UNIVERSIDADE DE BRASÍLIA
INSTITUTO DE CIÊNCIAS BIOLÓGICAS
PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA

Uma metanálise dos impactos do ruído aquático em peixes à luz da capacidade de produzir e perceber sons

MAYCON VEIGA CHAVES

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Dissertação apresentada ao Programa de Pós-Graduação em Ecologia (PGECL) do Instituto de Ciências Biológicas - Universidade de Brasília, como requisito parcial para obtenção do título de Mestre em Ecologia.

Orientador: Prof. Dr. Eduardo Bessa

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"Se, na verdade, não estou no mundo para simplesmente a ele me adaptar, mas para transformá-lo; se não é possível mudá-lo sem um certo sonho ou projeto de mundo, devo usar toda possibilidade que tenha para não apenas falar de minha utopia, mas participar de práticas com ela coerentes. "

Paulo Freire

"A presença da periferia na universidade é uma luta histórica, acumulada desde a defesa das cotas raciais, sociais e para alunos da rede pública. Nossa permanência nesse ambiente é necessária, somos quase sempre os primeiros das nossas famílias a acessar o nível superior, passamos diariamente por desafios para conseguir nos formar, pesquisar e construir as nossas narrativas. "

Max Maciel

DEDICATÓRIA

Dedico esta dissertação à minha vó, Helena Figueiredo da Veiga, *in memoriam*, uma mulher símbolo de amor, resistência e luta. Goiana, nascida e criada em Pirenópolis, viveu em prol da família, fazendo o possível e o impossível para garantir que seus filhos e filhas tivessem acesso à alimentação, saúde e educação. Assim como os rios e cachoeiras, que banham e dão vida ao Cerrado, Helena inundou todos (as) ao seu redor com muito carinho e amor. A saudade é enorme, mas carrego no peito cada lembrança da sua existência. Te amarei eternamente.

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> *English:* Thanks to Kieran Cox, Audrey Looby, and Francis Juanes, for their excellent partnership in the development of this research. Their collaborations were fundamental, and I will be forever grateful for their support, dedication, and care for the project and me.

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Aos meus familiares, que sempre me apoiam e fazem de tudo para me ajudar na realização dos meus sonhos. À minha mãe Maria Corina, que me inspira diariamente. Aos meus irmãos Robson Veiga e Magno Veiga, que sempre estiveram ao meu lado, me incentivando e aconselhando. Às minhas avós Maria Florentina e Helena Figueiredo, que são meus alicerces nessa vida. Ao meu sobrinho Guilherme Souza, meus tios (as) e primos (as), os quais amo imensamente.

RESUMO

A paisagem sonora natural de diversos ambientes, incluindo os ambientes aquáticos, onde o som se propaga mais eficientemente, tem sido alterada pela ação humana (e.g. embarcações, mineração, turbinas de hidrelétricas). Nesse contexto, os peixes que ficam nesses corpos d'água devem estar sofrendo mudanças fisiológicas e de comportamento. Já tiveram estudos que analisaram isso, mas uma nova síntese, incluindo o grande volume de estudos recentes sobre o assunto, se fazia necessária. Um fator especial que não foi considerado antes é a capacidade de produzir sons ou a acuidade auditiva do peixe. Nossa metanálise revisou impactos fisiológicos e comportamentais de ruídos antrópicos, biológicos, ambientais, tons e música sobre peixes. Também analisamos estes impactos em relação à ocorrência de vocalização ativa pelos peixes e à presença de aparelho Weberiano. Foram analisados 107 estudos sobre 66 gêneros, e os ruídos antrópicos, biológicos e tonais causaram aumento na atividade comportamental e/ou fisiológica. O ruído ambiente, músicas e tons (respostas fisiológicas) tiveram resultados conflitantes e requerem maior aprofundamento. Apesar de não apresentarem um resultado consistente em todos os tipos de ruído, percebemos que a vocalização aumentou a sensibilidade de peixes à música e a presença de aparelho de Weberiano aumentou a sensibilidade aos tons. No geral, percebe-se que sons com potencial efeito negativo devem ser observados na conservação dos peixes e sons com potenciais efeitos positivos podem ser úteis no bem-estar de peixes em cativeiro. Nosso estudo realça a importância de controlar a emissão de barulhos por atividades antrópicas e demonstra a importância de considerar a contribuição dos peixes de forma bidirecional à paisagem sonora (produção e percepção sonora) na avaliação de impactos.

Palavras-chave: Comportamento; Distúrbios; Fisiologia; Paisagem sonora; Poluição sonora.

ABSTRACT

The natural soundscape of many environments, including aquatic environments where sound propagates most efficiently, has been altered by human action (e.g. shipping, mining, hydroelectric turbines). In this context, the fish present in these water bodies must be undergoing physiological and behavioral changes. There have already been studies that have looked at this, but a new synthesis, including the large volume of recent studies on the subject, was needed. A special factor that has not been considered before is the ability to produce sounds or the hearing acuity of the fish. Our meta-analysis reviewed physiological and behavioral impacts of anthropogenic, biological, environmental noise, tones and music on fish. We also analyzed these impacts in relation to the occurrence of active vocalization by fish and the presence of Weberian apparatus. We analyzed 107 studies on 66 fish genera, and anthropogenic, biological, and tonal noises caused increased behavioral and/or physiological activity. Environmental noise, music, and tones (physiological responses) had conflicting results and require further study. Although they did not show a consistent result across all noise types, we noticed that vocalization increased fish sensitivity to music and the presence of Weberian apparatus increased sensitivity to tones. Overall, sounds with potential negative effects should be observed in fish conservation and sounds with potential positive effects may be useful in the welfare of captive fish. Our study highlights the importance of controlling noise emissions from anthropogenic activities and demonstrates the importance of considering the contribution of fish in a bidirectional manner (sound production and perception) to the soundscape in impact assessment.

Keywords: Behavior; Disturbance; Noise pollution; Physiology; Soundscape.

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INTRODUÇÃO GERAL

O grupo dos peixes é altamente diverso e exerce papéis ecológicos importantes no ambiente. Os peixes podem controlar teias alimentares por meio da predação, contribuem para a ciclagem de nutrientes e são considerados engenheiros do ecossistema (Villéger et al., 2017). Além disso, desempenham serviços ecossistêmicos valiosos para a vida humana, servindo como fonte de alimento (FAO, 2020). Mas, esses animais estão sendo afetados por inúmeros impactos, como por exemplo a sobrepesca, poluição química e a poluição sonora.

Os peixes usam vários sentidos para explorar o ambiente que habitam, e percebem a presença humana por meio de pistas químicas, visuais ou sonoras (Ladich, 2019; Samia et al., 2019). Devido à crescente poluição sonora como fator de perturbação nas últimas décadas (Hasan et al., 2018), tem sido dada atenção para os efeitos que a presença humana provoca no sistema auditivo dos peixes (Hawkins & Popper, 2014; Popper & Hawkins, 2019). Ao passo que os impactos da aproximação entre humanos e animais vem sendo bastante explorados, o detalhamento de como cada um dos componentes sensoriais é impactado (i.e., ver uma pessoa, perceber quimicamente a poluição despejada na água, ouvir ruídos antrópicos etc.) ainda é pouco estudado.

Os ambientes aquáticos não são silenciosos, mas as atividades humanas têm introduzido uma variedade de sons que interferem na paisagem sonora aquática (Popper & Hawkins, 2019), de forma intencional ou não. A paisagem sonora é composta por diferentes sons que constituem um determinado ambiente, produzidos por agentes naturais, biológicos ou antrópicos (Farina, 2014). Os sons produzidos por humanos também são chamados de ruídos antrópicos, e podem ser transitórios (e.g. barcos passando por uma área) ou contínuos (e.g. turbinas hidrelétricas em funcionamento) (Merchant et al., 2012). Independentemente de sua classificação, sabe-se que a velocidade de propagação do som é cerca de 4,5 vezes mais rápida na água em comparação ao ar (Palma et al., 2019). Portanto, animais aquáticos com sistema auditivo complexo podem perceber o som com mais intensidade.

De forma geral, os peixes possuem uma audição sensível. O ouvido interno desses animais desempenha funções de equilíbrio e auditivas, funciona por meio de estímulos mecanossensoriais, e possui estruturas como os canais semicirculares e órgãos terminais otolíticos (utrículo, sáculo e lagena) (Platt & Popper, 1981). A diversidade na anatomia do sistema auditivo dos peixes acompanha a diversidade filogenética, onde espécies podem apresentar a posição do ouvido interno em porções anatômicas distintas (Platt & Popper, 1981), e além disso, dispor de adaptações que melhorem a sensibilidade acústica, como por exemplo a ligação com cavidades de gás intracranianas (Schulz-Mirbach et al., 2013). Existem peixes que podem detectar sons menores que 50Hz até 500Hz, e algumas espécies especializadas que detectam frequências até 3–4 kHz (Ladich & Fay, 2013), percebendo com maior intensidade ruídos produzidos por humanos. Contudo, existem poucos estudos auditivos realizados em condições acústicas ideais, e os limiares auditivos são bem definidos apenas para algumas espécies (Popper & Hawkins, 2019). Ainda assim, Popper & Hawkins (2019) consideram que qualquer alteração ou interferência na paisagem sonora pode afetar a aptidão e a sobrevivência de peixes. Essa interferência é chamada de mascaramento acústico, a qual atrapalha a detecção de sons biologicamente relevantes (Fay & Simmons, 1999), como a comunicação acústica intraespecífica e pistas sonoras de predadores ou humanos aproximando-se.

Ruídos em ambientes aquáticos devem ser especialmente prejudiciais para peixes da Superordem Ostariophysi, que inclui Cypriniformes (as carpas), Characiformes (e.g. lambaris), Siluriformes (bagres) e Gymnotiformes (peixes elétricos). Este grupo representa cerca de 68% da ictiofauna de água doce do mundo (Nelson et al., 2016), e apresenta uma ligação específica e complexa entre o ouvido interno e a bexiga natatória, chamada aparelho Weberiano (Rosen & Greenwood, 1970). Essa estrutura possui uma cadeia dupla de ossículos derivados das costelas que melhora a audição de peixes ostariofisianos amplificando as vibrações que atingem a bexiga natatória (Diogo, 2009) à medida que os ossículos assumem o papel de alavancas transmitindo essas vibrações até o ouvido interno. Isso torna esses peixes especialmente sensíveis aos sons.

Além da capacidade de percepção sonora, alguns peixes possuem habilidades de produção de som. A plataforma FishSounds (fishsounds.net) apresenta um inventário abrangente sobre as pesquisas de produção sonora em peixes (Looby et al., 2021). Destaca-se que minha dissertação é fruto de uma parceria com Looby, Cox e Juanes, pesquisadores e membros da equipe FishSounds. Até o ano de 2020, cerca de 989 espécies de peixes capazes de produzir sons foram documentadas (Looby et al., 2022). Existem registros de sinais acústicos produzidos por peixes em vários contextos sociais, como por exemplo defesa de território, alimentação, encontros reprodutivos, comportamentos de natação em grupo e situações de agonia (Ladich, 2019; Ladich & Bass, 2011). As vocalizações em peixes variam suas propriedades espectrais e temporais, e podem ser geradas por vibração de músculos ligados à bexiga natatória, pela vibração da cintura peitoral ou também das nadadeiras (Ladich & Bass, 2011). Nesse contexto, um ambiente ruidoso dificulta a propagação desses sons (Fay &

Simmons, 1999; Kunc et al., 2014) e dificulta a realização do papel comportamental que o som tem para os peixes.

Há indícios de que o ruído antrópico pode causar uma série de efeitos na faixa auditiva dos animais, podendo ocorrer mascaramento, distração, dificuldade de comunicação e localização, e afetar até mesmo sinais visuais (Kunc et al., 2014). Além disso, o ruído pode interferir nas relações predador-presa, no forrageamento e alimentação em todos os estágios da história de vida (Cox et al., 2018; Kunc et al., 2016). Fisiologicamente, o ruído pode influenciar no aumento de glicocorticoides, o cortisol no caso dos peixes (Cox et al., 2018; Mickle & Higgs, 2018). Isso pode dificultar a reprodução, crescimento e imunidade. Além disso, afeta negativamente o metabolismo de diversas espécies (Kunc et al., 2016). Experimentos mostraram mudanças significativas na coesão e coordenação de movimento, o que afeta a estrutura dos cardumes (Herbert-Read et al., 2017). No entanto, sons variam muito em sua intensidade, timbre e frequência, mas ainda pouco se sabe sobre como as diferentes características desses sons afetam os peixes.

A maioria dos estudos sobre os impactos do ruído antrópico são realizados com peixes marinhos, concentrando-se principalmente em ruídos de barco a motor. Há evidências de que esse tipo de ruído afeta o cuidado parental (Nedelec et al., 2017), a sobrevivência, aumenta a taxa metabólica, diminui o comportamento anti-predador (Simpson et al., 2016) e, em alguns casos, resultam em habituação ao longo do tempo (Holmes et al., 2017), o que não é uma evidência da ausência de impacto (Blumstein, 2016). Recentemente, observou-se que o tipo de barco, a origem e a frequência do ruído podem causar efeitos diferentes nos peixes marinhos (McCormick et al., 2019).

As pesquisas realizadas em água doce focam nas consequências do ruído produzido por embarcações em corpos d’água com tráfego intenso. Por exemplo, esses ruídos afetam as respostas fisiológicas, aumentando taxas de consumo de oxigênio (Harding et al., 2018) e interferindo na percepção olfativa quando diminui as reações de medo ao sinal de alarme liberado na presença de predadores (Hasan et al., 2018). Empiricamente, por meio de um modelo matemático, identificaram que em níveis aumentados de ruído subaquático, cada espécie responderá de acordo com suas sensibilidades auditivas e adaptações comportamentais, sendo ela benéfica ou não para a relação predador-presa (Roca et al., 2020). Além disso, a proximidade da fonte sonora pode deixá-los vulneráveis a ataques ou à pesca (MacLean et al., 2020).

Neste estudo realizamos uma metanálise para investigar as consequências que os distúrbios na paisagem sonora aquática geram no comportamento e fisiologia de peixes à luz da capacidade de produzir e perceber sons. As metanálises são ferramentas robustas para explorar hipóteses ou pressupostos teóricos, sintetizando e comparando os resultados de estudos preexistentes de determinado campo de pesquisa (Harrison, 2011). Na literatura existem sínteses e revisões excelentes que tratam sobre os impactos da poluição sonora em ambientes aquáticos (Hawkins & Popper, 2014; Kunc et al., 2016; Mickle & Higgs, 2018; Popper & Hawkins, 2019), mas não avaliam de forma estatística os impactos nas espécies. Cox et al. (2018) realizaram a primeira síntese quantitativa global abordando o efeito da poluição sonora no comportamento e fisiologia dos peixes, reunindo dados de trabalhos de 1950 a 2015. Esse estudo identificou que os efeitos positivos ou negativos nas respostas comportamentais e fisiológicas dependem da fonte sonora: antrópico, ambiente, biológico, tons ou música (Cox et al., 2018). No entanto, os impactos não foram analisados à luz da produção de som ou da presença de um aparelho Weberiano nesses peixes. Aqui, incluímos tais características dos peixes, além de incluir 64 novos estudos à análise previamente feita com 43 estudos.

Observa-se que nos últimos anos houve um relevante crescimento na produção científica focada nos impactos da poluição sonora nos peixes. Trabalhos que avaliam a contribuição das espécies para a paisagem sonora também ganharam espaço na literatura. Essas avaliações possuem enfoques unidirecionais, analisando se as espécies produzem ruídos ou apenas se o ruído antrópico contribui, positivamente ou negativamente, para as espécies. Poucos estudos consideram uma interação bidirecional. Portanto, minha dissertação é a primeira análise global em que estamos avaliando como a capacidade das espécies de perceber e produzir sons influencia os impactos da poluição sonora no ambiente acústico.

INTRODUÇÃO

A paisagem sonora é composta por diferentes sons que constituem um determinado ambiente, produzidos por agentes naturais, biológicos ou antrópicos (Farina, 2014). Nas últimas décadas, as atividades humanas têm introduzido uma variedade de sons que interferem na paisagem sonora aquática (Popper & Hawkins, 2019). Construções, sonares, equipamentos de levantamento sísmico e motores de barco, são alguns exemplos de práticas humanas que têm prejudicado a vida marinha. Por exemplo, no caso dos barcos, estima-se que até o ano de 2030 a capacidade de ruído do transporte marítimo aumente em até 102% (Kaplan & Solomon, 2016). Sabe-se que a velocidade de propagação do som é cerca de 4,5 vezes mais rápida na água em comparação ao ar (Palma et al., 2019). Portanto, animais aquáticos com sistema auditivo complexo podem perceber o som com mais intensidade.

Em peixes, já foram documentados vários efeitos negativos do ruído antrópico. Entre eles, pode-se citar interferências comportamentais no cuidado parental (Nedelec et al., 2017), na sobrevivência e nas relações predador-presa (Simpson et al., 2016), no forrageamento e na alimentação (Cox et al., 2018; Kunc et al., 2016), e mudanças na estrutura dos cardumes (Herbert-Read et al., 2017). Além disso, alterações na faixa auditiva de algumas espécies (Kunc et al., 2014), aumento do estresse fisiológico (Cox et al., 2018; Mickle & Higgs, 2018), aumento da taxa metabólica (Harding et al., 2018; Kunc et al., 2016), e diminuição da percepção olfativa (Hasan et al., 2018) já foram diagnosticados em relação à fisiologia de peixes expostos a ruídos antropogênicos. Recentemente, identificaram que a origem e a frequência do ruído podem causar efeitos diferentes nos peixes (McCormick et al., 2019). A maioria dos estudos sobre os impactos do ruído antrópico são realizados com peixes marinhos, no entanto, de forma geral, sabe-se que os peixes são vulneráveis aos distúrbios da paisagem sonora devido a suas capacidades auditivas.

Os peixes possuem uma audição sensível e percebem o som por meio do ouvido interno, que desempenha funções vestibulares e auditivas, e funciona por meio de estímulos mecanossensoriais (Platt & Popper, 1981). Algumas espécies detectam sons menores que 50Hz até 500Hz (Popper & Hawkins, 2019), e espécies especializadas, como a carpa-comum (*Cyprinus carpio*), podem detectar frequências até 3–4 kHz (Ladich & Fay, 2013). Mas, os limiares auditivos são bem definidos apenas para algumas espécies (Popper & Hawkins, 2019). Em geral, os ruídos devem ser especialmente prejudiciais para peixes da Superordem Ostariophysi, que apresentam uma ligação específica e complexa entre o ouvido interno e a bexiga natatória, chamada aparelho Weberiano (Rosen & Greenwood, 1970). Essa estrutura possui uma cadeia dupla de ossículos derivados das costelas que melhora a audição de peixes ostariofisianos amplificando as vibrações que atingem a bexiga natatória (Diogo, 2009) à medida que os ossículos transmitem e amplificam essas vibrações até o ouvido interno. Isso torna esses peixes especialmente sensíveis aos sons.

Algumas espécies de peixes possuem habilidades de produção de som. Até o ano de 2020, foram documentadas cerca de 989 espécies de peixes capazes de produzir sons ativamente (Looby et al., 2022). Os peixes produzem sinais acústicos em vários contextos sociais, como por exemplo defesa de território, alimentação, encontros reprodutivos, natação e situações de agonia (Ladich, 2019; Ladich & Bass, 2011). Esses sinais possuem propriedades espectrais e temporais variadas, e podem ser gerados por vibração de músculos ligados à bexiga natatória, pela vibração da cintura peitoral ou também das nadadeiras (Ladich & Bass, 2011). Dessa forma, um ambiente ruidoso dificulta a propagação desses sons (Fay & Simmons, 1999; Kunc et al., 2014) e prejudica o papel comportamental sonoro para os peixes.

Os trabalhos recentes apresentam avaliações unidirecionais de impactos, ou seja, avaliam como os peixes contribuem para a paisagem sonora ou como o ruído afeta os peixes. A interação bidirecional entre esses fatores ainda é negligenciada. Portanto, o objetivo desta metanálise é investigar as consequências globais que os distúrbios na paisagem sonora aquática geram no comportamento e fisiologia de peixes à luz da capacidade de produzir e perceber sons. Nossas hipóteses são que os ruídos antrópicos, biológicos, ambientes e tonal aumentam as atividades comportamentais e fisiológicas de peixes, enquanto as músicas diminuem. Também esperamos que os efeitos dos ruídos no comportamento e na fisiologia de peixes com aparelho Weberiano apresentem maior intensidade, quando comparado aos efeitos em peixes não ostariofisianos. E ainda, que os efeitos dos ruídos no comportamento e na fisiologia de peixes produtores de som apresentem maior intensidade, quando comparado aos efeitos em peixes que não possuem produção de som documentada. Portanto, até agora e de acordo com nosso levantamento, esta é a primeira análise global em que estamos avaliando como a capacidade das espécies de perceber e produzir sons influencia os impactos da poluição sonora no ambiente acústico.

MATERIAL E MÉTODOS

Pesquisa Sistemática de Literatura

Utilizamos o banco de dados Thompson's Web of Science (www.webofscience.com/) para conduzir uma pesquisa sistemática na literatura. A pesquisa limitou-se a artigos revisados por pares publicados entre 1950 e 2021. Realizamos a busca no dia 23 de maio de 2021. Os termos específicos da pesquisa foram: fish AND (noise OR sound OR acoustic OR ecoacoustic OR bioacoustics) AND (behav* OR physiol* OR response OR morphology), resultando em 4.457 artigos potencialmente relevantes. Outros 528 artigos revisados por pares potencialmente relevantes foram obtidos por meio de outros mecanismos de pesquisa, incluindo ScienceDirect e JSTOR, e revisando minuciosamente as bibliografias de revisões relevantes.

Os títulos e resumos dos 4.985 estudos foram revisados para determinar quais artigos abordaram os efeitos do ruído no comportamento ou na fisiologia dos peixes (Figura 1b). Buscas em banco de dados podem gerar listas com artigos duplicados, em razão disso, identificamos e removemos estudos repetidos. Os artigos que preenchiam estes critérios (672) foram avaliados para identificar quais preenchiam os critérios de: pesquisa original, foco comportamental e/ou fisiológico, fonte sonora descrita, controle experimental, valor médio incluído, erro padrão e/ou desvio padrão, e o tamanho amostral (n) utilizado. Extraímos os dados dos grupos de tratamento e controle de cada estudo por meio de tabelas, texto e figuras.

Cento e sete estudos de 27 países cumpriram os critérios de pesquisa (Figura 1a). Oitenta e dois estudos realizaram experimentos em laboratório, e 26 estudos realizaram experimentos *in situ*. Apenas um estudo foi realizado em laboratório e *in situ*. Quando necessário, utilizamos o software de extração GetData Graph Digitizer (Fedorov, 2013) para recuperar dados de figuras. Reunimos um total de 3.432 pontos de dados dos 107 estudos que avaliaram o efeito do ruído no comportamento e/ou fisiologia dos peixes (Apêndice A, Tabela S1).

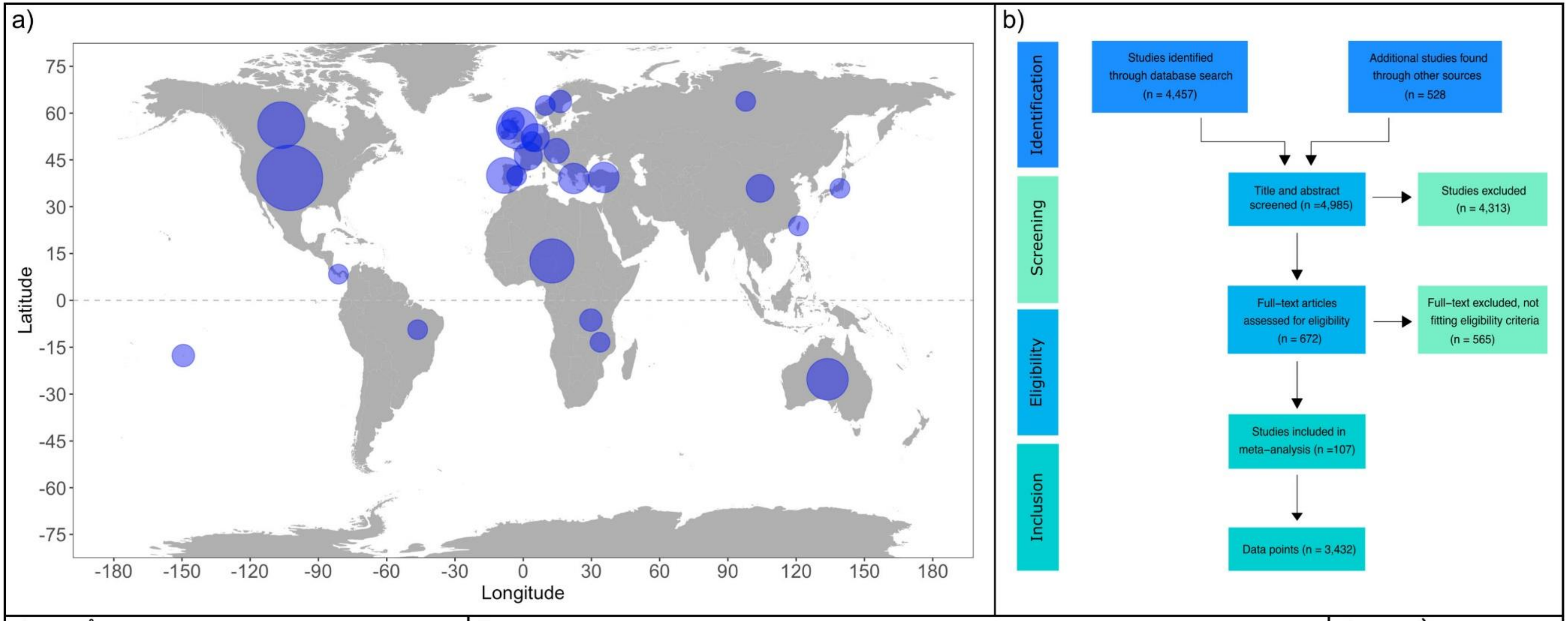

Figura 1. Resumo da pesquisa sistemática. (a) distribuição geográfica dos estudos utilizados nesta metanálise, onde o tamanho do círculo é proporcional ao número de estudos; (b) diagrama PRISMA descrevendo os processos de seleção de artigos para a metanálise sobre o efeito do ruído aquático no comportamento e na fisiologia dos peixes.

Obtenção de variáveis independentes dos peixes e dos sons

Para avaliar o efeito da capacidade de produção de som por determinados gêneros na resposta aos ruídos, definimos como categoria de “produtores de som”: "Yes" se pelo menos uma espécie do gênero tiver sido documentada por produzir sons ativamente (isto é, intencionais) ou "Unknow" se nenhuma espécie do gênero tiver uma documentação publicada de produção sonora ativa (Looby et al., 2022). Da mesma forma, avaliamos o efeito da presença de aparelho Weberiano na resposta aos ruídos registrando: a presença “Yes” se o gênero pertence à superordem Ostariophysi, ou ausência “No” se o gênero pertence a outro grupo, conforme informações taxonômicas disponíveis no FishBase (Froese & Pauly, 2021).

As fontes sonoras entraram em nossas análises como variáveis independentes, classificadas como ruídos antrópicos, biológicos, ambientes, tons e música. Essas variáveis foram obtidas diretamente dos textos dos artigos analisados. Incluímos dentro da categoria de ruídos Antrópicos, por exemplo, os sons de barcos a motor, pesquisa sísmica e ruído branco. Na categoria de ruídos Biológicos, por exemplo, sons de peixes coespecíficos e sons de cortejo. Nos ruídos Ambientes foram incluídos sons naturais do ambiente aquático, por exemplo os sons de um recife de coral. Nos Tons agrupamos os sons tonais contínuos e pulsos. E em Música agrupamos as músicas e sons binaurais (combinação de duas frequências de som para criar a percepção de um único).

Cálculo do Tamanho do efeito

Usamos o pacote ‘metafor’ (Viechtbauer, 2010) no programa R version 4.0.5 (R Core Team, 2021) para calcular os tamanhos e variações do efeito para cada estudo. Calculamos a diferença média (md) usando a Eq. (1), onde $\bar{Y}_1$ e $\bar{Y}_2$ são os valores médios do grupo de tratamento e controle, respectivamente.

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

Determinamos a diferença média padronizada (d de Hedge), que é uma indicação do efeito geral e dos pesos dos estudos com base em seus tamanhos de amostra e desvios padrão, usando Eq. (2). Os tamanhos das amostras são indicados por n_1 e n_2 com os desvios padrão s_1 e s_2.

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

Determinamos a variação para d de Hedge pela Eq. (3) (Hedges & Olkin, 1985).

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

Análise Estatística

Realizamos todas as análises no programa R version 4.0.5 (R Core Team, 2021). Criamos os gráficos de Floresta e Funil por meio dos pacotes ‘metafor’ e ‘MAd’ (Del Re & Hoyt, 2014; Viechtbauer, 2010) para definir os Tamanhos do efeito (ES) gerais, seus intervalos de confiança e verificar a presença de viés de publicação. Os gráficos foram elaborados para cada fonte sonora e separados de acordo com o tipo de estudo, comportamental ou fisiológico. Em seguida, plotamos os ES de cada fonte sonora em função da capacidade de produção de sons e da presença de aparelho Weberiano nos peixes, também separados em estudos comportamentais e fisiológicos. Realizamos ANOVAs de duas vias com testes post-hoc (Tukey Honest Significant Differences) que foram conduzidos nos dados de cada figura (portanto quatro ANOVAs), com a interação entre a fonte sonora e o aparelho weberiano ou estado de produção sonora executado em todos os casos.

RESULTADOS

Aspectos Gerais

Houve um aumento expressivo na quantidade de estudos publicados a partir do ano de 2015. Cerca de 67% dos estudos foram publicados no período de 2015 a 2021, sendo que o ano de 2020 apresentou o maior número de estudos (19), seguido por 2019 com 14 estudos (Figura 2a). Trinta e duas famílias de peixes foram utilizadas em investigações sobre o efeito dos sons nas respostas comportamentais e fisiológicas, e as famílias Sparidae, Cyprinidae e Clupeidae apresentaram maior representatividade de dados (Figura 2b). Ao todo, reunimos dados comportamentais e fisiológicos de 66 gêneros de peixes. Desses, 48 gêneros possuem produção de sons documentada e 18 gêneros ainda não possuem essa informação na literatura (Figura 2c). Além disso, 47 gêneros não apresentam aparelho Weberiano, apenas 19 possuem essa estrutura que liga a bexiga natatória ao ouvido interno (Figura 2c). Apenas nove gêneros apresentam as duas características, produção de sons e aparelho Weberiano (Apêndice B, Quadro S1).

A maioria dos dados comportamentais disponíveis focou em ruídos Antrópicos (49,7%) e ruídos Biológicos (34,2%), seguidos por Tons (12,4%) e ruídos Ambientes (3,7%). Até o momento e de acordo com nosso levantamento, nenhum estudo avaliou alterações comportamentais em peixes causadas por exposição à Música (Figura 3a). Quanto aos dados fisiológicos, observa-se que a maioria focou em ruídos Antrópicos (51,9%) e Músicas (31,7%), seguidos por Tons (12,8%), ruídos Ambientes (2,8%) e Biológicos (0,8%). Ao contrário dos estudos comportamentais, os estudos fisiológicos abordaram pouco as respostas aos ruídos Biológicos (Figura 3a). Os estudos acerca dos efeitos do som sobre peixes foram realizados, na maioria dos casos, com gêneros com produção de som conhecida. Destaca-se que, de acordo com nosso levantamento, há mais gêneros de peixes incluídos nesta metanálise em que se conhece a produção de som (70%) do que gêneros em que não se conhece (30%) (Figura 3b). Existem poucos estudos sobre o efeito de diferentes tipos de som sobre parâmetros comportamentais de peixes com aparelho Weberiano. Destaca-se que, até o momento, as respostas fisiológicas aos ruídos Biológicos e Ambientes não foram avaliadas em peixes com aparelho Weberiano (Figura 3c).

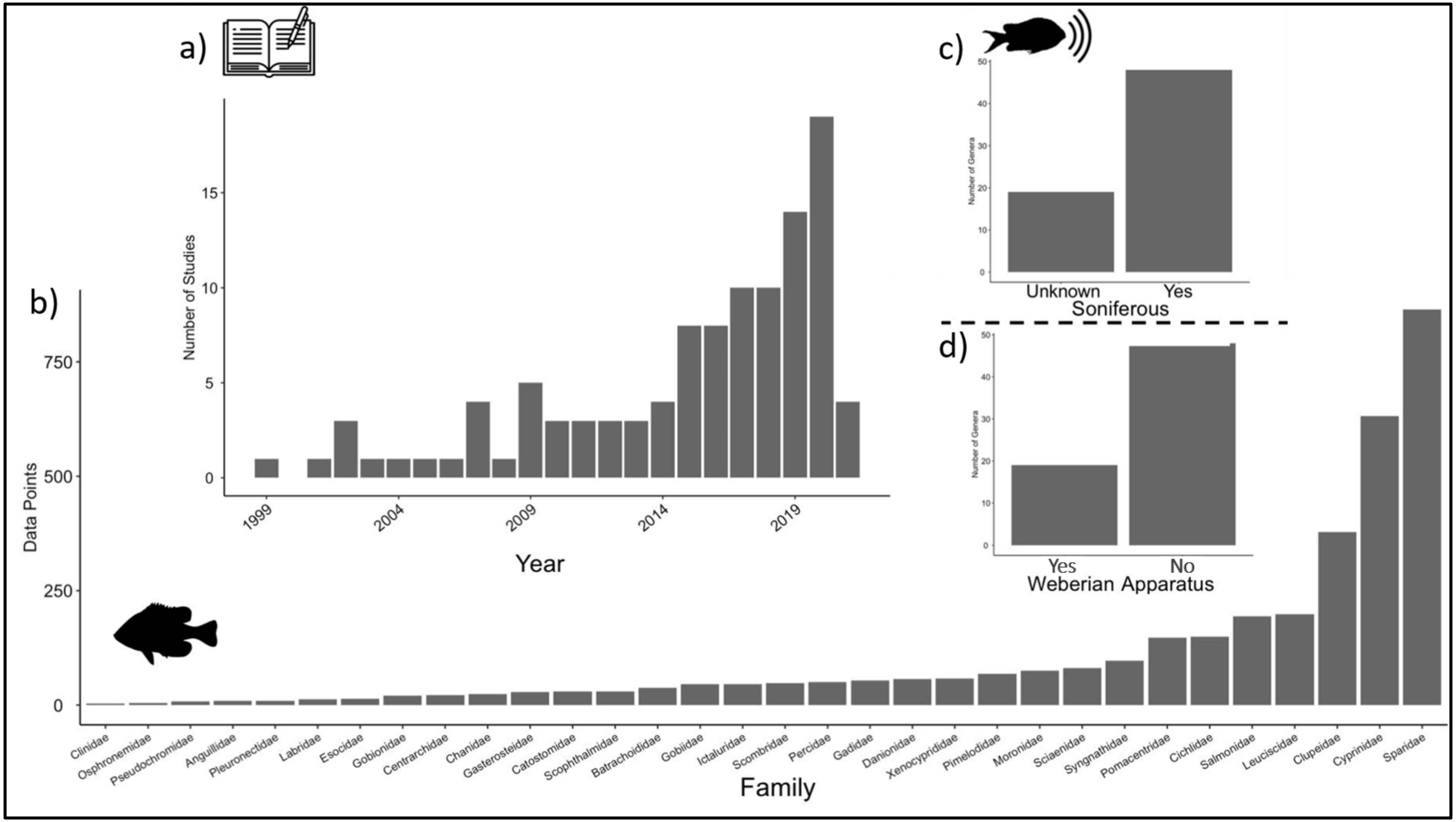

Figura 2. (a) Histórico por ano de publicação dos artigos utilizados nesta metanálise; (b) Número de pontos de dados por família taxonômica; (c) Proporção de gêneros que possuem a produção de som documentada e gêneros com tais informações desconhecidas; (d) Proporção de gêneros com a presença de aparelho Weberiano e gêneros sem essa estrutura.

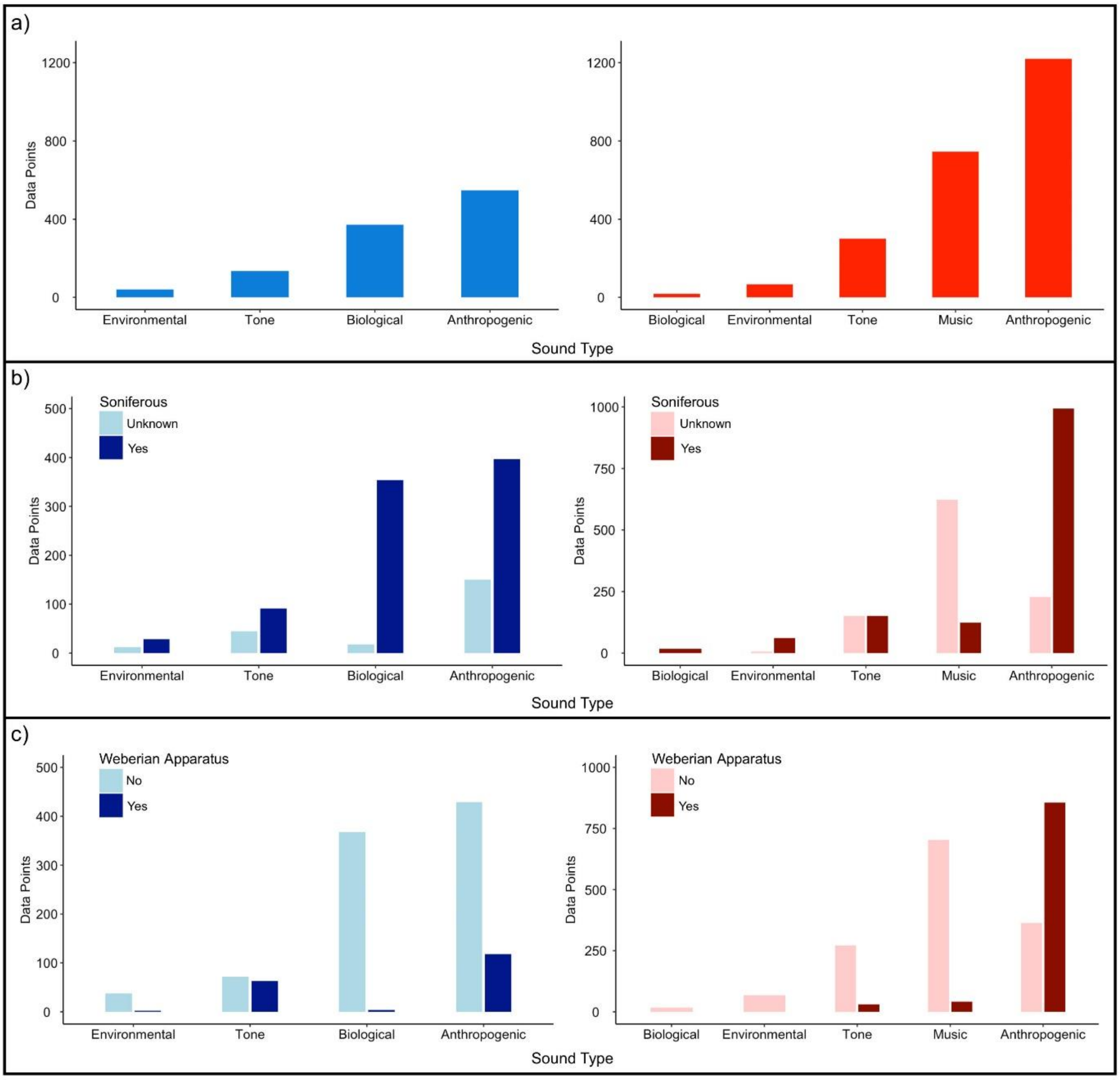

Figura 3. Número de pontos de dados utilizados nesta metanálise extraídos de estudos com foco comportamental (esquerda, azul) e com foco fisiológico (direita, vermelho). Separados por: (a) Tipo de som em todos os peixes; (b) Tipo de som em gêneros de peixes com produção de som documentada (tonalidade de cor forte) e gêneros com tais informações desconhecidas (tonalidade de cor fraca); (c) Tipo de som em gêneros com aparelho Weberiano (tonalidade de cor forte) e gêneros sem essa estrutura (tonalidade de cor fraca).

Metanálise

Os ruídos Antrópicos causaram aumento nas variáveis de resposta comportamentais e fisiológicas dos peixes. Os estudos com foco comportamental apresentaram um Tamanho de efeito (ES) geral de 1,63 com intervalos de confiança de 95% (IC) de 0,52 a 2,75, enquanto os estudos com foco fisiológico apresentaram um ES de 1,15 com IC de 95% de -0,46 a 2,75 (Figura 4a e 5a). Ruídos Biológicos também tendem a aumentar as variáveis de resposta comportamentais e fisiológicas, com ES gerais de 0,61 (IC -0,14 a 1,37) e 2,75 (IC -3,72 a 9,23), respectivamente (Figura 4b e 5b). Os ruídos Ambientes causaram leve redução das variáveis comportamentais (ES -0,13; IC -0,81 e 0,56; Figura 4c), e aumento das fisiológicas (ES 0,70; IC 0,02 e 1,37; Figura 5c). Os Tons apresentam uma tendência de aumento das variáveis comportamentais (ES 4,95; IC -0,62 e 10,51; Figura 4d) e de diminuição das fisiológicas (ES -13,07; IC -42,63 e 16,48; Figura 5d). As Músicas também tendem a diminuir as variáveis fisiológicas dos peixes, com ES de -55,17 (IC -162,68 e 52,35; Figura 5e).

A capacidade de produção sonora pelos peixes não explica os Tamanhos do efeito (ES) encontrados para as variáveis comportamentais (Apêndice A, Tabela S2a). Entretanto, foi significativa explicando os ES das variáveis fisiológicas ($F = 74,66$, $p < 0.0001$), e manteve-se significativa em interação com a fonte sonora ($F = 48,61$, $p < 0.0001$; Tabela S2b). A presença de aparelho Weberiano não explica os ES encontrados para as variáveis fisiológicas (Tabela S2d). Mas, foi significativa explicando os ES das variáveis comportamentais quando em interação com a fonte sonora ($F = 8,82$, $p < 0.0001$; Tabela S2c).

O teste post-hoc revelou que existe diferença significativa entre os Tamanhos do efeito (ES) encontrados para peixes com produção sonora documentada e peixes com essa informação ainda desconhecida, mas apenas para respostas fisiológicas em exposição à música (adjusted p value = 0; Figura 6a; Tabela S3b). O teste também mostrou que existe diferença significativa entre os ES encontrados para peixes com aparelho Weberiano e peixes sem estrutura, mas apenas para respostas comportamentais em exposição aos ruídos tonais (adjusted p value = 0; Figura 6b; Tabela S3c). Os Tamanhos do efeito (ES) das respostas comportamentais e fisiológicas aos ruídos antrópicos, biológicos e ambientes, visualmente, indicam diferenças entre as categorias das variáveis de produção sonora e presença de aparelho Weberiano (Figura 6). No entanto, o teste post-hoc aponta que essas diferenças não foram significativas.

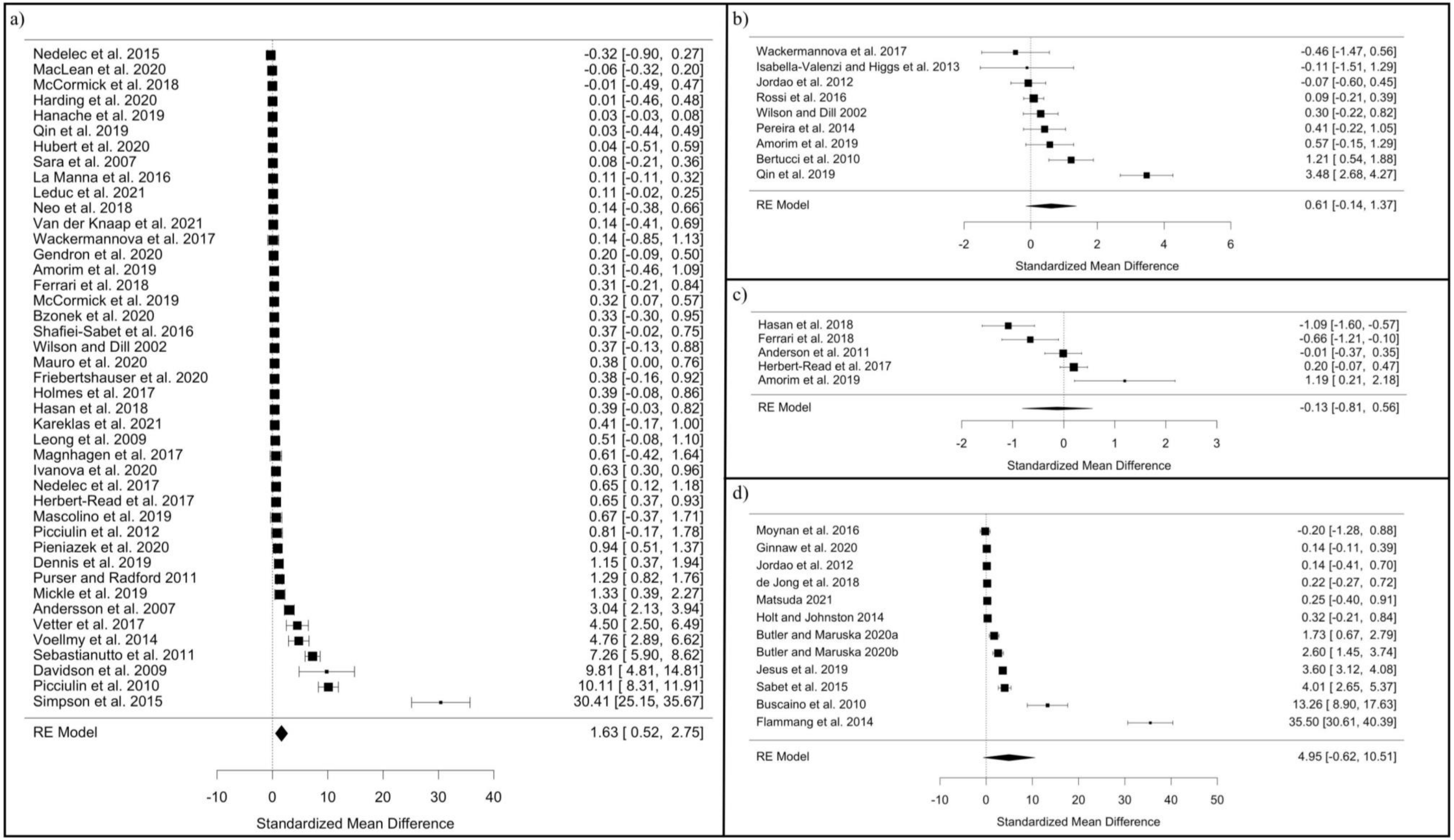

Figura 4. Gráficos Floresta ilustrando como vários ruídos aquáticos aumentam ou diminuem as respostas comportamentais dos peixes. Os estudos foram divididos nas seguintes categorias com base no tipo de ruído: (a) Ruído Antrópico; (b) Ruído Biológico; (c) Ruído Ambiente; (d) Tons. Autor(es) e ano de publicação estão listados dentro de cada gráfico. E, ao lado direito de cada gráfico observa-se o Tamanho do efeito e seu respectivo intervalo de confiança de 95%, representados no gráfico pelos quadrados (tamanho = peso relativo de cada estudo) e as barras. O losango na base de cada gráfico indica o Tamanho de efeito geral e seu intervalo de confiança.

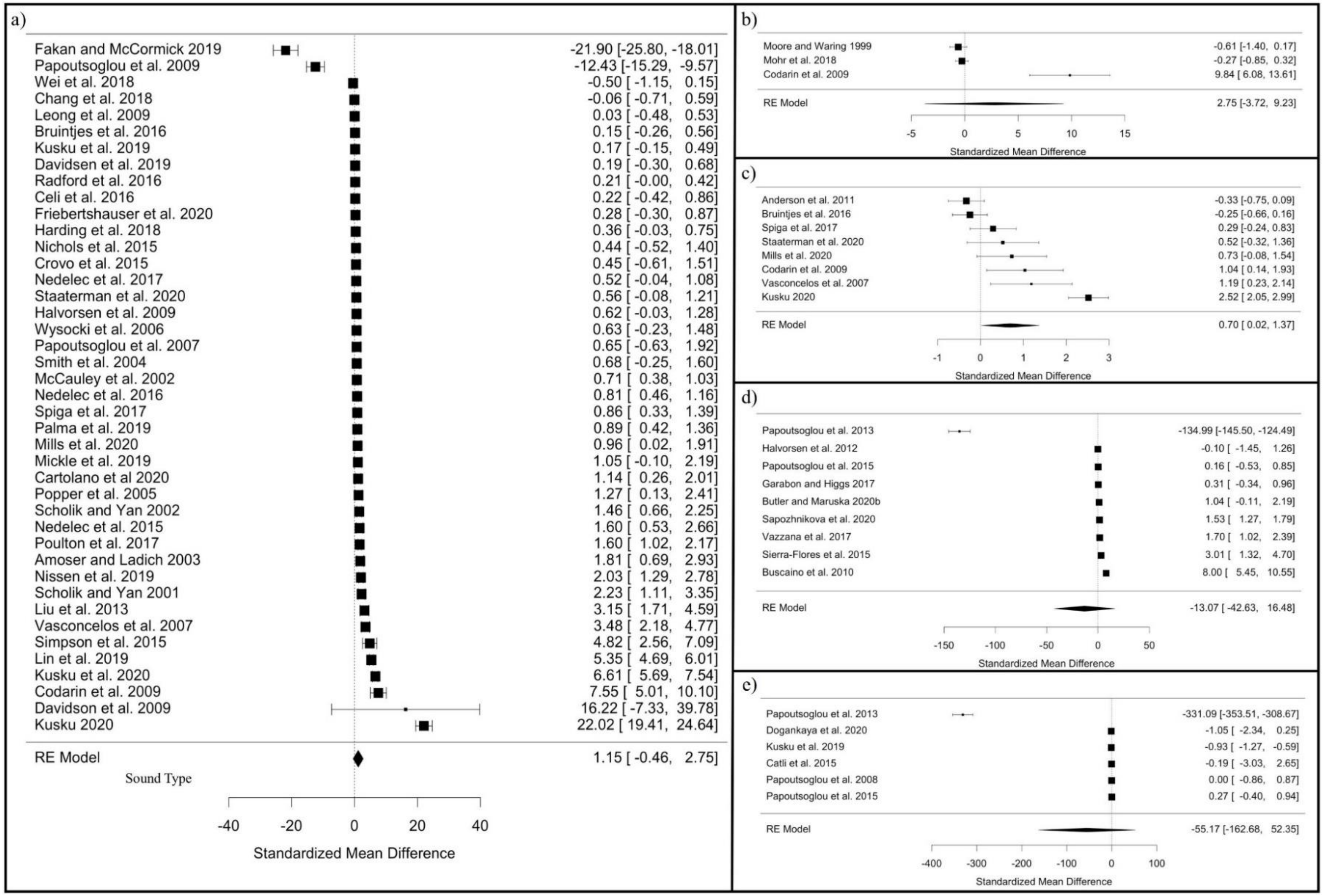

Figura 5. Gráficos Floresta ilustrando como vários ruídos aquáticos aumentam ou diminuem as respostas fisiológicas dos peixes. Os estudos foram divididos nas seguintes categorias com base no tipo de ruído: (a) Ruído Antrópico; (b) Ruído Biológico; (c) Ruído Ambiente; (d) Tons; (e) Música. Autor(es) e ano de publicação estão listados dentro de cada gráfico. E, ao lado direito de cada gráfico observa-se o Tamanho do efeito e seu respectivo intervalo de confiança de 95%, representados no gráfico pelos quadrados (tamanho = peso relativo de cada estudo) e as barras. O losango na base de cada gráfico indica o Tamanho de efeito geral e seu intervalo de confiança.

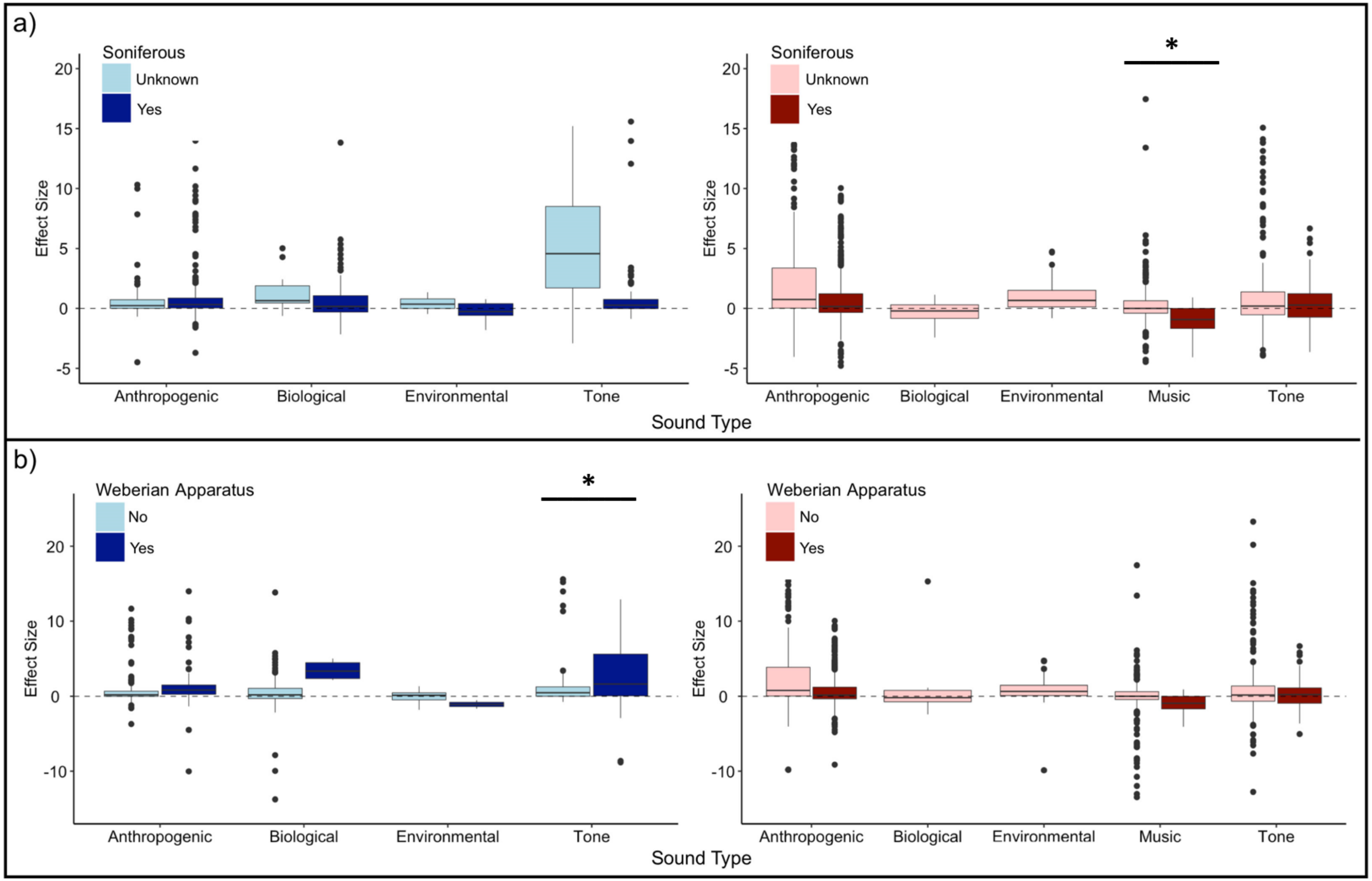

Figura 6. Tamanho do efeito dos tipos de som em respostas comportamentais (esquerda, azul) e fisiológicas (direita, vermelho) em função das capacidades de produzir e perceber sons. Produção: (a) Peixes com produção sonora documentada (tonalidade de cor forte) e peixes com tais informações desconhecidas (tonalidade de cor fraca); Percepção: (b) Peixes com aparelho Weberiano (tonalidade de cor forte) e peixes sem essa estrutura (tonalidade de cor fraca). As linhas centrais das caixas representam a mediana, as bordas superiores e inferiores da caixa representam os quartis de 75 e 25%, respectivamente, as linhas representam os valores máximo e mínimo excetuando-se os outliers, que estão representados como pontos. As barras e asterisco indicam comparações com diferença estatística significativa ao nível de 0.05 no teste post-hoc de Tukey.

DISCUSSÃO

Encontramos na literatura 107 estudos revisados por pares de 27 países, que tiveram como foco os impactos do ruído no comportamento e na fisiologia de peixes de água doce e salgada. Como esperávamos, os ruídos antrópicos e biológicos aumentam as variáveis resposta comportamentais e fisiológicas, enquanto as músicas diminuem as fisiológicas. Mas, curiosamente, os tons aumentam apenas as variáveis comportamentais e diminuem as fisiológicas, e os ruídos ambientes apresentaram efeito inverso. Também verificamos que os efeitos nas variáveis fisiológicas podem ser explicados pela capacidade de produzir sons, mas apenas em exposição à música. E os efeitos nas variáveis comportamentais podem ser explicados pela presença de aparelho Weberiano, mas apenas em exposição aos tons.

A ecologia comportamental de peixes é considerada um tópico quente na literatura. Houve um aumento na prevalência de estudos comportamentais nas últimas décadas, mas ainda existem lacunas importantes a serem preenchidas, principalmente em associação com outros tópicos ecológicos (Luiz et al., 2019). Nossa pesquisa apoia essa tendência, mostrando que o número de pesquisas sobre os efeitos dos sons no comportamento e fisiologia de peixes vem progredindo anualmente, embora se concentrem principalmente em países como Estados Unidos, Canadá, Itália, Reino Unido e Austrália. No geral, as avaliações de impactos antrópicos em peixes acompanham esse padrão geográfico, mostrando a escassez de estudos em regiões neotropicais (Bessa et al., 2017). Nesse sentido, evidencia-se a necessidade de realizar estudos que consideram a grande variedade de peixes e as diferentes fontes sonoras, sob diferentes condições (Popper & Hawkins, 2019), uma vez que cada espécie responde de uma forma e fornece resultados específicos.

Nossa metanálise identificou que os peixes com maior número de dados comportamentais e fisiológicos em resposta aos sons são das famílias Sparidae, Cyprinidae e Clupeidae. Essas famílias possuem espécies de peixes altamente comerciais, tanto para consumo humano como para atividades de pesca esportiva e aquarismo, como sargos, carpas e sardinhas. De fato os peixes desempenham serviços ecossistêmicos importantes para a vida humana (FAO, 2020; Pelicice et al., 2022 in prep.), e portanto, são necessários estudos que buscam compreender como os impactos antrópicos alteram características inerentes desses animais. Mas, para além disso, acreditamos e ressaltamos que essa não deve ser a única motivação, uma vez que os peixes participam de processos ecológicos essenciais, como controle de teias alimentares, ciclagem de nutrientes e podem ser considerados engenheiros do ecossistema (Villéger et al., 2017). Aqui, também identificamos que 70% dos gêneros estudados possuem informações de produção sonora ativa documentada (Looby et al., 2022). A produção ativa de sons é uma atividade comportamental prevalente em peixes, mas ainda requer validações, uma vez que algumas metodologias utilizadas apresentam falhas e incertezas, que muitas vezes não são claramente apresentadas nos estudos (Looby et al., 2022). Quanto à presença de aparelho Weberiano, apenas 29% dos gêneros estudados apresentam essa estrutura especializada. Um número relativamente baixo, uma vez que os peixes ostariofisianos representam cerca de 68% da ictiofauna de água doce do mundo (Nelson et al., 2016).

De forma geral, o ruído Antrópico demonstrou aumentar as variáveis de resposta comportamentais e fisiológicas. Este aumento está vinculado principalmente aos parâmetros comportamentais agonísticos, de forrageamento, movimento de natação, prevenção de predadores, comunicação e reprodução; e ainda aos parâmetros fisiológicos metabólicos, auditivos, e indicadores de estresse. O aumento em respostas comportamentais já foi observado, por exemplo, nas reações de defesa e alarme (Kareklas et al., 2021; Nedelec et al., 2017), no número de capturas de alimentos bem sucedidas e fracassadas (Purser & Radford, 2011; Voellmy et al., 2014), na velocidade de natação (Neo et al., 2018; Shafiei Sabet et al., 2016; Wilson & Dill, 2002), na natação desordenada (Andersson et al., 2007; Herbert-Read et al., 2017; Hubert et al., 2020; Mauro et al., 2020; Sarà et al., 2007), na reação de alerta aos predadores (La Manna et al., 2016), na taxa de vocalização (Picciulin et al., 2012) e no número de exibições visuais para atrair fêmeas (Mascolino et al., 2019). Quando o peixe é exposto a perturbações, sua primeira linha de defesa é a mudança repentina de comportamento para evitar a morte e custos metabólicos (Olla et al., 1980). Caso a perturbação não cesse ou não seja possível fugir, as mudanças no comportamento podem interferir em como o animal sente e responde ao ambiente (Schreck et al., 1997), prejudicando o equilíbrio homeostático. Nesse sentido, muitos estudos também demonstraram que o ruído antrópico aumenta os níveis de estresse dos peixes, por exemplo, observado pelo aumento de substâncias como o cortisol, ácido lático e glicose (e.g., Lin et al., 2019) e da taxa de ventilação (e.g., Kusku et al., 2020). Esses resultados estão de acordo com os encontrados por Cox et al. (2018), e juntos reforçam o alerta para as consequências graves do avanço de atividades antrópicas. A teoria prevê que alterações ou interferências na paisagem sonora podem causar danos significativos aos peixes, reversíveis e irreversíveis (Popper & Hawkins, 2019). Existe uma infinidade de atividades antrópicas que causam poluição sonora e interferem na vida marinha, entre as quais destaca-se o aumento da frota marítima (Kaplan & Solomon, 2016). Portanto, o cenário atual e as previsões futuras mostram a necessidade de regulação e definição de limiares seguros de ruído, para que seus efeitos não se tornem irreversíveis, e ainda demonstram a urgência de soluções que atenuem o excesso de ruído produzido por ações humanas.

O ruído Biológico também causou tendências de aumento nas variáveis de parâmetros comportamentais e fisiológicos. Já foi observado que a exposição aos sons de coespecíficos pode desencadear aumento no número de comportamentos agressivos (Wackermannova et al., 2017), no comportamento de evitação (Pereira et al., 2014), no desempenho vocal de machos (Jordão et al., 2012), e na atração de fêmeas reprodutivas (Isabella-Valenzi & Higgs, 2013). Fisiologicamente, já foi verificado que os chamados de coespecíficos aumentam os níveis de hormônio e do fluído seminal em machos (Moore & Waring, 1999), e a atividade cerebral em fêmeas (Mohr et al., 2018). Sons heteroespecíficos também já foram observados aumentando a velocidade de natação (Wilson & Dill, 2002) e a atividade cerebral de peixes (Mohr et al., 2018). Essas observações ressaltam que a comunicação acústica em peixes é importante para diversos contextos sociais (Ladich & Bass, 2011; Ladich & Fay, 2013), e que esses sons apresentam grande diversidade e complexidade (Parmentier et al., 2010), gerados por estruturas anatômicas distintas e com variedade nas características espectrais e temporais (Ladich & Bass, 2011). No entanto, apenas 34,2% dos dados avaliaram os impactos do ruído biológico no comportamento, e apenas 0,8% na fisiologia de peixes. A escassez de dados dificulta a definição de uma direcionalidade, como já observado em estudos anteriores (Cox et al., 2018; Ladich, 2019), apoiando a existência de lacunas no conhecimento sobre os efeitos de sons biológicos, intraespecíficos e interespecíficos, sobre o comportamento e fisiologia de peixes.

O ruído Ambiente provocou diminuição das variáveis comportamentais e aumento das fisiológicas. Embora nos últimos anos tenham surgido novos estudos que avaliaram o efeito do ruído ambiente no comportamento de peixes, o volume de dados ainda é baixo, o que torna difícil determinar uma tendência de direcionalidade. Além disso, os estudos que avaliaram o efeito desse tipo de ruído na fisiologia dos peixes apresentaram resultados divergentes. Por exemplo, já foi observado que em condições de ruído ambiente os peixes ficaram mais estressados, apresentando níveis elevados de cortisol, os rins foram mais afetados por parasitas, e o comportamento apresentou alta variabilidade (Anderson et al., 2011). Outra pesquisa observou que esse tipo de ruído não causou efeito na taxa de ventilação (Kusku, 2020), também indicador de estresse (Barreto & Volpato, 2006). O ruído ambiente já mostrou leve mascaramento na audição de peixes (Vasconcelos et al., 2007), mas em outro estudo não houve alteração na sensibilidade auditiva (Codarin et al., 2009). Acreditamos que essas divergências surgem por fatores relacionados ao tipo de ruído ambiente utilizado, pelo local de estudo e pelas metodologias empregadas nas avaliações. O que faz sentido, levando em consideração a alta diversidade de sons que compõem a paisagem sonora (Farina, 2014), e ainda o tempo que o peixe fica exposto ao estímulo acústico, uma vez que pode ocorrer habituação, assim como observado para outras fontes sonoras (e.g., Nedelec et al., 2016). Em geral, os impactos do ruído ambiente, em sua maioria negativos, já foram documentados para diversos grupos animais, e provocam alterações que vão desde o nível molecular ao nível de comunidade (Kight & Swaddle, 2011). Desse modo, os efeitos comportamentais e fisiológicos do ruído ambiente sobre os peixes precisam ser investigados de forma mais extensa e robusta.

Nossos resultados mostram que os Tons aumentam as variáveis de resposta comportamentais e diminuem as variáveis de resposta fisiológicas. O aumento nas variáveis comportamentais já era esperado, conforme observado para as respostas de alarme e a velocidade de natação (Shafiei Sabet et al., 2015), para a dissuasão e repulsão (Flammang et al., 2014; Jesus et al., 2019; Matsuda, 2021) e desordem do movimento coletivo (Ginnaw et al., 2020). Os tons também já apresentaram aumento nos níveis espectrais de sinais acústicos (Holt & Johnston, 2014), na latência para iniciar lutas em machos territoriais (Butler & Maruska, 2020a), e na motilidade, também aumentando parâmetros fisiológicos de estresse (Buscaino et al., 2010). Os tons são muito utilizados como barreiras não físicas em hidrelétricas (e.g., Jesus et al., 2019) e em aquiculturas (e.g., Flammang et al., 2014), como forma de impedir a fuga de peixes. Por um lado, essas barreiras sonoras protegem os peixes de serem mortos pelas turbinas e forçam os cardumes a seguirem um curso seguro no rio, mas acreditamos que ainda é necessário verificar as consequências a longo prazo para essas espécies migratórias. Observamos também que as atividades comportamentais são intensificadas pelos Tons em peixes com aparelho Weberiano. Esse resultado concorda com o encontrado para peixes ciprinídeos (ostariofisianos), que em contraste com peixes salmonídeos, exibiram uma forte reação de repulsão ao som tonal sinoidal (Jesus et al., 2019). Em ciprinídeos, os ruídos tonais causaram maiores mudanças no forrageamento (Shafiei Sabet et al., 2016), indicando interferências nas relações predador-presa, e no comportamento de natação (Matsuda, 2021; Shafiei Sabet et al., 2016), sinalizando maior reação de evitação. Esse padrão também foi encontrado na metanálise anterior, onde os tons aumentaram o forrageamento, movimento de natação e predação, embora Cox et al. (2018) não tenham avaliado as diferenças entre peixes ostariofisianos e não-ostariofisianos. A teoria prevê que peixes da Superordem Ostariophysi são mais sensíveis aos sons devido à presença de aparelho Weberiano, que amplifica o sinal sonoro recebido (Diogo, 2009), no entanto, é importante lembrar que o aparelho Weberiano não é a única adaptação auditiva dos peixes (Platt & Popper, 1981; Schulz-Mirbach et al., 2013). Portanto, nossos resultados sugerem a importância de considerar as capacidades auditivas especializadas em avaliações do efeito do ruído tonal, uma vez que esse tipo de som demonstrou afetar de forma mais intensa os peixes com aparelho Weberiano. Já a diminuição das variáveis fisiológicas que observamos, pode ser explicada pela forte influência de um único estudo (Papoutsoglou et al., 2013), no qual o grupo de peixes expostos aos tons apresentaram diminuição nos parâmetros de crescimento e atividade cerebral. Dessa forma, acreditamos que o efeito geral dos tons na fisiologia dos peixes precisa ser melhor investigado.

O resultado encontrado para a direcionalidade das variáveis fisiológicas em exposição às Músicas não foi conclusivo. Poucos estudos avaliaram o efeito da música sobre parâmetros fisiológicos, e a direcionalidade foi fortemente influenciada por um único estudo (Papoutsoglou et al., 2013). Ainda assim, encontramos uma tendência indicativa que os peixes produtores de som respondem de forma diferente à Música, mostrando que a capacidade de produzir sons explica os efeitos dessa fonte sonora nas respostas fisiológicas, comparado aos peixes sem registros de produção sonora ativa. Um estudo com *Cyprinus carpio,* espécie produtora de sons (ver Quadro S1), identificou que a música influenciou positivamente parâmetros fisiológicos de desempenho de crescimento e de eficiência de alimentação (Kusku et al., 2019). Esse padrão também já foi observado para juvenis da espécie *Oncorhynchus mykiss*, que exposta à música exibiu crescimento acelerado (Papoutsoglou et al., 2013). A pesquisa de Catli et al. (2015) também observou esse padrão, mas os autores apontam que os efeitos podem ser diferentes dependendo da velocidade que a música é tocada. Como mencionado anteriormente, a produção sonora ativa em peixes ainda precisa de testes em diferentes contextos, e com idades e sexos diversificados (Looby et al., 2022), embora este tipo de estudo possa ser complexo, irresoluto e ineficaz (Looby et al., 2022). Antes de tudo, é importante compreender como ocorreu a evolução dos sinais acústicos em peixes, combinando métricas acústicas contínuas e análises comparativas filogenéticas avançadas (Odom et al., 2021). Portanto, ainda é cedo para generalizar os efeitos da música em parâmetros comportamentais e fisiológicos, mas já existem resultados promissores na literatura que sugerem efeitos positivos, e abrem caminho para novas explorações e aplicações na aquicultura.

As especializações auditivas dos peixes e sua produção sonora influenciam os impactos causados pelos ruídos. Esperávamos que peixes produtores de sons e peixes com aparelho Weberiano fossem mais sensíveis a todas as fontes sonoras. No entanto, essas diferenças só foram observadas em exposição aos tons e à música. O que não deixa de ser uma observação importante, sugerindo por exemplo, que o ruído antrópico extremo pode afetar os peixes independente de suas especializações. Sendo assim, recomendamos que as análises de impactos sonoros sobre os peixes levem em consideração essa interação bidirecional. Assim, será possível realizar comparações mais robustas para melhorar nossa compreensão sobre quais espécies são mais vulneráveis a poluição sonora. Ressaltamos que, até onde sabemos, esta é a primeira análise quantitativa global que considera a capacidade de produzir e perceber sons como determinante no tamanho do efeito dos ruídos sobre os peixes.

Uma das limitações em metanálises é lidar com a grande variedade de metodologias utilizadas nos estudos. Durante as buscas na literatura, também é comum encontrar desequilíbrio nos tamanhos de amostra e insuficiência de dados, o que acaba gerando o descarte de estudos potenciais. Mas, essas divergências tornam-se bastante informativas, uma vez que por meio delas é possível traçar lacunas a serem preenchidas, como estudos que explorem os efeitos de sons biológicos, sons ambiente e música. Outra limitação se refere à categorização de peixes produtores ativos de sons. Embora os peixes produtores de som tenham ocorrências documentadas em todos os ambientes aquáticos e em quase todas as regiões do mundo, cerca de 96% das espécies de peixes carecem de experimentos publicados (Looby et al., 2022), assim, torna-se difícil categorizar uma espécie como não produtora de som, sendo mais comum que essa produção apenas não seja conhecida e tornando nossos resultados nessa categoria (produção de som desconhecida) pouco esclarecedora. Estudos futuros devem considerar essa discrepância de informações, e assim categorizar de forma mais robusta a produção sonora em peixes. Além disso, a direcionalidade das variáveis comportamentais e fisiológicas encontradas em nossa investigação não responde se os efeitos dos ruídos são positivos ou negativos para os peixes, portanto a inclusão desses fatores nas análises ainda é necessária.

Estudos sobre os efeitos dos ruídos em peixes são importantes para dar suporte, orientar e incentivar ações preventivas que garantam a conservação e o bem-estar dos peixes. Primeiramente, esperamos que esses dados sirvam como alerta para a necessidade de redução de práticas antrópicas ruidosas. Uma boa alternativa é a limitação de atividades antrópicas em áreas essenciais para a história de vida dos peixes, como sítios de reprodução e alimentação. Além disso, torna-se necessário definir limiares sonoros em áreas próximas a ambientes aquáticos considerados fundamentais para a conservação de animais aquáticos. Um grande problema atualmente é a exploração exacerbada de petróleo, que utiliza equipamentos extremamente ruidosos, causando impactos em diversos táxons (Hawkins & Popper, 2014; Kunc et al., 2016; Mickle & Higgs, 2018; Popper & Hawkins, 2019). A reprodução de sons naturais tem se tornado uma ferramenta promissora em processos de conservação e recuperação de ambientes aquáticos degradados. Essa estratégia foi utilizada em recifes de coral degradados da ilha continental Lizard Island, onde o enriquecimento acústico aumentou o desenvolvimento da comunidade de peixes em todas as principais guildas tróficas (Gordon et al., 2019). Utilizar músicas em aquiculturas também pode ser uma boa alternativa para impulsionar o crescimento dos peixes, e diminuir o estresse causado pelo confinamento. Portanto, sugerimos a limitação da produção de ruídos, especialmente em zonas sensíveis aos peixes, e a exploração de sons com efeitos positivos para recuperar populações de peixes ou aumentar seu bem-estar.

As diferentes fontes sonoras têm efeitos variados nos peixes, com ruídos antrópicos e biológicos aumentando as respostas comportamentais e fisiológicas, ao passo que a música diminui reações fisiológicas. Ainda há muitas lacunas em detalhes dessas relações, como os ruídos tonais em respostas fisiológicas, e de forma geral, os efeitos da exposição ao ruído ambiente e músicas. No entanto, ficou evidente, pelo menos em parte dos resultados, que espécies dotadas de aparelho Weberiano e produtoras de sons são mais sensíveis aos ruídos. Estes resultados são relevantes para a conservação dos peixes, que devem ser privados de ruídos prejudiciais especialmente em áreas de desova e alimentação, e podem ser aplicados ao bem-estar de espécies de produção. Com o aumento dos impactos antrópicos sobre a paisagem sonora, detalhar os impactos dos ruídos nos peixes, em especial relacionado à bidirecionalidade de produção e/ou percepção sonora aguçada, traz importantes contribuições para a conservação deste importante grupo.

CONSIDERAÇÕES FINAIS

O início do mestrado em meio a um cenário de incertezas gerou mudanças não previstas no meu projeto de dissertação. Meu projeto inicial tinha o objetivo de investigar como o ruído produzido pela presença de turistas altera o comportamento e fisiologia de peixes *Hyphessobrycon balbus* oriundos de rios com diferentes níveis de turismo de natureza. Dessa forma, dependíamos da presença de turistas e visitantes em locais como os córregos do Parque Nacional de Brasília. Esse projeto seria desenvolvido por meio de coletas em campo e testes experimentais em laboratório. Ambas as fases foram afetadas pelas restrições impostas pela pandemia, como o isolamento social e a suspensão de atividades presenciais.

Na esperança de que as atividades presenciais retornariam brevemente, o projeto inicial foi apresentado à banca de qualificação e aprovado com êxito. Entretanto, o período de isolamento se estendeu por mais tempo do que o esperado, o que impossibilitou o desenvolvimento do projeto. Nesse sentido, em consenso com meu orientador, resolvemos mudar a metodologia da dissertação para uma metanálise e, assim, investigar as consequências globais que os distúrbios na paisagem sonora aquática geram no comportamento e fisiologia de peixes de água doce e salgada. Um grupo de pesquisa internacional realizou um trabalho semelhante com estudos publicados até 2015, no entanto, diversos estudos novos surgiram na literatura a partir de 2015 até 2021. Movidos pela curiosidade de incluir novas variáveis nas análises e devido ao volume de dados novos, firmamos uma parceria com pesquisadores canadenses (Kieran Cox, Audrey Looby e Francis Juanes) para desenvolver o novo projeto.

Todo o processo de pesquisa nas bases de dados, seleção de artigos por títulos e resumos, leitura completa de artigos elegíveis e extração de dados foi realizado até novembro de 2021. Mas minha dissertação dependeu da inserção e análise parcial dos dados por estes parceiros, que tinham outras demandas em suas instituições de origem. Então, além da mudança de projeto no meio do mestrado, a dependência de algumas análises levou a não termos incluído ainda se os ruídos são positivos ou negativos para os peixes.

A pós-graduação, embora gratificante, é permeada de contratempos e desafios, e em um cenário pandêmico torna-se ainda mais desafiadora. Além dos problemas relacionados à elaboração da minha dissertação, os anos de 2020 e 2021 foram marcados por problemas de saúde e pessoais. Apesar disso, e com o apoio de professores e familiares, consegui superar os obstáculos, submeter um artigo com meu orientador para a revista Neotropical Ichthyology no dia 19 de julho de 2021 (Apêndice D), trabalhar em projetos paralelos, terminar minha dissertação, e ser contratado como professor de Biologia pela SEEDF em Santa Maria.

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APÊNDICE A – Tabelas suplementares

Tabela S1. Localização, Tipo de estudo e Número de pontos de dados dos artigos selecionados e extraídos nesta metanálise (n = 107)

(Continua)

Authors	Location	Behavioral	Physiological	#data points
Amorim et al. (2019)	France	X		19
Amoser & Ladich (2003)	Austria		X	122
Anderson et al. (2011)	USA	X	X	37
Andersson et al. (2007)	Sweden	X		12
Bertucci et al. (2010)	France	X		2
Bruintjes et al. (2016)	UK		X	12
Buscaino et al. (2010)	Italy	X	X	8
Butler & Maruska (2020b)	Tanzania	X	X	22
Butler & Maruska (2020a)	Tanzania	X		3
Bzonek et al. (2020)	Canada	X		8
Cartolano et al. (2020)	USA		X	2
Catli et al. (2015)	Turkey		X	30
Celi et al. (2016)	Italy		X	20
Chang et al. (2018)	Taiwan		X	30
Codarin et al. (2009)	Italy		X	35
Crovo et al. (2015)	USA		X	1
Davidsen et al. (2019)	Norway		X	4
Davidson et al. (2009)	USA	X	X	6
de Jong et al. (2018)	Portugal	X		15
Dennis et al. (2019)	USA	X		21
Doğankaya et al. (2020)	Turkey		X	27
Fakan & McCormick (2019)	Australia		X	22
Ferrari et al. (2018)	Australia	X		12
Flammang et al. (2014)	USA	X		12
Friebertshauser et al. (2020)	USA	X	X	30
Garabon & Higgs (2017)	Canada		X	12
Gendron et al. (2020)	Canada	X		9
Ginnaw et al. (2020)	UK	X		14
Halvorsen et al. (2009)	USA		X	20
Halvorsen et al. (2012)	USA		X	36
Hanache et al. (2019)	France	X		2
Harding et al. (2020)	Australia	X		4
Harding et al. (2018)	Malawi		X	4
Hasan et al. (2018)	Canada	X		8
Herbert-Read et al. (2017)	UK	X		20
Holmes et al. (2017)	Australia	X		15
Holt & Johnston (2014)	USA	X		16
Hubert et al. (2020)	Netherlands	X		4
Isabella-Valenzi & Higgs (2013)	Canada	X		19
Ivanova et al. (2020)	Canada	X		7
Jesus et al. (2019)	Portugal	X		24
Jordão et al. (2012)	Portugal	X		12
Kareklas et al. (2021)	Northern Ireland	X		4
Kusku et al. (2019)	Turkey		X	20

Tabela S1. Localização, Tipo de estudo e Número de pontos de dados dos artigos selecionados e extraídos nesta metanálise (n = 107)

(Continua)

Authors	Location	Behavioral	Physiological	#data points
Kusku (2020)	Turkey		X	50
Kusku et al. (2020)	Turkey		X	32
La Manna et al. (2016)	Italy	X		18
Leduc et al. (2021)	Brazil	X		9
Leong et al. (2009)	Portugal	X	X	3
Lin et al. (2019)	China		X	36
Liu et al. (2013)	China		X	30
Maclean et al. (2020)	Canada	X		6
Magnhagen et al. (2017)	Sweden	X		60
Mascolino et al. (2019)	Italy	X		3
Matsuda (2021)	Japan	X		10
Mauro et al. (2020)	Spain	X		68
McCauley et al. (2003)	Australia		X	2
McCormick et al. (2018)	Australia	X		16
McCormick et al. (2019)	Australia	X		24
Mickle et al. (2019)	Canada	X	X	20
Mills et al. (2020)	French Polynesia		X	16
Mohr et al. (2018)	USA		X	10
Moore & Waring (1999)	UK		X	4
Moynan et al. (2016)	USA	X		6
Nedelec et al. (2015)	Scotland	X	X	18
Nedelec et al. (2016)	French Polynesia		X	4
Nedelec et al. (2017)	Australia	X	X	8
Neo et al. (2018)	Netherlands	X		8
Nichols et al. (2015)	USA		X	3
Nissen et al. (2019)	USA		X	48
Palma et al. (2019)	Portugal		X	12
Papoutsoglou et al. (2007)	Greece		X	300
Papoutsoglou et al. (2008)	Greece		X	416
Papoutsoglou et al. (2010)	Greece		X	199
Papoutsoglou et al. (2013)	Greece		X	117
Papoutsoglou et al. (2015)	Greece		X	324
Pereira et al. (2014)	Portugal	X		5
Picciulin et al. (2010)	Italy	X		6
Picciulin et al. (2012)	Italy	X		12
Pieniazek et al. (2020)	Canada	X		8
Popper et al. (2005)	Canada		X	37
Poulton et al. (2017)	UK		X	2
Purser & Radford (2011)	UK	X		10
Qin et al. (2019)	China	X		12
Radford et al. (2016)	France		X	20
Rossi et al. (2016)	Australia	X		2
Sapozhnikova et al. (2020)	Russia		X	15
Sarà et al. (2007)	Italy	X		48
Scholik & Yan (2001)	USA		X	40
Scholik & Yan (2002)	USA		X	40

Tabela S1. Localização, Tipo de estudo e Número de pontos de dados dos artigos selecionados e extraídos nesta metanálise (n = 107)

(Conclusão)

Authors	Location	Behavioral	Physiological	#data points
Sebastianutto et al. (2011)	Italy	X		5
Shafiei Sabet et al. (2016)	Netherlands	X		12
Shafiei Sabet et al. (2015)	Netherlands	X		24
Sierra-Flores et al. (2015)	Scotland		X	23
Simpson et al. (2015)	UK	X	X	5
Smith et al. (2004)	USA		X	4
Spiga et al. (2017)	UK		X	9
Staaterman et al. (2020)	Panama		X	12
van der Knaap et al. (2021)	Belgium	X		2
Vasconcelos et al. (2007)	Australia		X	14
Vazzana et al. (2017)	Italy		X	8
Vetter et al. (2017)	USA	X		3
Voellmy et al. (2014)	UK	X		9
Wackermannova et al. (2017)	Portugal	X		8
Wei et al. (2018)	China		X	24
Wilson & Dill (2002)	Canada	X		378
Wysocki et al. (2006)	Austria		X	6

Tabela S2. Resumo dos resultados das ANOVAs de duas vias separadas por tipo de estudo (comportamental ou fisiológico) e pelas variáveis de produção sonora e presença de aparelho Weberiano

a) Behaviour Soniferous

	Df	Sum Sq	Mean Sq	F value	Pr (>F)
Sound Source	3	2278	759	34.88	**2.00E-16**
Actively Soniferous	1	11	11	0.53	0.47
Sound Source*Soniferous Status	3	42	14	0.65	0.58
Residuals	1086	23647	22		

b) Physiology Soniferous

Sound Source	4	562895	140724	6.71	**2.30E-05**
Actively Soniferous	1	1566428	1566428	74.66	**2.00E-16**
Sound Source*Soniferous Status	3	3059803	1019934	48.61	**2.00E-16**
Residuals	2342	49136623	20981		

c) Behaviour Weberian apparatus

Sound Source	3	2278	759	35.71	**< 2e-16**
Weberian apparatus	1	40	40	1.9	0.17
Sound Source*Weberian apparatus	3	563	188	8.82	**8.90E-06**
Residuals	1086	23098	21		

d) Physiology Weberian apparatus

Sound Source	4	562895	140724	6.14	**6.50E-05**
Weberian apparatus	1	1256	1256	0.05	0.81
Sound Source*Weberian apparatus	2	65779	32890	1.44	0.24
Residuals	2343	53695818	22918		

Tabela S3. Resumo dos resultados dos testes post-hoc TukeyHSD (Tukey Honest Significant Differences) que avaliou as diferenças entre as variáveis de produção sonora e presença de aparelho Weberiano em função da fonte sonora. Resultados separados por tipo de estudo, comportamental ou fisiológico

a) Behaviour Soniferous

	Observed Means Difference	Lower Interval	Upper Interval	Adjusted P-Value
Anthropogenic: Yes-Unknown	0.422	-0.936	1.78	0.982
Biological: Yes-Unknown	-1.028	-4.452	2.396	0.985
Environmental: Yes-Unknown	-0.59	-5.479	4.3	1
Tone: Yes-Unknown	0.674	-1.928	3.276	0.994

b) Physiology Soniferous

Anthropogenic: Yes-Unknown	0.8105	-32.9	34.56	1
Music: Yes-Unknown	-210.1512	-255.4	-164.89	**0**
Tone: Yes-Unknown	-34.7439	-87.6	18.13	0.541

c) Behaviour Weberian apparatus

Anthropogenic: Yes-No	0.543	-0.9132	1.999	0.95
Biological: Yes-No	3.201	-3.8397	10.242	0.866
Environmental: Yes-No	-1.091	-11.252	9.069	1
Tone: Yes-No	-3.983	-6.3989	-1.567	**0**

c) Physiology Weberian apparatus

Anthropogenic: Yes-No	-5.081	-35.1	24.92	1
Music: Yes-No	35.669	-40.5	111.82	0.899
Tone: Yes-No	19.26	-73	111.5	1

APÊNDICE B – Quadros suplementares

Quadro S1. Informações sobre produção sonora (Soniferous) e presença de aparelho Weberiano (Weberian apparatus) dos gêneros de peixes incluídos nesta metanálise (n = 67)

Genus	Soniferous	Weberian apparatus	Genus	Soniferous	Weberian apparatus
Acanthopagrus	Unknown	No	*Hypophthalmichthys*	Unknown	Yes
Ameiurus	Yes	Yes	*Ictalurus*	Yes	Yes
Amphiprion	Yes	No	*Larimichthys*	Yes	No
Anguilla	Yes	No	*Lepomis*	Yes	No
Argyrosomus	Yes	No	*Luciobarbus*	Unknown	Yes
Astatotilapia	Yes	No	*Metriaclima*	Unknown	No
Betta	Yes	No	*Micropterus*	Yes	No
Boreogadus	Yes	No	*Myxocyprinus*	Unknown	Yes
Campostoma	Unknown	Yes	*Neogobius*	Yes	No
Carassius	Yes	Yes	*Nibea*	Yes	No
Chanos	Unknown	Yes	*Oncorhynchus*	Yes	No
Chromis	Yes	No	*Opsanus*	Yes	No
Clupea	Yes	No	*Oreochromis*	Yes	No
Coregonus	Yes	No	*Pagrus*	Unknown	No
Couesius	Unknown	Yes	*Perca*	Yes	No
Cynotilapia	Yes	No	*Phoxinus*	Unknown	Yes
Cyprinella	Yes	Yes	*Pimelodus*	Yes	Yes
Cyprinus	Yes	Yes	*Pimephales*	Yes	Yes
Danio	Unknown	Yes	*Pomacentrus*	Yes	No
Dascyllus	Yes	No	*Pomatoschistus*	Yes	No
Dicentrarchus	Unknown	No	*Porichthys*	Yes	No
Esox	Yes	No	*Pseudochondrostoma*	Unknown	Yes
Etheostoma	Yes	No	*Pseudochromis*	Unknown	No
Gadus	Yes	No	*Pseudopleuronectes*	Unknown	No
Gasterosteus	Yes	No	*Rutilus*	Yes	Yes
Gobio	Yes	Yes	*Salmo*	Yes	No
Gobius	Yes	No	*Sander*	Yes	No
Gobiusculus	Yes	No	*Schizopygopsis*	Unknown	Yes
Halichoeres	Yes	No	*Sciaena*	Yes	No
Halobatrachus	Yes	No	*Scophthalmus*	Yes	No
Haplochromis	Yes	No	*Sparus*	Unknown	No
Heterostichus	Unknown	No	*Stegastes*	Yes	No
Hippocampus	Yes	No	*Thunnus*	Yes	No

Quadro S2. Descrição dos parâmetros comportamentais e fisiológicos avaliados pelos estudos incluídos nesta metanálise, com seus respectivos exemplos

Study Type	Sound Source	Parameter	Specific Examples
Behaviour	Anthropogenic	Agonistic Behaviour, Communication, Foraging Behaviour, Predator Avoidance, Reproduction, Stress Response, Swimming Behaviour	Food-handling error, discrimination error, unsuccessful strikes, feeding time, darting behaviors, prey speed and distance, startle rate, startle responses, distance between conspecifics, swimming speed
	Biological	Agonistic Behaviour, Communication, Feeding, Swimming Behaviour	Aggressive behaviours, lateral displays, aggression level, calling and grunt rate, approach frequency, swimming depth and speed
	Environmental	Agonistic Behaviour, Foraging, Maintenance Behaviour, Swimming	Vocalizations, angular difference, nearest-neighbor, swimming speed, relative position, feeding rate
	Tone	Agonistic Behaviour, Communication, Foraging Behaviour, Reproduction, Swimming Behaviour	Territorial behavior, conflict, calling Rate, knock duration, drum number, pulses per call, discrimination error, handling error, avoidance behaviour, nearest-neighbor, swimming speed and depth, number of challenges
Physiology	Anthropogenic	Auditory, Circulatory, Immune and Endocrine Systems, Growth, Metabolism, Stress Responses	Hearing threshold, particle acceleration thresholds, cortisol concentration, food consumption, width-length ratio, liver lipids, immunoglobulin, tumor necrosis factor, heart rate, lactic acid, ventilation rate
	Biological	Auditory System, Plasma, Reproduction	Hearing threshold, testosterone, milt
	Environmental	Auditory, Immune, and Endocrine System, Growth, Body Condition, Metabolism, Reproduction, Stress	Food conversion rate, condition factor, hearing threshold, cortisol concentration
	Music	Circulatory and Nervous Systems, Growth, Metabolism	Blood condition factor, feed conversion ratio, organ health, serotonin, noradrenaline, dopamine
	Tone	Auditory, Circulatory, and Endocrine System, Growth, Metabolism, Stress	Hearing threshold, plasma protein, lactate, and cortisol concentration, mortality, condition factor, food conversion rate, growth rate, serotonin, noradrenaline, dopamine

APÊNDICE C – Figuras suplementares

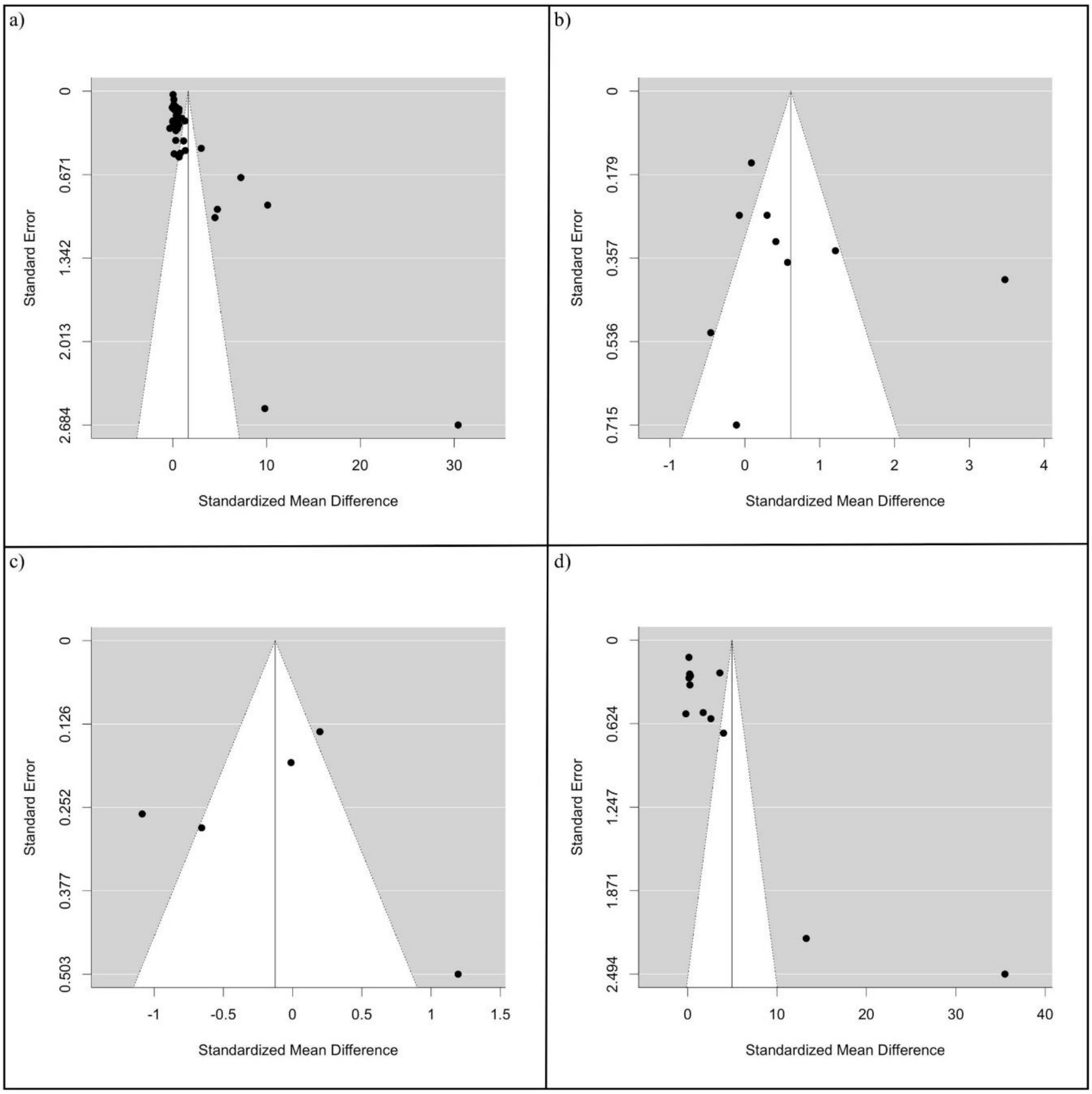

Figura S1. Gráficos Funil dos Tamanhos dos efeitos em parâmetros comportamentais de acordo com o tipo de som. (a) Ruído Antrópico; (b) Ruído Biológico; (c) Ruído Ambiente; (d) Tons.

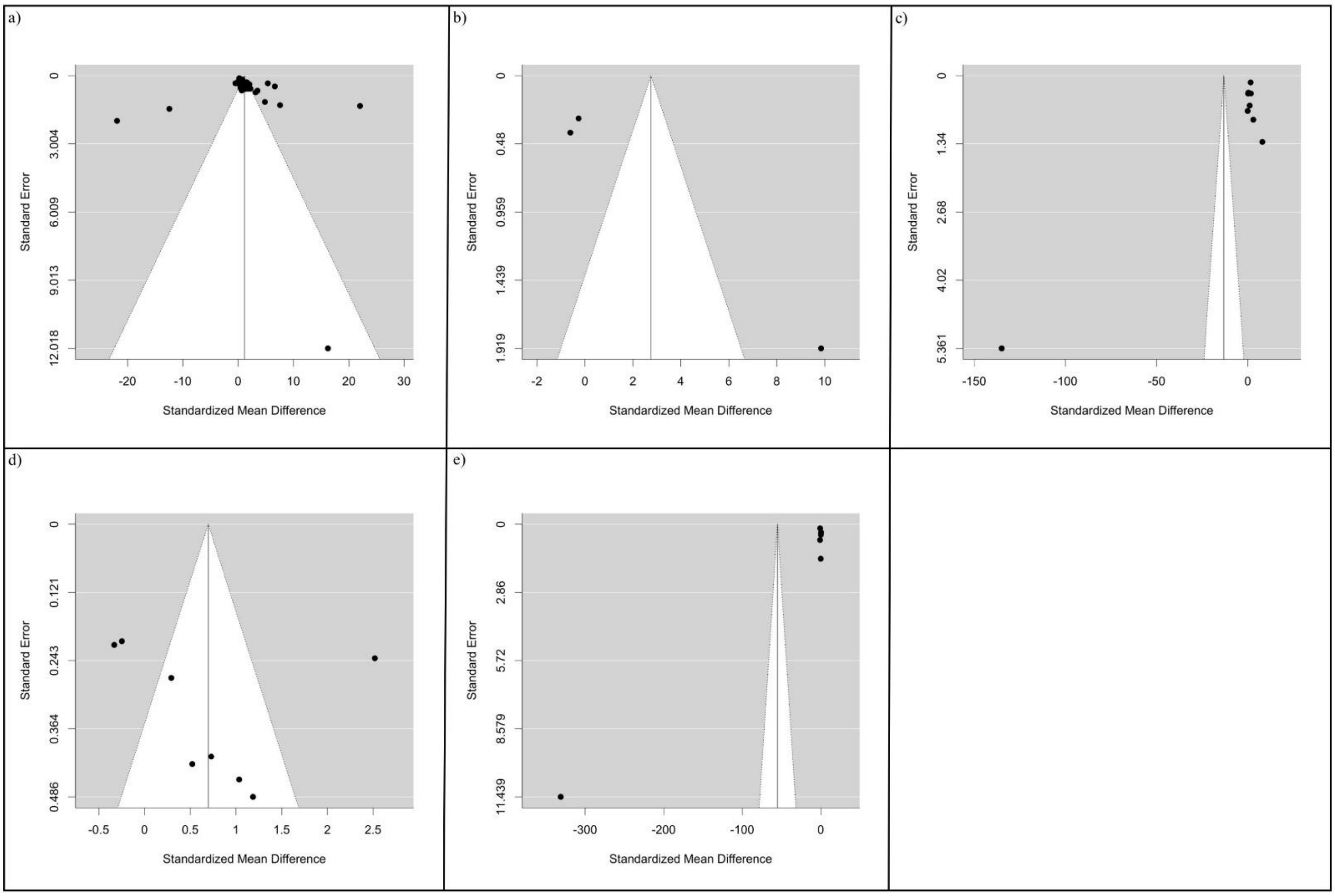

Figura S2. Gráficos Funil dos Tamanhos dos efeitos em parâmetros fisiológicos de acordo com o tipo de som. (a) Ruído Antrópico; (b) Ruído Biológico; (c) Ruído Ambiente; (d) Tons; (e) Música.

APÊNDICE D – Artigo Submetido à Neotropical Ichthyology

Neotropical Ichthyology

Population dynamics of Neotropical fishes under fishing pressure: growth and mortality parameters

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Keywords (English):	Conservation, Human disturbance, Overcatch, Natural Mortality, Fishing Mortality
Palavras-chave or Palabras clave:	Captura excessiva, Conservação, Distúrbios antrópicos, Mortalidade natural, Mortalidade por pesca

Population dynamics of Neotropical fishes under fishing pressure: growth and mortality parameters

Abstract

Overfishing is a recurrent problem in fish stocks, which can result in overexploitation of populations. Present legislation guarantees the development of sustainable fishing, but there are still flaws in the enforcement system. The main objective of this work is to evaluate how fishing has affected the population dynamics of commercially important Neotropical fishes, through growth and mortality data. We pooled assessments of population parameters from 24 species. Fishing proved to be one of the factors determining the growth of individuals within a population. For 11 species, natural causes were the most important factor in total mortality, for 13 species fishing was more relevant, therefore they were considered overexploited. Population parameters should be constantly monitored, since any change caused by fishing or environmental conditions can turn an underexploited stock into an overexploited one. Conservation actions should consider biological and ecological aspects of the species, and social and economic aspects of the fishing community, to reverse a state of overfishing or avoid collapse in fish populations.

Resumo

A pesca excessiva é um problema recorrente nos estoques pesqueiros, que pode resultar em sobreexplotação de populações. Existem legislações vigentes que garantem o desenvolvimento da pesca sustentável, mas ainda existem falhas no sistema de fiscalização. O objetivo principal deste trabalho é avaliar como a pesca tem afetado a dinâmica populacional de peixes Neotropicais com importância comercial, por meio de dados de crescimento e mortalidade. Agrupamos avaliações de parâmetros populacionais de 24 espécies. A pesca demonstrou ser um dos fatores que agem na determinação do crescimento de indivíduos dentro da população. Para 11 espécies as causas naturais apresentaram maior importância para a mortalidade total, para 13 espécies a pesca foi a fonte mais relevante de mortalidade, sendo consideradas sobreexplotadas. Parâmetros populacionais devem ser constante monitorados, uma vez que qualquer alteração causada pela pesca ou por condições ambientais pode tornar um estoque subexplotado em sobreexplotado. Ações de conservação devem considerar aspectos biológicos e ecológicos da espécie, e aspectos sociais e econômicos da comunidade pesqueira, para reverter um estado de sobrepesca ou evitar o colapso nas populações de peixes.

Keywords: Conservation, Human disturbance, Overcatch

Palavras-chave: Captura excessiva, Conservação, Distúrbios antrópicos

Running Head

Growth and mortality of populations under fishing pressure

Introduction

Short-term fish consumption is threatening marine and freshwater environments and jeopardizing future fish populations. Overfishing is one of the practices that raises global concern. According to the State of World Fisheries and Aquaculture (SOFIA), global fishery production in 2018 reached a record 96.4 million tons, and about 34.2% of fish stocks are harvested at biologically unsustainable levels (FAO, 2020). These numbers may be even higher, as some countries have not reported data to the Food and Agriculture Organization of the United Nations (FAO) in recent years.

Unsustainable fishing is more severe in developing countries. This scenario is due to the inadequacy of these countries to the environmental and screening standards required by fishery certification organizations (Sampson et al., 2015), the recent acquisition of technology for more predatory fishing, or because population growth and fish ingestion is increasing (Guillen et al., 2019). In addition, developing countries are more vulnerable to the occurrence of illegal and unreported fishing, which puts fish populations and the ecosystem at risk (Agnew et al., 2009).

In South America, there are typical examples of this scenario of intense exploitation in developing countries. In Brazil, according to the last Statistical Bulletin of Fisheries and Aquaculture - 2011 of the Ministry of Fisheries and Aquaculture, the production of extractive fisheries was 803.3 thousand tons, an increase of 2.3% over the previous year (Brazil, 2011). In Colombia the overall landings of industrial fleets during 2020 reached 41.86 thousand tons, tuna being the most important species captured (Altamar et al., 2020). In Peru, just in February 2021, the fishery landing was 234.3 thousand tons, a harvest 49.6% higher compared to the same month of the previous year (Peru, 2021).

Fisheries legislation around the world, even when well established, is rarely enforced to the satisfaction of the public. Brazil, for example, is ruled by law nº 11.959, of 29 June 2009 (Brazil, 2009) which governs the sustainable development, inspection, preservation and conservation of fishing. However, most of the fishery resources are exploited, overexploited or collapsed due to inefficient management (Castello-Pablo, 2007; Castello, 2008; Kalikoski et al., 2009). Management models have some limitations, such as the economic and social focus overriding biological and ecological arguments (Castello-Pablo, 2007).

Intense exploitation of species can destabilize population dynamics, causing collapse or even local extinctions of a population (Lande et al., 2003). One of the reasons for population instability in fish stocks is changes in demographic parameters, caused mainly by overfishing of large animals (Anderson et al., 2008). Understanding population structure and dynamics is essential for developing sustainable management and conservation strategies for fish stocks (Pauly et al., 2002; Peixer et al., 2007).

The parameters of growth and mortality (natural mortality and fishing mortality) are the most used in stock assessments (Sparre, Venema, 1997). A good assessment uses biological references to inform the status of fish stocks, and thus subsidizes decisions by stakeholders (Cooper, 2006). In addition, knowing the characteristics of the population allows for the identification and estimation of threats that may trigger an extinction process (Lacy, 1993), helping determine urgent actions to reverse the decline scenario.

Thus, the main objective of this work is to evaluate how fishing has affected the population dynamics of commercially important fishes in the Neotropical Region through growth and mortality data, and to identify possible conservation actions to avoid overexploitation of fish stocks.

Material and Methods

We conducted searches in the Google Scholar virtual search engine (https://scholar.google.com.br) and the Web of Science main collection. Search results were limited to full peer-reviewed articles published by 2020 in English, Portuguese, or Spanish. In Google Scholar, the search terms were "fishing" AND "mortality rates" AND ("characiformes" OR “siluriformes"), which returned 458 articles. To expand the search, we used the terms "fishing mortality" AND "natural mortality" AND "growth" in Web of Science, which returned 552 articles. We analyzed the titles and abstracts of the articles to see which ones were conducted in the Neotropical region. In addition, whether the articles estimated population dynamics parameters such as growth rate, total mortality, natural mortality, and fishing mortality. We selected 19 articles that met the search criteria.

Results

Regions and data sources

We pooled 33 assessments of population parameters from 19 studies (Tab. 1). In total, we used 24 species, eight Characiformes, eight Siluriformes, seven Perciformes and one Batrachoidiformes. Studies in Brazil were conducted in the Amazon Basin (Isaac, Ruffino, 1996; Ruffino, Isaac, 1999; Santos Filho, Batista, 2009; Freire, Freitas, 2013), Paraguay Basin (Mateus, Penha, 2007; Peixer et al., 2007; Penha, Mateus, 2007), Upper Paraná Basin (Lizama, Ambrósio, 2004; Novaes, Carvalho,

2011) and through landings data from the southeastern coast of Brazil (Vianna et al., 2000; Castro et al., 2002).

Studies in Colombia have been conducted in the Amazon Basin (Córdoba et al., 2013; Bonilla-Castillo et al., 2018), in the Sinú River Basin (Olaya-Nieto et al., 2015), and through landing data from the coastal region (Caiafa et al., 2011). One study was conducted using landing data from the coast of Peru (Caramantin-Soriano et al., 2008), and another from the coast of Puerto Rico (Acosta, Appeldoorn, 1992). In Venezuela one study was conducted in Lake Maracaibo, connected to the Caribbean Sea (Ferrer-Montaño, Morales, 2013) and one study in the Los Frailes Archipelago (González et al., 2019).

Population parameters

The asymptotic length values ($L\infty$) of the studies included in this work ranged from 12 to 180 cm, with the lowest value for the species *Astyanax schubarti* and the highest for *Pseudoplatystoma metaense* (previously known as *P. tigrinum*). The growth rate coefficient (K) ranged from 0.13 to 0.77/year. Three catfish species represented the lowest value (*Pseudoplatystoma fasciatum*, *Zungaro jahu* and *Pseudoplatystoma corruscans*) and *Cichla temensis* obtained the highest coefficient (Tab. 1).

Total Mortality (Z) ranged from 0.41 to 3.35/year, where the species *Pseudoplatystoma corruscans* presented the lowest value and *Scomber japonicus peruanus the* highest. The Natural Mortality (M) ranged from 0.28/year (*Zungaro jahu*) to 1.36/year (*Haemulon plumieri*). In the analysis of Fishing Mortality (F) the values ranged from 0.10/year to 2.78/year, where the lowest value and the highest value corresponded to *Hemisorubim platyrhynchos* and *Scomber japonicus peruanus,* respectively. For 13 species, fishing was the most important source of mortality, and for 11 species natural causes were the most important for total mortality.

The exploitation rate (E) ranged from 0.12 to 0.84.Thirteen species were overexploited, four were approaching the optimal exploitation limit, and seven were underexploited (Tab. 1).

Discussion

Factors that interfere with growth parameters

In addition to fishing; evolutionary mechanisms, reproductive or even the growth potential of each species in the studied region can interfere with growth parameters (Lizama, Ambrósio, 2004). Diet type and the trophic level occupied by the species are also factors that can determine growth trend (Novaes, Carvalho, 2011). A clear example is the species *Hoplias malabaricus*, in which the specialized diet and the high trophic level exert pressure on growth, slowing it (Novaes, Carvalho, 2011).

It is well accepted that growth parameters are different interspecifically, but it is important to highlight the variation that may occur intraspecifically. According to Sparre, Venema (1997) growth parameters within the same species can vary from one population to another according to environmental conditions. Growth curves of the species *Brycon amazonicus* indicated that there are differences in growth in relation to its distribution in the watershed (Santos Filho, Batista, 2009). Fish from Madeira, Purus, Lower and Middle Solimões River showed the growth rate coefficient (K) at 0.72/year, 0.57/year, 0.54/year and 0.43/year, respectively (Santos Filho, Batista, 2009). These differences can be explained by environmental conditions (Mateus, Penha, 2007; Caiafa et al., 2011), such as water temperature and quality (Sparre, Venema, 1997; Caramantin-Soriano et al., 2008), and by fishing, which may have induced compensatory mechanisms in the populations (Santos Filho, Batista, 2009).

The most commonly used method to estimate the growth parameters applies the FISAT package (FAO - ICLARM Stock Assessment Tools) in the ELEFAN program (Electronic Length Frequency Analysis), which considers Von Bertalanffy's method (1934)to obtain the growth curve. The resulting parameters are: $L\infty$ = asymptotic maximum mean length; and K = growth rate coefficient, which determines how fast the fish approaches its $L\infty$ (Sparre, Venema, 1997). Body size is an important variable because it helps predict life history characteristics of species (Caramantin-Soriano et al., 2008).

The growth parameters are inversely proportional. According to Sparre, Venema (1997) fish with lower $L\infty$ tend to have a high K value, and vice versa. This relationship was evident for most of the species included in this work, but there are exceptions. For example, *Astyanax altiparanae* and *Astyanax schubarti*, which are small fish, had low K values of 0.26 and 0.25, respectively (Tab. 1). This pattern is typical of species with short life cycles in floodplains (Lizama, Ambrósio, 2004).

In summary, individual, population, or environmental factors are important and can interfere with growth within a population. However, in the evaluation of growth parameters in the studies pooled here, these explorations remained in the theoretical field, since no work directly analyzed their effects on $L\infty$ and K. It becomes necessary to verify which factors affect with greater intensity the growth curve of the analyzed species. As previously discussed, fishing can also exert effects on growth parameters, and it is important to estimate them in order to understand the population dynamics of fish species. All articles addressed this scenario, which will be discussed in more detail below.

Level of fish stocks' exploitation

The estimation of fish stocks exploitation considers parameters of total, natural and fishing mortality. Natural Mortality (M) is that created by all causes except fishing (Sparre, Venema, 1997), such as disease and predation. There are several methods estimating M that can be divided according to the parameters used in the formulas (Liu et al., 2020): i) based on maximum age; ii) based on growth coefficient (K); iii) based on K, asymptotic length ($L\infty$) and water temperature; and iv) based on K and maximum age.

Most of the studies pooled in this work used the empirical formula of Pauly (1980), which requires the growth parameters and the average temperature of the environment in which the species is found: $\ln M = - 0.0152 - 0.279 * \ln L\infty + 0.6543 * \ln K + 0.463 \ln T^o$. Only one paper (Acosta, Appeldoorn, 1992) used Ralston's (1987) formula, an adaptation of Pauly's (1980) formula for snappers and groupers: $M = -0.0666 + 2.53(K)$.

Similar to Natural Mortality, there are several methods for estimating Total Mortality (Z). Most studies have used the Beverton, Holt (1956) method: $Z = K^*\{(L\infty - L_{mean})/(L_{mean} - L')\}$, which takes into account the average length in the catch and the K and $L\infty$ parameters of the Von Bertalanffy equation. Where L_{mean} is the average length of fish with length L' or greater, where L' is the lower bound length. According to Sparre, Venema (1997), when L and L' are not known, it is possible to use a mathematic equivalent equation that considers the first-catch size: $Z = K^*\{(L\infty - \overline{Lc})/(\overline{Lc} - Lc)\}$. Where Lc is the length at which 50% of the fish entering the net are retained and $\overline{Lc}$ (Acosta, Appeldoorn, 1992; Caramantin-Soriano et al., 2008; Caiafa et al., 2011; Ferrer-Montaño, Morales, 2013; Olaya-Nieto et al., 2015; Bonilla-Castillo et al., 2018; González et al., 2019) is the average length of the total catch (Sparre, Venema, 1997). Other methods used to estimate Z were: the Linearized Length-Converted Catch Curve (Acosta, Appeldoorn, 1992; Caramantin-Soriano et al., 2008; Caiafa et al., 2011; Ferrer-Montaño, Morales, 2013; Olaya-Nieto et al., 2015; Bonilla-Castillo et al., 2018; González et al., 2019) and Hoenig's method (1983): $\ln (Z) = 1.44 - 0.982 \ln (t_{max})$(Penha, Mateus, 2007).

To obtain the Fishing Mortality Rates (F) the studies used the equation: $F = Z - M$, an important parameter because it can be controlled and regulated (González et al., 2019). To estimate the Exploitation Rate of the stock (E) they calculated the proportion of deaths caused by fishing, being represented by the relation: $E = F / Z$. We calculated E when this parameter was not provided in the articles.

Natural Mortality has a positive correlation with growth rates (Isaac, Ruffino, 1996; Ruffino, Isaac, 1999), where populations with low growth rates have low M. Occasionally exceptions can occur, such as for the species *Cichla temensis*, which had a high growth rate and low natural mortality (Freire, Freitas, 2013).

What may explain this variation is that, according to Pauly (1980), natural mortality is composed of physiological mortality (only due to disease, old age or both), selective mortality (same as physiological, but making fish accessible to predation) and random mortality (unrelated to physiological mechanisms, only related to the number of possible encounters with predators). Furthermore, Pauly's (1980) empirical formula is associated with fish size, growth speed and water temperature (Sparre, Venema, 1997). Therefore, it is considered difficult to get good estimates from this parameter, also being a major source of uncertainty in stock assessments (Mateus, Penha, 2007). Still, it is a key parameter for modeling population dynamics (Sparre, Venema, 1997; Mannini et al., 2020).

A stock is considered overexploited or underexploited when the Exploitation Rate (E) is above or below 0.5, respectively, and in equilibrium when E approaches 0.5 (Pauly, 1983). We know that E is the fraction between fishing mortality and total mortality. Therefore, the species that presented fishing as the main cause of mortality were considered overexploited. Note that when we calculated the E of the species *Lutjanus synagris*, not provided in the source article, we observed a high value of 0.68, i.e., overexploited. However, Acosta, Appeldoorn (1992) did not consider the stock threatened by overfishing, stating that it is susceptible to low overexploitation levels.

As seen earlier, about 46% of the species (eleven out of twenty-four) had higher natural mortality than that caused by fishing. Consequently, for these eleven species, stocks were not considered threatened by overfishing. In the case of *Astyanax schubarti*, researchers attribute this result to the low exploitation of the species, and also point out that these animals have a rapid and natural renewal in the environment (Lizama, Ambrósio, 2004). In fact, *A. schubarti* has an average fecundity of almost five thousand oocytes per female, being also considered highly viable and contributing to the replacement of the population in the future (Rodrigues et al., 1995).

On the other hand, 13 species presented fishing as the main cause of Total Mortality (Z). Isaac, Ruffino (1996) consider that, to avoid overexploitation, the optimal fishing mortality would be around 0.4/year. However, this value depends on other factors, such as recruitment (Sparre, Venema, 1997) and is different for each species and for the situation in which the population finds itself. For the species *Cynoscion jamaicensis,* researchers relate the increase in fishing mortality to the increase in fishing effort and the use of more invasive fishing tools, such as bottom trawling (Castro et al., 2002).

The biggest problem with trawling is bycatch. This practice catches species other than the target species and is detrimental to several populations (Vianna et al., 2000). These multi-species fisheries have contributed to increased fishing mortality and exploitation rate of *Porichthys porosissimus* and *Cynoscion jamaicensis* (Vianna et al., 2000; Castro et al., 2002).

In general, these results draw attention and demonstrate how several fishes are being exploited at levels inappropriate for the species' life history, some almost reaching their limit. As for natural mortality, there are few biological explanations for the values found in the literature. However, Santos Filho, Batista (2009), who attribute the differences in M values to the biotic integrity of the

Amazon Basin sub-system in which the species *Brycon amazonicus* was evaluated, stand out. They suggest the existence of three distinct populations (Santos Filho, Batista, 2009) may explain high M values for the species in one sub-system and lower ones in another. Studies in other areas pointed to increased water temperature (Al-Ansi et al., 2002), predation (Benoît et al., 2011), starvation (Byström et al., 2006), diseases and factors that increase susceptibility to pathogens (Snieszko, 1958) as causes of high natural mortality. As for fishing mortality and exploitation rate, the studies elucidate some factors that may interfere with these parameters, such as the conservation strategies adopted for the region.

Conservation Strategies

It is important to know the species' biology and to establish alternative and appropriate strategies for each region. Some authors suggest using behavioral aspects of the species, its interspecific and environmental ecological interactions (Castro et al., 2002) to define pertinent actions. The main suggestions for the conservation of fish stocks by researchers are: establishment of no-take areas, especially in spawning sites (Isaac, Ruffino, 1996; Vianna et al., 2000; Ferrer-Montaño, Morales, 2013); definition and adequacy of minimum catch sizes (Isaac, Ruffino, 1996; Ruffino, Isaac, 1999; Caiafa et al., 2011; Ferrer-Montaño, Morales, 2013); increasing mesh size in nets and reducing the use of fishing traps (e.g. cages and baskets) (González et al., 2019); raising the awareness of the productive sector (Castro et al., 2002; Caiafa et al., 2011), with the creation and introduction of environmental education tools (Isaac, Ruffino, 1996); evaluating the effectiveness of the management actions by the environmental agencies (Penha, Mateus, 2007) and adopting participatory fisheries management.

For long-distance migratory species, the situation is more delicate. According to Córdoba et al. (2013), species with these characteristics are more vulnerable to habitat degradation and dam construction. The species *Brachyplatystoma rousseauxii* performs large migrations and was considered overexploited by Córdoba et al. (2013), who, to avoid population collapse, suggested a multilateral process of broadly participatory coordination between Colombia and neighboring countries.

The introduction of adequate fishing policies requires monitoring. In Brazil, for example, there are flaws in the current system of fisheries control by government organs and their representatives (Santos Filho, Batista, 2009). A clear example of the lack of enforcement is the scenario presented for *Pseudoplatystoma tigrinum*, in which the decrease in the average size of individuals and the increase in catches, below the limit set by law, have increased in recent years (Ruffino, Isaac, 1999). With this in mind, the adoption of participatory management in Brazilian fisheries becomes a necessary alternative. Participatory management occurs when government and fishery resource users come together in the administration of fisheries (Kalikoski et al., 2009). This advance in fisheries science can promote conservation by bringing the population and management institutions closer together (Castello, 2008). However, it is necessary that governmental agents are prepared to adopt this type of management, and that training occurs for managers and the fishing community (Kalikoski et al., 2009). Another worrisome scenario are the places without any kind of regulation. For example, Lake Maracaibo in Venezuela where, according to Ferrer-Montaño, Morales (2013), fisheries operated in open access regime, putting fish populations in the region at risk.

In general, stock assessments are fundamental for understanding the dynamics of fish populations and are of great importance for the management of species in any area (Penha, Mateus, 2007). For certain species, these assessments have provided the development of actions that control overfishing. In the case of the fish *Hemisorubim platyrhynchos* and *Sorubim lima*, the establishment of a minimum catch size seems to have helped prevent overfishing of stocks (Penha, Mateus, 2007). In the Cuiabá River Basin there is also a fishing restriction for small individuals, which may have contributed to the species *Pinirampus pirinampu*, *Pseudoplatystoma fasciatum*, *Zungaro jahu*, and *Pseudoplatystoma corruscans* being considered not threatened by overfishing (Mateus, Penha, 2007). However, the existence of a minimum catch size is not always sufficient. For example, even with catch restrictions, the species *Colossoma macropomum* and *Pseudoplatystoma tigrinum* were considered overfished (Tab. 1). This can be explained by the excessive removal of small animals, even with the defined minimum sizes, impairing reproductive success in the population (Isaac, Ruffino, 1996; Ruffino, Isaac, 1999; Peixer et al., 2007). But, one must also ensure that large individuals are not taken before they contribute to the genetic diversity of the population (Penha, Mateus, 2007). This becomes a problem when the removal of these individuals affects the age structure of the population and reduces its longevity (Mateus, Penha, 2007).

We believe that fishing moratorium in certain environments, minimum catch sizes, environmental education, and participatory fisheries management have potential for success. We also suggest the creation of areas for the practice of sport fishing, such as catch-and-release, ensuring that the species continues to reproduce and the population persists (Cooke et al., 2006) without banning this recreational activity, interaction with nature, and source of income for many families, especially in developing countries (Gupta et al., 2015). In addition, invasive fishing gear must be regulated.

Taking into consideration the studies used in this work, one can see that many studies do not suggest conservation and management actions. Such informed recommendations are essential to define species-specific strategies. Many fish stocks are not assessed or sometimes incompletely assessed, but according to FAO (1995) the absence of adequate scientific information should not be used as a reason for postponing or failing to take conservation measures.

Limitations and Future Directions

Studies on fish population dynamics lack a standard. For example, some studies estimate growth parameters but do not estimate mortality parameters (e.g., Campos et al., 2015). Others estimate growth parameters and natural mortality, but do not estimate total and fishing mortality (e.g., Cutrim, Batista, 2005). In addition, there are several methods to estimate the Total Mortality (Z). This estimation depends on the growth data available for the population under study. For example, Catarino et al. (2014) estimated Z with linearized catch curve method, considering that the density of the stock decreased proportionally with fish age.

A viable alternative would be to estimate Z using different methods in the same study, as in Castro et al. (2002). By doing this, it is possible to evaluate which method best describes the stock situation, since fishing mortality and exploitation rate depend directly on the value of Z. In addition, it allows the data to be comparable with later studies, since comparing information estimated by different methods leads to biases in the interpretation of the results.

We also suggest estimating Natural Mortality (M) by various methods, as in Bonilla-Castillo (2018). It is worth noting a recent methodology developed by Liu et al. (2020) called Tree-Based Set Learning Models, which does not need to specify a mathematical formula between the predictors and the response variable. The authors further suggest that combining traditional models with tree-based models can improve predictions and lead to better scenario interpretation (Liu et al., 2020). The importance of accounting for uncertainty regarding M during stock assessment is emphasized to avoid management biases, as results may be underestimated or overestimated (Mannini et al., 2020).

Classic stock assessment models should consider the hydrological regime to which the species is subjected (Isaac, Ruffino, 1996) seems that these models are not well applicable in floodplains. It is emphasized that the results presented in Tab. 1 are valid only for the periods specified. Therefore, population parameters of each species needs to be continually monitored (Castro et al., 2002), we suggest annual assessments. This constant assessment is essential because changes in the dynamics of the species caused by fishing or environmental changes can transform an underexploited population into an overexploited one (Santos Filho, Batista, 2009).

Overfishing is an anthropogenic disturbance that negatively impacts fish populations. We found evidence that fishing exerts pressure on the growth trend of some species. However, it is important to note that other factors, such as evolutionary and environmental ones, also determine individual growth decrease or increase within a population. High fishing mortality has contributed to the overexploitation of fish stocks. Even though for some species the stock is not considered threatened by overfishing, it is necessary to continue monitoring their population parameters to avoid such threat. Thus, managers and the fishing community will have complete information to define relevant conservation actions, considering biological, ecological, social, and economic aspects.

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Tab. 1. Growth and mortality data from all articles used in this work. Where: N = number of individuals; $L\infty$ = asymptotic length (cm); K = annual growth rate; Z = annual total mortality; M = annual natural mortality; F = annual fishing mortality; E = exploitation rate ([1] number of individuals was not clear; [2] Average Z between Beverton & Holt and Ault & Ehrhardt; [3] Assessments for the same species in different locations; [4] Z calculated using Length-Converted Capture Curve; [5] Z calculated by Hoening's method; [6] M calculated by Ralston's method)

Country	Authors	Species	Period	N	$L\infty$	K	Z	M	F	E
Brazil	Castro et al. (2002)	*Cynoscion jamaicensis*	1993-1995	5449	39.00	0.40	1.80	0.85	0.95	0.53
			1997-1998	16016	40.00	0.41	2.11	0.86	1.25	0.59
	Freire, Freitas (2013)	*Cichla temensi*	2011-2012	1627	43.58	0.77	1.76	0.40	1.36	0.77
	Isaac, Ruffino (1996) [1]	*Colossoma macropomum*	1992	-	121.20	0.23	1.37	0.45	0.95	0.69
			1993	-	118.50	0.23	1.28	0.44	0.93	0.73
	Lizama, Ambrósio (2004)	*Astyanax altiparanae*	1993-1994	1844	18.00	0.26	2.13	0.79	1.34	0.63
		Astyanax schubarti	1993-1994	661	12.00	0.25	1.65	0.86	0.79	0.48
	Mateus, Penha (2007)	*Pinirampus pirinampu*	2000-2001	908	90.60	0.30	1.11	0.58	0.53	0.48
		Pseudoplatystoma fasciatum	2000-2001	1283	122.40	0.13	0.64	0.31	0.33	0.52
		Zungaro jahu	2000-2001	488	172.00	0.13	0.45	0.28	0.17	0.38
		Pseudoplatystoma corruscans	2000-2001	1445	149.70	0.13	0.41	0.29	0.12	0.29
	Novaes, Carvalho (2011)	*Hoplias malabaricus*	2005	426	35.18	0.32	1.24	0.71	0.54	0.44
	Peixer et al. (2007) [2]	*Piaractus mesopotamicus*	1996	5146	87.20	0.34	1.52	0.62	0.90	0.59
			1997	4921	86.50	0.34	1.66	0.63	1.03	0.62
	Penha, Mateus (2007) [5]	*Hemisorubim platyrhynchos*	2000	913	64.00	0.22	0.62	0.52	0.10	0.17
		Sorubim cf. lima	2000	817	56.00	0.25	0.87	0.58	0.29	0.33
	Ruffino, Isaac (1999)	*Pseudoplatystoma tigrinum / P. metaense* (current)	1993	1690	180.00	0.29	1.22	0.47	0.75	0.61
			1995	2576	180.00	0.29	1.41	0.47	0.94	0.67
	Santos Filho, Batista (2009) [3]	*Brycon amazonicus*	1998-1999	2510	51.00	0.57	1.20	1.06	0.14	0.12
			1998-1999	1560	51.10	0.72	1.76	1.24	0.52	0.30
			1998-1999	561	43.20	0.54	1.39	1.07	0.32	0.23
			1998-1999	820	46.90	0.43	1.06	0.90	0.16	0.15
	Vianna et al. (2000)	*Porichthys porosissimus*	1995-1996	2897	37.00	0.28	2.33	0.63	1.70	0.73
Colombia	Bonilla-Castillo et al. (2018) [4]	*Prochilodus nigricans*	2009-2017	10884	35.70	0.37	1.58	0.87	0.71	0.45
	Caiafa et al. (2011) [4]	*Caranx hippos*	2005-2006	1151	91.00	0.38	1.76	1.12	0.63	0.36
	Córdoba et al. (2013)	*Brachyplatystoma rousseauxii*	1995-1997	4116	153.3	0.22	1.14	0.41	0.73	0.64
	Olaya-Nieto et al. (2015) [4]	*Cynopotamus atratoensis*	2001-2002	1893	43.40	0.29	0.97	0.72	0.25	0.26
Peru	Caramantin-Soriano et al. (2008)[4]	*Scomber japonicus peruanus*	1996	178067	40.20	0.38	1.68	0.52	1.16	0.68
			1997	720608	42.20	0.39	2.56	0.52	2.13	0.80
			1998	2464686	41.50	0.39	3.35	0.53	2.78	0.84
Puerto Rico	Acosta, Appeldoorn (1992) [4,6]	*Lutjanus synagris*	1988	1308	45.00	0.23	1.65	0.53	1.13	0.68
Venezuela	Ferrer-Montaño, Morales (2013) [1,4]	*Cynoscion acoupa*	2009	-	98.10	0.26	1.23	0.53	0.70	0.57
	Gonzalez et al. (2019) [4]	*Haemulon plumieri*	2014	2967	30.95	0.67	3.31	1.36	1.95	0.59

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	Gonzalez et al. (2019) [4]	*Haemulon plumieri*	2014	2967	30.95	0.67	3.31	1.36	1.95	0.59

APÊNDICE E – Texto da metanálise em Inglês para submissão

A meta-analysis of the impacts of aquatic soundscape under the light of the fish's ability to produce and perceive sounds

ABSTRACT

The natural soundscape of many environments, including aquatic environments where sound propagates most efficiently, has been altered by human action (e.g. shipping, mining, hydroelectric turbines). In this context, the fish present in these water bodies must be undergoing physiological and behavioral changes. There have already been studies that have looked at this, but a new synthesis, including the large volume of recent studies on the subject, was needed. A special factor that has not been considered before is the ability to produce sounds or the hearing acuity of the fish. Our meta-analysis reviewed physiological and behavioral impacts of anthropogenic, biological, environmental noise, tones and music on fish. We also analyzed these impacts in relation to the occurrence of active vocalization by fish and the presence of Weberian apparatus. We analyzed 107 studies on 66 fish genera, and anthropogenic, biological, and tonal noises caused increased behavioral and/or physiological activity. Environmental noise, music, and tones (physiological responses) had conflicting results and require further study. Although they did not show a consistent result across all noise source, we noticed that vocalization increased fish sensitivity to music and the presence of Weberian apparatus increased sensitivity to tones. Overall, sounds with potential negative effects should be observed in fish conservation and sounds with potential positive effects may be useful in the welfare of captive fish. Our study highlights the importance of controlling noise emissions from anthropogenic activities and demonstrates the importance of considering the contribution of fish in a bidirectional manner (sound production and perception) to the soundscape in impact assessment.

Keywords: Behavior; Disturbance; Noise pollution; Physiology; Soundscape.

INTRODUCTION

The soundscape is made of different sounds that constitute a given environment, produced by natural, biological or anthropogenic agents (Farina, 2014). In recent decades, human activity has introduced a variety of sounds that interfere with the aquatic soundscape (Popper & Hawkins, 2019). Constructions, sonars, seismic measuring equipment and boat engines are some examples of human devices that have harmed marine life. In relation to boats, for example, it is estimated that by the year 2030 the noise capacity of maritime transport will increase by up to 102% (Kaplan & Solomon, 2016). The speed of sound is about 4.5 times greater in water compared to air (Palma et al., 2019). Therefore, aquatic animals with complex auditory system can perceive sound more intensely.

In fish, several negative effects of anthropogenic noise have been documented. Among them, we can mention behavioral interferences in parental care (Nedelec et al., 2017), survival and predator-prey relationships(Simpson et al., 2016), foraging and feeding (Cox et al., 2018; Kunc et al., 2016), and changes in shoal coordination(Herbert-Read et al., 2017). In addition, changes in the auditory range of some species(Kunc et al., 2014), increased physiological stress(Cox et al., 2018; Mickle & Higgs, 2018), increased metabolic rate (Harding et al., 2018; Kunc et al., 2016), and decreased olfactory perception (Hasan et al., 2018) have already been diagnosed in relation to the physiology of fish exposed to anthropogenic noises. Recently, it was recognized that the origin and frequency of noise can cause different effects in fish (McCormick et al., 2019). Although most studies on the impacts of anthropogenic noise are performed with marine fish, it is known that fish in general are vulnerable to soundscape disturbances due to their auditory abilities.

Fish have sensitive hearing and perceive sound through the inner ear, which performs vestibular and auditory functions, and works through mechanosensory stimuli (Platt & Popper, 1981). Some species detect sounds below 50Hz to 500Hz(Popper & Hawkins, 2019), and specialized species such as common carp (*Cyprinus carpio*), can detect frequencies up to 3–4 kHz (Ladich & Fay, 2013). Notwithstanding, the hearing thresholds are well defined only for a few species (Popper & Hawkins, 2019). In general, noises should be especially harmful to fish of the Superorder Ostariophysi, which present a specific and complex connection between the inner ear and the swimming bladder, called Weberian apparatus (Rosen & Greenwood, 1970). This structure has a double chain of rib-derived ossicles that improves the hearing of ostariophysian fish by amplifying the vibrations that reach the swimming bladder (Diogo, 2009). Such apparatus makes ostariophysians especially sensitive to sounds.

Some fish species also have sound production skills. By the year 2020, about 989 species of fish capable of actively producing sounds were documented (Looby et al., 2022). Fish produce acoustic signals in various social contexts, such as territory defense, feeding, reproductive encounters, swimming and distress (Ladich, 2019; Ladich & Bass, 2011). These signals have varied spectral and time properties, and can be generated by vibration of muscles attached to the swimming bladder, by the vibration of the pectoral waist (Ladich & Bass, 2011). Thus, a noisy environment makes these sounds difficult to spread (Fay & Simmons, 1999; Kunc et al., 2014) impairs the behavioral role of sound for fish.

Recent studies present unidirectional impact assessments, i.e., they either assess how fish contribute to the soundscape or how noise affects fish. The bidirectional interaction between these factors is still neglected. Therefore, the aim of our meta-analysis is to identify the global consequences that disturbances in the aquatic soundscape cause in the behavior and physiology of fish under the light of the fish's ability to produce and perceive sounds. Our hypotheses are that the anthropogenic, biological, environmental and tonal noises increase the behavioral and physiological activities of fish, while music reduces. We also expect the effects of noise on the behavior and physiology of fish with Weberian apparatus to be higher when compared to the effects on non-ostariophysian fish. Furthermore, the effects of noise on the behavior and physiology of soniferous fish should be more intense when compared to the effects on fish without documented sound production. Therefore, so far and according to our survey, this is the first global analysis in which we are evaluating how the ability of species to perceive and produce sounds influences the response to noise pollution.

MATERIAL AND METHODS

Systematic Literature Search

We used the Thompson's Web of Science (www.webofscience.com/) database to conduct a systematic search in the literature. The search was limited to peer-reviewed articles published between 1950 and 2021. We conducted the search on May 23, 2021. Its specific terms were: fish AND (noise OR sound OR acoustic OR ecoacoustic OR bioacoustics) AND (behav* OR physiol* OR response OR morphology), resulting in 4,457 potentially relevant articles. A librarian validated the search. Another 528 potentially relevant peer-reviewed articles were obtained through other research mechanisms, including ScienceDirect and JSTOR. We also thoroughly searched the bibliographies of relevant reviews for different articles, which were also included.

Database searches can generate lists with duplicate articles, so we identified and removed repeated studies. The titles and abstracts of the 4,985 studies were reviewed to determine which studies addressed the effects of noise on fish behavior or physiology (Figure 1b). The articles that met these criteria (672) were evaluated to identify which met the further criteria of: original research, behavioral and/or physiological focus, described sound source, experimental control, mean value, standard error and/or standard deviation included, and the sample size (n) used. We extracted data from the treatment and control groups of each study through tables, text and figures.

One hundred and seven studies from 27 countries attended the search criteria (Figure 1a). Eighty-two studies carried out laboratory experiments, and 26 studies conducted in *situ* field trials. Only one study was conducted in both laboratory and field. When necessary, we use the GetData Graph Digitizer (Fedorov, 2013) extraction software to retrieve data from figures. We gathered a total of 3,432 data points from the 107 studies that evaluated the effect of noise on fish behavior and/or physiology (Appendix A, Table S1).

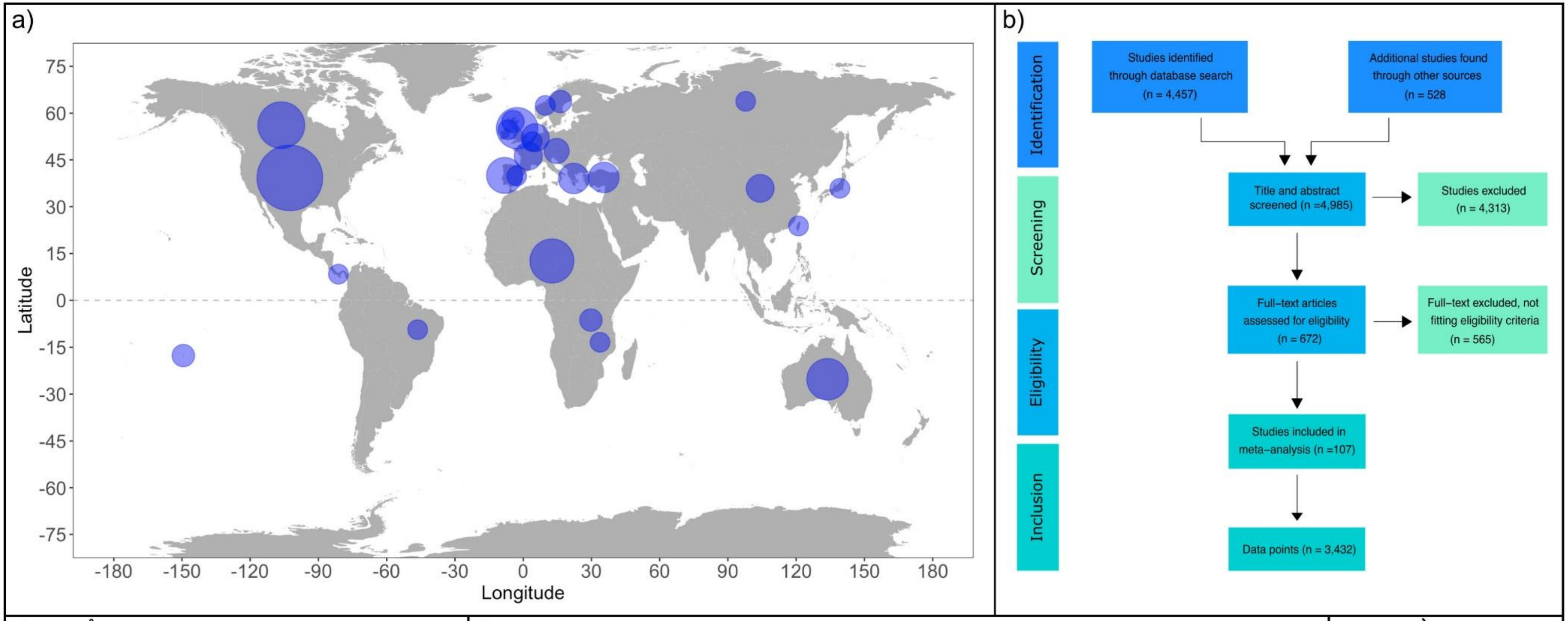

Figure 1. Summary of systematic search. (a) geographical distribution of the studies used in this metanalysis, where the size of the circle is proportional to the number of studies; (b) PRISMA diagram describing the processes of article selection.

Independent variables of fish and sounds

To evaluate the effect of sound production by certain genus on the response to noise, we defined as "soniferous" categories: "Yes" if at least one species in the genus had been documented for actively producing sounds (i.e., intentional) or "Unknow" if no species of the genus had published documentation of active sound (Looby et al., 2022). Similarly, we evaluated the effect of the presence of weberian apparatus on the response to noises by recording the presence, "Yes" if the genus belonged to the superorder Ostariophysi, or absence, "No" if the genus belonged to another group, according to taxonomic information available in FishBase (Froese & Pauly, 2021).

The sound sources entered our analyses as independent variables, classified as anthropogenic noises, biological noises, environmental noises, tones and music. These variables were obtained directly from the texts of the analyzed articles. We included in the category of anthropogenic noises, for example, the sounds of motorboats, seismic research and white noise. In the category of biological noises, for example, conspecific fish sounds and courting sounds. In the environmental noises were included natural sounds of the aquatic environment, for example the sounds of a coral reef, waves or river rapids. In the Tones we grouped the continuous tones and pulses (beeps). In Music we grouped songs and binaural sounds (combination of two sound frequencies to create the perception of a single one).

Effect Size Calculation

We used the 'metafor' (Viechtbauer, 2010) in the R version 4.0.5 (R Core Team, 2021) to calculate the effect sizes and its variations for each study. We calculate the mean difference (md) using Eq. (1), where $\bar{Y}_1$ and $\bar{Y}_2$ are the mean values of the treatment and control group, respectively.

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

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

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

We determined the variation for Hedge's d using Eq. (3) (Hedges & Olkin, 1985).

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

Statistical analysis

We performed all analyses in the program R version 4.0.5 (R Core Team, 2021). We created the Forest plots to define the general effect sizes (ES) and their confidence intervals; and the Funnel plots to check for publication bias using the 'metafor' and 'MAd' packages for both (Del Re & Hoyt, 2014; Viechtbauer, 2010). The graphs were elaborated for each sound source and separated according to the study type, behavioral or physiological. Following, we plot the ES of each sound source according to the sound production capacity and the presence of Weberian apparatus in the fish, we also separated them in behavioral or physiological studies. We performed two-way ANOVAs with post-hoc tests (Tukey Honest Significant Differences) on the data of each figure (therefore four ANOVAs), with the interaction between the sound source and the Weberian apparatus or sound production state performed in all cases.

RESULTS

General Aspects

There was a significant increase in the number of studies published from 2015 on. About 67% of the studies were published from 2015 to 2021, and the year 2020 had the highest number of studies (19), followed by 2019 with 14 studies (Figure 2a). Thirty-two fish families were used in studies on the effect of sounds on behavioral and physiological responses, and the families Sparidae, Cyprinidae and Clupeidae presented greater data representativeness (Figure 2b). In all, we gathered behavioral and physiological data from 66 fish genera. Of these, 48 genera have documented sound production and 18 genera do not have this information in the literature yet (Figure 2c). In addition, 47 genera do not present Weberian apparatus, while only 19 have this structure that connects the swimming bladder to the inner ear (Figure 2c). Only nine genera have both characteristics, sound production and Weberian apparatus (Appendix B, Box S1).

Most of the behavioral characteristics available focused on anthropogenic noises (49.7%) and biological noises (34.2%), followed by Tones (12.4%) and Environmental noises (3.7%). To date and according to our survey, no study has evaluated behavioral changes in fish caused by exposure to music (Figure 3a). Regarding physiological data, it is observed that most studies focused on anthropogenic noises (51.9%) and Music (31.7%), followed by Tones (12.8%), Environmental (2.8%) and Biological (0.8%) noises. Unlike behavioral studies, physiological studies have seldom addressed responses to Biological noises (Figure 3a). Studies on the effects of sound on fish were conducted, in most cases, with genera with known sound production. It is noteworthy that, according to our survey, there are more fish genera included in this metanalysis in which sound production is known (70%) than genera in which it is unknown (30%) (Figure 3b). There are few studies on the effect of different sound source on the behavioral parameters of fish with Weberian apparatus. It is noteworthy that, to date, physiological responses to biological and environmental noises have not been evaluated in fish with Weberian apparatus (Figure 3c).

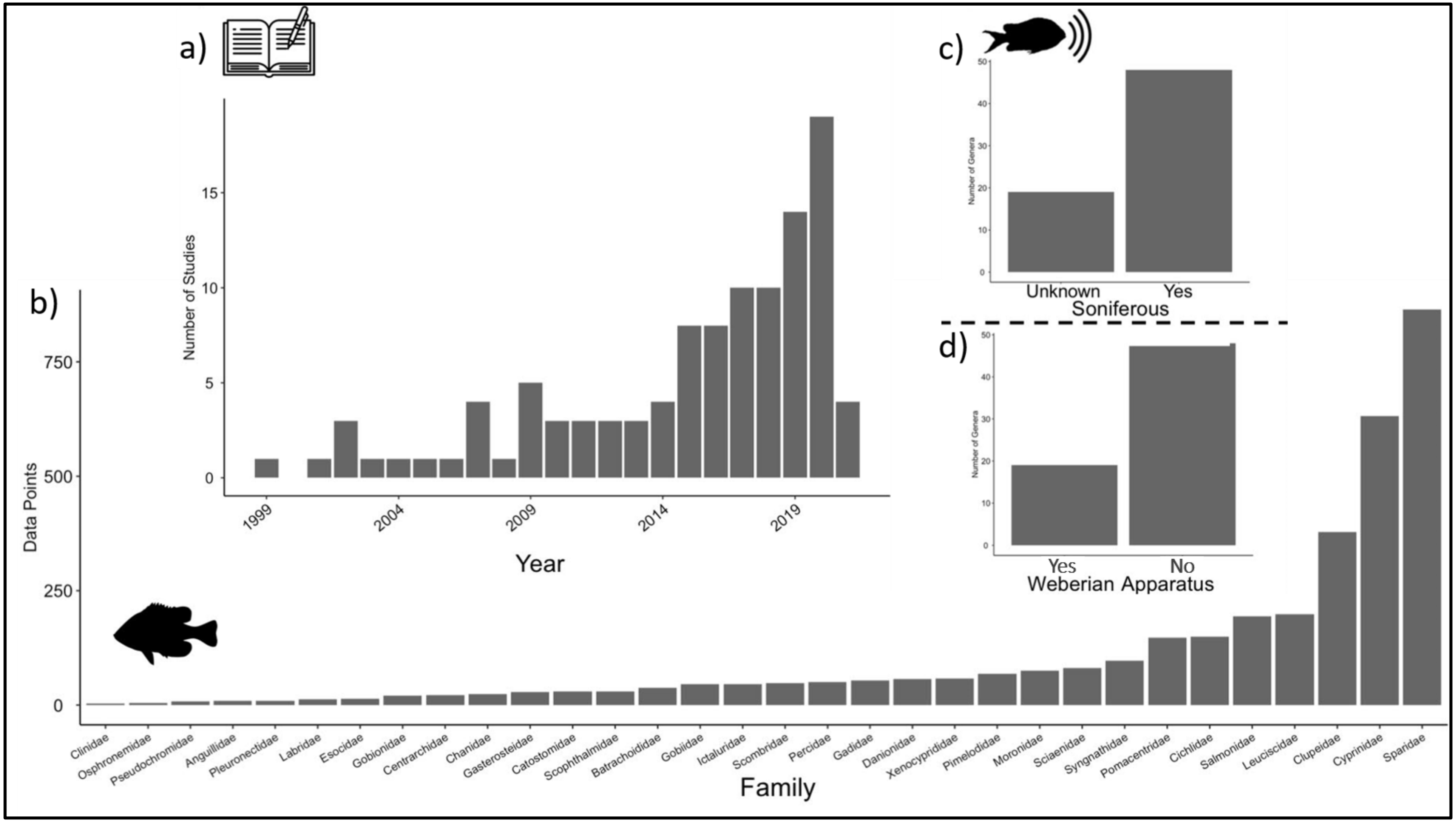

Figure 2. (a) history of yearly publication of the articles used in this metanalysis; (b) Number of data points per taxonomic family; (c) Proportion of soniferous genera and genera without documented sound production; (d) Proportion of genera with and without Weberian apparatus.

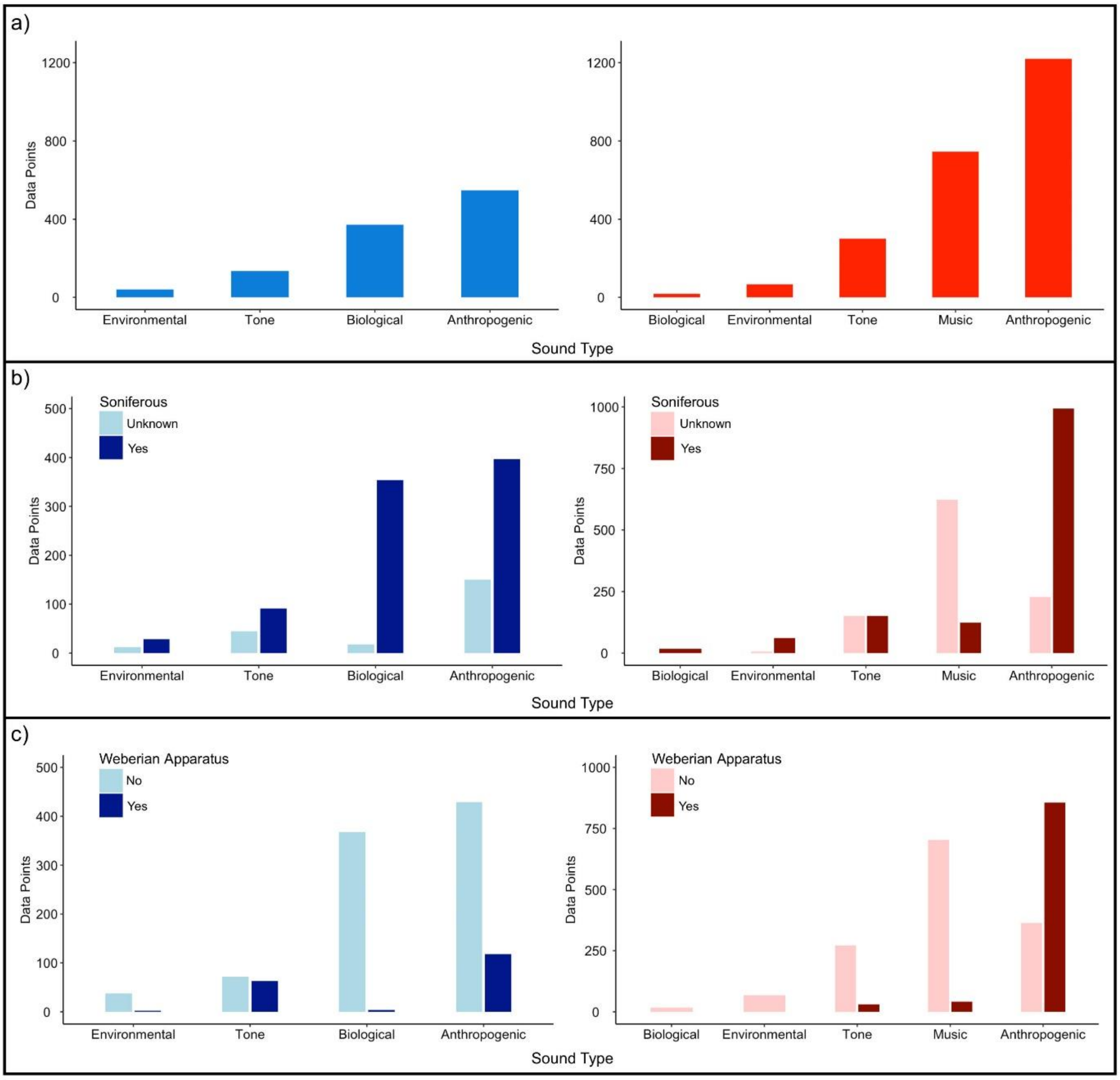

Figure 3. Number of data points used in this meta-analysis extracted from studies with behavioral focus (left, blue) and with physiological focus (right, red). Separated by: (a) Sound source in all fish; (b) Sound source in soniferous fish genera (dark color) and genera with unknown sound production (light color); (c) Sound source in genera with (dark color) and without (light color) Weberian apparatus.

Meta-analysis

Anthropogenic noises caused an increase in the behavioral and physiological response variables of fish. The studies with behavioral focus presented a general effect size (ES) of 1.63 with confidence intervals of 95% (CI) from 0.52 to 2.75, while the studies with physiological focus presented an ES of 1.15 with CI of 95% from -0.46 to 2.75 (Figure 4a and 5a). Biological noises also tend to increase behavioral and physiological response variables, with general ES 0.61 (CI -0.14 to 1.37) and 2.75 (CI -3.72 to 9.23), respectively (Figure 4b and 5b). Environmental noise caused a slight reduction in behavioral variables (ES -0.13; CI -0.81 to 0.56; Figure 4c), and an increase in physiological variables (ES 0.70; CI 0.02 to 1.37; Figure

5c). Tones present a tendency to increase behavioral (ES 4.95; CI -0.62 to 10.51; Figure 4d) and to decrease physiological variables (ES -13.07; CI -42.63 and 16.48; Figure 5d). The Music also tends to decrease physiological variables of fish, with ES of -55.17 (CI -162.68 to 52.35; Figure 5e).

Sound production does not explain the Effect Sizes (ES) found for behavioral variables (Appendix A, Table S2a). However, it was significant explaining the ES of the physiological variables ($F = 74.66$, $p < 0.0001$), and remained significant in interaction with the sound source ($F = 48.61$, $p < 0.0001$; Table S2b). The presence of Weberian apparatus does not explain the ES for physiological variables (Table S2d). However, it was significant explaining the ES of behavioral variables when interacting with the sound source ($F = 8.82$, $p < 0.0001$; Table S2c).

The post-hoc test revealed that there is a significant difference between the Effect Sizes (ES) for soniferous fish and fish without documented sound production, but only for physiological responses in exposure to music (adjusted p value = 0; Figure 6a; Table S3b). The test also showed that there is a significant difference between the ESs found for fish with Weberian apparatus and fish without structure, but only for behavioral responses in exposure to tones (adjusted p value = 0; Figure 6b; Table S3c). The Effect Sizes (ES) of behavioral and physiological responses to anthropogenic, biological and environmental noises appear to indicate differences between the categories of the sound production variables and the presence of Weberian apparatus (Figure 6). However, the post-hoc test indicates that these differences were not significant.

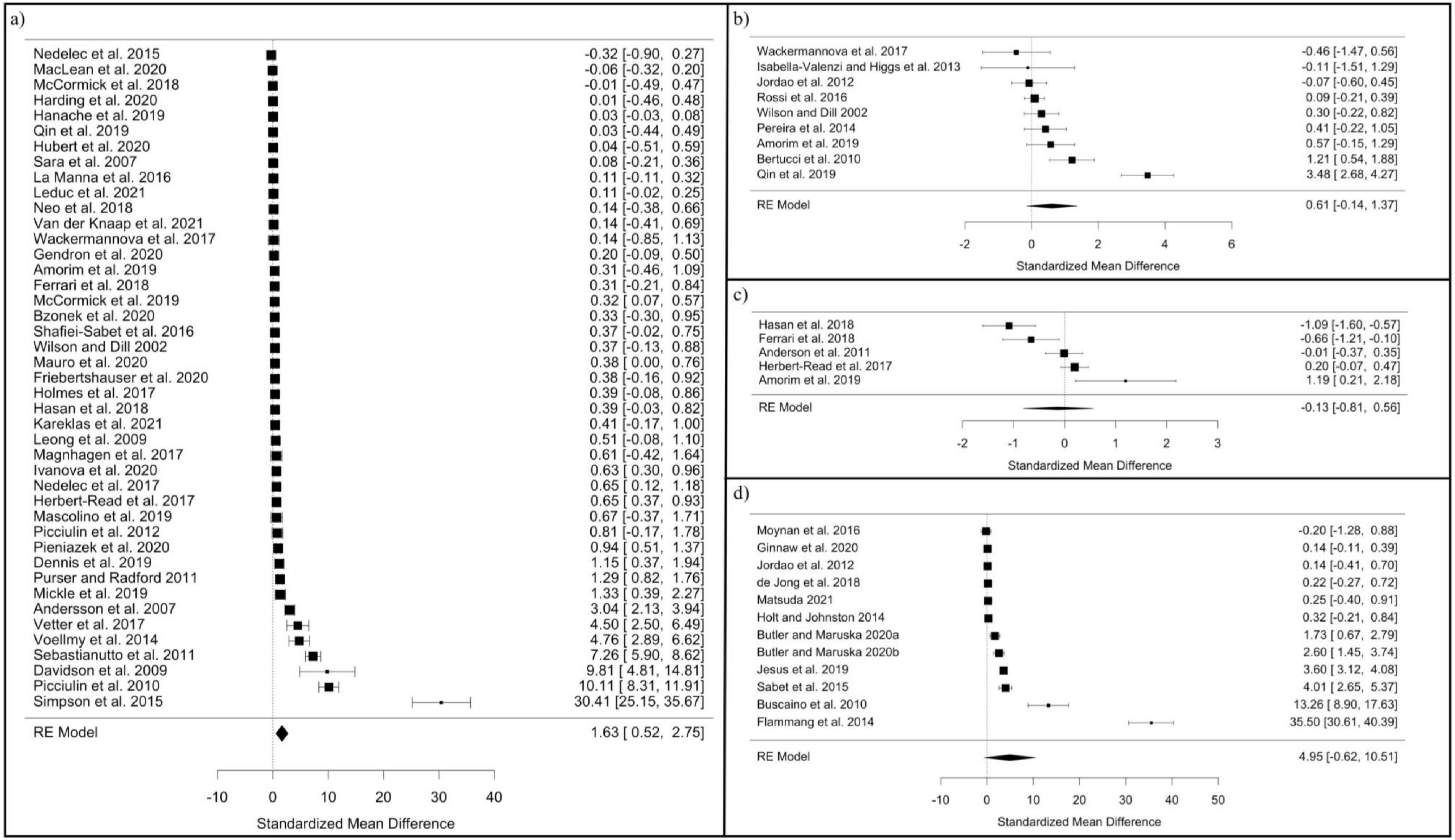

Figure 4. Forest plots illustrating how various aquatic noises increase or decrease the behavioral responses of fish. The studies were divided into the following categories based on the sound source: (a) Anthropogenic Noise; (b) Biological Noise; (c) Environmental Noise; (d) Tones. Author(s) and year of publication are listed within each chart. On the right side of each chart is the Effect Size and its respective 95% confidence interval, represented in the graph by the squares (size = relative weight of each study) and the bars. The diamond at the base of each chart indicates the overall effect size and its confidence interval.

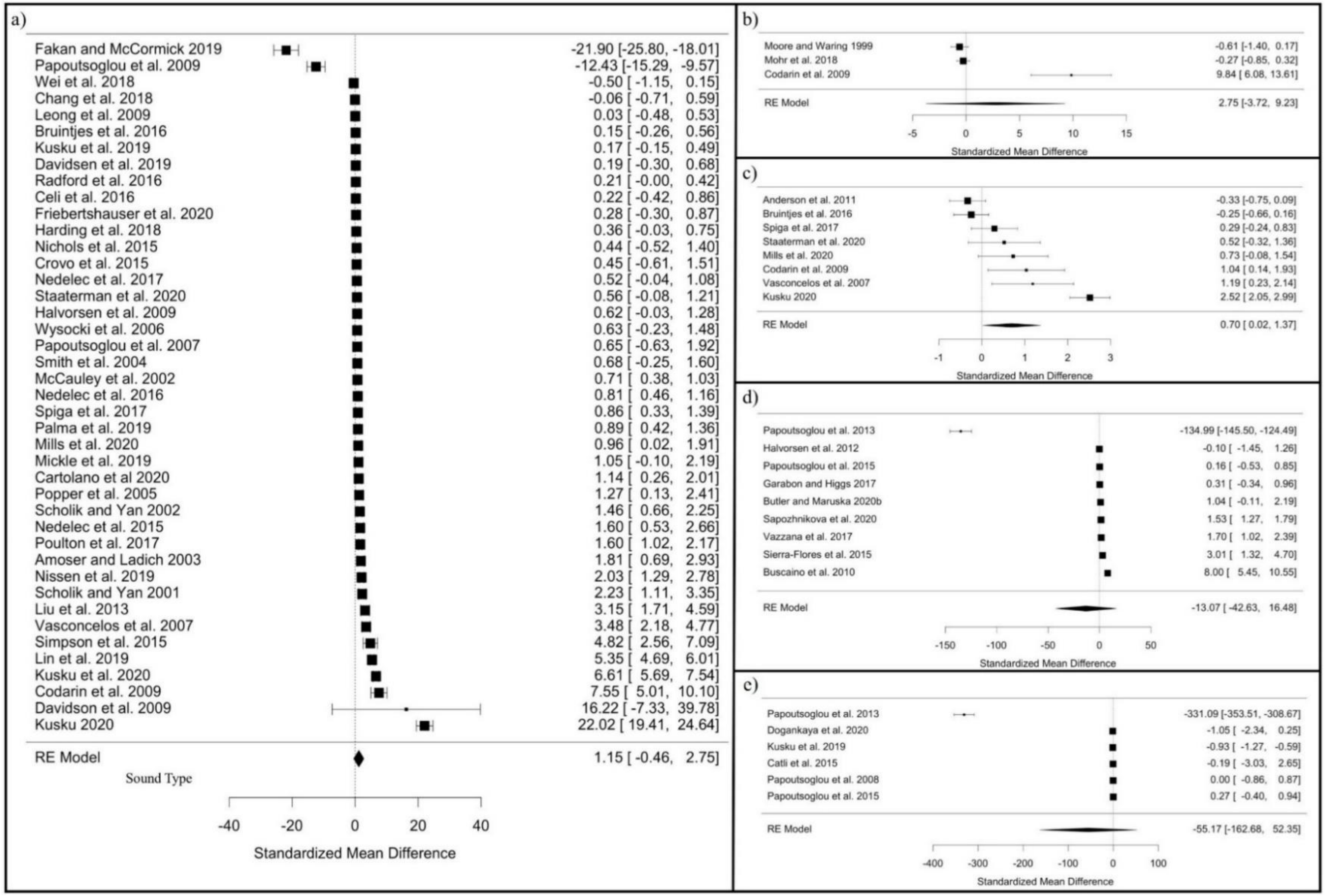

Figura 5. Forest plots illustrating how various aquatic noises increase or decrease the physiological responses of fish. The studies were divided into the following categories based on the sound source: (a) Anthropogenic Noise; (b) Biological Noise; (c) Environmental Noise; (d) Tones. Author(s) and year of publication are listed within each chart. On the right side of each chart is the Effect Size and its respective 95% confidence interval, represented in the graph by the squares (size = relative weight of each study) and the bars. The diamond at the base of each chart indicates the overall effect size and its confidence interval.

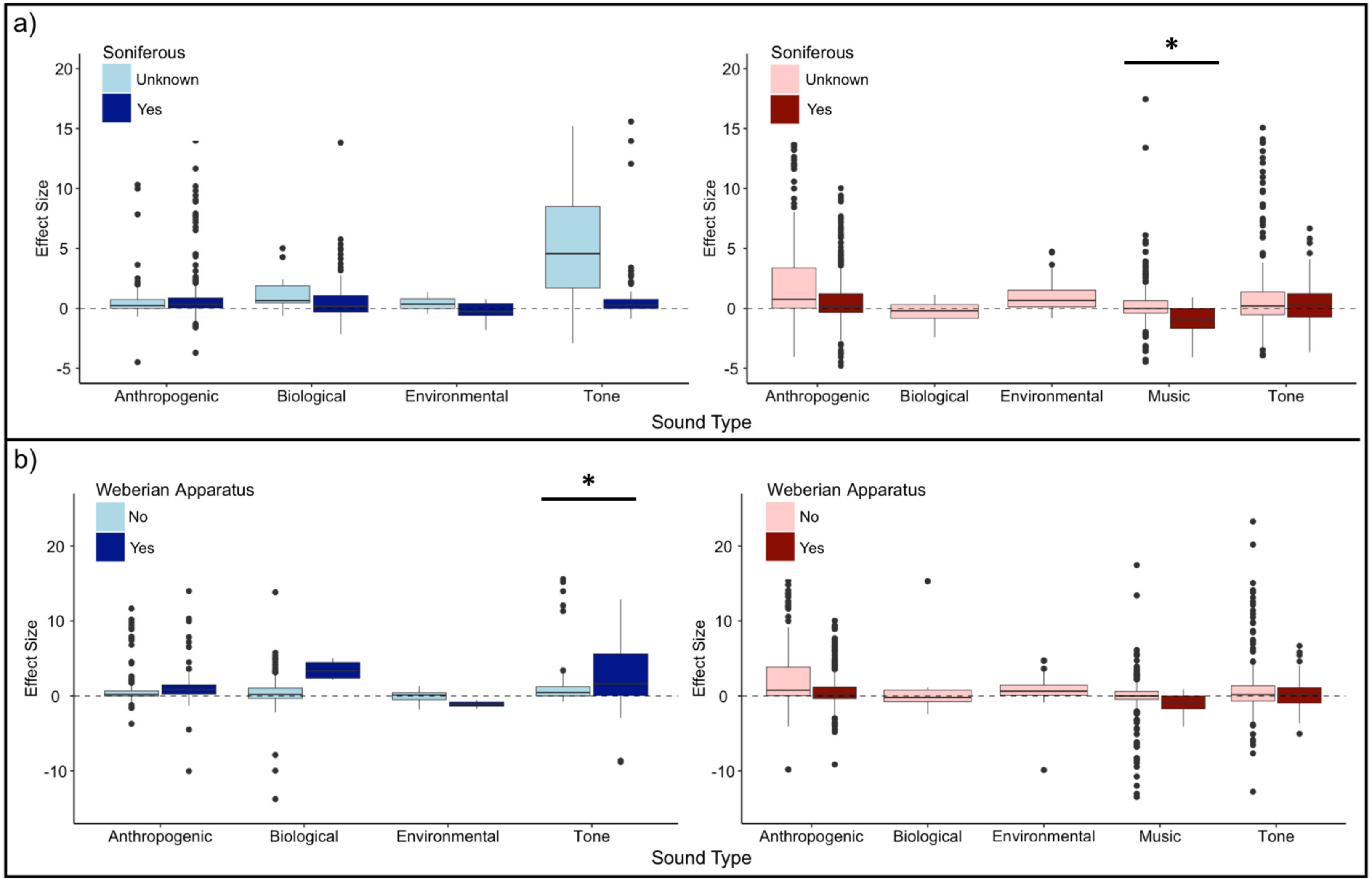

Figure 6. Effect sizes of sound source on behavioral (left, blue) and physiological (right, red) responses as a function of the ability to produce and perceive sounds. Production: (a) Fish with documented (dark color) and fish with unknown sound production (light color); Perception: (b) Fish with Weberian apparatus (dark color) and fish without this structure (light color). The center lines of the boxes represent the median, the upper and lower edges of the box represent the quartiles of 75 and 25%, respectively, the lines represent the maximum and minimum values except for the outliers, which are represented as points. The bars and asterisk indicate statistically significant difference at the level of 0.05 in the Tukey post-hoc test.

DISCUSSION

We found 107 peer-reviewed studies from 27 countries in the literature focusing the impacts of noise on the behavior and physiology of freshwater and saltwater fish. As we expected, anthropogenic and biological noises increase behavioral and physiological response variables, while the Music decreases physiological responses. Interestingly, the tones increase only the behavioral variables and decrease the physiological variables, while the environmental noises had the opposite effect. We also found that the effects on physiological variables can be explained by the ability to produce sounds, but only in relation to Music; and the effects on behavioral variables can be explained by the presence of Weberian apparatus, but only in relation to Tones.

The behavioral ecology of fish is considered a hot topic in the literature. There has been an increase in the prevalence of behavioral studies in recent decades, but there are still important gaps to be filled, especially in association with other ecological (Luiz et al., 2019). Our research supports this trend, showing that the number of research on the effects of sounds on fish behavior and physiology has been progressing annually, although they focus mainly on countries such as the United States, Canada, Italy, the United Kingdom and Australia. In general, the evaluations of anthropogenic impacts on fish follow this geographical pattern, showing the scarcity of studies in neotropical regions (Bessa et al., 2017). In this sense, the need to carry out studies that consider the wide variety of fish and the different sound sources under different conditions is evident (Popper & Hawkins, 2019), since each species respond differently and provide specific results.

Our meta-analysis identified that the families with most behavioral and physiological data in response to sounds are Sparidae, Cyprinidae and Clupeidae. These families have highly commercial fish, as much for human consumption as for sport fishing and aquarism, such as seabreams, carps, and sardines. In fact, fish perform important ecosystem services to humans (FAO, 2020; Pelicice et al., 2022 in prep.), therefore, studies seeking to understand how anthropogenic impacts alter the inherent characteristics of these animals are needed. But in addition, we believe and emphasize that usefulness to humans should not be the only motivation, since fish participate in essential ecological processes, such as food chain control, nutrient cycling and ecosystem engineering (Villéger et al., 2017). Here, we also identified that 70% of the studied genera are known to be soniferous (Looby et al., 2022). The active sounds production is a prevalent behavioral activity in fish, but still requires validations, since some methodologies used present flaws and uncertainties, which are often not clearly presented in the studies (Looby et al., 2022). Regarding the presence of Weberian apparatus, only 29% of the studied genera present this specialized structure. A relatively low number, since ostariophysian fish represent about 68% of the world's freshwater ichthyofauna (Nelson et al., 2016).

In general, anthropogenic noise has been shown to increase behavioral and physiological response variables. This increase is mainly linked to the agonistic behavioral parameters, foraging, swimming, predator avoidance, communication and reproduction; and also to metabolic, auditory physiological parameters, and stress indicators. The increase in behavioral responses has already been observed, for example, in defense and alarm reactions (Kareklas et al., 2021; Nedelec et al., 2017), in the number of successful and failed food catches (Purser & Radford, 2011; Voellmy et al., 2014), at swimming speed (Neo et al., 2018; Shafiei Sabet et al., 2016; Wilson & Dill, 2002), in erratic swimming (Andersson et al., 2007; Herbert-Read et al., 2017; Hubert et al., 2020; Mauro et al., 2020; Sarà et al., 2007), in the alarm reaction to predators (La Manna et al., 2016), in the vocalization rate (Picciulin et al., 2012) and in the number of visual courtship displays (Mascolino et al., 2019). When fish is exposed to disturbances, its first line of defense is the sudden change of behavior to prevent death and metabolic costs (Olla et al., 1980). If the disturbance does not stop or fish cannot escape, changes in behavior may interfere with how the animal feels and responds to the environment (Schreck et al., 1997), impairing the homeostatic balance. In this sense, many studies have also demonstrated that anthropogenic noise increases the stress levels of fish, for example, observed by the increase in substances such as cortisol, lactic acid and glucose (e.g., Lin et al., 2019) and ventilation rate (e.g., Kusku et al., 2020). These results are in accordance with those found by Cox et al. (2018), and together reinforce the warning that the advance of anthropogenic activities have serious consequences. The theory predicts that changes or interferences to the soundscape can cause significant reversible and irreversible damage to fish (Popper & Hawkins, 2019). There are a multitude of anthropogenic activities that cause noise pollution and interfere with marine life, among which stands out the increase in the maritime fleet (Kaplan & Solomon, 2016). Therefore, the current scenario and future forecasts reinforce the need for regulation and definition of safe noise thresholds, so that noise impacts do not become irreversible. They also demonstrate the urgency of solutions that attenuate the excessive noise produced by human actions.

Biological noise also caused increasing trends in behavioral and physiological variables. It has been observed that exposure to conspecific sounds can trigger an increase in the number of aggressive (Wackermannova et al., 2017), in avoidance (Pereira et al., 2014), in the vocal performance of males (Jordão et al., 2012), and in the attraction of reproductive females (Isabella-Valenzi & Higgs, 2013) . Physiologically, it has been verified that conspecific calls increase hormone and seminal fluid levels in males (Moore & Waring, 1999), and brain activity in females (Mohr et al., 2018). Heterospecific sounds have also been observed to increase swimming speed (Wilson & Dill, 2002) and brain activity (Mohr et al., 2018). These observations highlight that acoustic communication in fish is important for various social contexts (Ladich & Bass, 2011; Ladich & Fay, 2013), and that these sounds present great diversity and complexity (Parmentier et al., 2010), generated by distinct anatomical structures and with various spectral and duration characteristics (Ladich & Bass, 2011). However, only 34.2% of the data evaluated the impacts of biological noise on behavior, and only 0.8% on fish physiology. The scarcity of data makes it difficult to define a directionality, as already observed in previous studies(Cox et al., 2018; Ladich, 2019), supporting the existence of gaps in knowledge about the effects of intra- and interspecific biological sounds on fish behavior and physiology.

Environmental noise caused a decrease in behavioral variables and an increase in physiological variables. Although in recent years new studies have evaluated the effect of environmental noise on fish behavior, the volume of data is still low, which makes it difficult to determine a directionality trend. Furthermore, studies evaluating the effect of this noise source on fish physiology showed divergent results. For example, it has been observed that in environmental noise conditions fish became more stressed, presenting high cortisol levels, the kidneys were more affected by parasites, and the behavior presented high variability (Anderson et al., 2011). Another study observed that this noise source did not have an effect on the ventilation (Kusku, 2020) an indicator of stress (Barreto & Volpato, 2006). The environmental noise has already shown slight masking in the hearing of (Vasconcelos et al., 2007), but in another study there was no change in auditory (Codarin et al., 2009). We believe that these divergences arise from factors related to the type of environmental noise used, the study site and the methodologies used in the evaluations. This makes sense, taking into account the high diversity of sounds that comprise the soundscape (Farina, 2014), and also the duration of fish exposure to the acoustic stimulus, since habituation may occur, as observed for other sound sources (e.g., Nedelec et al., 2016). In general, the impacts of environmental noise are mostly negative and have already been documented for various animal groups, causing changes ranging from molecular level to community level (Kight & Swaddle, 2011). Thus, the behavioral and physiological effects of environmental noise on fish need to be investigated more extensively.

Our results show that tones increase behavioral response variables and decrease physiological response variables. The increase in behavioral variables was already expected, as observed for alarm responses and swimming speed (Shafiei Sabet et al., 2015), for deterrence and repulsion (Flammang et al., 2014; Jesus et al., 2019; Matsuda, 2021) and shoal movement disorder (Ginnaw et al., 2020). The tones have also shown an increase in spectral levels of acoustic (Holt & Johnston, 2014), in latency to start fights in territorial males (Butler & Maruska, 2020a), and in motility, also increasing physiological parameters of stress (Buscaino et al., 2010). The tones are widely used as non-physical barriers (e.g., Jesus et al., 2019) and in aquaculture (e.g., Flammang et al., 2014), as a way to prevent fish from escaping. On the one hand, these sound barriers protect fish from being killed by turbines and force schools to follow a safe course in the river, but we believe that it is still necessary to verify the long-term consequences for these migratory species. We also observed that behavioral activities are intensified by tones in fish with Weberian apparatus. This result agrees with that found for cyprinid fish (ostariophysians), which in contrast to salmonid fish, exhibited a strong reaction of repulsion to the synoidal tonal sound (Jesus et al., 2019). In cyprinids, the tonal noises caused greater changes in foraging (Shafiei Sabet et al., 2016), indicating interferences in predator-prey relationships and swimming behavior (Matsuda, 2021; Shafiei Sabet et al., 2016), signaling a greater avoidance reaction. This pattern was also found in the previous meta-analysis, where the tones increased foraging, swimming movement and predation, although Cox et al. (2018) have not evaluated the differences between ostariophysian and non-ostariophysian fish. The theory predicts that fish from the Ostariophysi Superorder are more sensitive to sounds due to the presence of Weberian apparatus, which amplifies the sound signal (Diogo, 2009) however, it is important to remember that the Weberian aparatus is not the only auditory adaptation of fish (Platt & Popper, 1981; Schulz-Mirbach et al., 2013). Therefore, our results suggest the importance of considering the specialized auditory abilities on evaluations of the tonal noise, since this sound source has been shown to affect more intensely the fish with Weberian apparatus. On the other hand, the decrease in the physiological variables we observed can be explained by the strong influence of a single study (Papoutsoglou et al., 2013), in which the group of fish exposed to the tones showed a decrease in growth and brain activity. Thus, we believe that the general effect of tones on fish physiology needs to be further investigated.

The result found for the directionality of physiological variables in exposure to music was not conclusive. Few studies have evaluated the effect of music on physiological parameters, and the directionality was strongly influenced by a single study (Papoutsoglou et al., 2013). Nevertheless, we found an indicative trend that soniferous fish respond differently to music, showing that the ability to produce sounds explains the effects of this source on physiological responses, compared to fish with unknown sound production. A study with *Cyprinus carpio*, a sound-producing species (see Box S1), identified that music positively influenced physiological parameters of growth performance and feeding efficiency (Kusku et al., 2019). This pattern has also been observed for juveniles of the species *Oncorhynchus mykiss*, which exposed to music exhibited accelerated growth (Papoutsoglou et al., 2013). The study of Catli et al. (2015) also noted this pattern, but the authors point out that the effects may be different depending on the speed of the music played. As mentioned earlier, active sound production in fish still needs tests in different contexts, and with diverse ages and sexes (Looby et al., 2022), although this type of study may be complex, irresolute and ineffective(Looby et al., 2022). First of all, it is important to understand how the evolution of acoustic signals occurred in fish, combining continuous metrics and advanced phylogenetic comparative (Odom et al., 2021). Therefore, it is still too early to generalize the effects of music on behavior and physiology, but there are already promising results in the literature that suggest positive effects, and pave the way for new explorations and applications in aquaculture.

The auditory specializations of fish and their sound production capacity influence the impacts caused by noise. We expected that soniferous fish and fish with Weberian devices would be more sensitive to all sound sources. However, these differences were only observed in exposure to tones and music. This is an important observation, suggesting, for example, that extreme anthropogenic noise can affect fish regardless of their specializations. Therefore, we recommend that the analyses of sound impacts on fish take into account this bidirectional interaction. With this it will be possible to make more robust comparations to improve our understanding of which species are most vulnerable to noise pollution. We emphasize that, as far as we know, this is the first global quantitative analysis that considers the ability to produce and perceive sounds as determinant in the effect size of noise on fish.

One of the limitations in meta-analyses is how to deal with the wide variety of methodologies used in the studies. During the literature search it is also common to find imbalance in sample sizes and insufficient data, which ends up generating the exclusion of potential studies. Nevertheless, these divergences become very informative, since with them it is possible to draw gaps to be filled, such as studies that explore the effects of biological sounds, environmental sounds and music. Another limitation refers to the categorization of active sound-production in fish. Although soniferous fish are documented in all aquatic environments and in almost all regions of the world, about 96% of fish species lack published experiments (Looby et al., 2022), thus, it becomes difficult to categorize a species as a non-sound producer, being more common that this production is not known and making our results in this category (unknown sound production) little informative. Future studies should consider this information discrepancy, and thus better categorize sound production in fish. Moreover, the directionality of the behavioral and physiological variables found in our investigation does not answer whether the effects of noise are positive or negative for fish, so the inclusion of these factors in the analyses is still necessary.

Studies on the effects of noise on fish are important to support, guide and encourage protective actions that ensure the conservation and welfare of fish. First, we hope that these data will serve as a warning to the need to reduce noisy anthropogenic practices. A good alternative is the limitation of anthropogenic activities in areas essential to fish life history, such as breeding and feeding sites. In addition, it is necessary to set sound thresholds in areas close to fundamental environments for the conservation of aquatic animals. A major problem today is the exagerated oil exploration, which uses extremely noisy equipment, causing impacts on various taxa (Hawkins & Popper, 2014; Kunc et al., 2016; Mickle & Higgs, 2018; Popper & Hawkins, 2019). The reproduction of natural sounds has become a promising tool in conservation and recovery of degraded aquatic environments. This strategy was used in degraded coral reefs on lizard island, where acoustic enrichment increased the development of the fish community in all major trophic guilds (Gordon et al., 2019). Using music in aquaculture can also be a good alternative to boost fish growth and decrease confinement stress. Therefore, we suggest limiting noise pollution, especially in important areas for fish, and exploring sounds with positive effects to recover fish populations or increase their welfare.

The different sound sources have varied effects on fish, with anthropogenic and biological noises increasing behavioral and physiological responses, while music decreases physiological reactions. There are still many gaps in the details of these relationships, such as the tonal noises in physiological responses, and in general, the effects of exposure to environmental noise and music. However, it was evident, at least in part of our results, that species with Weberian apparatus and soniferous fish are more sensitive to noise. These results are relevant for fish conservation, which should be protected against harmful noise especially in reproductive and feeding areas. They can also be applied to the well-being of production species. With the increase in anthropogenic impacts on the soundscape, detailing the impacts of noise on fish brings important contributions to the conservation of this important group, especially related to the bidirectionality of production and/or accurate sound perception.

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Table S1. Location, study type and Number of data points for the articles selected and extracted in this meta-analysis (n = 107)

(Continua)

Authors	Location	Behavioral	Physiological	#data points
Amorim et al. (2019)	France	X		19
Amoser & Ladich (2003)	Austria		X	122
Anderson et al. (2011)	USA	X	X	37
Andersson et al. (2007)	Sweden	X		12
Bertucci et al. (2010)	France	X		2
Bruintjes et al. (2016)	UK		X	12
Buscaino et al. (2010)	Italy	X	X	8
Butler & Maruska (2020b)	Tanzania	X	X	22
Butler & Maruska (2020a)	Tanzania	X		3
Bzonek et al. (2020)	Canada	X		8
Cartolano et al. (2020)	USA		X	2
Catli et al. (2015)	Turkey		X	30
Celi et al. (2016)	Italy		X	20
Chang et al. (2018)	Taiwan		X	30
Codarin et al. (2009)	Italy		X	35
Crovo et al. (2015)	USA		X	1
Davidsen et al. (2019)	Norway		X	4
Davidson et al. (2009)	USA	X	X	6
de Jong et al. (2018)	Portugal	X		15
Dennis et al. (2019)	USA	X		21
Doğankaya et al. (2020)	Turkey		X	27
Fakan & McCormick (2019)	Australia		X	22
Ferrari et al. (2018)	Australia	X		12
Flammang et al. (2014)	USA	X		12
Friebertshauser et al. (2020)	USA	X	X	30
Garabon & Higgs (2017)	Canada		X	12
Gendron et al. (2020)	Canada	X		9
Ginnaw et al. (2020)	UK	X		14
Halvorsen et al. (2009)	USA		X	20
Halvorsen et al. (2012)	USA		X	36
Hanache et al. (2019)	France	X		2
Harding et al. (2020)	Australia	X		4
Harding et al. (2018)	Malawi		X	4
Hasan et al. (2018)	Canada	X		8
Herbert-Read et al. (2017)	UK	X		20
Holmes et al. (2017)	Australia	X		15
Holt & Johnston (2014)	USA	X		16
Hubert et al. (2020)	Netherlands	X		4
Isabella-Valenzi & Higgs (2013)	Canada	X		19
Ivanova et al. (2020)	Canada	X		7
Jesus et al. (2019)	Portugal	X		24
Jordão et al. (2012)	Portugal	X		12
Kareklas et al. (2021)	Northern Ireland	X		4
Kusku et al. (2019)	Turkey		X	20

Table S1. Location, study type of and number of data points for the articles selected and extracted in this meta-analysis (n = 107).

(Continua)

Authors	Location	Behavioral	Physiological	#data points
Kusku (2020)	Turkey		X	50
Kusku et al. (2020)	Turkey		X	32
La Manna et al. (2016)	Italy	X		18
Leduc et al. (2021)	Brazil	X		9
Leong et al. (2009)	Portugal	X	X	3
Lin et al. (2019)	China		X	36
Liu et al. (2013)	China		X	30
Maclean et al. (2020)	Canada	X		6
Magnhagen et al. (2017)	Sweden	X		60
Mascolino et al. (2019)	Italy	X		3
Matsuda (2021)	Japan	X		10
Mauro et al. (2020)	Spain	X		68
McCauley et al. (2003)	Australia		X	2
McCormick et al. (2018)	Australia	X		16
McCormick et al. (2019)	Australia	X		24
Mickle et al. (2019)	Canada	X	X	20
Mills et al. (2020)	French Polynesia		X	16
Mohr et al. (2018)	USA		X	10
Moore & Waring (1999)	UK		X	4
Moynan et al. (2016)	USA	X		6
Nedelec et al. (2015)	Scotland	X	X	18
Nedelec et al. (2016)	French Polynesia		X	4
Nedelec et al. (2017)	Australia	X	X	8
Neo et al. (2018)	Netherlands	X		8
Nichols et al. (2015)	USA		X	3
Nissen et al. (2019)	USA		X	48
Palma et al. (2019)	Portugal		X	12
Papoutsoglou et al. (2007)	Greece		X	300
Papoutsoglou et al. (2008)	Greece		X	416
Papoutsoglou et al. (2010)	Greece		X	199
Papoutsoglou et al. (2013)	Greece		X	117
Papoutsoglou et al. (2015)	Greece		X	324
Pereira et al. (2014)	Portugal	X		5
Picciulin et al. (2010)	Italy	X		6
Picciulin et al. (2012)	Italy	X		12
Pieniazek et al. (2020)	Canada	X		8
Popper et al. (2005)	Canada		X	37
Poulton et al. (2017)	UK		X	2
Purser & Radford (2011)	UK	X		10
Qin et al. (2019)	China	X		12
Radford et al. (2016)	France		X	20
Rossi et al. (2016)	Australia	X		2
Sapozhnikova et al. (2020)	Russia		X	15
Sarà et al. (2007)	Italy	X		48
Scholik & Yan (2001)	USA		X	40
Scholik & Yan (2002)	USA		X	40

Table S1. Location, Type of study and Number of data points for the articles selected and extracted in this meta-analysis (n = 107).

(Conclusão)

Authors	Location	Behavioral	Physiological	#data points
Sebastianutto et al. (2011)	Italy	X		5
Shafiei Sabet et al. (2016)	Netherlands	X		12
Shafiei Sabet et al. (2015)	Netherlands	X		24
Sierra-Flores et al. (2015)	Scotland		X	23
Simpson et al. (2015)	UK	X	X	5
Smith et al. (2004)	USA		X	4
Spiga et al. (2017)	UK		X	9
Staaterman et al. (2020)	Panama		X	12
van der Knaap et al. (2021)	Belgium	X		2
Vasconcelos et al. (2007)	Australia		X	14
Vazzana et al. (2017)	Italy		X	8
Vetter et al. (2017)	USA	X		3
Voellmy et al. (2014)	UK	X		9
Wackermannova et al. (2017)	Portugal	X		8
Wei et al. (2018)	China		X	24
Wilson & Dill (2002)	Canada	X		378
Wysocki et al. (2006)	Austria		X	6

Table S2. Summary of the two-way ANOVAs results separated by study type (behavioral or physiological) and by the variables of sound production and presence of Weberian apparatus.

a) Behaviour Soniferous

	Df	Sum Sq	Mean Sq	F value	Pr (>F)
Sound Source	3	2278	759	34.88	**2.00E-16**
Actively Soniferous	1	11	11	0.53	0.47
Sound Source*Soniferous Status	3	42	14	0.65	0.58
Residuals	1086	23647	22		

b) Physiology Soniferous

	Df	Sum Sq	Mean Sq	F value	Pr (>F)
Sound Source	4	562895	140724	6.71	**2.30E-05**
Actively Soniferous	1	1566428	1566428	74.66	**2.00E-16**
Sound Source*Soniferous Status	3	3059803	1019934	48.61	**2.00E-16**
Residuals	2342	49136623	20981		

c) Behaviour Weberian apparatus

	Df	Sum Sq	Mean Sq	F value	Pr (>F)
Sound Source	3	2278	759	35.71	**< 2e-16**
Weberian apparatus	1	40	40	1.9	0.17
Sound Source*Weberian apparatus	3	563	188	8.82	**8.90E-06**
Residuals	1086	23098	21		

d) Physiology Weberian apparatus

	Df	Sum Sq	Mean Sq	F value	Pr (>F)
Sound Source	4	562895	140724	6.14	**6.50E-05**
Weberian apparatus	1	1256	1256	0.05	0.81
Sound Source*Weberian apparatus	2	65779	32890	1.44	0.24
Residuals	2343	53695818	22918		

Table S3. Synthesis of the post-hoc results of the TukeyHSD (Tukey Honest Significant Differences) test, which evaluated the diferences between sound production and presence of Weberian apparatus variables in relation to sound type. Results are separated by study type, behavioral or physyiological.

a) Behaviour Soniferous

	Observed Means Difference	Lower Interval	Upper Interval	Adjusted P-Value
Anthropogenic: Yes-Unknown	0.422	-0.936	1.78	0.982
Biological: Yes-Unknown	-1.028	-4.452	2.396	0.985
Environmental: Yes-Unknown	-0.59	-5.479	4.3	1
Tone: Yes-Unknown	0.674	-1.928	3.276	0.994

b) Physiology Soniferous

Anthropogenic: Yes-Unknown	0.8105	-32.9	34.56	1
Music: Yes-Unknown	-210.1512	-255.4	-164.89	**0**
Tone: Yes-Unknown	-34.7439	-87.6	18.13	0.541

c) Behaviour Weberian apparatus

Anthropogenic: Yes-No	0.543	-0.9132	1.999	0.95
Biological: Yes-No	3.201	-3.8397	10.242	0.866
Environmental: Yes-No	-1.091	-11.252	9.069	1
Tone: Yes-No	-3.983	-6.3989	-1.567	**0**

c) Physiology Weberian apparatus

Anthropogenic: Yes-No	-5.081	-35.1	24.92	1
Music: Yes-No	35.669	-40.5	111.82	0.899
Tone: Yes-No	19.26	-73	111.5	1

Box S1. Information on the sound production (Soniferous) and presence of Weberian apparatus in the fish genus included in this metanalysis (n = 67)

Genus	Soniferous	Weberian apparatus	Genus	Soniferous	Weberian apparatus
Acanthopagrus	Unknown	No	*Hypophthalmichthys*	Unknown	Yes
Ameiurus	Yes	Yes	*Ictalurus*	Yes	Yes
Amphiprion	Yes	No	*Larimichthys*	Yes	No
Anguilla	Yes	No	*Lepomis*	Yes	No
Argyrosomus	Yes	No	*Luciobarbus*	Unknown	Yes
Astatotilapia	Yes	No	*Metriaclima*	Unknown	No
Betta	Yes	No	*Micropterus*	Yes	No
Boreogadus	Yes	No	*Myxocyprinus*	Unknown	Yes
Campostoma	Unknown	Yes	*Neogobius*	Yes	No
Carassius	Yes	Yes	*Nibea*	Yes	No
Chanos	Unknown	Yes	*Oncorhynchus*	Yes	No
Chromis	Yes	No	*Opsanus*	Yes	No
Clupea	Yes	No	*Oreochromis*	Yes	No
Coregonus	Yes	No	*Pagrus*	Unknown	No
Couesius	Unknown	Yes	*Perca*	Yes	No
Cynotilapia	Yes	No	*Phoxinus*	Unknown	Yes
Cyprinella	Yes	Yes	*Pimelodus*	Yes	Yes
Cyprinus	Yes	Yes	*Pimephales*	Yes	Yes
Danio	Unknown	Yes	*Pomacentrus*	Yes	No
Dascyllus	Yes	No	*Pomatoschistus*	Yes	No
Dicentrarchus	Unknown	No	*Porichthys*	Yes	No
Esox	Yes	No	*Pseudochondrostoma*	Unknown	Yes
Etheostoma	Yes	No	*Pseudochromis*	Unknown	No
Gadus	Yes	No	*Pseudopleuronectes*	Unknown	No
Gasterosteus	Yes	No	*Rutilus*	Yes	Yes
Gobio	Yes	Yes	*Salmo*	Yes	No
Gobius	Yes	No	*Sander*	Yes	No
Gobiusculus	Yes	No	*Schizopygopsis*	Unknown	Yes
Halichoeres	Yes	No	*Sciaena*	Yes	No
Halobatrachus	Yes	No	*Scophthalmus*	Yes	No
Haplochromis	Yes	No	*Sparus*	Unknown	No
Heterostichus	Unknown	No	*Stegastes*	Yes	No
Hippocampus	Yes	No	*Thunnus*	Yes	No

Box S2. Description of the behavioral and physiological parameters evaluated by the studies included in this metanalysis, with their respective examples.

Study Type	Sound Source	Parameter	Specific Examples
Behaviour	Anthropogenic	Agonistic Behaviour, Communication, Foraging Behaviour, Predator Avoidance, Reproduction, Stress Response, Swimming Behaviour	Food-handling error, discrimination error, unsuccessful strikes, feeding time, darting behaviors, prey speed and distance, startle rate, startle responses, distance between conspecifics, swimming speed
	Biological	Agonistic Behaviour, Communication, Feeding, Swimming Behaviour	Aggressive behaviours, lateral displays, aggression level, calling and grunt rate, approach frequency, swimming depth and speed
	Environmental	Agonistic Behaviour, Foraging, Maintenance Behaviour, Swimming	Vocalizations, angular difference, nearest-neighbor, swimming speed, relative position, feeding rate
	Tone	Agonistic Behaviour, Communication, Foraging Behaviour, Reproduction, Swimming Behaviour	Territorial behavior, conflict, calling Rate, knock duration, drum number, pulses per call, discrimination error, handling error, avoidance behaviour, nearest-neighbor, swimming speed and depth, number of challenges
Physiology	Anthropogenic	Auditory, Circulatory, Immune and Endocrine Systems, Growth, Metabolism, Stress Responses	Hearing threshold, particle acceleration thresholds, cortisol concentration, food consumption, width-length ratio, liver lipids, immunoglobulin, tumor necrosis factor, heart rate, lactic acid, ventilation rate
	Biological	Auditory System, Plasma, Reproduction	Hearing threshold, testosterone, milt
	Environmental	Auditory, Immune, and Endocrine System, Growth, Body Condition, Metabolism, Reproduction, Stress	Food conversion rate, condition factor, hearing threshold, cortisol concentration
	Music	Circulatory and Nervous Systems, Growth, Metabolism	Blood condition factor, feed conversion ratio, organ health, serotonin, noradrenaline, dopamine
	Tone	Auditory, Circulatory, and Endocrine System, Growth, Metabolism, Stress	Hearing threshold, plasma protein, lactate, and cortisol concentration, mortality, condition factor, food conversion rate, growth rate, serotonin, noradrenaline, dopamine

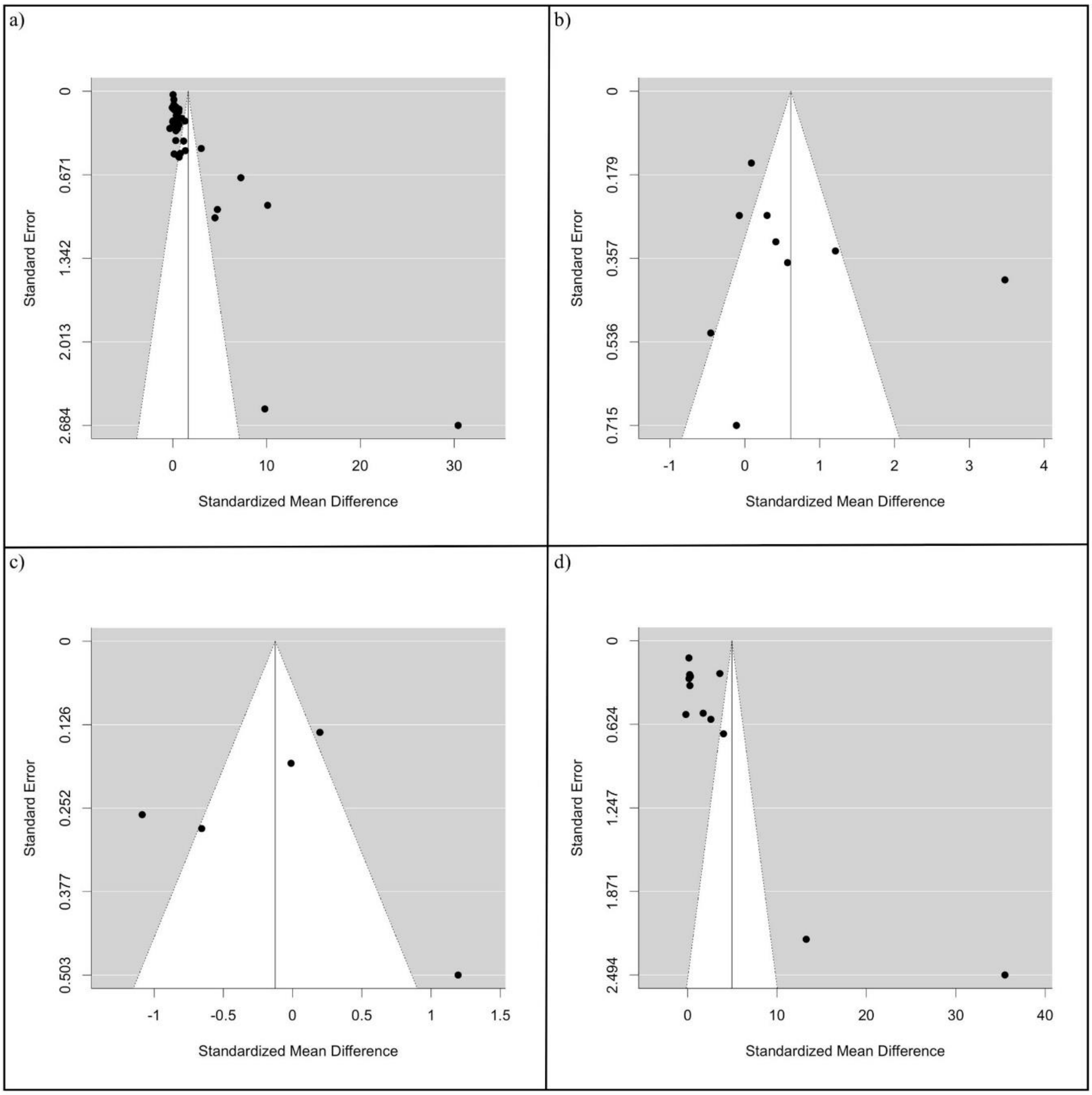

Figura S1. Funnel graph of the effect sizes of behavioral parameters in relation to the sound type. (a) Anthropogenic noise; (b) Biological sounds; (c) Environmental sounds; (d) Tones; (e) Music.

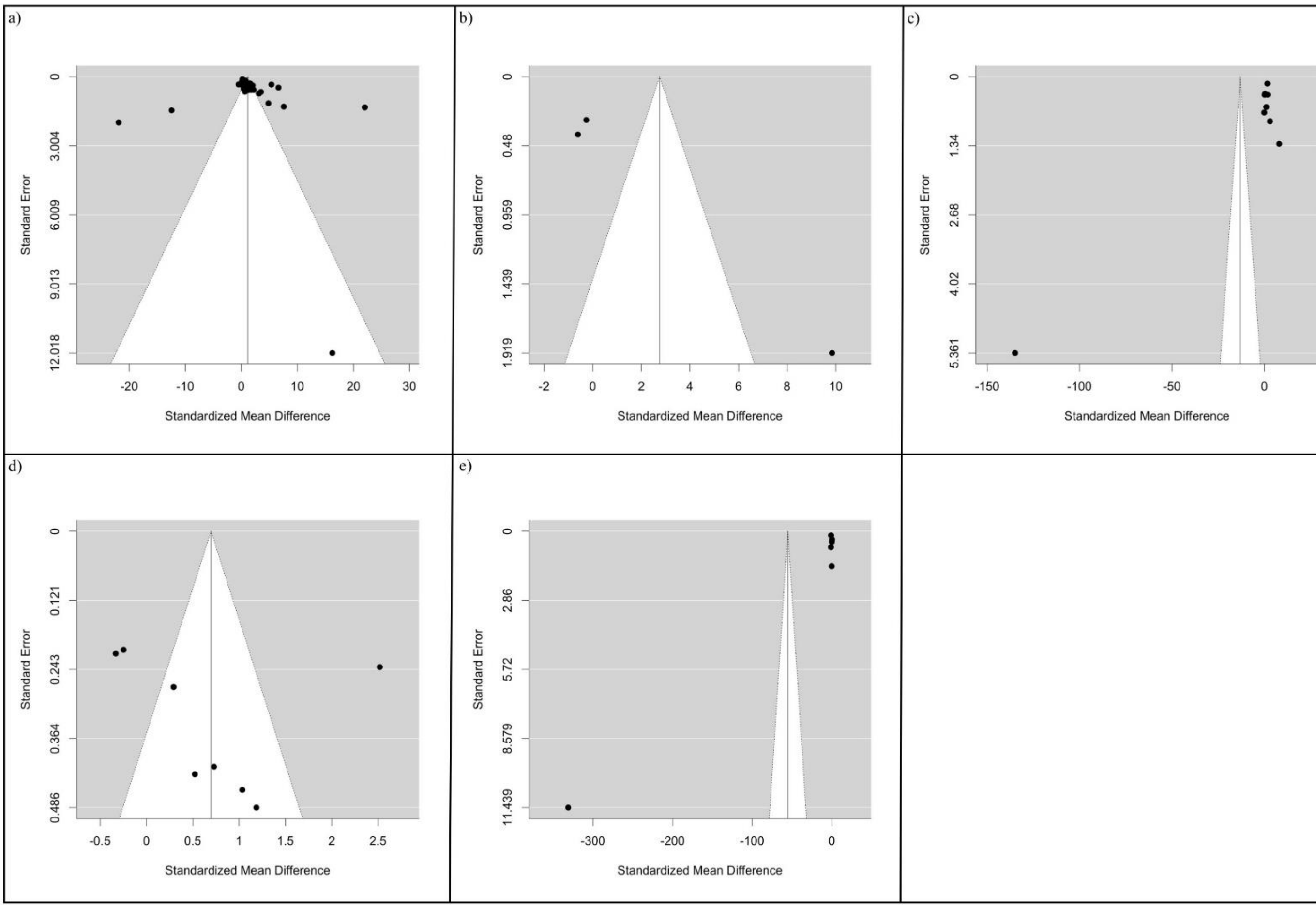

Figure S2. Funnel graph of the effect sizes of physiological parameters in relation to the sound type. (a) Anthropogenic noise; (b) Biological sounds; (c) Environmental sounds; (d) Tones; (e) Music.