of various larval invertebrate species (e.g., barnacles and bivalves) due to increased settlement (Jolivet et al. 2016; Stanley, Wilkens, and Jeffs 2014), while settlement of coral larvae decreased (Lecchini et al. 2018).
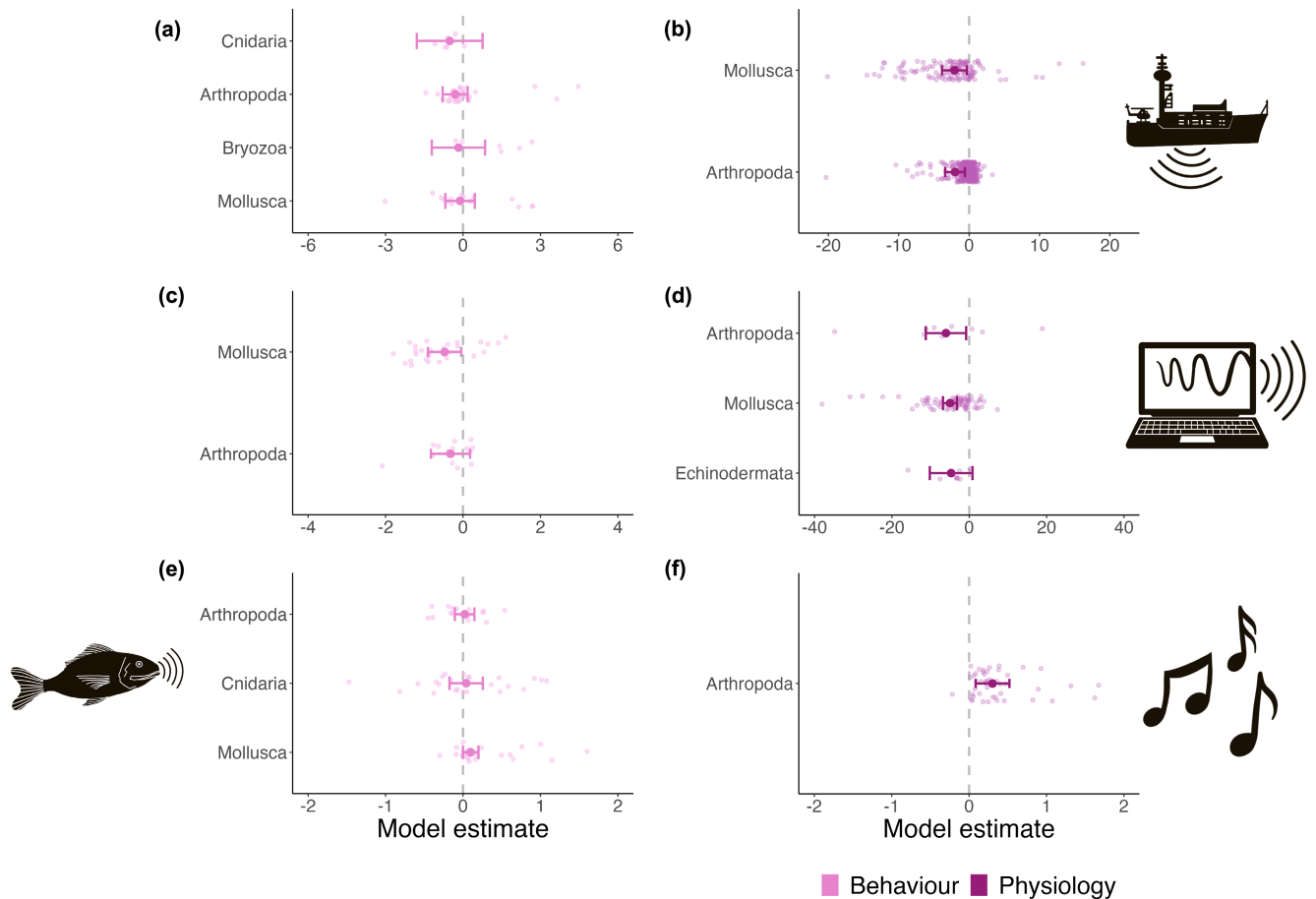
FIGURE 5 | Model estimates and 95% confidence intervals (CIs) of the behavioral (light pink) and physiological (dark pink) responses of aquatic invertebrate taxa to sounds, derived from meta-analytic multivariate mixed-effect models which evaluated responses to (a) and (b) anthropogenic noise, (c) and (d) synthetic sounds, (e) environmental sounds, and (f) music. Points illustrate the transformed effect size data that were used in each model. The vertical dotted line indicates an effect size of zero and non-overlapping 95% CIs are significant. Annelida and zooplankton were excluded from these models due to insufficient data.

This trend supports the findings that larval invertebrates use sounds to identify suitable habitats (Simpson et al. 2011, 2005; Vermeij et al. 2010) but suggests that the acoustic stimuli used are not limited to natural sounds (and increased recruitment to unsuitable habitats may not be beneficial in the long-term). Notably, behavioral impacts were not always consistent between similar taxa. For example, increased valve gape was considered a stress response in mussels (Wale et al. 2019), but the same behavior was found to improve the growth rate of oysters (Charifi et al. 2018).

We observed an array of physiological responses to anthropogenic noise related to or independent of behavioral responses. Invertebrate genetics and morphology were significantly impacted, causing damage and downregulation of various genes, hair cell damage, and reduced body size and strength (e.g., Day et al. 2019; Zhao et al. 2021). Despite these trends, size and condition were not always impacted in the months following noise exposure, possibly due to the added dynamic of in situ ecological pressures (Przeslawski et al. 2018). Biochemical parameters, most often stress bioindicators extracted from invertebrate hemolymph, were also significantly impacted (Solé et al. 2023). However, certain biochemical parameters such as hepatopancreas index might have more limited applications, and elevated

glucose has only recently been supported as a stress response to acoustic exposure (Fitzgibbon et al. 2017; Simon et al. 2015; Solé et al. 2023). While the effects were less pronounced likely due to limited data, physiological defence responses were also detrimentally impacted (e.g., Carter, Tregenza, and Stevens 2020). Additionally, anthropogenic noise increased development failure and accelerated metamorphosis, negatively impacting larval shell growth and body mass in mussels (Jolivet et al. 2016). Conversely, no significant differences in development were found in crab larvae when exposed to seismic survey noise (Pearson et al. 1994), suggesting that some taxa may be more resistant. Finally, larvae and zooplankton survival were less impacted than other response categories (McCauley et al. 2017; Pearson et al. 1994), but more studies are needed to sufficiently evaluate invertebrate mortality. Overall, physiological responses to noise were generally more pronounced than behavioral, which could indicate that altered physiology compounded on behavioral changes (e.g., decreased foraging success leading to elevated stress levels), or that physiological effects are associated with more severe sound exposures (Hawkins and Popper 2017; Kunc, McLaughlin, and Schmidt 2016).

Synthetic sound exposure, such as linear sweeps, negatively influenced invertebrate behavior and physiology. In addition to

broad impacts, studies incorporating synthetic sounds can effectively test how aquatic invertebrates respond to specific sound frequencies and modulations (e.g., Hubert et al. 2022). Defence, movement, and foraging behaviors were all impacted, but the largest effects were on defence. Estimates of movement and foraging responses may have been less pronounced than defence behaviors as these were the most data-limited response categories (i.e., a single study for each category). These behavioral changes could be induced through several mechanisms, including masking of relevant acoustic cues or disturbance leading to decreased risk-taking (Hubert et al. 2022, 2018). There were also negative effects on invertebrate physiological responses including morphology, genetics, and biochemistry. Morphological responses to synthetic sounds were quantified through damaged hair cells following exposure to tones (Solé et al. 2021, 2018, 2017, 2016), allowing for the relationship between sound exposure and hearing impairment to be examined directly. Significant effects on genetics were also detected through changes in gene expression, including increases in genes linked to stress responses (Peng et al. 2016; Tu et al. 2021). Further, examples of biochemical responses included effects on enzyme activity in sea slugs and sea urchins (Tu et al. 2021; Vazzana et al. 2020).

Our examination of environmental sounds provided insight into the varied invertebrate behavioral responses to animal and reef sounds, and we did not identify any research on physiological responses. One study showed decreased foraging success of crabs in the wild exposed to predatory fish sounds (Hughes, Mann, and Kimbro 2014). In contrast, environmental sounds had positive effects on larval recruitment, which supports further exploration of acoustic enrichment techniques (Gordon et al. 2019; Simpson et al. 2005). The single examination of movement found that the activity levels of various larvae slightly increased in response to reef sounds (Stocks et al. 2012). Further research incorporating animal bioacoustics and physiological responses to environmental sounds would help substantiate these findings.

Similar to acoustic exposure studies on fishes, limited research has been conducted on the effects of music on aquatic invertebrate physiology (Cox et al. 2018; Ren et al. 2021). Music was shown to positively influence invertebrate development, survival, and biochemistry, but these insights were drawn from a single study (Ren et al. 2021). While environmental enrichment is increasingly being considered in fish aquaculture settings and music welfare research is beginning to develop (Arechavala-Lopez et al. 2022; Barcellos et al. 2018; Kriengwatana, Mott, and ten Cate 2022), studies on invertebrates remain limited (e.g., Pereira 2015). Expanding the field of acoustic enrichment research could nonetheless have substantial applications for improving invertebrate aquaculture and welfare.

In addition to examining the responses of aquatic invertebrates to sound exposure, we quantified the effects of each sound category on invertebrate taxa. Behavioral and physiological responses were typically consistent within each sound source analysis (e.g., behavioral responses to anthropogenic noise), and arthropods and molluscs were most likely to have pronounced physiological responses to anthropogenic and synthetic sounds. The responses to synthetic sounds may have been most detrimental since these sounds do not occur naturally in aquatic ecosystems and can have sound characteristics less constrained by natural forces. In general, the behavioral responses of taxa were less notable, though synthetic sounds did elicit significantly negative responses in molluscs. Decapod crustaceans and cephalopods especially have several physiological adaptations that could increase their hearing sensitivity (e.g., acceleration detection) and therefore adverse responses to noise, which should be incorporated into aquatic ecosystem assessments (Solé et al. 2023). Additionally, the studies we identified were heavily biased towards arthropods and molluscs in countries outside of equatorial regions. Therefore, more acoustic exposure research on a variety of invertebrate taxa from different regions is critical as some groups are particularly understudied (e.g., annelids and echinoderms), and research on many ecologically and commercially important invertebrates is still absent (Solé et al. 2023).

While the responses of cetaceans, pinnipeds, and fishes to sound exposure have been more extensively studied than aquatic invertebrates, key differences between these groups highlight the importance of continued research efforts on invertebrates (Duarte et al. 2021). Aquatic invertebrate phyla, body plans, and ontogenetic stages are notably more diverse than those of fishes and marine mammals, so sound exposure impacts are likely to be less uniform and generalizations should be made with caution (Aguilar de Soto 2016). While there are some similarities in sound detection anatomy among these groups, invertebrate taxa have receptor systems consisting of unique combinations of internal statocysts and epidermal flow detectors (Duarte et al. 2021; Solé et al. 2023). Unlike fishes, aquatic invertebrates do not have accessory hearing structures (e.g., swim bladder connections) that allow them to sense the pressure component of sound, so are likely only sensitive to particle motion (Solé et al. 2023). Sound exposure studies on aquatic invertebrates should therefore measure particle motion in addition to sound pressure levels and frequency (Nedelec et al. 2016). Further, particle motion travels both through the water as well as the epibenthos so some aquatic invertebrates (e.g., hermit crabs) are also impacted by epibenthic vibrations (Roberts and Elliott 2017; Roberts and Laidre 2019).

The diverse responses of aquatic invertebrate taxa to sounds suggests that species will experience both behavioral and physiological impacts while navigating rapidly changing underwater soundscapes (Duarte et al. 2021). These adjustments have the potential to affect individual fitness (e.g., growth rate) as well as populations (Hawkins and Popper 2017)—for example, noise exposure can cause species emigration, which may impact population structures, create unbalanced predator–prey dynamics, or lead to reduced recruitment through impaired larval development (Peng, Zhao, and Liu 2015). Reduced populations could also negatively affect the productivity of fisheries, although no significantly negative effects of noise on invertebrate catch rates have yet been reported (Solé et al. 2023). Additionally, sound exposure can change social interactions in a variety of ways including altered signal characteristics and communication, mating behaviors, and group cohesion (Fisher et al. 2021). For invertebrate species that are dominant in underwater soundscapes, such as snapping shrimp, any changes to their health and behaviors could lead to acoustically mediated feedback loops further exacerbating the extent of environmental changes (Gordon et al. 2018;

Spiga 2016). More holistic assessments of underwater soundscapes and how invertebrates interact with them will provide greater insight into the larger ecosystem implications of anthropogenic noise and other global changes.

Meta-analyses are an effective technique for reaching transparent conclusions and evaluating ecological trends but nonetheless have limitations (Del Re 2015). Some of the challenges in our meta-analysis included the widely differing behavioral and physiological responses among diverse invertebrate phyla (and uncertainty of the response directionality in some cases), varied methodologies of the selected studies (e.g., laboratory and field environments), and an inability to include relevant data due to its published format (e.g., mean or variability not available) or lack of peer-review (e.g., government reports). There are also notable difficulties with conducting laboratory bioacoustic studies, including the sound field within tanks not matching those of natural aquatic environments and the complex relationship between sound pressure and particle motion (Dinh and Radford 2021; Hawkins and Popper 2017; Nedelec et al. 2016). Additionally, there was some indication of publication bias for physiological responses to anthropogenic noise and synthetic sounds, which suggests that significant results may have been published more frequently in these categories. We recommend cautious interpretations of these data as the ESs and model estimates could be inflated, and we emphasize the importance of publishing all results to avoid bias in subsequent meta-analyses. Future work should consider these issues as well as continue to assess the impacts of various sound sources and acoustic enrichment on a diversity of aquatic invertebrates, especially understudied and ecologically important groups, early life stages, freshwater species, and sound-producing taxa (e.g., sea urchins; Coquereau et al. 2016; Rountree, Juanes, and Bolgan 2020; Solé et al. 2023), in addition to ensuring that these data are accessible to future meta-analyses.

Our study illustrates that rapidly changing underwater acoustic conditions, including increased noise pollution and altered soundscapes (Duarte et al. 2021; Gordon et al. 2018), can significantly impact aquatic invertebrates at various life stages. While the literature on the effects of sounds on aquatic invertebrates is growing, our study is the first to quantitatively analyze and categorize responses to a variety of sound types across a range of invertebrate species. Since increasingly prevalent underwater noise poses a global threat to aquatic ecosystems and their inhabitants, we also highlight the necessity to develop management strategies and policies surrounding acoustic exposure that consider the wide array of marine and freshwater invertebrates that could be impacted.

Author Contributions

Hailey L. Davies: conceptualization, data curation, formal analysis, investigation, methodology, project administration, validation, visualization, writing – original draft, writing – review and editing. **Kieran D. Cox:** conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, project administration, resources, supervision, validation, visualization, writing – original draft, writing – review and editing. **Kelsie A. Murchy:** data curation, writing – original draft, writing – review and editing. **Hailey M. Shafer:** data curation, visualization, writing – original draft, writing – review and editing. **Audrey Looby:** validation, writing – original draft, writing – review and editing. **Francis Juanes:** conceptualization, funding acquisition, investigation, project administration, supervision, writing – review and editing.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data and code that support the findings of this study are openly available in Borealis at https://doi.org/10.5683/SP3/EV6QQH.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.