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Sound the Alarm: A Meta-Analysis on the Effect of Aquatic Noise on Fish Behavior and Physiology

Running Title: Meta-Analysis on the Effects of Noise on Fish

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Abstract

The aquatic environment is increasingly bombarded by a wide variety of noise pollutants, whose range and intensity are increasing with each passing decade. Yet little is known about how aquatic noise affects marine communities. To determine the implications that changes to the soundscape may have on fishes, a meta-analysis was conducted focusing on the ramifications of noise on fish behavior and physiology. Our meta-analysis identified 42 studies that produced 2,354 data points, which in turn indicated that anthropogenic noise negatively affects fish behavior and physiology. The most predominate responses occurred within foraging ability, predation risk, and reproductive success. Additionally, anthropogenic noise was shown to increase the hearing thresholds and cortisol levels of numerous species while tones, biological, and environmental noise were most likely to affect complex movements and swimming abilities. These findings suggest that the majority of fish species are sensitive to changes in the aquatic soundscape, and depending on the noise source, species responses may have extreme and negative fitness consequences. As such this global synthesis should serve as a warning of the potentially dire consequences facing marine ecosystems if alterations to aquatic soundscapes continue on their current trajectory.

Introduction

The range and intensity of anthropogenic noise in aquatic environments has increased considerably in recent decades, yet little is known about its effects on marine communities (Popper and Hastings, 2009; Popper and Fay, 2011; Simmonds *et al.*, 2014). Specifically, low-frequency ambient noise levels in the open ocean have increased by 3.3 dB per decade since the 1950's, representing a doubling of the noise budget every decade (McDonald *et al.,* 2006; Frisk 2012). Recent research suggests that these increases in noise occur regardless of an area's protection designation. Anthropogenic noise now doubles background sound levels in over half of all protected units within the continental United States, and 14% of habitats critical to endangered species are exposed to a tenfold increase in sound levels relative to the natural soundscape (Buxton *et al.,* 2017). Although derived from terrestrial parks, this phenomenon is likely more severe in marine protected areas as sound travels five times faster in water than air, therefore, moving greater distances in less time, with less attenuation (Hawkins and Myrberg; 1983; Finfer *et al.*, 2008). Additionally, coastal regions are three times more populated than the global average, resulting in 40% of the global population living within 100 km of the coastline (Cohen *et al.,* 1997; Small & Nicholls 2003). This influx of anthropogenic activity indicates that noise production is centered around coastlines. In all cases, increased noise levels are positively correlated with transportation, development, and resource extraction; all of which are increasing to keep pace with the ever-expanding global economy (Frisk 2012; Buxton *et al.,* 2017).

The majority of sound produced by anthropogenic activities is considered to be noise pollution as it contains little to no intentional information (Popper and Hastings, 2009; Pijanowski *et al.*, 2011). Many fish species have adaptations that have increased their abilities to detect and produce sound, including the roughly 800 fish species from 109 families known to be soniferous, however, these adaptations have also made them susceptible to noise pollution (Kaatz 2002; Popper and Hastings, 2009; Picciulin *et al.*, 2010; Shannon *et al.,* 2016). Investigations into the potential implications of noise on marine life have determined that these disturbances would likely first lead to physiological followed by behavioral changes (Kight and Swaddle, 2011; Gedamke *et al.,* 2016). Depending on the intensity and duration of exposure, noise pollution has the potential to temporarily or permanently alter auditory thresholds, mask the detection of important environmental cues, and lead to increased mortality due to predation (Bass and Clark, 2003; Ladich, 2008; Popper and Hastings, 2009; Picciulin *et al.,* 2010; Simpson *et al.,* 2016). Despite the concerns regarding increasing anthropogenic noise, the monitoring and regulation of this pollutant has been limited (Simmonds *et al.,* 2014). This is in part due to a lack of understanding the effects of noise on aquatic organisms (Bass and Clark, 2003; Popper and Hastings, 2009).

To determine the implications that disturbances in the aquatic soundscape may have on marine and freshwater fishes, we conducted a meta-analysis addressing the effect of noise on fish behavior and physiology. Meta-analyses are an effective method for assessing ecological trends (Mann, 1990; Côté & Sutherland 1997; Harrison 2011), as they allow for generalizable conclusions to be reached through the utilization of data from multiple sources (Cadotte *et al.,* 2012). Although high-quality syntheses of noise pollution in both the terrestrial and aquatic environments have been conducted (see Popper and Hastings, 2009; Radford *et al.,* 2014; Shannon *et al.,* 2016), these studies have been limited to thorough reviews or vote counting methods that lack statistical power and were therefore unable to quantify the impact to species (Harrison 2011). Through this analysis we reveal the main sources of noise that fishes are exposed to both experimentally and in the wild: anthropogenic noise, biological noise, environmental noise, tones, and music. We also examined how species responses, including foraging ability, movement, responses to predation and reproductive ability, were affected by the various noise sources. This study constitutes the first global quantitative synthesis addressing the effect of noise pollution on fish behavior and physiology.

Methods

Systematic Literature Search

Thompson's Web of Science was used to conduct a systematic literature search. Search results were limited to peer-reviewed articles published between 1950 and 2015. The specific search terms were 'fish' and 'noise or sound or acoustic or ecoacoustics or bioacoustics' and 'behav* or physiol* or response or morphology', which returned 2,817 potentially relevant peer-reviewed articles. An additional 526 potentially relevant peer-reviewed articles were retrieved through other search engines including ScienceDirect and JSTOR, and by thoroughly reviewing bibliographies of relevant reviews. The titles and abstracts of the 3,343 studies were reviewed to determine which papers addressed the effects of anthropogenic noise on fish behavior or physiology (Fig. 1; Moher *et al.,* 2009). Articles that met these criteria (452) were then further evaluated to identify those that met the criteria of: original research, behavior or physiology focus, listed sound source, experimental control, included mean value, listed standard error or standard deviation, and the sample size stated.

Forty-two studies from 11 countries met the search criteria (Fig. S1). Thirty-six of the studies were conducted within a range of laboratory settings, and six of the studies were conducted in situ. We then extracted the sample size, mean, and standard deviation of the treatment and control groups from each study. All data were obtained from tables and text when possible; if necessary, the reliable and accurate extraction software GraphClick was used to retrieve data from figures (Boyle *et al.,* 2013). A total of 2,354 data points were collected from the 42 studies (Fig. S2).

Effect Size Calculation

The Metafor package was used in R-studio to calculate the effect sizes and variances for each study (Viechtbauer, 2010; R Core Team, 2013). Mean difference (md) was calculated using Eq. (1), where $\bar{Y}_1$ and $\bar{Y}_2$ are the mean values of the treatment and control group, respectively.

$$\mathrm{md} = \bar{Y}_1 - \bar{Y}_2 \qquad (1)$$

The standardized mean difference (Hedge's d), which is an indication of the overall effect and weights of studies based on their sample sizes and standard deviations, was determined using Eq. (2). Sample sizes are indicated by n_1 and n_2 with standard deviations s_1 and s_2.

$$d = \frac{\bar{Y}_1 - \bar{Y}_2}{\sqrt{\frac{(n_1-1)s_1^2+(n_2-1)s_2^2}{n_1+n_1-2}}} \qquad (2)$$

The variance for Hedge's d was determined via Eq. (3) (Hedges and Olkin, 1985).

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

To account for the large amount of dissimilarity present within the response variables, the directionality of each study was determined to ensure that negative and positive effect sizes represented negative and positive responses, respectively. For example, for a response variable such as growth rate, an increase would result in a positive effect size, while an increase in a response variable such as cortisol (a common stress hormone) would also lead to a positive effect size, despite being an undesirable response. Accounting for the directionality of each response variable is thus a critical step for a meta-analysis of this nature.

Statistical Analyses

Separate analyses were conducted on studies addressing behavioral and physiological responses, which were further split according to sound source: anthropogenic noise, environmental noise, tones, music, and biological noise. We considered biological noise both a positive and negative source, *e.g.* mating calls vs. aggressive conspecifics calls, therefore studies examining positive and negative biological noises were split accordingly and analyzed separately. Furthermore, in rare cases when studies evaluated the effect of both behavior and physiology or multiple noise sources, each case was treated independently as effect sizes for each sound source were never pooled during the analysis.

To determine which aspects of species behavior and physiology would be affected by the various sound sources, the response variables for each study were grouped into the following behavioral categories: foraging, movement, predation avoidance, reproduction, social interactions, and vocalization; and the following physiological categories: auditory system, blood chemistry, body condition, body size and growth, fatty acid, immune system, neurotransmitters, organ health, reproduction, and stress (Table S3 & S4).

The analysis was conducted in R-studio (R Core Team, 2013; R Studio, 2015). Forest and funnel plots were generated for each of the sound sources within the behavioral and physiological categories using the 'metafor' and 'MAd' packages to determine the summary effect and confidence intervals of each model, and establish if any potential publication bias was present (Viechtbauer, 2010; Del Re and Hoyt 2014). Separate linear mixed effect models were used to determine which of the behavioral and physiological categories effect sizes differed from the 'zero' (no effect) line. A separate linear mixed effect model was run for each of the sound sources within the behavioral and physiological categories, which used response category as a fixed factor and study as a random effect. The resulting model value and standard deviations were then plotted as a visual indication of how each response variable was affected by the various sound sources.

Results

Effect of Noise on Behavior and Physiology

Forest plots indicated that behavioral and physiological responses varied strongly based on sound source. Anthropogenic noise had a significantly negative effect on fish behavior and physiology, as studies addressing behavioral responses yielded an overall effect size (ES) of -4.73 with 95% confidence intervals (CI) of -8.75 and -0.70, while studies addressing physiological responses had an ES of -1.35 with 95% CI of -2.07 and -0.63 (Fig. 2a; Fig. 3a). These results indicate that there is a negative impact of 4.73 and 1.35 standard deviations to behavior and physiology when fish are exposed to anthropogenic noise, compared to control groups. Tones also had a negative (but not significant) impact on behavior and physiology with overall ES's of -10.5 (CI -23.43, 2.42) and -6.75 (CI -15.62, 2.12), respectively (Fig. 2b; Fig. 3b). Biological noise that was deemed to be adverse, had a negative, but non-significant effect on behavior (ES -0.61, CI -1.16, 0.07; Fig. 2c), while positive biological noise had no effect on fish behavior (ES 0.08, CI -0.41, 0.57; Fig. 2d). A single study addressed the effect of biological noise on fish physiology, and indicated that noises from positive biological sources do not affect fish physiology (ES 0.61, CI -0.17, 1.40; Fig. 3c). Fish behavior was not affected by environmental noise (ES 0.01, CI -0.35, 0.37; Fig. 2e), while fish physiology was negatively affected (ES -0.67, CI -1.29, 0.06; Fig. 3d). No studies addressing how fish respond behaviorally to music were conducted, however, studies addressing the effect of music on fish physiology indicated that music has a positive, although not significant, effect on fish physiology (ES 41.36, CI -39.60, 122.32; Fig. 3e). Funnel plots indicated that there was a minor but acceptable amount of publication bias within studies focusing on fish behavior and physiology (data not shown).

Behavioral Responses to Aquatic Noises

Anthropogenic noise increased movement (mixed-effects model: Estimate=18.52, DF= 155, t-value= 3.53, and P= 0.00) and reproduction (mixed-effects model: Estimate= 17.78, DF= 155, t-value= 3.09, and P= 0.002) related behaviors, which included swimming depth, directional changes, schooling adjustments, swimming speed, and the time parents spent caring for their nests (Fig. 4a; Table S5). In contrast, anthropogenic noise decreased predation responses, including starting responses, time until caught and responses to predatory strikes (mixed-effects model: Estimate= -9.02, DF= 155, t-value= -1.69, and P= 0.092), as well as social interactions *e.g.*, encounters won and number of social interactions (mixed-effects model: Estimate= -7.34, DF= 150, t-value= -1.23, and P= 0.220), although both decreases were not significant. Foraging behaviors, however, significantly decreased due to anthropogenic noise (mixed-effects model: Estimate= -12.17, DF= 155, t-value= -2.24, and P= 0.027), indicating that the proportion and number of food items consumed, foraging efficiency, and discrimination error, were all negatively affected by anthropogenic noise. Substantial variation existed in the vocalization response to anthropogenic noise, with both positive and negative responses with no unanimous direction observed (mixed-effects model: Estimate= 0.81, DF= 10, t-value= 0.05, and P= 0.960).

Tones significantly increased foraging (mixed-effects model: Estimate= 15.98, DF= 51, t-value= 2.27, and P= 0.03), movements (mixed-effects model: Estimate= 17.94, DF= 51, t-value= 2.78, and P= 0.01), and predation responses, (mixed-effects model: Estimate= 21.01, DF= 51, t-value= 2.69, and P= 0.01). These increases were associated with activities that included food handling error, discrimination error, swimming speed, and startle responses (Fig. 4b; Table S5). As with anthropogenic noise, species vocalization responses to tones showed a large amount of variation, with no clear directionality (mixed-effects model: Estimate= 0.23, DF= 4, t-value= 0.03, and P= 0.98).

Negative biological noise induces significant increases in behaviors related to foraging (mixed-effects model: Estimate= 1.33, DF= 319, t-value= 3.55, and P= 0.001), movement (mixed-effects model: Estimate= 0.28, DF= 319, t-value= 5.4, and P= 0.000), and social interactions (mixed-effects model: Estimate= 1.21, DF= 2, t-value= 1.86, and P= 0.204), while positive biological noise had no impact on species vocalizations (mixed-effects model: Estimate= -0.1, DF= 4, t-value= -0.23, and P= 0.833; Fig. 4c,d; Table S5). Specifically, exposure to negative biological noise increased species bite rate, the amount of time they spent isolated, and their aggression.

Neither movement nor vocalization-related behaviors increased or decreased when exposed to environmental noise (mixed-effects model: Estimate= -0.07, DF= 18, t-value= -0.53, and P= 0.600: mixed-effects model: Estimate= 0.22, DF= 18, t-value= 0.85, and P= 0.408; Fig. 4e; Table S5)

Physiological Responses to Aquatic Noises

Anthropogenic noise caused significant increases in the auditory system (mixed-effects model: Estimate= 2.63, DF= 18, t-value= 4.11, and P= 0.001), and stress levels (mixed-effects model: Estimate= 1.72, DF= 991, t-value= 2.11, and P= 0.035) indicating that hearing threshold (including the inability to hear conspecifics) and cortisol levels increase when exposed to anthropogenic noise (Fig. 5a; Table S6).

Neither reproduction nor neurotransmitters showed a significant response to positive biological noise (mixed-effects model: Estimate= -2.43, DF= 2, t-value= -1.83, and P= 0.209: mixed-effects model: Estimate= -0.01, DF= 2, t-value= -0.01, and P= 0.995; Fig. 5b).

Environmental noise led to positive response within the auditory system, which was predominately due to increases in species hearing thresholds when exposed to environmental noise (mixed-effects model: Estimate= 1.02, DF= 2, t-value= 5.16, and P= 0.036). However, none of the other areas tested, which included blood chemistry, body condition, size and growth, immune system, organ health, reproduction, and stress exhibited significant positive or negative responses to environmental noise (Fig. 5c; Table S6).

Exposure to music caused decreases in response variables associated with blood chemistry, body condition, size and growth, fat stores, and organ health, and increased neurotransmitters, although all of these alterations were subject to large amounts of variation and none of them were significant (Fig. 5d; Table S6).

Tones significantly increased body condition, measured as carcass moisture and condition factor (mixed-effects model: Estimate= 95.63, DF= 214, t-value= 8.29, and P= 0.000). No responses to tones were observed within any of the other physiological responses tested (Fig. 5e; Table S6).

Discussion

Given growing concerns surrounding species' responses to the ever-increasing bombardment of noise in aquatic environments, there is a pressing need for innovative ways to evaluate this issue (Popper and Hastings, 2009; Popper and Fay, 2011). Unfortunately, understanding how species respond to noise pollution is greatly obstructed by a lack of concrete knowledge (Hawkins *et al.,* 2015). To further our understanding of fish responses to aquatic noise we analyzed 42 peer-reviewed studies from 11 countries, focusing on the impact of noise on fish behavior or physiology. The studies included freshwater, estuarine and marine species and were conducted in variety of field and laboratory settings. The resulting 2,354 data points were used to develop models summarizing trends across studies as well as specific responses.

Recent research suggests that all stages of species' life histories may be negatively affected by anthropogenic noise (see Popper and Hastings, 2009; Radford et al 2014; Shannon *et al.,* 2016). Our findings support this trend as anthropogenic noise was shown to increase movement, nest care, hearing thresholds and stress levels, while decreasing foraging-related behaviors. Increases in movement were attributed to directional changes and alterations to swimming behaviors, the majority of which appeared to be responses to perceived predation and were energetically costly (Fraser and Gilliam 1992). Increased parental care also carries additional costs with implications for both parents and offspring, as nest care is a strenuous and time-consuming activity that can exhaust certain species, especially those with complex mating strategies, to the point of death (Williams, 1966; Alonso-Alvarez and Velando 2012; Bose et al., 2015). Increased hearing thresholds and cortisol levels were associated with an increase in stress-related hormones, and suggest that anthropogenic noise has the potential to cause both short and long-term physiological effects. As the potential consequences of hearing threshold increases are well documented within mammals, if fishes respond in a similar fashion then it is likely that the development of the auditory cortical will be severely impaired (Fay and Popper, 2000; Chang and Merzenich 2003). Recovery from threshold shifts will vary according to the stimulus as well as the auditory sensitivity of the affected species (Clark 1991). However, alterations to a species ability to forage and move through its environment have the potential to impede many species at all life history stages (Slabbekoorn *et al.*, 2010). Our results indicate that across a wide range of experimental and natural exposure conditions, anthropogenic noise can have adverse effects on fish behavior and physiology, which are not limited to specific responses or species. These findings quantify Popper and Hastings' (2009) concerns surrounding the potential implications of anthropogenic noise on fishes, and advance the notion that this issue is in urgent need of further attention and regulation.

In general, similar to anthropogenic noise, exposure to pure tones appeared to have a negative, but weaker, effect on fish behavior and physiology. The lack of statistical significance in these results is potentially a function of a low sample size in the studies summarized here, as tones have a long history of eliciting adverse physiological responses in fishes (see Popper and Clarke 1976), especially in relation to species' hearing thresholds (Slabbekoorn *et al.*, 2010; Kight and Swaddle 2011). In unique cases, tones increase auditory thresholds at a wider range of frequencies than anthropogenic noise (Scholik and Yan 2001), indicating that, much like anthropogenic noise, tones have the potential to negatively affect fish behavior and physiology across a wide range of species and conditions. Results of mixed effect models indicated that tones caused increased foraging, movement, and predation related responses. Furthermore, tones caused an increase in body condition-related response variables; the majority of which were attributed to increases in carcass moisture. Alterations to movement, foraging, and predation responses suggest that species exposed to tones will be more likely to startle, and experience discrimination or handling errors when feeding. Species exposed to tones will likely alter their swimming depth and speed, increase time spent in isolation, and potentially modify schooling shape or direction. These alterations in activity levels support and possibly explain the mechanisms behind fishes fleeing from seismic exploration. Fishes within these areas become more susceptible to predation, and school less effectively, resulting in decreased fitness and potentially size, which in turn, drastically reduces trawler and longline catch rates within surrounding waters (Hirst and Rodhouse 2000; Wardle *et al.*, 2001). Although untested to date, if decreasing catch rates are any indication, aquatic soundscapes may play more of a role in shaping fisheries and recent declines than currently assumed.

Unfortunately, investigations into how biological noise affects fishes are extremely rare and require extensive further inquiry. Additionally, the necessity to split these studies based on the nature of the sounds further reduces the likelihood of detecting overarching trends. However, despite this current lack of existing research, results generally supported our predictions. As expected, negative biological noises were determined to have an adverse effect on fish behavior, whereas studies investigating positive biological noise all resulted in positive responses, but these responses failed to elicit a significant effect size. This is likely due to the low number of studies considered, as it has been suggested and well supported that species, especially those with anatomical modifications for sound projection or reception, can recognize and potentially evaluate sounds related to biological interactions (Fay and Popper 2000; Horne 2008). The lack of research into this topic is understandable given the difficulty associated with replicating natural soundscapes under laboratory conditions; mostly due to issues surrounding the balance between sound pressure and particle velocity within a closed environment (Akamatsu *et al.*, 2002). As such, there is a dire need to address this issue and conduct more in situ research to increase the acoustic validity of testing environments (Slabbekoorn, 2016).

Our results unanimously showed that fish physiology is negatively affected by environmental noise. However, as only a single study addressed how environmental noise affects fish behavior, results surrounding behavioral responses were inconclusive and not considered indicative of a trend. Much like anthropogenic noise, environmental noise caused an increase in species' hearing thresholds. Although hearing impairment is an obvious response to extreme environmental noises (Kight and Swaddle 2011), the effect that hearing loss will have on species' life history is not as evident since studies investigating the long-term consequences of hearing loss are rare, and inferring potential consequences is essential. Over 800 species from 109 families are known to produce sounds (Kaatz 2002; Rountree *et* *al.*, 2006), with distinct variation between sounds existing at the species, population and even gender level (Kihslinger and Klimley 2002; Ueng *et al.*, 2007). The inability to hear and thus communicate with conspecifics could impact critical interactions such as agonistic communication, courtship, and spawning (Myrberg, 1997; McKibben and Bass 1998; Aalbers, 2008) and have dire fitness consequences (Brumm and Slabbekoorn, 2005; Wysocki and Ladich 2005). Given that anthropogenic noise elicited similar but more predominant hearing shifts, species living within areas subjected to intense anthropogenic and environmental noise, like exposed coastlines along shipping routes, are likely bombarded with acoustic stimuli to the point that the previously listed consequences become extremely probable.

The finding that music may positively affect fish physiology, although potentially comical to some, does represent a potential point of interest. These studies occurred within aquatic facilities, where mechanical noise can produce a stressful environment (Papoutsoglou *et al.*, 2008). One of the observed effects was that classical music increased dopamine levels in fish. Dopamine neuropathways are essential for positive reinforcement learning and occur across all animal phyla, including vertebrates (Barron *et al.*, 2010). This result suggests that classical music may be interpreted as a positive stimulation and could be used as an environmental enrichment tool to improve animal welfare, which in turn can result in improved growth rates (Newberry, 1995) for fish hatcheries.

It is worth noting that under these experimental conditions, a lack of significance does not necessarily indicate that these areas of species behavior or physiology will not be affected by noise pollution. As meta-analyses draw from the existing literature, unbalanced samples sizes and insufficient data are inevitable and represent areas in need of further study. This is evident in the area of study concerning environmental noise, music, and biological noise, which are currently data insufficient and require further research. However, as these findings indicate that multiple fish species respond similarly to noise across a wide range of experimental conditions, our study aligns with current reviews on the topic (see Popper and Hastings, 2009; Radford et al 2014; Shannon *et al.*, 2016), but is the first to do so in a robust quantitative fashion through the use of meta-analysis.

These findings also illuminate an ongoing debate within soundscape research: the study of species responses to aquatic noise in laboratory conditions. Some have concluded that sound fields within tanks will never match those of natural aquatic environments (Akamatsu *et al.*, 2002). Species, however, may be adapted to detect sound under a wider variety of conditions than previously considered. For example, as natural habitats are far more structurally complex than the experimental designs used in these studies, it is reasonable to assume that species whose hearing capabilities and sound production evolved within these habitats are well suited to detect noise despite distortion. Although currently untested, noise distortion under experimental conditions may not be magnitudes more severe than that of noise propagating through a kelp forest, coral reef or other complex habitats. Undoubtedly, a large portion of the information embedded within the noise has the potential to be lost in an experimental setting, however, this loss may not differ drastically from natural conditions and thus the extent to which studies conducted in imperfect sound fields should be discredited remains a topic in need of further inquiry.

It is now well-recognized that to regulate, monitor and predict the effect that aquatic noise has on fishes, increasing our knowledge of marine soundscapes is essential (Hawkins *et al.*, 2015), especially as aquatic soundscapes continue to be subjected to anthropogenic activity. A major limitation of this effort is the lack of understanding of how sound affects marine organisms (Bass and Clark, 2003; Popper and Hastings, 2009; Simmonds *et al.*, 2014). Our findings suggest that aquatic noise, depending largely on the source, has the potential to disturb species' ability to interact with conspecifics, forage efficiently, produce viable offspring, and school effectively, while inducing potentially reversible hearing loss. These findings are likely not limited to fishes; although a thorough synthesis is still lacking, recent research suggests that invertebrates may be just as susceptible to noise pollution. Solan and colleagues (2016) determined that invertebrate species, even those that do not communicate via acoustics, can exhibit a suite of behavioral responses when exposed to shipping and construction-related noise. These behavioral responses can ultimately alter how species mediate key ecosystem processes, possibly undermining the ecosystem services provided by benthic invertebrates.

Our study illustrates how the ever increasing, potentially unstoppable, bombardment of aquatic noise may negatively affect the majority of marine species. However, it is important to remember that fish and other marine organisms have not evolved in a quiet environment (Slabbekoorn *et al.*, 2008). Although most of the responses observed in this synthesis are associated with an inability to function properly, not all responses resulted in permanent damage (Bass and Clark, 2003; Ladich, 2008; Popper and Hastings, 2009; Picciulin *et al.*, 2010). This result suggests that despite unregulated noise pollution in marine soundscapes having the potential to drastically affect organisms, there is also the option of regulation and recovery within these systems. As anthropogenic noise is easily the most negative of the sound sources that exists within any body of water, and noise pollution is increasing exponentially, this global synthesis should serve as a warning and echo the growing concerns regarding the potentially dire consequences for marine ecosystems if noise continues to climb in an unregulated manner.

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Figure Captions

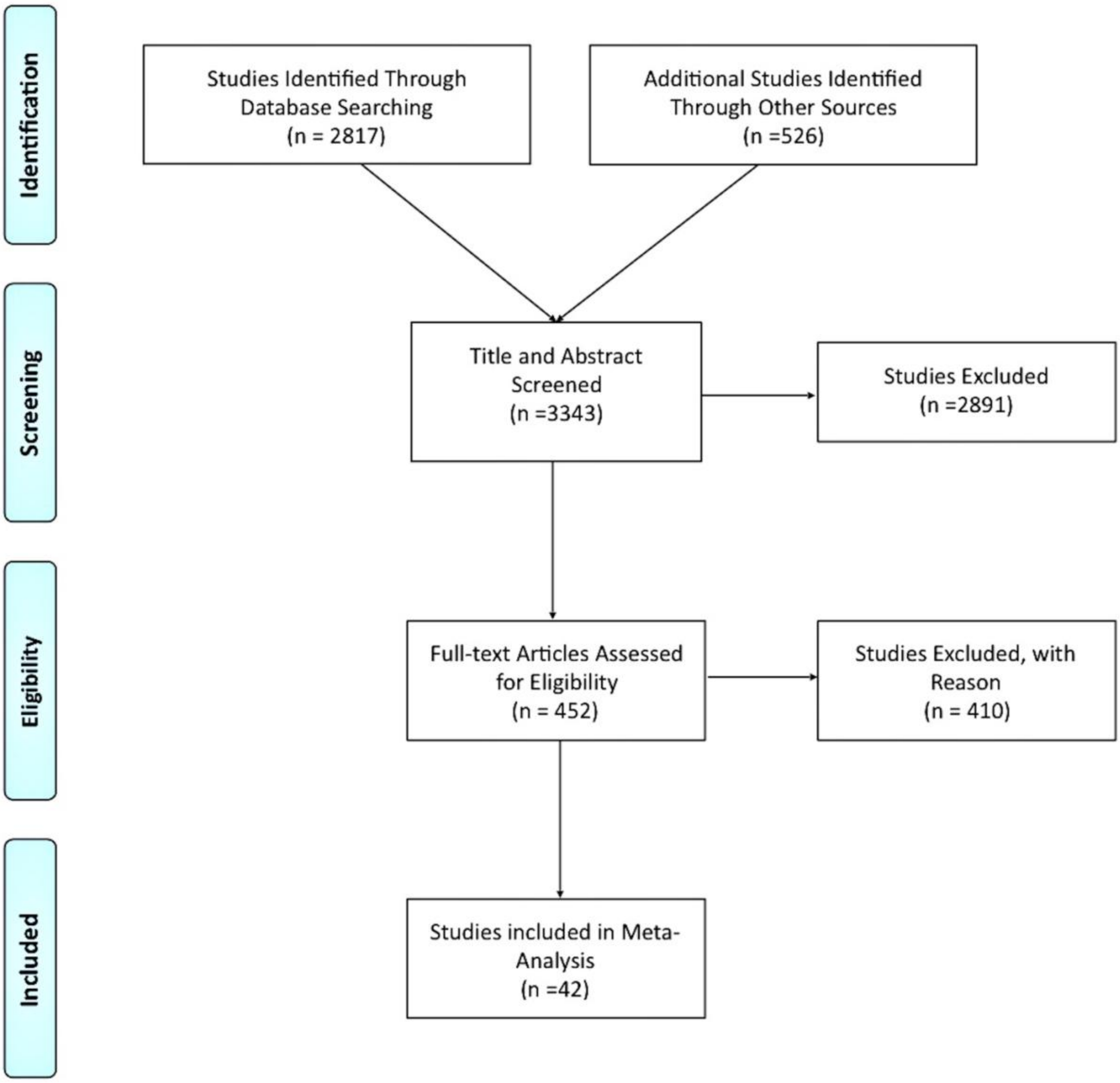
Figure 1. A PRISMA diagram outlining the selection processes of papers for the meta-analysis on the effect of aquatic noise on fish behavior and physiology.

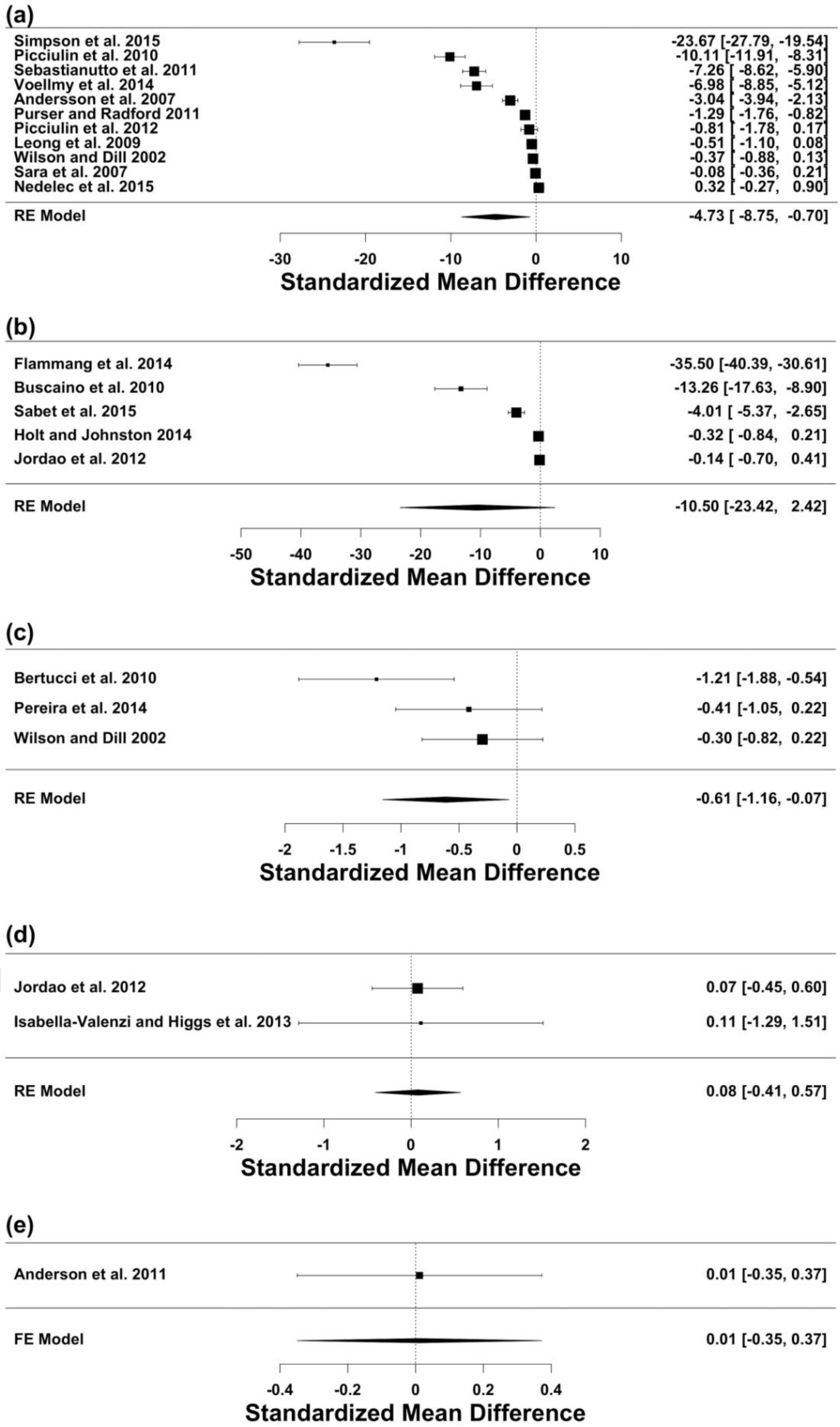
Figure 2. Forest plots illustrating how various aquatic noises affect fish behavior. Studies were divided into the following categories based on noise source: a) Anthropogenic Noise b) Tones c) Negative Biological Noise d) Positive Biological Noise e) Environmental Noise. Author(s) and publication year are listed within each plot.

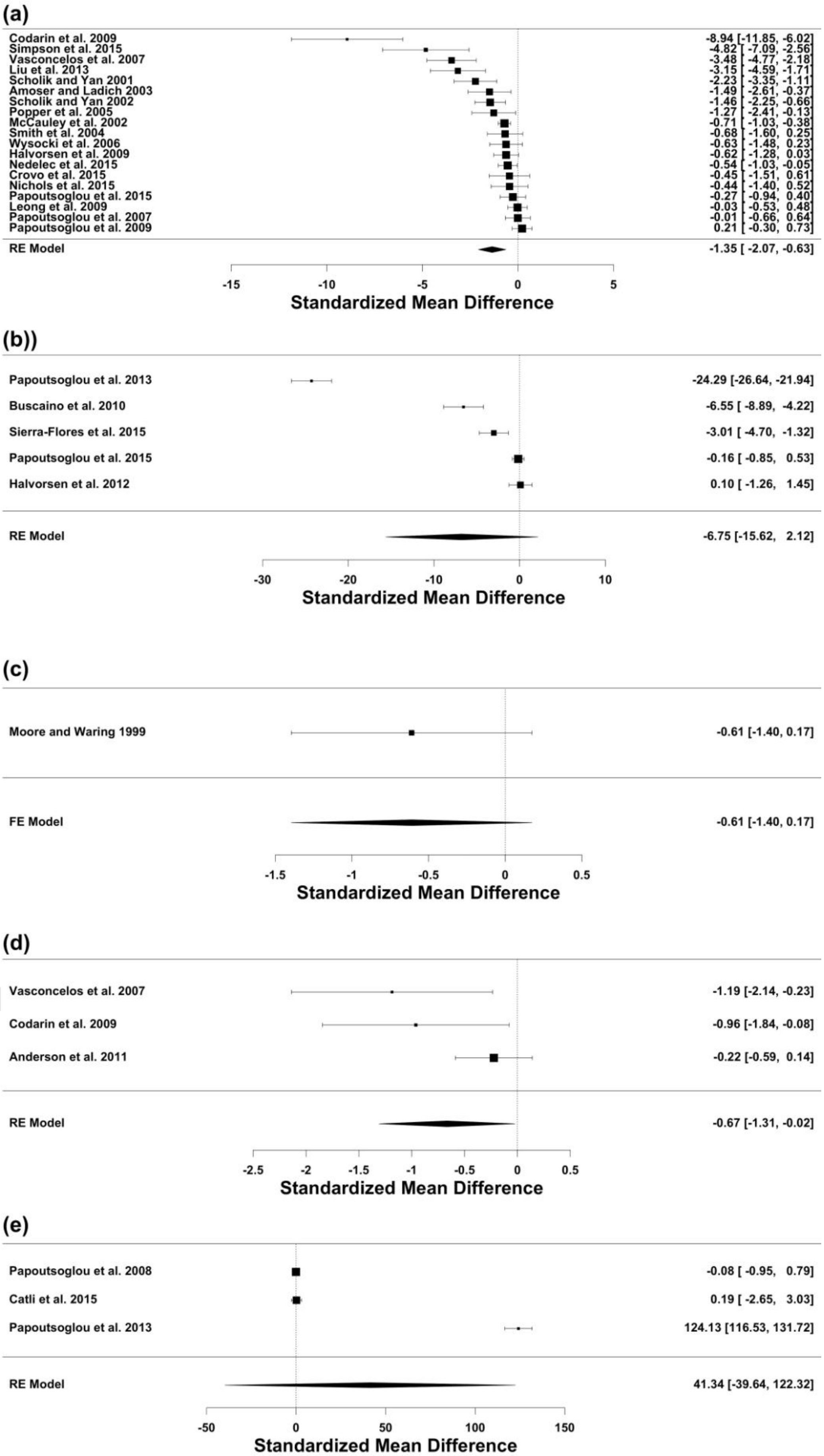
Figure 3. Forest plots illustrating how various aquatic noises affect fish physiology. Studies were divided into the following categories base on noise source: a) Anthropogenic Noise b) Tones c) Positive Biological Noise d) Environmental e) Music. Author(s) and publication year are listed within each plot.

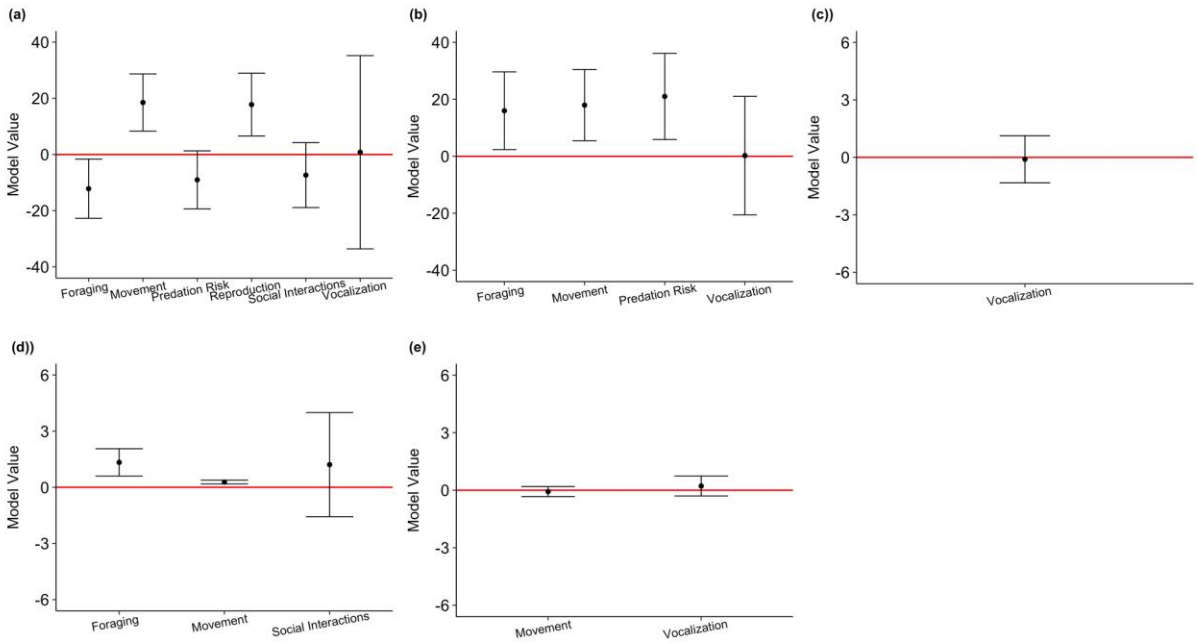
Figure 4: Fish behavioral responses to aquatic noise, derived via separate mixed effect models evaluating fish responses to each noise source: a) Anthropogenic Noise b) Tone c) Positive Biological Noise d) Negative Biological Noise e) Environmental Noise. Horizontal lines indicate the 0 effect size or 'no change' line.

Figure 5: Fish physiology responses to aquatic noise derived via separate mixed effect models evaluating fish responses to each noise source: a) Anthropogenic Noise b) Positive Biological Noise c) Environmental Noise d) Music e) Tone. Horizontal lines indicate the 0 effect size or 'no change' line.


Identification
Studies Identified Through Database Searching (n = 2817)
Additional Studies Identified Through Other Sources (n =526)
Screening
Title and Abstract Screened (n =3343)
Studies Excluded (n =2891)
Eligibility
Full-text Articles Assessed for Eligibility (n = 452)
Studies Excluded, with Reason (n = 410)
Included
Studies included in Meta-Analysis (n =42)


(a)
Simpson et al. 2015
Picciulin et al. 2010
Sebastianutto et al. 2011
Voellmy et al. 2014
Andersson et al. 2007
Purser and Radford 2011
Picciulin et al. 2012
Leong et al. 2009
Wilson and Dill 2002
Sara et al. 2007
Nedelec et al. 2015
RE Model
-23.67 [-27.79, -19.54]
-10.11 [-11.91, -8.31]
-7.26 [-8.62, -5.90]
-6.98 [-8.85, -5.12]
-3.04 [-3.94, -2.13]
-1.29 [-1.76, -0.82]
-0.81 [-1.78, 0.17]
-0.51 [-1.10, 0.08]
-0.37 [-0.88, 0.13]
-0.08 [-0.36, 0.21]
0.32 [-0.27, 0.90]
-4.73 [-8.75, -0.70]
-30 -20 -10 0 10
Standardized Mean Difference
(b)
Flammang et al. 2014
Buscaino et al. 2010
Sabet et al. 2015
Holt and Johnston 2014
Jordao et al. 2012
RE Model
-35.50 [-40.39, -30.61]
-13.26 [-17.63, -8.90]
-4.01 [-5.37, -2.65]
-0.32 [-0.84, 0.21]
-0.14 [-0.70, 0.41]
-10.50 [-23.42, 2.42]
-50 -40 -30 -20 -10 0 10
Standardized Mean Difference
(c)
Bertucci et al. 2010
Pereira et al. 2014
Wilson and Dill 2002
RE Model
-1.21 [-1.88, -0.54]
-0.41 [-1.05, 0.22]
-0.30 [-0.82, 0.22]
-0.61 [-1.16, -0.07]
-2 -1.5 -1 -0.5 0 0.5
Standardized Mean Difference
(d)
Jordao et al. 2012
Isabella-Valenzi and Higgs et al. 2013
RE Model
0.07 [-0.45, 0.60]
0.11 [-1.29, 1.51]
0.08 [-0.41, 0.57]
-2 -1 0 1 2
Standardized Mean Difference
(e)
Anderson et al. 2011
FE Model
0.01 [-0.35, 0.37]
0.01 [-0.35, 0.37]
-0.4 -0.2 0 0.2 0.4
Standardized Mean Difference


(a)
Codarin et al. 2009
-8.94 [-11.85, -6.02]
Simpson et al. 2015
-4.82 [-7.09, -2.56]
Vasconcelos et al. 2007
-3.48 [-4.77, -2.18]
Liu et al. 2013
-3.15 [-4.59, -1.71]
Scholik and Yan 2001
-2.23 [-3.35, -1.11]
Amoser and Ladich 2003
-1.49 [-2.61, -0.37]
Scholik and Yan 2002
-1.46 [-2.25, -0.66]
Popper et al. 2005
-1.27 [-2.41, -0.13]
McCauley et al. 2002
-0.71 [-1.03, -0.38]
Smith et al. 2004
-0.68 [-1.60, 0.25]
Wysocki et al. 2006
-0.63 [-1.48, 0.23]
Halvorsen et al. 2009
-0.62 [-1.28, 0.03]
Nedelec et al. 2015
-0.54 [-1.03, -0.05]
Crovo et al. 2015
-0.45 [-1.51, 0.61]
Nichols et al. 2015
-0.44 [-1.40, 0.52]
Papoutsoglou et al. 2015
-0.27 [-0.94, 0.40]
Leong et al. 2009
-0.03 [-0.53, 0.48]
Papoutsoglou et al. 2007
-0.01 [-0.66, 0.64]
Papoutsoglou et al. 2009
0.21 [-0.30, 0.73]
RE Model
-1.35 [-2.07, -0.63]
-15 -10 -5 0 5
Standardized Mean Difference
(b))
Papoutsoglou et al. 2013
-24.29 [-26.64, -21.94]
Buscaino et al. 2010
-6.55 [-8.89, -4.22]
Sierra-Flores et al. 2015
-3.01 [-4.70, -1.32]
Papoutsoglou et al. 2015
-0.16 [-0.85, 0.53]
Halvorsen et al. 2012
0.10 [-1.26, 1.45]
RE Model
-6.75 [-15.62, 2.12]
-30 -20 -10 0 10
Standardized Mean Difference
(c)
Moore and Waring 1999
-0.61 [-1.40, 0.17]
FE Model
-0.61 [-1.40, 0.17]
-1.5 -1 -0.5 0 0.5
Standardized Mean Difference
(d)
Vasconcelos et al. 2007
-1.19 [-2.14, -0.23]
Codarin et al. 2009
-0.96 [-1.84, -0.08]
Anderson et al. 2011
-0.22 [-0.59, 0.14]
RE Model
-0.67 [-1.31, -0.02]
-2.5 -2 -1.5 -1 -0.5 0 0.5
Standardized Mean Difference
(e)
Papoutsoglou et al. 2008
-0.08 [-0.95, 0.79]
Catli et al. 2015
0.19 [-2.65, 3.03]
Papoutsoglou et al. 2013
124.13 [116.53, 131.72]
RE Model
41.34 [-39.64, 122.32]
-50 0 50 100 150
Standardized Mean Difference


(a)
(b)
(c))
(d))
(e)
Model Value
40
20
0
-20
-40
6
3
-3
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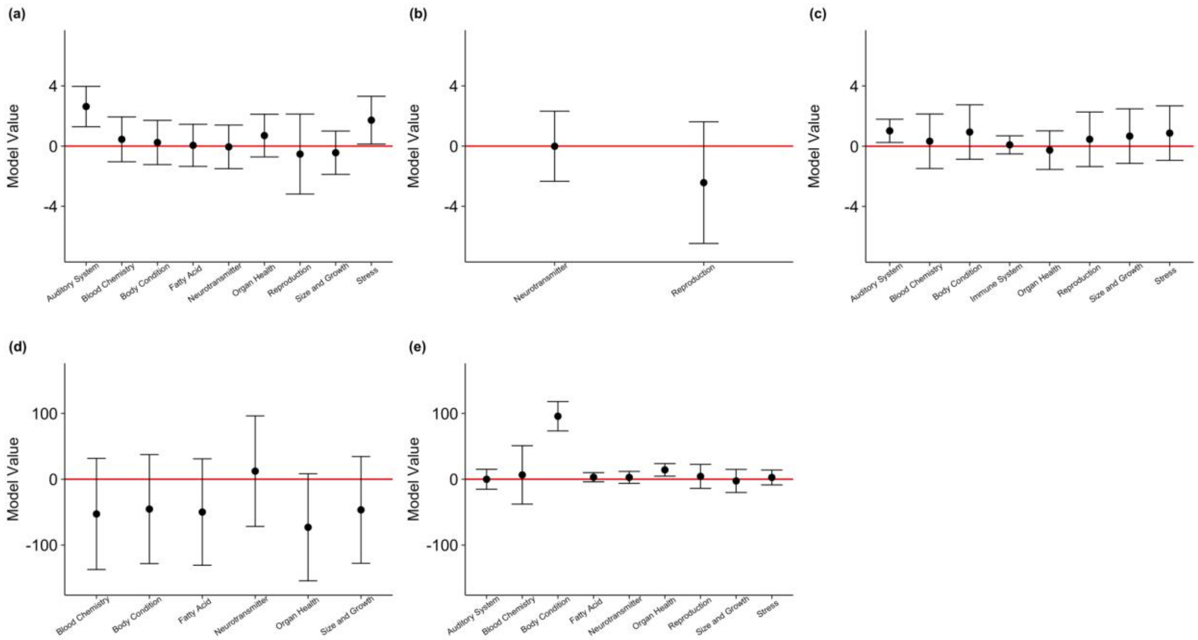
Foraging
Movement
Predation Risk
Reproduction
Social Interactions
Vocalization


(a)
(b)
(c)
(d)
(e)
Model Value
4
0
-4
100
-100
Auditory System
Blood Chemistry
Body Condition
Fatty Acid
Neurotransmitter
Organ Health
Reproduction
Size and Growth
Stress
Immune System