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Informing acoustic deterrence through quantification of innate behavioural responses of fish to short-duration pure tones

by

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Thesis for the degree of Doctor of Philosophy

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Abstract

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Informing acoustic deterrence through quantification of innate behavioural responses of fish to short-duration pure tones

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This thesis aimed to inform acoustic deterrence through quantification of innate behavioural responses of fish to short-duration pure tones. To fulfil this aim, a set of objectives were developed, returning to first principles, to achieve optimum avoidance using startle responses as a proxy for deterrence: (1) determine the startle response threshold in goldfish to pure tone acoustic stimuli; (2) quantify innate responses of goldfish responding to a 120 ms pure tone acoustic stimulus in presence and absence of band-limited (100 – 2500 Hz) random noise; (3) utilise the temporal characteristics of fish sounds to inform acoustic deterrence and identify the optimal temporal sound characteristics to elicit an avoidance response. All experiments used goldfish – a species with well-understood hearing abilities. Prior to commencing experiments with fish, a methodological study was undertaken, which provided a unique set up in which a cylindrical tank was submerged in a large water body to produce a heterogeneous and replicable sound field for subsequent experiments. The first of the experiments identified the optimum frequency to elicit a startle response in individual goldfish as being different to the frequency of best hearing. The second found that adding background noise introduced stochastic resonance, whereby the noise acted as a primer for responses to a pure tone acoustic stimulus. The meta-analysis concluded that it was not possible to generalise the temporal characteristics, such as pulse period or pulse duration, that would be ideal for acoustic deterrents. Towards the end of the thesis, the ideal conditions for implementing acoustic deterrents successfully were discussed, as well as how the experimental findings can be built upon for future studies. This research may help alleviate the ecological impacts of river infrastructure and environmental stressors such as invasive species.

Key words: Acoustic deterrence, fish passage, behavioural guidance, particle motion, stochastic resonance, auditory evoked behavioural response

Dedication

In the name of Allah, the Most Gracious the Most Merciful

To my parents, husband, grandparents, and my wholly supportive friends and family. This could not have been done without your love, care, and guidance. And to Rufus.

In memory of Grandad Tom

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$p_{rms} = \frac{A}{\sqrt{2}}$ Equation 1 8

$SPL = 20\log_{10}\frac{p_{rms}}{p_0}$ Equation 2 8

$c = \sqrt{\frac{B}{\rho}}$ Equation 3 8

$Z = \frac{p}{u}$ Equation 4 9

$Z = \rho c$ Equation 5 9

$a = u \times 2\pi f$ Equation 6 13

$\xi = \frac{u}{2\pi f}$ Equation 7 13

$a = -\frac{\nabla P}{\rho}$ Equation 8 33

$SPL = 20\log_{10}\frac{p}{10^{-6}}$ Equation 9 40

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List of Accompanying Materials

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Research Thesis: Declaration of Authorship

Print name: Amelia Holgate

Title of thesis: Informing acoustic deterrence through quantification of innate behavioural responses of fish to short-duration pure tones

I declare that this thesis and the work presented in it are my own and has been generated by me as the result of my own original research.

I confirm that:

1. This work was done wholly or mainly while in candidature for a research degree at this University;
2. Where any part of this thesis has previously been submitted for a degree or any other qualification at this University or any other institution, this has been clearly stated;
3. Where I have consulted the published work of others, this is always clearly attributed;
4. Where I have quoted from the work of others, the source is always given. With the exception of such quotations, this thesis is entirely my own work;
5. I have acknowledged all main sources of help;
6. Where the thesis is based on work done by myself jointly with others, I have made clear exactly what was done by others and what I have contributed myself;
7. Parts of this work have been published as:-

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Definitions and Abbreviations

A.1 Species List

A.1.1 Fish Families

Acipenseridae Sturgeons

Anguillidae Freshwater eels

Ariidae Sea catfishes

Balistidae Triggerfish

Batrachoididae Toadfishes

Blenniidae Combtooth blennies

Callichthyidae Armoured catfishes

Carcharhinidae Requiem sharks

Carangidae Jacks and pompanos

Carapidae Pearlfishes

Centrarchidae Sunfishes

Chaetodontidae Butterflyfishes

Cichlidae Cichlids

Clupeidae Herrings and sardines

Cottidae Sculpins

Cyprinidae Minnows and Carps

Cyprinodontidae Pupfishes

Doradidae Thorny catfishes

Escocidae Pikes

Gadidae Cods and haddocks

Gasterosteidae Sticklebacks

Glaucosomatidae Pearl perches

Gobiidae Gobies

Haemulidae Grunts

Holocentridae Soldierfishes and Squirrelfishes

Ictaluridae North American freshwater catfishes

Labridae Wrasses and parrotfishes

Lotidae Hakes and burbots

Mochokidae Squeakers

Mormyridae Elephantfishes

Moronidae Temperate basses

Mugilidae Mullets

Odontobutidae Freshwater sleepers

Ophidiidae Cusk eels

Osphronemidae Gouramies

Osteoglossidae Arowanas

Ostraciidae Boxfishes

Pempheridae Sweepers

Percidae Perches

Pimelodidae Long-whiskered catfishes

Plecoglossidae Ayu fish

Poeciliidae Poeciliids

Pomacentridae Damselfishes

Prochilodontidae Flannel-mouthed characins

Salmonidae Salmonids

Sciaenidae Drums or croakers or meagre

Serranidae Groupers

Serrasalmidae Piranhas and pacus

Syngnathidae Pipefishes

Terapontidae Grunters

Triglidae Searobins

Tripterygiidae Triplefin blennies

Zeidae Dories

A.1.2 Fish Species

Abudefduf abdominalis Green damselfish

Abramis bjoerkna Silver bream

Abramis brama common bream

Acanthodoras cataphractus Spiny catfish

Acipenser fulvescens Lake sturgeon

Agamyxis pectinifrons Whitebarred catfish

Alburnus alburnus Common bleak

Alosa aestivalis Blueback herring

Alosa fallax Twait shad

Alosa pseudoharengus Alewife

Alosa sapidissima American Shad

Amblydoras affinis Thorny catfish sp.

Amphichthys cryptocentrus Bocon toadfish

Amphiprion akallopisos Skunk clownfish

Amphiprion akindynos Barrier reef anemonefish

Amphiprion chrysopterus Orange-fin anemonefish

Amphiprion chrysogaster Mauritian anemonefish

Amphiprion clarkii Yellowtail clownfish

Amphiprion frenatus Tomato clownfish

Amphiprion latifasciatus Madagascar anemonefish

Amphiprion melanopus Fire clownfish

Amphiprion nigripes Maldive anemonefish

Amphiprion ocellaris Clown anemonefish

Amphiprion percula Orange clownfish

Amphiprion perideraion Pink anemonefish

Amphiprion polymnus Saddleback clownfish

Anguilla anguilla European eel

Anguilla rostrata American eel

Argyrosomus japonicus Japanese meagre

Argyrosomus regius Meagre

Ariopsis seemanni Tete sea catfish

Astatotilapia burtoni Cichlid sp.

Atractoscion nobilis White seabass

Balistes vetula Queen triggerfish

Bathygobius soporator Frillfin goby

Batrachoides gilberti Large-eye toadfish

Batrachomoeus trispinosus Three-spined toadfish

Bairdiella chrysoura American silver perch

Brienomyrus brachyistius Elephantfish sp.

Brycon orbignyanus Piracanjuba

Carassius auratus Goldfish

Carassius carassius Crucian carp

Carapus boraborensis Pinhead pearlfish

Carapus homei Pearlfish sp.

Carapus mourlani Star pearlfish

Carcharhinus plumbeus Sandbar shark

Chaetodon auriga Threadfin butterflyfish

Chaetodon kleinii Sunburst butterflyfish

Chaetodon multicinctus Pebbled butterflyfish

Chaetodon ornatissimus Ornate butterflyfish

Chaetodon unimaculatus Teardrop butterfly fish

Chelon labrosus Thicklip grey mullet

Chelon ramada Thinlip mullet

Chromis chromis Mediterranean damselfish

Chromis viridis Blue-green damselfish

Clupea harengus Atlantic herring

Codoma ornata Ornate shiner

Copadichromis conophorus Mchenga

Corydoras paleatus Peppered cory

Cottus bairdii Mottled sculpin

Cottus carolinae Banded sculpin

Cottus gobio Bullhead

Cottus paulus Pygmy sculpin

Cottus perifretum Chabot bullhead

Cottus rhenanus Rhineland Sculpin

Ctenopharyngodon idella Grass carp

Cynoscion guatucupa Stripped weakfish

Cynoscion nebulosus Spotted seatrout

Cynoscion othonopterus Gulf weakfish

Cynoscion regalis Weakfish

Cynoscion xanthulus Orangemouth weakfish

Cynotilapia afra Afra cichlid

Cyprinella galactura Whitetail shiner

Cyprinella venusta Blacktail shiner

Cyprinodon bifasciatus Cuatro Cienegas pupfish

Cyprinus carpio Common carp

Danio rerio Zebrafish

Dascyllus albisella Hawaiian dascyllus

Dascyllus aruanus Whitetail dascyllus

Dascyllus flavicaudus Yellowtail dascyllus

Dascyllus trimaculatus Threespot dascyllus

Dicentrarchus labrax European sea bass

Doryichthys deokhatoides Dwarf pipefish

Dorosoma cepedianum Gizzard shad

Epinephelus guttatus Red hind

Epinephelus marginatus Dusky grouper

Epinephelus morio Red grouper

Epinephelus striatus Nassau grouper

Etheostoma crossopterum Fringed darter

Etheostoma nigripinne Blackfin darter

Etheostoma oophylax Guardian darter

Eupomacentrus partitus Bicolour damselfish

Eutrigla gurnardus Grey gurnard

Esox Lucius Northern pike

Etroplus maculatus Orange chromide

Forcipiger flavissimus Yellow longnose butterflyfish

Forcipiger longirostris Longnose butterflyfish

Forsterygion lapillum Common triplefin

Gadus morhua Atlantic cod

Gaidropsarus mediterraneus Shore rockling

Gasterosteus aculeatus Three-Spined Stickleback

Genypterus chilensis Red cusk-eel

Genypterus maculatus Black cusk-eel

Glaucosoma buergeri Deepsea jewfish

Glaucosoma hebraicum Western Australia dhufish

Gnathonemus petersii Peter’s elephantnose fish

Gobio gobio Gudgeon

Gobius cobitis Giant goby

Gobius cruentatus Red-mouthed goby

Gobius niger Black goby

Gobius paganellus Rock goby

Gomphosus varius Bird wrasse

Haemulon flavolineatum French grunt

Halobatrachus didactylus Lusitanian toadfish

Hemichromis bimaculatus African jewelfish

Hemichromis guttatus Spotted jewelfish

Hemidoras morrisi Thorny catfish sp.

Hemitaurichthys polylepis Pyramid butterflyfish

Heniochus chrysostomus Threeband pennantfish

Herotilapia multispinosa Rainbow cichlid

Hippocampus comes Tiger tail seahorse

Hippocampus reidi Longsnout seahorse

Holocentrus rufus Longspine squirrelfish

Hypophthalmichthys nobilis Bighead carp

Hypophthalmichthys molitrix Silver carp

Ictalurus furcatus Blue catfish

Ictalurus punctatus Channel catfish

Ictiobus cyprinellus Bigmouth buffalo

Iheringichthys labrosus Long-whiskered catfish sp.

Johnius macrorhynus Big-snout croaker

Knipowitschia panizzae Adriatic dwarf goby

Knipowitschia punctatissima Italian spring goby

Labeotropheus fuelleborni Blue mbuna

Lampetra fluviatilis European river lamprey

Leiostomus xanthurus Spot croaker

Lepomis cyanellus Green sunfish

Lepomis humilis Orangespotted sunfish

Lepomis macrochirus Bluegill

Lepomis megalotis Longear sunfish

Lepomis microlophus Redear sunfish

Lepomis punctatus Spotted sunfish

Limanda limanda Common dab

Luciobarbus bocagei Iberian barbel

Macrodon atricauda Southern king weakfish

Macropodus opercularis Paradise fish

Marcusenius macrolepidotus Bulldog

Maylandia aurora Cichlid sp.

Maylandia callainos Cobalt zebra

Maylandia emmiltos Cichlid sp.

Maylandia fainzilberi Cichlid sp.

Maylandia zebra Zebra mbuna

Megalodoras uranoscopus Giant Raphael catfish

Melanogrammus aeglefinus Haddock

Melichthys piceus Black triggerfish

Menticirrhus saxatilis Northern kingfish

Merlangius merlangus Whiting

Micropogonias furnieri Whitemouth croaker

Micropogonias undulatus Atlantic croaker

Micropterus coosae Redeye bass

Micropterus henshalli Alabama Bass

Mycteroperca jordani Gulf grouper

Mycteroperca venenosa Yellowfin grouper

Myripristis kuntee Shoulderbar soldierfish

Myripristis violacea Lattice soldierfish

Neogobius melanostomus Round goby

Nenoniphon sammara Sammara squirrelfish

Notropis analostanus Satinfin shiner

Oncorhynchus kisutch Coho salmon

Oncorhynchus mykiss Rainbow trout

Oncorhynchus tshawytscha Chinook salmon

Ophidion rochei Roche's snake blenny

Opsanus tau Oyster toadfish

Opsanus beta Gulf toadfish

Oreochromis mossambicus Mozambique tilapia

Oreochromis niloticus Nile tilapia

Osmerus eperlanus European smelt

Osteoglossum bicirrhosum Silver arawana

Ostracion meleagris Whitespotted boxfish

Oxydoras niger Ripsaw catfish

Padogobius martensii Padanian goby

Parablennius parvicornis Rockpool blenny

Paratilapia polleni Poleni cichlid

Pelates quadrilineatus Fourlined terapon

Pempheris adspersa New Zealand bigeye

Pempheris oualensis Blackspot sweeper

Perca fluviatilis European perch

Perccottus glenii Chinese sleeper

Petrocephalus catostoma Churchill

Petrotilapia nigra Cichlid sp.

Piaractus mesopotamicus Small-scaled pacu

Pimelodus pictus Pictus catfish

Pimephales notatus Flathead minnow

Pimephales promelas fathead minnow

Plagioscion squamosissimus South American silver croaker

Platydoras armatulus Striped Raphael catfish

Platichthys flesus European Flounder

Platydoras hancockii Blue-eye catfish

Plecoglossus altivelis Ayu sweetfish

Poecilia mexicana Atlantic molly

Pogonias cromis Black drum

Pollachius pollachius Pollock

Pollimyrus adspersus Elephantfish sp.

Pollimyrus castelnaui Dwarf stonebasher

Pollimyrus isidori Elephantfish sp.

Pollimyrus Marianne Elephantfish sp.

Polyodon spathula American paddlefish

Pomatoschistus canestrinii Canestrini's Goby

Pomatoschistus marmoratus Marbled goby

Pomatoschistus microps Common goby

Pomatoschistus minutus Sand goby

Pomatoschistus pictus Painted goby

Porichthys notatus Plainfin midshipman

Premnas biaculeatus Spinecheek anemonefish

Prochilodus argenteus Flannel-mouthed characins sp.

Prochilodus costatus Flannel-mouthed characins sp.

Prochilodus lineatus Flannel-mouthed characins sp.

Pseudochondrostoma duriense **Northern straight-mouth nase**

Pseudorasbora parva Topmouth gudgeon

Pungitius pungitius Nine-spine stickleback

Pygocentrus nattereri Red-bellied piranha

Rhinecanthus aculeatus White-banded triggerfish

Rhinecanthus rectangulus Wedge-tail triggerfish

Rutilus rutilus Common roach

Salmo salar Atlantic salmon

Salmo trutta Brown trout

Salvelinus fontinalis Brook trout

Sander vitreus Walleye

Sanopus astrifer Whitespotted Toadfish

Sargocentron diadema Crown squirrelfish

Schizopygopsis younghusbandi tu-fish

Sciaena umbra Brown meagre

Sciaenops ocellatus Red drum

Sebastiscus marmoratus False kelpfish

Serrasalmus compressus Compressus Piranha

Serrasalmus eigenmanni Eigenmann's Piranha

Serrasalmus elongatus Slender piranha

Serrasalmus maculatus Maculatus piranha

Serrasalmus manueli Manuel's piranha

Serrasalmus marginatus Piranha sp.

Serrasalmus rhombeus Redeye piranha

Serrasalmus sanchezi Sanchez’s piranha

Serrasalmus spilopleura Speckled piranha

Solea Solea Common sole

Sprattus sprattus European sprat

Squalius cephalus Chub

Steatocranus tinanti Slender lion head cichlid

Stizostedion lucioperca Zander

Syngnathoides biaculeatus Alligator pipefish

Syngnathus fuscus Northern pipefish

Syngnathus louisianae Chain pipefish

Synodontis angelicus Angel squeaker

Synodontis decorus Clown squeaker

Synodontis eupterus Featherfin squeaker

Synodontis grandiops Upside-down catfish sp.

Synodontis marmorata Upside-down catfish sp.

Synodontis nigriventris Upside-down catfish sp.

Synodontis nigromaculatus Spotted squeaker

Synodontis schoutedeni Yellow marbled catfish

Terapon jarbua Grunter sp.

Thalassoma duperrey Saddle wrasse

Trachurus symmetricus Pacific jack mackerel

Trachurus trachurus Atlantic horse mackerel

Tramitichromis intermedius Cichlid sp.

Trisopterus luscus Pouting

Trichopsis pumila Pygmy gourami

Trichopsis schalleri Threestripe gourami

Trichopsis vittata Croaking gourami

Tropheus brichardi Cichlid sp.

Tropheus duboisi Cichlid sp.

Umbrina canosai Argentine croaker

Umbrina cirrosa Shi drum

Zeus faber John Dory

Zosterisessor ophiocephalus Grass goby

A.1.3 Other Species

Accipiter nisus Eurasian sparrow hawk

Malurus cyaneus Superb fairy-wren

Parus caeruleus Eurasian blue tit

Platycercus elegans Crimson rosella

Tursiops truncatus Bottlenose dolphin

A.2 General Terms

A priori	Knowledge considered to be true without being based on previous experience or observation
Anechoic	Free from echo
Bathydemersal	An organism living and feeding on the bottom of the water column below 200 m
Benthopelagic	Organisms living and feeding near the bottom as well as in midwaters or near the surface
Conspecific	Organisms belonging to the same species
Cortisol	A hormone produced in response to stress
Demersal	Bottom feeding organisms
Electrophysiological	Electrical properties of biological cells and tissues
Habituation	The long-term process whereby without adequate recovery time from exposure to a stimulus, or with a series of frequent exposures over time
Heterospecific	Organisms belonging to a different species
Near-field	The region immediately adjacent to the vibrating surface of a sound source
Impedance	The resistance to the propagation of sound waves through different mediums
Isotropic	A physical property which has the same value when measured in different directions
Lateral line/Neuromast	A sensory organ consisting of a visible line along the side of a fish which detect pressure and vibration.
Omnidirectional	Receiving or transmitting signals in all directions
Otolith	Three organs within the inner ear; the Saccule, Utricle, and Lagena, which contain structures known as otoliths that enable fish to detect particle acceleration
Otophysan	A superorder of fishes that possess a Weberian apparatus that improves their hearing capacities

Particle motion	The change in position of a particle with respect to time; in acoustics, particle motion is vibratory motion in which the particles move back and forth around a point. Usually, it is described as particle acceleration, velocity or displacement.
Pelagic	Organisms living in the open sea
Perilymphatic fluid	Extracellular fluid found in the inner ear
Sound pressure	The local pressure deviation from the ambient (average or equilibrium) atmospheric pressure, caused by a sound wave
Stochastic resonance	A phenomenon in which a signal that is normally too weak to be detected by a sensor, can be boosted by adding white noise to the signal
Swim bladder	An internal gas-filled organ that contributes to the buoyancy of many teleost fish, allowing them to control water depth. It also functions as a resonating air chamber in the production of or sensitivity to sound
Transducer	An electronic device that converts energy from one form to another
Weberian ossicles	An anatomical structure comprised of four pairs of bones that connect the swim bladder to the inner ear, allowing fish to detect acoustic pressure

A.3 Symbols

A	Amplitude (RMS) of a wave
a	Acceleration
B	Bulk modulus
c	Speed of sound
c'	Response criterion
cm	Centimetre
d'	Discriminability criterion
dB	Decibel
dB$_{\mathrm{ht}}$	Decibel (hearing threshold)
df	Degrees of freedom
f	Frequency
g	Gram
Hz	Hertz
k	Number of studies
kHz	Kilohertz
L	Litre
m	Metre
min	Minute
mm	Millimetre
ms	Millisecond
N	Number of individuals
n	Sample size
p	Acoustic pressure
p_0	Reference pressure of the medium of transmission
p_{atm}	Atmospheric pressure
p_{max}	Maximum acoustic pressure
p_{rms}	Root mean square pressure

PA_e	Experimental particle acceleration
PA_p	Predicted particle acceleration
ppm	Parts per million
S^2	Corrected sample variance
s^2	Sample variance
s	Second
T	Period
u	Acoustic flow velocity (particle velocity)
V	Volt
Z	Specific acoustic impedance
Z_H	Standard deviation unit of a hit
Z_{FA}	Standard deviation unit of a false alarm
Δp	Change in pressure
λ	Wavelength
µm	Micrometre
µPa	Micropascal
ξ	Displacement
π	Pi
ρ	Density
Σ	Sum
σ	Standard deviation
°	Degrees
℃	Degrees Celsius

A.4 Abbreviations

AC	Acoustic Cue
AEBR	Acoustically Evoked Behavioural Response
AEP	Auditory Evoked Potential
AIC	Akaike Information Criterion
CBS	Cranial Bone Stridulation
CDT-SIS	Centre for Doctoral Training – Sustainable Infrastructure Systems
CEE	Collaboration for Environmental Evidence
EIA	Environmental Impact Assessment
FM	Fin Movement
GLM	Generalised Linear Model
GLMM	Generalised Linear Mixed Model
ICER	International Centre for Ecohydraulics Research
IUCN	International Union for Conservation of Nature
JTS	Jaw or Teeth Stridulation
PA	Particle Acceleration
PD	Pulse Duration
PGM	Pectoral Girdle Muscle
PP	Pulse Period
PPS	Pulses Per Second
PTS	Permanent Threshold Shift
RMS	Root Mean Square
ROC	Receiver Operating Curve
NR	Not Recorded
SD	Sound Duration
SDT	Signal Detection Theory
SNR	Signal to Noise Ratio

SPL	Sound Pressure Level
SSM	Swimbladder Sonic Muscle
TTS	Temporary Threshold Shift
U	Unknown
UK	United Kingdom
USA	United States of America

Thesis Structure

This research project informed acoustic deterrence through quantification of innate behavioural responses of goldfish to short-duration pure tones. Each data chapter is related to a research objective identified to address the overall aim. Chapter 1 gives a broad perspective as to why this research is necessary, and the aims and objectives of the project. Chapter 2 consists of a literature review providing a detailed narrative considering the role of acoustics in freshwater ecosystems, the requirement for acoustic deterrents and their current challenges and shortcomings. The methods used throughout the experiments are outlined in Chapter 3.

Chapter 4 is a methodological study in which the acoustic field of experimental tanks were quantified to create the most reproducible setup. This setup was then used for the experimental work covered in Chapter 5 and Chapter 6. Each data chapter gives an introduction, methods specific to that study, results, and a discussion. These chapters cover three experiments in which the startle responses of goldfish were observed to acoustic pure tones. Chapter 5 identifies the most appropriate frequency for applying acoustic deterrence, whilst the two experiments in Chapter 6 quantified the responses of goldfish to pure tones in presence of band-limited random noise.

The final data chapter – Chapter 7 – consisted of a meta-analysis that reviewed fish sounds and whether the temporal characteristics of the calls can inform acoustic deterrence. Chapter 8 provides a discussion of the findings throughout all the data chapters and Chapter 9 summarises the research project, giving conclusions and future recommendations.

Chapter 1 Research Introduction

1.1 Introductory Statement

Anthropogenic stressors are transforming the global system. Land-system change, freshwater use, biogeochemical flows, amongst others, all contribute to the interactions between physical, chemical, and biological processes, the effects of which are likely to be exacerbated by feedbacks (Steffen *et al.*, 2015). Global change and anthropogenic stressors thus contribute to biodiversity loss and, inevitably, loss of ecosystem functions and services (Oliver *et al.,* 2015). This will, therefore, have detrimental impacts on the world's biota and will indirectly impact human health (Diaz *et al.,* 2006). For example, loss of ecosystem services affects food provision, construction materials and mental health (Diaz *et al.,* 2006). Anthropogenic stressors have been widely reported to affect human health (Ochoa-Hueso, 2017; Paseka *et al.,* 2019; amongst others), marine species and terrestrial species (Ávila *et al.,* 2018; Gamelon *et al.,* 2019; amongst others). However, freshwater species remain largely underrepresented within the current literature (Flitcroft *et al.,* 2019).

Populations of freshwater species have declined 83.0% since 1970 and efforts from the scientific community are essential in preventing further deterioration (WWF, 2018). For freshwater fish, this means conserving the 15,000 extant species (IUCN, 2019). Multiple approaches have been executed to reduce population decline at river infrastructure (e.g., inlet screens; Yorkshire Water, 2019). Of particular interest are behavioural deterrents that have been implemented to reduce fish mortality at places of harm (Maes *et al.,* 2004), or to control the dispersal of invasive species (Vetter *et al.,* 2017). For behavioural deterrents to be effective there must be a comprehensive understanding of how fish behave in response to a stimuli and what stimulus characteristics will elicit a desirable reaction.

This thesis will focus on informing acoustic deterrence through quantification of innate behavioural responses of fish to short-duration pure tones. Further, there will be focus on how alteration of background noise, as well as investigating how using fish sounds can help inform acoustic deterrents and ultimately increase the efficacy of the acoustic deterrent. Thus, undertaking research in this field will provide an insight into the fundamentals of fish behaviour whilst simultaneously benefitting applications in acoustic deterrent development.

1.2 Aims and Objectives

1.2.1 Vision

The requirement for a fully systematic approach in acoustic deterrent development should consider the frequency, Signal-to-Noise Ratio (SNR) and signal characteristics that will elicit a desired response based on the hearing abilities and behaviour of the target species. Therefore, it is essential to return to fundamentals in fish behaviour to understand what will constitute an effective acoustic deterrent. This research developed a set of methodology for goldfish (*Carassius auratus*), for whom there is currently no literature on use of acoustic deterrents.

1.2.2 Research Aim

To inform acoustic deterrence through quantification of innate behavioural responses of fish to short-duration pure tones.

1.2.3 Research Questions

Research Question 1

Which frequency (of a 120 ms pure tone) evokes an innate response in goldfish using the least acoustic energy?

Hypothesis: The frequency of greatest response is that of the most physiologically sensitive hearing level, as determined by the audiogram.

Research Question 2

What effect does noise have on the startle responses of goldfish to a 120 ms pure tone?

Hypothesis: The signal (pure tone) will be masked by the background noise, inhibiting the startle response of the goldfish.

Research Question 3

Do all fishes respond to a particular set of temporal sound characteristics (e.g., pulse rate, duration)?

Hypothesis: Fishes do not share similar temporal characteristics of the sounds they produce; however they may be similar according to context, sound production mechanism or the habitat in which they reside.

1.2.4 Research Objectives

Research Objective 1

Determine the startle response threshold in goldfish to pure tone acoustic stimuli.

Research Objective 2

To quantify innate responses of goldfish responding to a 120 ms pure tone acoustic stimulus in presence and absence of band-limited (100 – 2500 Hz) random noise.

Research Objective 3

Utilise the temporal characteristics of fish sounds to inform acoustic deterrence and identify the optimal temporal sound characteristics to elicit an avoidance response.

1.2.5 Summary

A summary of the PhD aims and objectives are provided below, outlining the experiments chosen to fulfil each of the objectives (Figure 1), as well as the predicted results and a summary of the methods (Table 1).

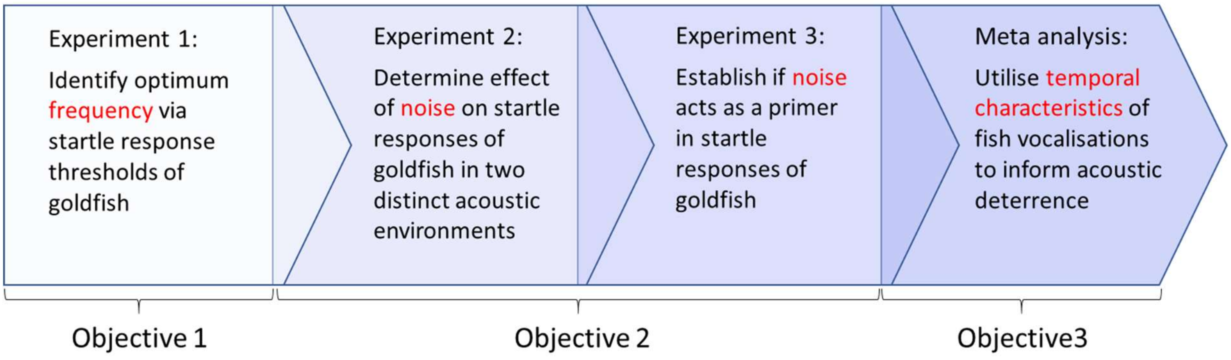


Figure 1 The experiments chosen to fulfil each of the PhD objectives. Objective 1 is covered in Chapter 5, whilst Objective 2 is the objective of Chapter 6 and Objective 3 can be found in Chapter 7.

Table 1 The overall issue, PhD aims and objectives with the corresponding data collection and summary of methods.

Issue	Aim	Objectives	Results	Methods
Acoustic deterrents are used to conserve native and control invasive fish populations	Informing acoustic deterrence through quantification of innate behavioural responses of fish to short-duration pure tones	Determine startle response thresholds of goldfish responding to 120 ms pure tone acoustic stimuli (Chapter 5)	• Startle responses compared across frequencies. • Startle response threshold. • Evaluation of the relationship between the startle threshold and hearing threshold.	A laboratory experiment presenting six different frequencies at four SPLs to individual goldfish.
		Evaluate startle responses of goldfish to 120 ms pure tone acoustic stimuli in distinct acoustic environments (Chapter 6)	• Compare startle responses across two acoustic environments. • Determine if individuals tolerate the stimulus.	Laboratory experiment presenting pure tones to individual goldfish: 1) In presence or absence of band-limited random noise.
			• Establish if noise acts as a masker or a primer for eliciting startle response.	2) In presence of different SPLs of band-limited random noise.
		Utilise temporal characteristics of fish sounds to inform acoustic deterrence (Chapter 7)	• Determine if the sounds produced are consistent under a variety of contexts, mechanisms and habitat-specific factors.	Meta-analysis of existing literature involving fish sound production.

1.3 Framing and Embedding

This iPhD project was conducted through the Centre for Doctoral Training – Sustainable Infrastructure Systems (CDT-SIS). The work aimed to address global infrastructure and sustainability issues by contributing to the advancement to acoustic deterrent technology. This technology is currently implemented at a variety of infrastructure, such as locks (UMRACP, 2018), power stations (Maes *et al.,* 2004) and water treatment works (Fish Guidance Systems Ltd., 2020). Development of this technology will result in lower capital costs in debris-filled waterways compared to physical screens that require regular maintenance (Piper *et al.,* 2019). Additionally, use of more sophisticated technology will prevent fish entrainment, which may lead to fines

(Castro, pers. comm., 2019). Therefore, the project aims to encourage and facilitate industry to develop its infrastructure sustainably.

The International Centre for Ecohydraulics Research (ICER) conducts research for a variety of themes: fish passage; hydropower; fish response to environmental stimuli; habitat modelling and restoration; amongst others. This research adds to the existing body of research investigating response to environmental stimuli. Currently, investigation in ICER is focused on response of fish to stimuli such as light, optic flows, sonic bubbles, electricity and acoustics.

Chapter 2 Literature Review

2.1 Acoustics

Sounds are generated by a mechanical disturbance in a compressible medium that propagates away from a source (Popper and Hawkins, 2018). The source moves, releasing kinetic energy into the medium, which forms a longitudinal wave (Popper and Hawkins, 2018). The particles associated with this wave move back and forth at the same location forming compressions and rarefactions where the particles are more densely and sparsely packed respectively (Figure 2). This is unlike a transverse wave where the particles move with the wave (Hansen, 1951). Thus, sound is characterised by both particle motion and sound pressure. Sound pressure refers to the increase and decrease in pressure from compression and rarefaction whereas particle motion describes the movement of the particles in the medium using the vector quantities acceleration, displacement, and velocity (Popper and Hawkins, 2018).

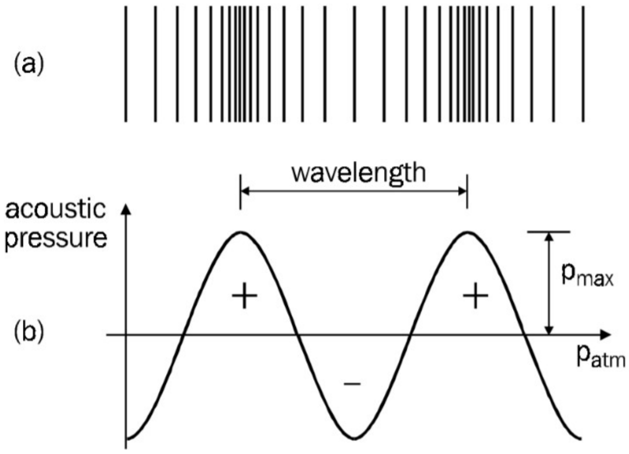


Figure 2 Representation of a sound wave showing a) compressions and rarefactions caused by a soundwave in air and b) pressure variations above and below atmospheric pressure (where p_{max} is maximum pressure and p_{atm} is atmospheric pressure) [Hansen, 1951].

Pure tone sound waves exhibit pressure fluctuations that repeat sinusoidally, known as harmonic motion (Fahy and Thompson, 2015). As a sound wave propagates, the amplitude of the wave relates to the amount of acoustic energy it carries. To quantify the magnitude of the pressure fluctuation, measurements may be taken of the peak-to-peak pressure amplitude, zero-to-peak amplitude, or Root Mean Square (RMS) amplitude in which the sound pressure is squared, averaged and then the square root is taken (Hansen, 1951). Most commonly, the RMS value is used to describe the amplitude of the sound pressure. The RMS pressure level, p_{rms} measured in Pascal, is commonly used to describe the amplitude, A, of a pure tone such that:

$$p_{rms} = \frac{A}{\sqrt{2}} \quad \text{Equation 1}$$

Additionally, the amplitude of the acoustic pressure variations is described logarithmically by the decibel (dB), typically using the RMS pressure amplitude, *p*, and reference pressure of the medium of transmission, p_0 (1 µPa in water). This is described as the Sound Pressure Level (SPL, dB):

$$SPL = 20\log_{10}\frac{p_{rms}}{p_0} \quad \text{Equation 2}$$

An in-depth explanation of decibels and decibel arithmetic can be found in Fahy and Thompson (2015).

Pure tone sound waves are also characterised by the wavelength (λ), the distance travelled by the wave in one oscillation; the frequency (f), the number of oscillations per second; the period (T), the time taken for one oscillation of the wave to pass a fixed point (Hansen, 1951). The frequency and period are related by $T = 1/f$ and the speed of sound (c), the frequency and the wavelength are related by $c = f\lambda$ (Hansen, 1951).

The ability of sound to travel through a particular medium is explained by how a longitudinal wave is able to transmit through it. The characteristics that determine the sound speed of linear longitudinal compressive waves, *c*, are the density, ρ, and the compressibility of the medium, described by the bulk modulus, *B* (Rolling and Vogt, 1960):

$$c = \sqrt{\frac{B}{\rho}} \quad \text{Equation 3}$$

As the medium becomes increasingly compressible (lower bulk modulus) and dense, the sound speed increases. Therefore, in air, the speed of propagation is ~344 m s^{-1}, whereas in water, a denser but lower compressibility (high bulk modulus) fluid, it is ~1480 m s^{-1} (Leighton, 1994). However, the speed of the acoustic wave in water is not constant and may be influenced by temperature, salinity, or hydrostatic pressure (Urick, 1983).

Simple harmonic motion will produce a single sinewave (a tone), however irregular motion, like that of complex waves, will produce a wave that combines multiple pure tones. These waves can also be analysed in the frequency domain, often by a fast Fourier transform that describes a sine wave by a single frequency, but a complex wave is described by multiple frequencies (see Hansen, 1951).

Propagation of acoustic waves varies depending on the proximity to the source and the conditions of the surrounding environment (Figure 3). In the near-field, the acoustic pressure and particle velocity are not in phase, whereas in the far-field, the two are in phase (Urick, 1983). If the conditions of the environment are such that the waves can propagate unrestricted, the field is described as the free field. However, a reverberant field exists if there is at least one reflection from a boundary. If a wave encounters a boundary, the energy may be reflected, absorbed or transmitted. At a hard surface, the absorption is far less than that of a rough surface, and the reflection is much higher. The contribution of the reflected sound to the total sound field increases with increasing reflected incident sound, and a continuation of sound will exist if the source is turned off, known as reverberation (Hansen, 1951).

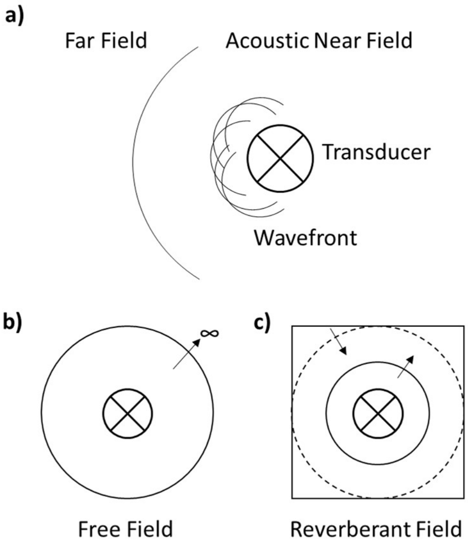


Figure 3 Representation of acoustic fields showing **a**) the near and far-field, **b**) the free field and **c**) the reverberant field.

Another phenomenon that may inhibit the propagation of sound is specific acoustic impedance. The specific acoustic impedance, *Z*, is a ratio of acoustic pressure to acoustic flow velocity, *u*, (Leighton, 1994):

$$Z = \frac{p}{u} \qquad \text{Equation 4}$$

The specific acoustic impedance also is related to the density of the medium, *ρ*, and the speed of sound in that medium, *c*, (Leighton, 1994):

$$Z = \rho c \qquad \text{Equation 5}$$

This has a real value if there is no absorption, taking a value of *ρc* for plane progressive waves, where *ρ* is the density of water and *c* is the speed of sound underwater (Leighton, 1994). Despite these special constraints on validity, when researchers convert from acoustic pressure to particle velocity, the relationship $\frac{p}{u} = \rho c$ is commonly used (Leighton, 1994).

Thus, specific acoustic impedance is a measure of how easily a sound wave can propagate through a given medium. Mediums with different specific acoustic impedances encounter impedance mismatch when a sound wave is transmitted from the first to the second medium (Berg, 2020). Consequently, some of the wave is transmitted and some of the wave is reflected. The greater the difference between the impedance of the two materials, the greater the reflection.

2.2 Shallow Water Acoustics

Shallow water systems consider depths of up to 10 acoustic wavelengths at a given frequency and often refer to coastal waters, estuaries, rivers, lakes and other smaller bodies of water (Lynch and Newhall, 2017). These systems often possess a diverse range of acoustic soundscapes, differing in SPL and spectral characteristics (Wysocki *et al.*, 2007a). The close top and bottom boundaries (i.e., the water surface and the substrate) act as scatterers that reflect incident sound and introduce surface and bottom reverberation. Shallow waters also exhibit a phenomenon called volume reverberation that originates from biota, bubbles, flow obstructions, and other scatterers in the water column (Hawkins and Myrberg, 1983; Lynch and Newhall, 2017). Such reverberation is difficult to predict since the position and characteristics of scatterers are usually unknown (Lynch and Newhall, 2017). Volume reverberation is generally stronger in shallow waters due to increased turbulence that introduces bubbles and suspended sediments (Lynch and Newhall, 2017).

Turbulence is common in shallow waters and contributes to the diverse acoustic environment by causing variation in the SPL via an increase in water velocity (Tonolla *et al.,* 2009). High water velocities increase both turbulence and bubble formation, which increases midrange frequency SPLs and a narrow band of low-frequency SPLs (Tonolla *et al.,* 2009). At low discharges, for example, riffles are dominated by middle frequencies (125 – 2000 Hz), whereas at high discharges they are dominated by low frequencies (<125 Hz) (Tonolla *et al.,* 2009). Conversely, pools contain slower flowing water and are much deeper, meaning low frequencies are likely to dominate. This is also observed in lakes, backwaters and ponds, which display main energies in the low frequencies (Wysocki *et al.,* 2007a). However, not all frequencies propagate freely within the water column. This is because the wavelength of the cut-off frequency is four times the depth of the water for a rigid bottom (Urick 1983). If the water is shallower, the sound cannot propagate as an acoustic wave and is rapidly attenuated (Fine and Lenhardt, 1983; Forrest *et al.,* 1993). Thus, low-frequency bands (<125 Hz) can travel some distance through the water column, however, midrange (125 – 2000 Hz) and high frequencies (>2 kHz) are attenuated over short distances (Tonolla *et al*., 2009).

The spatial and temporal uncertainty of noise sources in shallow water environments makes the determination of ambient noise difficult (Lynch and Newhall, 2017). Most commonly, ambient noise is categorised as shipping and industry, wind and waves, and biological noise (Urick, 1983). High levels of ambient noise in shallow waters may be both naturally occurring and anthropogenic. For example, in high energy rivers and during flooding, fishes may encounter SPLs of 150 – 160 dB re 1 µPa, such as in the Nyack floodplain of the Flathead River, United States of America (USA) (Tonolla *et al.,* 2011). SPLs at man-made structures such as hydropower dams have also been recorded above 180 dB for high frequency bands and 160 – 175 dB for low-frequency bands (Nestler *et al.,* 1992). Impacts of noise at river infrastructure, particularly in small rivers, are rarely investigated (Section 2.5.1) and increased noise levels in regions that were previously quiet may have significant ecological impacts.

Small boats such as jet skis produce broadband sounds overlaid with harmonic tones (100 – 1000 Hz) with source levels of 92 – 140 dB re 1 µPa (Erbe, 2013), whilst large craft such as ferries and container ships have source levels in excess of 200 dB re 1 µPa (Simard *et al.,* 2016; Gassmann *et al.,* 2017). Such large ships are rarely able to travel in freshwaters, although boat noises have been recorded at 153 dB re 1 µPa in the river Danube and in two Austrian Lakes (Wysocki and Ladich*,* 2005). Underwater noise from vessels may result in large sound differences between loud and quiet stretches, such as in the river Ganges which has differences of approximately 63 dB re 1 µPa (Dey *et al.,* 2019). Quiet stretches with less traffic, such as secluded lakes and backwaters in Austria have ambient noise levels in the 81 – 99 dB re 1 µPa (Wysocki *et al.,* 2007a).

Shallow waters are dominated by sound at a wide variety of frequencies. Despite this, noisy waters possess a band of frequencies in which there is very little sound at 125 – 250 Hz (Lugli *et al*., 2003; Lugli and Fine, 2007; Lumsdon *et al*., 2017). This region is present in many spectra such as in the river Serchio, Italy (Lugli and Fine, 2003), and Danube, Austria (Amoser and Ladich, 2005). This band is described as the 'quiet window' and is commonly used by biota for both conspecific and intraspecific communication (Lugli and Fine, 2003; Ladich and Schleinzer, 2015; Radford *et al.*, 2015). The width and energy of the window may differ between water bodies due to the characteristics of the substrate, flow velocity and depth (Wysocki *et al*., 2007a; Tonolla *et al*., 2009; Lynch and Newhall, 2017).

2.2.1 Tank Acoustics

Small tanks have complex soundscapes owing to their small size, the elasticity of the tank walls, and the large impedance differences between water and air at the tank boundaries (Rogers *et al.,* 2016). For example, a rectangular tank made from glass or acrylic has five hard surfaces (four sides and a bottom), as well as the water surface in close proximity to each other. In such circumstances, there is a large degree of scattering from all the boundaries. The tank characteristics, particularly the tank size, shape, and impedance difference, give rise to reverberation, in which the acoustic field cannot be regarded as homogeneous and may introduce misleading particle motion data when using point pressure measurements (Akamatsu *et al.,* 2002; Gray *et al.,* 2016).

To increase sound field inhomogeneity, an open body of water should be selected with a depth and width greater than the wavelength being considered (Akamatsu *et al.,* 2002). However, inhomogeneity may be avoided with corrections of the tank size and stimulus (see Akamatsu *et al.,* 2002; Okumura *et al.,* 2002). These corrections will minimise resonance effects that, in a closed boundary system, introduce standing waves (Akamatsu *et al.,* 2002). For example, the propagation of frequencies well below the resonant frequency (the frequency at which the tank vibrates) are similar and will prevent resonance effects. Thus, the use of frequencies below the resonance frequency is preferred (Okumura *et al.,* 2002). Nevertheless, most of the tanks used previously did not have these corrections and possessed inhomogeneous and irreproducible sound fields (Rogers *et al.,* 2016).

For species that live in the open water, the acoustics in tanks compared to the natural landscape are intrinsically different. For example, a behavioural study on sea bass (*Dicentrarchus labrax*) would not be suitable for a small tank, but should be conducted *in situ* (Debusschere *et al.,* 2014), in a pen (Hubert *et al.,* 2020), or in a large tank (Neo *et al.,* 2014). For species inhabiting noisy locations with lots of reverberation, such as shallow waters, there would be some similarities between the tank and the natural environment. However, *ex situ* studies are less reflective of the fish's natural environment and the true behaviour of the species (Slabbekoorn, 2016). Regardless, the use of tanks allows control of environmental factors, and the constraint of fish provides an accurate determination of their behaviour, which would be unfeasible in the field (Akamatsu *et al.,* 2002; Gray *et al.,* 2016).

In acoustic experiments, inhomogeneous sound fields mean the level received by a subject varies according to their position within the experimental arena. In the problem we consider, the received SPL and particle motion experienced by a fish would be subject to a high level of uncertainty. Additionally, the complex nature of the sound field makes it challenging to reproduce.

2.3 Measurement of Underwater Sound Fields in Small Tanks

A variety of instrumentation can be used to measure underwater sound fields, such as passive sonar arrays that are deployed in the ocean (Maranda, 2008). However, for small tank experiments, the use of much smaller scale instrumentation is more appropriate to measure sound pressure and particle motion. Sound pressure is usually mapped using a single hydrophone in several positions (Zeddies *et al.,* 2012; Zielinski and Sorenson, 2017; Currie *et al.,* 2019). This provides an accurate visualisation of the pressure field and facilitates observation of the variation of SPL within a tank that would not be obtained by just recording the source level. Mapping the sound pressure can identify factors such as an inhomogeneous sound field, which may affect the outcomes of behavioural studies. Additionally, illustrating this data in sound maps allows for the determination of the received SPL by a subject at any position in the tank. Due to the ease of measurement, sound pressure is more frequently measured than particle motion (Radford *et al*., 2012; Lepper *et al*., 2014).

Unlike sound pressure, particle motion provides information about the direction of the propagating wave and may be expressed as velocity, acceleration or displacement vectors (Nedelec *et al.,* 2016; Popper and Hawkins, 2018). Particle velocity, acceleration and displacement are related by:

$$a = u \times 2\pi f \qquad \text{Equation 6}$$

and

$$\xi = \frac{u}{2\pi f} \qquad \text{Equation 7}$$

where a = acceleration (m s^{-2}), u = particle velocity (m s^{-1}), $2\pi f$ = angular frequency (f = frequency in Hz) and ξ = displacement (m) (Nedelec *et al.,* 2016).

Common methods of measuring particle motion underwater are calculating the pressure gradient between two hydrophones, using velocity sensors, or using accelerometers (Martin *et al.,* 2016). Accelerometers are the most accurate for measuring frequencies in the hearing range of fishes but are expensive to obtain commercially (Nedelec *et al*., 2016; Popper *et al.,* 2019). Despite the range of equipment available for particle motion mapping, accuracy between methods is variable and the repeatability of measurements is low (Nedelec *et al.,* 2016; Anderson, 2013; Campbell *et al.,* 2019). Similarly, there are no internationally agreed standard units for particle motion measurements and, thus, comparing studies becomes difficult (Nedelec *et al.,* 2016).

When mapping particle motion, it is necessary to control hydrodynamic cues that influence the readings (Popper and Hawkins, 2018). Doing so would lead to values that are too high and that do not represent the true particle motion. Additionally, the hydrodynamic near-field may be the dominant source of particle motion at close range and low-frequency, since it is generated near the sound source and from the oscillations of the propagating waves (Rogers and Cox, 1988). This must be considered when mapping in close proximity to the transducer and must also be considered during experimental set-up, so it does not affect fish behaviour.

Particle acceleration (PA) may be most relevant for understanding fish behaviour since it is closest to the auditory system functioning in fish and is most relevant in stimulating the otolith (Enger, 1966; Popper *et al.,* 2019; Section 2.4). This poses biological relevance since fish communication occurs in the acoustic near field, where particle motion contains more energy than sound pressure (Lugli and Fine, 2007; Popper and Hawkins, 2018; Nedelec *et al.,* 2016). Studies may map a form of particle motion: particle velocity via calculation (Zeddies *et al.,* 2012; Currie *et al.,* 2020; 2021), PA via an accelerometer (Zeddies *et al.,* 2012; Zielinski and Sorensen, 2016, 2017) or particle displacement via four (Flores Martin *et al.,* 2021) or eight (Zeddies *et al.,* 2010a, b) hydrophones. Nevertheless, it is uncommon to map particle motion in fish behaviour studies (Popper *et al.,* 2019). Hence, there is a requirement to increase particle motion mapping in tank studies to further understand fish behaviour.

2.4 Fish Hearing

Hearing allows fish to obtain vital information about their surroundings, which may not be possible by other sensory means (Popper and Hawkins, 2019). For example, sound has advantages to taste and vision since it is multidirectional and is continuously available, and thus helps fish to understand the soundscape in a particular location. Sound production and detection assist with predator avoidance, prey location, which results in diverse inter and intraspecific behaviours (Slabbekoorn *et al.,* 2010).

There is considerable variation among the ear structures of teleost fishes, resulting in a diverse range of hearing capabilities, even amongst species in the same family (Popper and Coombs, 1982; Popper and Schilt, 2008). Nevertheless, unrelated fish with similar ear structures are likely to exhibit similar functional mechanisms (Popper *et al.,* 1982). Teleost fish have a bilateral pair of ears that are situated on either side of the cranium. The basic structure of the ear of teleost fish (Figure 4) has three dorsally located semi-circular canals and three fluid-filled otolith organs: the utricle, saccule and lagena (Popper *et al.,* 1988; Popper *et al.,* 2003). The otolith has a greater density than the rest of the fish and the surrounding water and, thus, moves at a different amplitude and phase, providing the fish with cues of the motion of its own body (Braun and Coombs, 2000; Popper and Hawkins, 2019). The inner ear, thus, provides the fish with information about posture and balance, and also facilitates hearing (Popper *et al.,* 2003).

The direct stimulation of the otolith organs via the movement of particles at a range of frequencies gives rise to hearing in fishes, which all fish are likely able to detect (Popper *et al.,* 2003; Radford *et al.,* 2012; Nedelec *et al.,* 2016). The otolith may also indirectly respond to sound pressure that is transformed into particle motion at gas-filled structures, such as the swim bladder (Popper and Fay, 1999). Fish that are most sensitive to sound pressure possess Weberian ossicles that facilitate sound transmission from the swim bladder to the inner ear (Ladich, 2000). The gas contained within the swim bladder fluctuates as a response to changing sound pressure, facilitating particle motion that is detected by the otolith (Fay, 1984; Popper *et al.,* 2014). Species such as otophysans (e.g., Tete sea catfish, *Ariopsis seemanni*; Lechner and Ladich, 2008 and zebrafish, *Danio rerio*; Bird *et al.,* 2020) possess Weberian ossicles that allow them to have increased hearing ability and sensitivity (Ladich, 2012). Other specialised mechanisms, such as gas-filled vesicles, also exist that allow some fish to have improved hearing of sound pressure. Gas-filled vesicles that are in direct contact with the auditory system, or with the perilymphatic fluid in the inner ear facilitate increased hearing abilities in 10 unrelated families (Tavolga, 1971; Popper *et al.*, 2003), such as mormyridae (e.g., *Brienomyrus brachyistius*; Yan and Curtsinger, 2000) and clupeidae (e.g., Atlantic herring, *Clupea harengus*; Mann *et al.,* 2001).

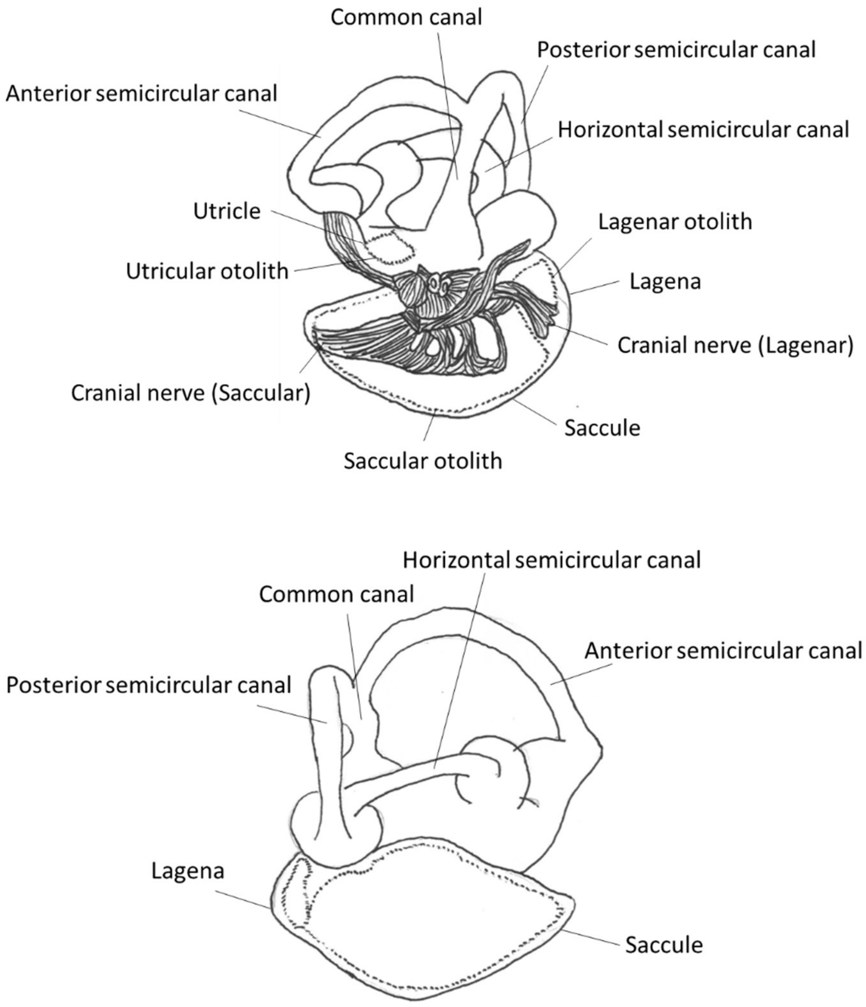


Figure 4 A drawing of the right ear of the arawana (*Osteoglossum bicirrhosum*), with medial (top) and lateral (bottom) view (see Popper, 1981).

The lateral line, like the otolith, also contributes to the hearing abilities of fish. The mechanism is instigated by pressure differences in the fluid in the lateral line pores, which produces acceleration of the fluid and stimulation of the lateral line hair cells (Braun and Coombs, 2000; Higgs and Radford, 2012). Both the otolith and the lateral line detect particle displacement, meaning differentiation between the contribution of the two to hearing is challenging since the inputs for auditory and lateral line nerves lie in close contact, meaning electrophysiological techniques to measure hearing are likely to detect both inputs (Coombs and Montgomery, 1999; Higgs *et al.,* 2006).

The lateral line and otolith may have functional overlap. In some studies, it is stated that the lateral line may only detect very near-field stimuli (Braun and Sand, 2013), whereas other cases found that there is a similar contribution of the inner ear and the lateral line to hearing (e.g., mottled sculpin, *Cottus bairdii*; Braun and Coombs, 2000). Similarly, some state that near-field hearing does not imply that the lateral line system must be involved, yet some highlight that electrophysiological recordings ignore the contribution of the lateral line to hearing, particularly under 400 Hz where the lateral line is most sensitive (Higgs and Radford, 2012).

2.4.1 Audiograms

An audiogram is a plot of the hearing threshold of an individual, which shows the minimum point of hearing for a set of frequencies. Audiograms have been obtained for numerous species of animals, including many species of fish. However, particle motion thresholds have also been derived for some species of fish (e.g., red drum, *Sciaenops ocellatus*; Horodysky *et al.,* 2008). For fish and other biota, numerous methods have been adopted to determine the hearing threshold, with all being advantageous in some way but often resulting in variation in hearing threshold due to methodological differences between the techniques (Radford *et al.,* 2012; Ladich and Fay, 2013).

One method is the Auditory Evoked Potential (AEP), which is an electrophysical measure of the function of the auditory pathway in response to sound stimuli (Ladich and Fay, 2013; Sliwinska-Kowalska, 2015). For fish, the AEP is performed by placing a recording electrode subdermally, a reference electrode in the dorsal midline and a ground electrode near the body of the fish (Mann *et al.,* 2007; Radford *et al.,* 2012). The AEP is quick, minimally invasive and has been used to obtain audiograms for over 100 fish species (Ladich and Fay, 2013). Alternatively, audiograms may be obtained behaviourally via methods involving training periods, such as instrumental avoidance conditioning (e.g., shock avoidance; Weiss, 1966), respiratory conditioning (e.g., restraining a fish and subjecting it to a conditioned stimulus and a shock pulse that inhibits respiration, and the conditioned response is anticipatory of the shock; Fay and MacKinnon, 1968) and positive reinforcement (e.g., training fish to associate a tone with receiving food; Yan and Popper, 1991), amongst others. Historically, some behavioural studies involved an in-air speaker (Fay, 1969) whilst some involved an underwater speaker (Offutt, 1968). Hence, those involving an in-air speaker would have experienced impedance at the air-water interface and obtained inaccurate hearing threshold readings. Different experimental conditions have led to discrepancies between thresholds, such as with the goldfish whose hearing thresholds obtained behaviourally vary up to 58 dB re 1 µPa (at 2000 Hz) (Enger, 1966; Offutt, 1968), however, it is impossible to determine which of the behavioural audiograms is more valid (Ladich and Fay, 2013).

Differences also exist between hearing thresholds obtained via AEP and behavioural techniques. A reason for this is the signal duration used in the study, which alters the detection threshold. AEP generally uses shorter tone bursts than behavioural studies, which means the detection thresholds in AEP studies are likely to be more sensitive those obtained behaviourally (Fay and Coombs, 1983; Ladich and Fay, 2013). Nevertheless, for the AEP technique a precise short tone burst is difficult to create at low frequencies, meaning at low frequencies the hearing threshold may be higher (Ladich and Fay, 2013). Even when replicating experiments, the acoustic field in small tanks may be heterogeneous (Section 2.2.1), which makes replication problematic (Akamatsu *et al.,* 2002). Thus, efforts should also be made to improve the sound field and replicability of experiments. Additionally, AEP recordings may detect inputs from both the auditory and lateral line nerves (Section 2.4), however, this is more pronounced at frequencies less than 400 Hz (Enger, 1967; Higgs and Radford, 2012).

An alternative behavioural method of determining the hearing threshold of fish is the Acoustically Evoked Behavioural Response (AEBR) (Zeddies and Fay, 2005; Alderks and Sisneros, 2013). The AEBR uses the startle response, or the Mauthner reflex, which is mediated by the Mauthner cells in teleost fish when evoked by acoustic or vibrational stimulation (Eaton *et al.,* 1977). Using the AEBR method, the hearing threshold is identified by determining the lowest SPLs over a range of frequencies at which a reaction (i.e., an avoidance response) is elicited. This technique has been applied to larval fish (Table 2) whose audiogram cannot be achieved by other methods. The AEBR is, thus, an overestimation of the absolute hearing threshold because the stimulus should be sufficiently loud enough to evoke a startle response, yet it is also a measure of behavioural avoidance and, thus, may be useful in other applications such as acoustic deterrence (i.e., it may be possible to use the behavioural response to a tone to work out the frequency of optimum avoidance when applied to an acoustic deterrence setting). This technique has not been undertaken for cypriniformes.

Table 2 A summary of the AEBR studies (NR – not recorded).

Reference	Species	Life Stage
Zeddies and Fay, 2005	• Zebrafish (*Danio rerio)*	larval
Alderks and Sisneros, 2013	• Plainfin midshipman (*Porichthys notatus)*	larval
Kastelein *et al.,* 2008	• Seabass (*Dicentrarchus labrax*) • Thicklip mullet (*Chelon labrosus*) • Pouting (*Trisopterus luscus*) • Atlantic cod (*Gadus morhua*) • Pollock (*Pollachius pollachius*) • Horse mackerel (*Trachurus trachurus*)	NR

To determine the particle motion audiogram rather than sound pressure, PA thresholds, which observe the minimum PA an individual can detect at certain frequencies, may be used. PA thresholds are most commonly measured, as opposed to particle displacement or velocity, since it is considered to be most similar to the auditory system functioning in fish and most relevant in stimulating the otolith (Enger, 1966; Popper *et al.,* 2019).

The PA threshold has been developed using a variety of techniques including pressure differences between two hydrophones (Holt and Johnston, 2010), accelerometers (Wysocki *et al.,* 2009; Radford *et al.,* 2012) and shaker tables (Radford *et al.,* 2012; Mooney *et al.,* 2010). The PA threshold may be similar for some species, but the SPL threshold may differ. For example, goldfish, triplefin (*Forsterygion lapillum*) and New Zealand bigeye (*Pempheris adspersa*) have similar PA thresholds but dissimilar sound pressure thresholds, reflective of their hearing specialisations, with goldfish being the most sensitive and triplefin the least (Radford *et al.,* 2012).

The instrumentation and methodology used to obtain PA thresholds create inconsistencies between studies (Radford *et al.,* 2012). For example, there was over a 40 dB re 1 µm s^{-2} difference between the accelerometer and the two hydrophone-derived thresholds for bigeye (Radford *et al.,* 2012). Nevertheless, the only comparative study is between New Zealand bigeye, triplefin and goldfish, so further research is required. For other tested species, only one PA threshold exists. Between the species tested, the PA thresholds vary between them (Figure 5). To determine whether PA thresholds are consistent for all species would involve repeating obtaining PA threshold data using shaker tables, which eliminate any sound pressure stimuli (Radford *et al.,* 2012). Despite this, the lower frequencies (~100 – 300 Hz) are often the most sensitive frequency among fishes responding to PA, whilst individuals are less sensitive to frequencies above ~400 Hz.

This may be due to the contribution of the lateral line, which has increased sensitivity at the lower frequencies (Holt and Johnston, 2010).

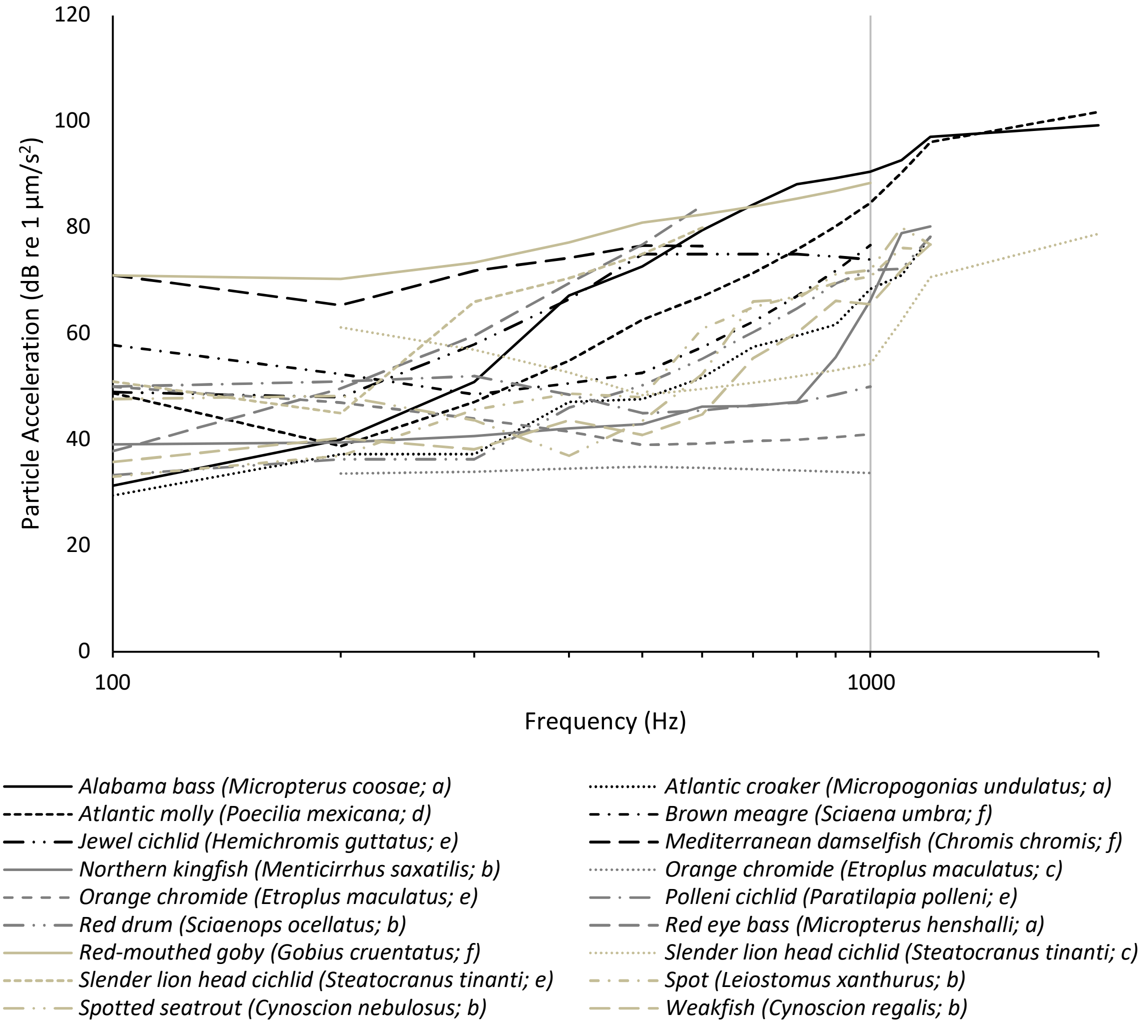


Figure 5 PA thresholds of 18 fish species. [References: a) Holt and Johnston, 2010; b) Horodysky *et al.,* 2008; c) Ladich and Schulz-Mirbach, 2013; d) Schulz-Mirbach *et al.,* 2010; e) Schulz-Mirbach *et al.,* 2012; f) Wysocki *et al.,* 2009.]

2.5 Acoustic Communication in Fishes

Acoustic stimuli have a significant role in information acquisition and communication amongst fishes, with all fishes having some form of hearing but not all producing vocalisations (Ladich, 2014; Putland *et al.,* 2018). A wealth of literature has identified that fish possess multi-sensory hearing and sound-generating organs that allow them to communicate in various contexts such as agonistic interactions, courtship and conspecific communication to manipulate school and shoal cohesion (Lugli and Fine, 2003; Ladich and Schleinzer, 2015*;* Radford *et al.*, 2015). Conversely, some predatory species are known to make use of sound from soniferous fishes for their own adaptive advantage. For example, the bottlenose dolphin's diet (*Tursiops truncates*) consists of up to 80% soniferous fishes (Burros and Myrberg, 1987).

Sonograms and oscillograms are used to characterise fish vocalisations across a wide frequency spectrum (Fine and Parmentier, 2015). This has allowed for the identification of a variety of sounds exhibited by fishes including grunts, pops, and drumming (Maruska and Mensinger, 2009; Tellechea *et al.,* 2011a; Radford *et al.,* 2012). These sounds are most commonly facilitated by intrinsic and extrinsic drumming muscles or stridulation (Fine and Parmentier, 2015). The intrinsic drumming muscles are attached to the swimbladder wall, which rapidly contract and vibrate the swimbladder itself, producing sounds (Smith, 1905; Ladich *et al.,* 2006). Intrinsic drumming muscles are often associated with the production of long-duration tonal notes, such as in the oyster toadfish (*Opsanus tau*; Fine *et al.,* 2009; Fine and Parmentier, 2015). Extrinsic muscles may originate in various locations, and thus a greater variety of sounds are observed (Ladich *et al.,* 2006). Some may attach directly (e.g., Mochokid catfish, *Synodontis nigromaculatus* and *S. nigriventris*; Ladich and Bass, 1996) or indirectly (e.g., Nile tilapia, *Oreochromis niloticus*; Longrie *et al.,* 2009) to the swim bladder and may produce a fast (e.g., red-bellied piranha, *Pygocentrus nattereri*; Millot *et al.,* 2011) or slow vibration (e.g., pearlfish, *Carapus boraborensis;* Parmentier *et al.,* 2008). The faster the muscles contract, the higher the frequency of sound that is produced. Stridulation is a result of friction of skeletal elements spine abduction or adduction (e.g., featherfin squeaker, *S. eupterus*; Parmentier *et al.,* 2010a) and grinding of teeth (e.g., French grunt, *Haemulon flavolineatum*; Bertucci *et al.,* 2014).

Some species such as the blackfin darter (*Etheostoma nigripinne*; Johnston and Johnson, 2000a) are able to produce multiple calls, which suggests some fish are able to discriminate between different frequencies, signals and signal sources (Ladich, 2014). Upon detection of a nearby predator, fish may be able to adapt acoustic signalling by reducing the number of signals, reducing sound levels or terminating calling (Ladich, 2019). For example, upon detection of the bottlenose dolphin, male silver perch *(Bairdiella chrysoura)* reduce the SPL of their call by 9 dB re 1 µPa (Luczkovich *et al.,* 2000), and gulf toadfish *(Opsanus beta)* also decrease their calling activity to reduce predation threats (Remage-Healey *et al.,* 2006). The sound preferences of fish may also determine their migratory pathways (Febrina *et al.,* 2015). For example, ayu *(Plecoglossus altivelis)* have been shown to avoid 100 Hz tones and show a preference for 200 Hz tones emitted at a fish ladder in the Sawanami River, Japan (Febrina *et al.,* 2015), meaning their movement trajectories can be modified by using acoustic cues.

There are a large variety of mechanisms and vocalisations amongst fishes, yet most are broadband sounds less than 500 Hz (Slabbekoorn *et al.*, 2010). The quiet window has ecological significance for fish communication since the frequency band coincides with the hearing and vocalisation range of a variety of species (Wysocki *et al.,* 2007a; Speares *et al.,* 2011; Ladich and Fay, 2013). Generally, fishes communicate over a short range so there is no requirement to use stimuli that are able to traverse over long distances, such as those above the cut-off frequency. Signalling below the cut-off frequency (the frequency that is four times the depth of the water for a rigid bottom) facilitates quick attenuation of the signal since the signal cannot propagate as an acoustic wave under these conditions (Urick, 1983; Forrest *et al.,* 1993). Additionally, these signals may be inhibited via masking in the presence of natural or anthropogenic masking noise.

2.5.1 Anthropogenic Noise, Stress Levels and Mitigation

Anthropogenic noise in freshwaters usually originates from shipping, road traffic, recreation, and the power industry (Risch and Parks, 2017). These noise sources lie within the frequency band 10 – 1000 Hz, which overlaps with the quiet window used for communication by fishes (Putland and Mensinger, 2020). Despite a recent focus on how anthropogenic noise affects marine biota, artificial noise in freshwater environments has been largely neglected (Gammel and O'Brien, 2013; Risch and Parks, 2017). The main impacts of noise on marine species are noise-dependent stress that may affect fitness (Holt and Johnston, 2015), masking that may lead to a reduction in detection distance for courting, and masking that may affect predator-prey relationships (Slabbekoorn *et al.,* 2010). Despite this, shallow freshwaters are naturally noisier than their marine equivalents. Notwithstanding, recent evidence suggests that road traffic noise masks the acoustic signals of blacktail shiner (*Cyprinella venusta*), a freshwater fish species (Holt and Johnston, 2015). Additionally, studies have shown evidence of recreational boat use altering fish behaviour (Amoser *et al.,* 2004), diamond exploration potentially masking vocalisations (Mann *et al.,* 2009), and shipping increasing production of the stress hormone, cortisol (Wysocki *et al*., 2006).

Measuring stress (measured behaviourally: swimming at the surface, erratic swimming behaviour; physiologically: increased cortisol levels) amongst fish due to acoustic stimuli is difficult to quantify (Hastings and Popper, 2005). Stressful behaviours are characterised as those including gasping at the surface, locking of fins to the side of the fish, and erratic swimming behaviour such as swimming continuously in circles or swimming into the sides of the tank (Vowles, pers. comm., 2020). Smith *et al.* (2004a) exposed goldfish to 10 min of white noise (0.1 – 10.0 kHz, at 170 dB re 1 µPa) and recorded that cortisol levels were significantly higher than the control period after 10 min of continuous exposure, however after 60 min continuous exposure, the cortisol levels were lower. Similarly, Wysocki *et al.* (2006) played 153 dB re 1 µPa of underwater ship recordings continuously for 30 min to three species: the common carp (*Cyprinus carpio;* a fish possessing

Weberian ossicles) and the gudgeon (*Gobio gobio;* a fish possessing Weberian ossicles), the European perch (*Perca fluviatilis;* a fish without Weberian ossicles but likely to detect particle motion). The three species listed represent individuals across the continuum of fish hearing ability (Fay and Popper, 2012). Wysocki *et al.* (2006) also played white noise to the three species at 156 dB re 1 µPa but no increase in cortisol was observed when the fish were exposed to continuous noise.

Anthropogenic noise and other acoustic stimuli may lead to temporary hearing loss in fishes. This may arise in individuals exposed to low levels of sound for a long period, or shorter exposure to high levels of sound, referred to as Temporary Threshold Shift (TTS; Lonsbury-Martin *et al.,* 1987). The effects and recovery of species are diverse according to the characteristics of the stimulus, the exposure conditions and the recovery environment (Popper and Hawkins, 2019). For example, goldfish had 5 dB of TTS after 10 minutes of exposure to band-limited noise (0.1 – 10.0 kHz, approximately 170 dB re 1 µPa; Smith *et al.,* 2004a, b), whilst there was no TTS in rainbow trout *(Oncorhynchus mykiss)* after nine months of exposure to 0.2 – 2.0 kHz broadband noise with an overall SPL of 150 dB re 1 µPa in an aquaculture facility (Wysocki *et al.,* 2007b). Again, after stimulation with five presentations of a small seismic air-gun array, each presentation having a received mean peak SPL of 205 – 210 dB re 1 µPa, goldfish showed no TTS, whereas northern pike *(Esox Lucius;* a hearing generalist) and sandbar shark *(Carcharhinus plumbeus;* a hearing specialist) showed 10 – 25 dB re 1 µPa of hearing loss that recovered within 24 hr after exposure (Popper *et al.,* 2005). Thus, both short-duration intense (e.g., the aforementioned air gun ray) and long-duration quiet (e.g., nine-month noise exposure) stimuli have the potential to cause TTS with significant hair cell damage (Smith *et al.,* 2006, 2011) but this would be limited for healthy, captive fishes when exposed to short-duration pure tones <145 dB re 1 µPa used in this thesis. Nevertheless, recovery of injured, low-fitness fishes in the wild would be slow and would make them more susceptible to predation (Popper and Hawkins, 2019). Permanent Threshold Shift (PTS) has not been reported for fishes, so a definitive SPL and frequency for this do not currently exist (Hastings and Popper, 2005; Smith *et al.,* 2011).

A number of initiatives have been implemented to monitor and reduce noise pollution in waterways, with the majority in marine waters. For example, the European Union has adopted the Marine Strategy Framework Directive (MSFD 2008/56/EC) under descriptor 11, which monitors underwater noise and ensures noise is not at levels that would adversely affect the marine environment. Equivalent monitoring has been implemented in the UK for Good Environmental Status, under the UK Marine Strategy (2019). The Environmental Impact Assessment (EIA) Directive (2011/92/EU) also monitors the impacts of public and private developments to limit ecological disturbance. In the United Kingdom (UK), EIAs assessing noise impacts follow the guidelines set out in the Sound Exposure Guidelines for Fishes and Sea Turtles (Popper *et al.,* 2014). The guidelines set out injury criteria, TTS and PTS criteria as well as behavioural impacts to fishes with and without a swimbladder, which helps to determine the risk. The guidelines also refer to the fact that behavioural changes may occur in migratory species, hence creating periods of heightened sensitivity. For example, mortal injury in fish where the swim bladder is involved in hearing is estimated at 229 – 234 dB re 1 µPa (Popper *et al.,* 2014). This has been implemented in projects such as the North Wales Connection Project proposed by the National Grid (National Grid, 2018), and the Norfolk Vanguard Offshore Wind Farm (Barnham, 2019). Nevertheless, outdated guidelines using dB_{ht} (Nedwell *et al.,* 2007) are still being used in industry (Taylor *et al.,* 2021), despite being discarded by the scientific community (see Popper *et al.,* 2014; Sisneros *et al.,* 2015).

2.6 Acoustic Deterrents

Sound travels faster underwater than chemical cues and attenuates slower than light, making it an ideal stimulus for the behavioural manipulation of fish. However, exploiting the natural responses of fishes to acoustic stimuli is not something novel. In the 2nd century, fishermen were known to strike the surface of the ocean to attract fish (Oppian and Diaper, 2015). More recently, fishermen in northern Laos are known to use the sounds of cans to guide fish into traps (Hortle *et al.*, 2016). Yet, since the early 1990s, conservation and invasive species management have promoted the use of sound as a deterrent (Turnpenny and Nedwell, 2003; Jesus *et al.,* 2018; Deleau *et al.,* 2019).

Notable uses of deterrents are to guide or deter fish, such as rerouting them to safe passages at hydropower stations, invasive species control, or to deter fish from abstraction points and pumping systems (Maes *et al.*, 2004; Zielinski *et al.*, 2014; Jesus *et al.*, 2018). Acoustic deterrents consist of an underwater transducer that produces an omnidirectional sound field, with the signal characteristics (e.g., pulse rate, broadband, sweep) dependent on the target species' hearing abilities (Putland and Mensinger, 2019). The sound is amplified and projected underwater in various locations and depths (Turnpenny and Nedwell, 2003; Putland and Mensinger, 2019). For a behavioural deterrent to be effective, as a minimum, the target individuals must be able to detect the stimulus and have sufficient time and capability to move away (Kemp *et al.*, 2012; Vetter *et al.*, 2015). This technology has an advantage over conventional physical screens that tend to become obstructed by debris (Zielinski *et al.*, 2014). Hence, if acoustic deterrents can be developed and maintained at a low cost, they may have the potential to supplement physical screens (Deleau *et al.,* 2019; Piper *et al.*, 2019).

Table 3 Comparison of acoustic deterrent studies for six orders, showing sample size (number of data points); auditory sensitivity for that order; frequency range (for the stimulus); median frequency (for the stimulus); SPL (of the stimulus); deterrence (the proportion of studies where fish avoided the stimulus <50% or >50% or not recorded (NR)). Data were taken from Putland and Mensinger (2019), screened for use in this context and added to according to suitable literature that was not in the original review.

Order	Sample Size	Auditory Sensitivity (Hz)	Frequency Range (Hz)	Median Frequency (Hz)	SPL (dB re 1 µPa)	Deterrence (%)
Anguilliformes	9	10-300[a]	11.8-1000	18	150-192	<50% = 33.3 >50% = 0.0 NR = 66.7
Clupeiformes	21	200-4000 10,000-100,000[b, c]	20-420,000	600	158-218	<50% = 14.3 >50% = 14.3 NR = 71.4
Cypriniformes	19	100-7000[d, e]	0-10,000	320	140-174	<50% = 26.3 >50% = 36.8 NR = 36.8
Gadiformes	5	50-300[f, g]	20-50,000	600	158-214	<50% = 40.0 >50% = 0.0 NR = 60.0
Perciformes	7	10-500[h]	20-10,000	375	150-174	<50% = 28.6 >50% = 42.9 NR = 28.6
Salmoniformes	36	10-1000[i, j]	10-10,000	150	140-190	<50% = 44.4 >50% = 11.1 NR = 44.4

a) Jerkø, 1989; b) Mann *et al.,* 1997; c) Mann *et al.,* 2001; d) Lovell *et al.,* 2006; e) Vetter *et al.,* 2018; f) Buerkle, 1968; g) Chapman and Hawkins, 1973; h) Karlsen, 1992; i) Van der Walker, 1966; j) Hawkins and Johnstone, 1978.

Acoustic deterrents have been employed at numerous sites including the Doel nuclear power plant, Belgium (Maes *et al.,* 2004); the Hinkley Point nuclear power station, UK (Turnpenny and Nedwell*,* 2003); and the Don Sahong Hydropower Plant, Laos (Hortle *et al.,* 2016). Despite use in industry, acoustic deterrents operate with varying degrees of efficacy (Table 3; Appendix A: A literature review by Putland and Mensinger (2019) was built upon for use in this thesis), with none being completely effective (Putland and Mensinger, 2019). The current understanding is that pure tones are ineffective acoustical deterrents (Nedwell *et al*., 2003; Vetter *et al*., 2015, 2017; Gu *et al*., 2017), meaning sweeps and complex sounds have been studied more recently (Vetter *et al*., 2015; Jesus *et al*., 2018). Despite this, the deterrence efficacy for complex sounds is frequently <50% (Table 4). This may be due to unclear methodological principles in experimental design. For example, Maes *et al.* (2004) tested a low-frequency stimulus because few species have been tested using low-frequency sound. Similarly, it may be because the stimulus is played at a frequency outside the hearing range and that noise has not been taken into account.

Table 4 A summary of the stimulus type, sample size and deterrence efficacy (the proportion of studies where fish avoided the stimulus <50% or >50% or not recorded (NR)). Data were taken from Putland and Mensinger (2019), screened for use in this context and added to according to suitable literature that was not in the original review.

Broadband or Pure?	Stimulus Type	Sample size	Deterrence (%)
Broadband	Continuous	18	<50% = 22.2 >50% = 22.2 NR = 55.6
	Crescendo	5	<50% = 20.0 >50% = 0.0 NR = 80.0
	Pulse	6	<50% = 16.7 >50% = 0 .0 NR = 83.3
Pure	Chirp	20	<50% = 30.0 >50% = 10.0 NR = 60.0
	Continuous	35	<50% = 42.9 >50% = 14.3 NR = 42.9
	Pulse	31	<50% = 41.9 >50% = 22.6 NR = 35.5

Ambient noise levels may influence deterrent efficiency but are rarely recorded in the literature (Kemp *et al*., 2012; Putland and Mensinger, 2019). Ambient noise levels were recorded (Appendix A) for 10 out of 199 samples (i.e., 8.4%), which equated to 5 out of 28 studies. For locations with considerable anthropogenic noise, the stimulus must be played at a sufficiently high SPL to elicit a reaction, thus it is important that the SNR is recorded. It is apparent that the selection of parameters appears to be somewhat *ad hoc,* and the process of trial and error seen throughout the literature is unlikely to increase the effectiveness of acoustic deterrents (Deleau *et al.,* 2019, 2020).

Acoustic deterrent research shows a bias towards the northern hemisphere, since studies mostly take place in North America and Europe (Figure 6), with most of the data being obtained in the USA (39%) and the UK (23%). Similarly, there is a bias towards certain taxonomic orders: Clupeiformes, Salmoniformes, Cypriniformes, and Perciformes (Figure 7). The bias towards Clupeiformes is likely due to the impingement of species such as herring at power station intakes (Popper and Schilt, 2008), whereas attention towards Salmoniformes such as Atlantic salmon (*Salmo salar*) is owing to their high recreational and commercial value. Most of the research in the later 20th century focused on Salmoniformes (Figure 8) despite them not possessing specialised hearing (Hawkins and Johnstone, 1978). There has since been a focus on other taxa such as Cypriniformes (Figure 8) that are highly invasive in the USA, particularly in the Great Lakes (Vetter *et al.,* 2017). Additionally, Anguilliformes have also been recipients of more recent deterrent research due to protection under legislation throughout Europe (EU Eel Regulation EC 1100/2007).

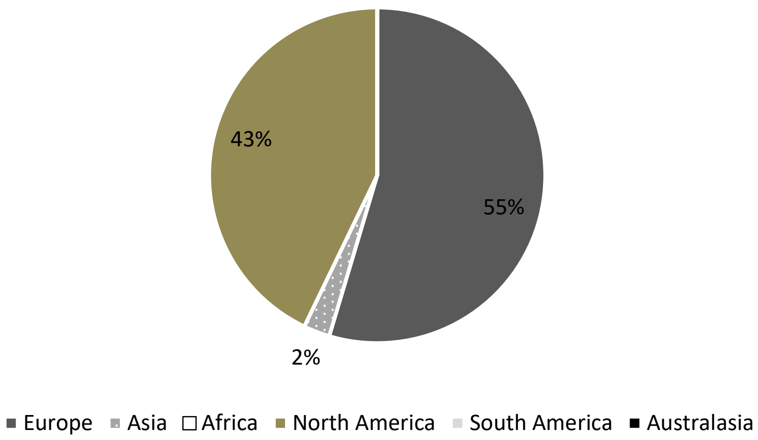


Figure 6 Studies investigating acoustic deterrence of fish presented in a pie chart to observe biases in geographic areas (see Appendix A).

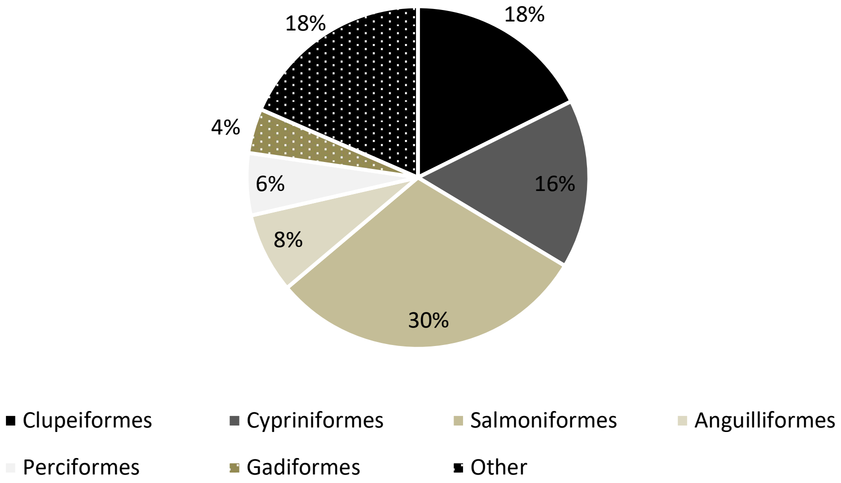


Figure 7 Studies investigating acoustic deterrence of fish presented in a pie chart to observe biases in taxonomic order per order (see Appendix A).

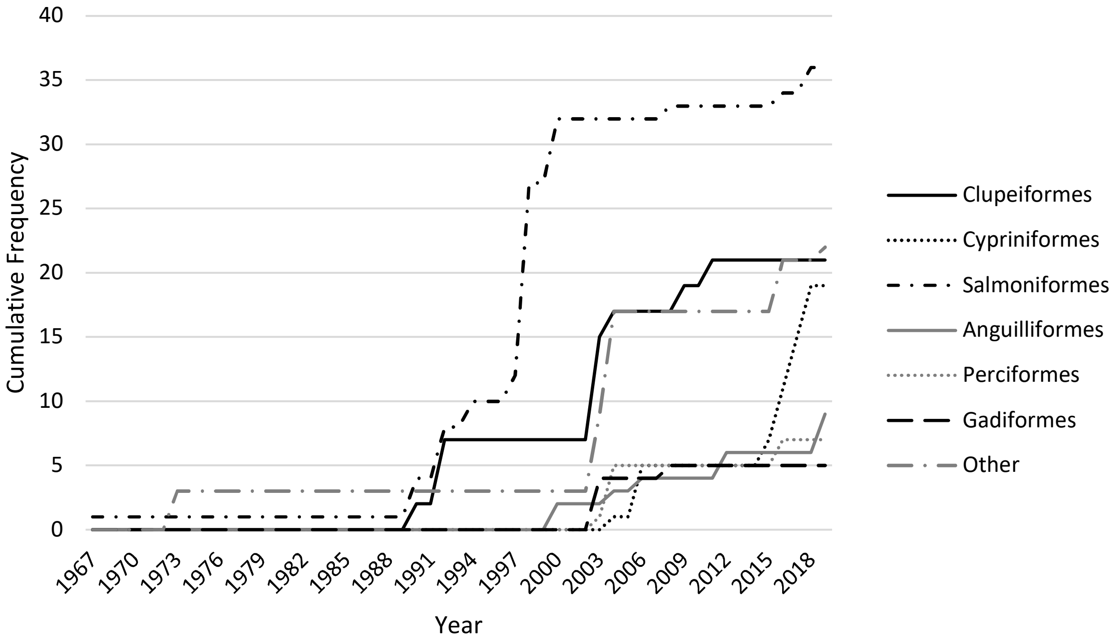


Figure 8 The number of fish acoustic deterrent studies per order, expressed as cumulative frequency (See Appendix A).

In the past, acoustic deterrent research and application have used hearing thresholds to inform behavioural reactions (Turnpenny and O'Keefe, 2005). Turnpenny and O'Keefe (2005) recommended the use of the dB_{ht} metric to determine the reaction of the target species and, thus, to increase the efficacy of deterrents. This scale involves the SPL and frequency range of the species' hearing and measures sound relative to this hearing threshold (Nedwell *et al.,* 2003). Hence, the dB_{ht} metric implies that the relationship between a strong behavioural response and the hearing threshold is uniform. For example, "+30 dB is the threshold of visible reaction in more sensitive individuals whilst +70 dB elicits a strong aversive reaction". Turnpenny and O'Keefe (2005) describe this as "advice in advance" and also state "if auditory sensitivity is the key factor, then simply increasing the acoustic emission of the system may be a way of achieving improved performance for these species" (Turnpenny and Nedwell, 2003). Such an assumption was not evidence-based and has been dismissed by some researchers (Popper *et al.,* 2014; Sisneros *et al.,* 2016).

Many in the scientific community have discouraged the use of dB_{ht} and have emphasised that it cannot be used to predict behavioural responses (Sisneros *et al,* 2016; Popper *et al.,* 2014). To improve on this, Popper *et al.* (2014) issued guidelines which are currently used in the UK. Separate recommendations were given for different circumstances (e.g., pile driving), different injury types (e.g., mortal injury, TTS, behaviour) and different fish (no swim bladder, swim bladder with no involvement in hearing, swim bladder with involvement in hearing). Despite rigorous documentation of injuries, the classification of risk was subjective since many injuries were categorised as ‘low’, ‘medium’ or ‘high’ risk at ‘near’, ‘intermediate’, and ’far’ distances. This was largely due to a lack of literature, particularly for behavioural studies.

Another approach for increasing deterrent effectiveness is to increase the SPL (Turnpenny and Nedwell, 2003). Nevertheless, increasing the SPL of the deterrent may cause damage to the auditory system or induce TTS (Section 2.5.1). The TTS has been observed at 158 dB re 1 µPa for goldfish and the pictus catfish (*Pimelodus pictus*), however, the pictus catfish took a longer time to recover - up to 14 days after exposure, compared to three days for goldfish (Amoser and Ladich, 2003). Additional research found that, when applied to bighead carp (*Hypophthalmichthys nobilis*) and silver carp (*H. molitrix)*, TTS is species-specific (Nissen *et al.,* 2019), meaning an acoustic deterrent must induce an anti-predator response but be sympathetic to the limitations of the fish’s auditory system.

Chapter 3 Methodology

3.1 Study Species

The goldfish (Figure 9) is a member of the *Cyprinidae* family of fishes. Originally inhabiting streams and lakes in East Asia, the goldfish was first domesticated in the 11th century (Balon, 2004). Until now, the goldfish is a hugely popular aquarium and outdoor pond fish. As well as its recreational popularity, the goldfish has been a beneficial species in aquatic ecology, contributing to the advancement of various fields such as evolutionary developmental biology (Ota and Abe, 2016), neuroendocrine signalling (Popesku *et al.,* 2008), and fish auditory systems (e.g., neural mechanisms, Fay, 1982; physiology, Lanford *et al.,* 2000; and hearing thresholds, Smith *et al.* 2011).

Figure 9 Image of a young, sexually mature goldfish.

Since the 1960s in particular, the goldfish has been a keystone species in understanding fish hearing (Popper and Clarke, 1976; Fay, 1984; amongst others). This is because, goldfish possess Weberian ossicles that facilitate sound transmission to the inner ear, which enables them to detect sound pressure as well as particle motion (Figure 10). Goldfish hearing thresholds are well-studied and are known to be highly sensitive (Kenyon *et al.,* 1998; Ladich and Fay, 2013). The threshold of best hearing obtained behaviourally for goldfish is between 350 Hz and 1500 Hz, at SPLs between 52 and 80 dB re 1 µPa. The threshold of best hearing obtained electrophysiolocically (i.e., via AEP) is 300 to 800 Hz, at SPLs between 63 and 84 dB re 1 µPa (Figure 11). Goldfish are also known to have directional hearing that enables them to localise sound sources (Moulton and Dixon, 1967). They also exhibit temporal discrimination (Fay, 1982) and frequency discrimination (Fay, 1989).

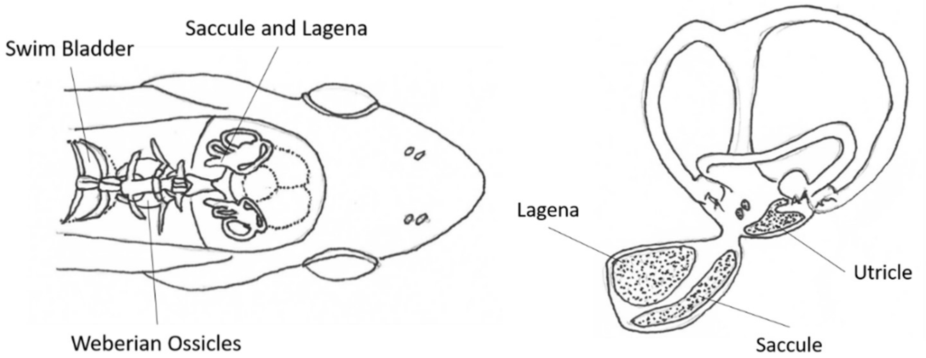


Figure 10 Relative positions of the ear, the Weberian ossicles, and the swim bladder within the body of the goldfish. Sensory epithelia within the goldfish ear. The posterior part of the ear has the saccule and the lagena. The anterior part of the ear contains the utricle (see Lanford *et al.,* 2000).

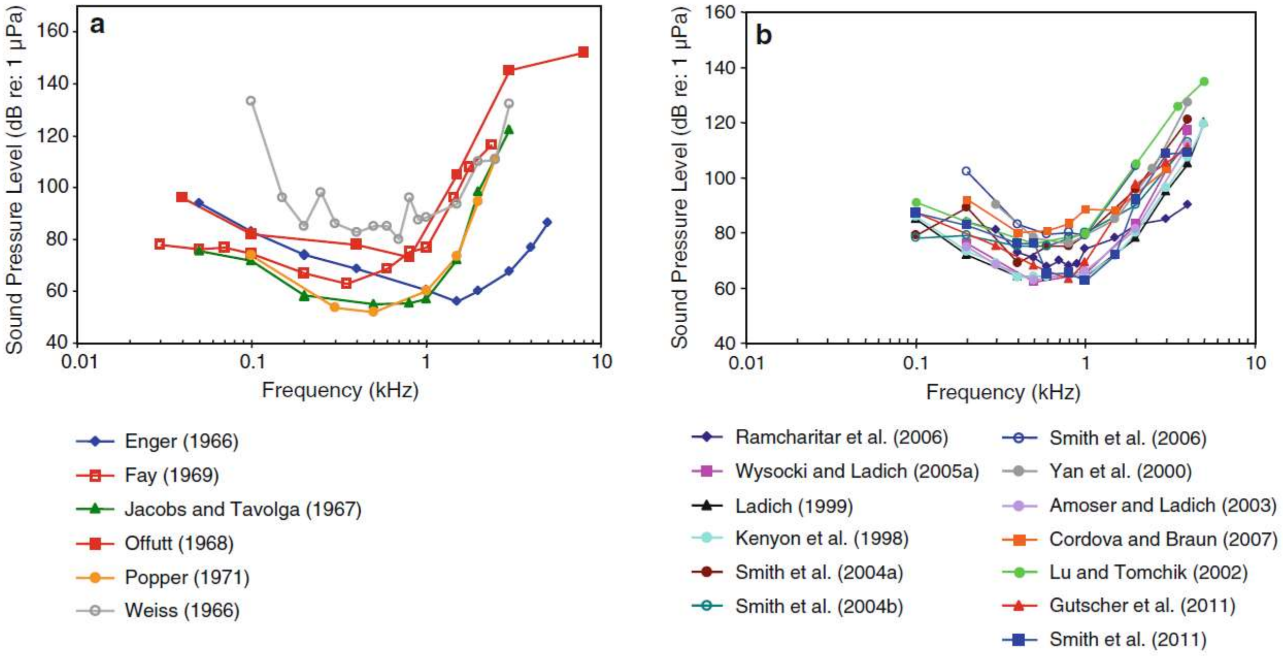


Figure 11 Comparisons of **a)** behavioural and **b)** AEP audiograms for goldfish. [Source: Ladich and Fay, 2013].

Goldfish are a globally invasive species causing widespread ecological damage, such as parasite dispersal and increased water turbidity from bottom feeding (see Lorenzoni *et al.,* 2010; Beatty *et al.,* 2016; Trujillo-González *et al.,* 2018). The fish inhabit both lotic and lentic environments, preferring slower flowing environments, meaning they have invaded rivers and lakes alike (Haynes *et al.,* 2011; Lorenzoni *et al.,* 2007). Currently, there is no literature on the use of acoustic deterrents for invasive goldfish management, however, there is a wealth of literature on other carp species such as common carp (Murchy *et al.,* 2016), bighead carp (Vetter *et al.,* 2017) and silver carp (Vetter *et al.,* 2015).

3.2 Experimental Setup

To meet PhD Objective 1 and 2 (Table 1), laboratory experiments were carried out in facilities at the University of Southampton, UK. The first of which was a still water tank that was used to conduct a methodological study at the ICER Experimental Facility. Data was collected in an experimental arena (86.0 cm length [referred to as horizontal distance, as it was horizontal to the researcher when collecting data] x 30.8 cm width [referred to as vertical distance, as it was vertical to the researcher when collecting data] x 30.2 cm height) situated within a custom-made still water rectangular acrylic tank (300.0 cm length x 30.8 cm width x 30.2 cm height; 12.0 mm thickness; 27.0 cm water depth; temperature: mean [sd], 18.8 [1.4] °C) in September 2019. The tank was situated on concrete blocks and surrounded by air on all sides (Figure 12). Two underwater transducers (Electro-Voice UW-30; maximal output 153 dB re 1 µPa at 1 m for 150 Hz, Lubell Labs, Columbus, OH, USA) were suspended centrally, 13.5 cm from the bottom of the tank and 5.0 cm away from custom-made baffles that flanked the experimental arena.

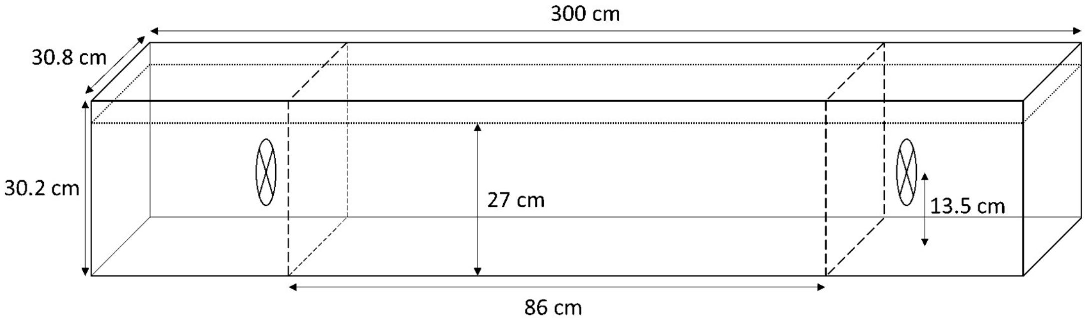


Figure 12 The rectangular in-air tank (300.0 cm length × 30.8 cm width × 30.2 cm height) and experimental arena (86.0 cm length × 30.8 cm width × 30.2 cm height) in relation to the water level (dotted line, 27.0 cm water depth). Two transducers were suspended centrally at either end of the experimental arena and behind an acoustic baffle (dashed line).

The second and primary facility was the A. B. Wood laboratory, University of Southampton. For the methodological study, a white medium density polyethylene cylindrical arena (modified 100 L Round Water Tank; 55.5 cm diameter × 45.0 cm height; 4.0 mm thickness; 30.0 cm water depth; Direct Water Tanks, Retford, Nottinghamshire, UK) situated on a concrete floor (Figure 13). The water depth was 3 cm deeper than the rectangular in-air tank due to practicality, however the sound waves would propagate in the same manner for both water depths. An underwater transducer (Electro-Voice UW-30) was suspended centrally 1.0 cm from the bottom of the tank. The vertical and horizontal distance were established to aid acoustic data collection; the measurements were vertical and horizontal for the researcher, when conducting the acoustic mapping data.

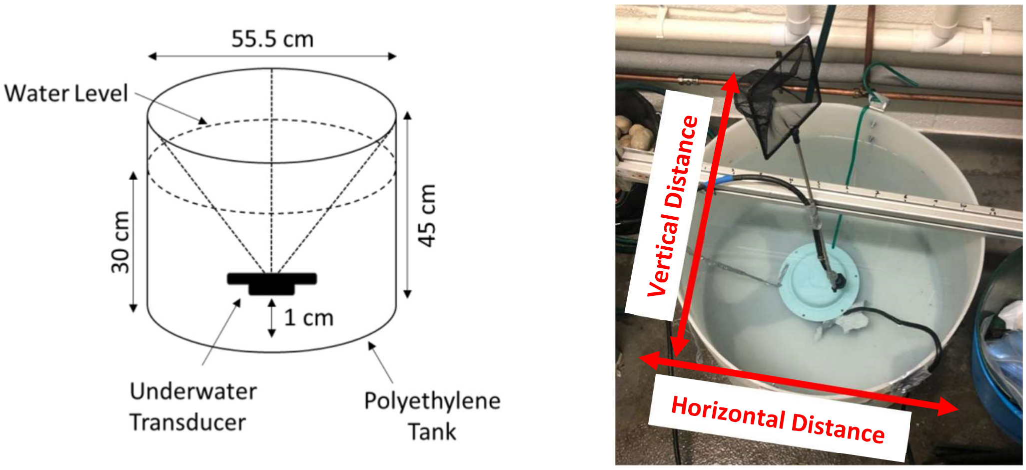


Figure 13 The experimental set up used to fulfil the methodological study, showing the cylindrical tank (experimental arena, 45.0 cm height × 55.5 cm diameter) in relation to the water level (dashed line, 30.0 cm depth). The transducer was suspended (dotted line) 1.0 cm above the bottom of the tank. The vertical and horizontal distance have been labelled and were used for the researcher to undertake acoustic mapping.

The same cylindrical arena was used to carry out all the remaining experiments. All trials with goldfish were conducted in the A. B. Wood laboratory. The arena was mounted on a bespoke metal frame and suspended in a large tank (8.0 m length × 8.0 m width × 5.0 m depth; Figure 14). An underwater transducer (Electro-Voice UW-30) was suspended 70 cm below the arena. The vertical and horizontal distance were established to aid acoustic data collection. A webcam (C920; HD 1080p; 30 frames s^{-1}; Logitech Pro, Switzerland) was situated directly above the arena.

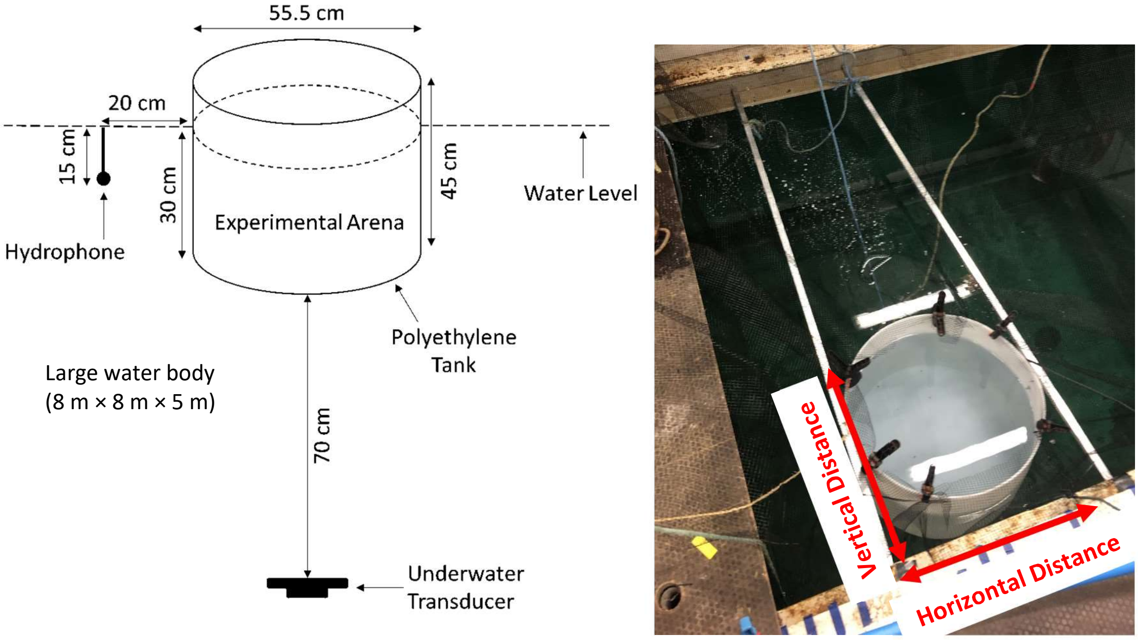


Figure 14 The experimental set up used to fulfil PhD objectives 1 and 2, showing the cylindrical tank (experimental arena, 45.0 cm height × 55.5 cm diameter) inside a large tank (8.0 m length x 8.0 m width x 5.0 m depth) in relation to the water level (dotted line, 30.0 cm depth). The transducer was suspended 70 cm below the tank, and a hydrophone placed 15 cm below the water level and 20 cm away. The vertical and horizontal distance have been labelled and were used for the researcher to undertake acoustic mapping.

3.3 **Acoustic Stimuli and Mapping**

Acoustic stimuli were produced in MATLAB (Release 2019b, The Mathworks, Inc., Natick, Massachusetts, USA) using a laptop connected to a DAQ (NI USB-6212; National Instruments, Berkshire, UK), transmitting the signal through an amplifier (Prosound Power AMP 200; frequency response: 20 Hz – 20 kHz) and emitted via an underwater transducer (Electro-Voice UW-30). Use of artificial stimuli allowed for control of the specific acoustic components tested. Each pure tone signal consisted of a sinusoidal 120 ms tone ramped with a 20 ms Hanning taper. Although latencies of Mauthner cell activation in goldfish is 5 – 10 ms, the tone was played at 120 ms so that it was sufficiently short to elicit a startle response but long enough to enable the frequency spectrum to be well defined at this lower signal duration (Eaton, 1977; Zeddies and Fay, 2005).

For acoustic mapping in the rectangular arena (Chapter 4), the sound pressure field was also mapped using a calibrated hydrophone (8103, manufacturer-calibrated sensitivity -211 dB re: 1 V/ µPa, Brüel & Kjær, Hertfordshire, UK) attached to a manual slider (80 measurements, each 5.0 cm apart), and recorded at three depths (7.0 cm, 13.5 cm, 20.0 cm, measured from the water surface). For experiments in the cylindrical arena (Chapter 5 and Chapter 6), the sound pressure field was measured and mapped prior to starting any trials using a calibrated hydrophone (8105, manufacturer-calibrated sensitivity -205 dB re: 1 V/ µPa; Brüel & Kjær, Hertfordshire, UK) attached to a manual slider (76 measurements, each 5.0 cm apart). Point measurements were recorded at three depths (5.0 cm, 15.0 cm, 25.0 cm, measured from the water surface).

For any setup, the ambient sound was recorded within the experimental arena, which was the electrical noise floor of the measurement system being used. The stimuli were then calibrated such that the desired SPL was reached in the centre of the experimental arena. The sound pressure field was then mapped using the hydrophone. The sound pressure data was then imported into MATLAB and the SPL (in dB) was calculated. The SPL data was then used to plot colourised maps in MATLAB.

The data capture and stimulus generation were synchronised to facilitate computation of the PA. Both SPL and PA were quantified to create 3D maps of the sound field. The PA, a, was calculated as:

$$a = -\frac{\nabla P}{\rho} \qquad \text{Equation 8}$$

where ρ is the ambient density in and ∇P is the pressure gradient (Kinsler *et al.,* 1982).

The pressure gradient was calculated using the measurements of the pressure signal. The RMS of the pressure difference was calculated independently in three directions (x, y and z), in which the difference between the two pressures was computed and then the RMS of that difference was calculated. The pressure gradient was obtained as the difference in sound pressure between measurement points. The RMS PA, in each direction, was calculated as the pressure gradient (dP/dx in Pa m^{-1}) and water density (kg m^{-3}). The total RMS PA was attained by combining the values in all three directions, with the results expressed in decibels (dB re 1 mm s^{-2}). Subsequently, the PA was represented in maps.

3.4 **Fish Maintenance**

Goldfish were obtained from Hampshire Carp Hatcheries, Southampton, UK, and transported in oxygenated water to ICER Facility, University of Southampton (50° 56’16.3” N, 1°24’15.9” W) where they were maintained in husbandry tanks (1.5 m length × 1.0 m width × 0.8 m height, filled to 60.0 cm) containing ~1200 L of aerated, filtered and dechlorinated water. They were maintained under an artificial photoperiod (dependent on the time of year) and fed once daily (Tetra goldfish flakes; protein: 42.0%). Ammonia, nitrites, nitrates, pH (API Freshwater Master Test Kit) and temperature were monitored daily. A water change of 25.0% was conducted weekly and a 50.0% water change was conducted prior to receiving a new batch of fish or as necessary to maintain ammonia, nitrate and nitrite levels below 0.5 ppm, 60.0 ppm and 0.3 ppm, respectively. Prior to experimenting on any fish, ethical approval was received from the University of Southampton.

All the experiments were carried out in compliance with guidelines established by the current UK animal protection law established by the Home Office (Animal Welfare Act 2006). All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. The study was reviewed by the Animal Welfare and Ethics Review Body and approval granted by the University of Southampton Ethics and Research Governance committee (Experiment 1: 52155, 54900.A1; Experiment 2a: 63874; Experiment 2b: 69464). The number of goldfish used was reduced where possible in accordance with the Three Rs of Research (replacement, refinement and reduction; NC3Rs, 2014). Individuals were handled with care, and handling time was kept to a minimum. There was no evidence of stress or fatigue from exposure to the acoustic stimulus in any of the experiments, regardless of the SPL and frequency of the stimulus.

3.5 Quantifying Startle Responses

Fish behaviour was quantified through the startle response (Figure 15). A startle response was defined as a change in body tortuosity with a sudden increase in swimming speed or a change in swimming direction (Kastelein *et al.,* 2008). Startle responses were recorded in binary terms as present or absent, thus residuals followed a binomial distribution.

Behaviour was recorded using overhead video cameras and startle responses were documented by manually reviewing the video footage twice. The time of the signal presentation was noted and the videos were reviewed in absence of sound. If a startle response occurred at the time of the signal presentation, the startle would be recorded as present, and if not, it would be recorded as absent. The responses were documented twice to determine the error in reviewing and recording the behaviour. Videos were always reviewed without sound and in a random order to reduce bias in documenting responses.

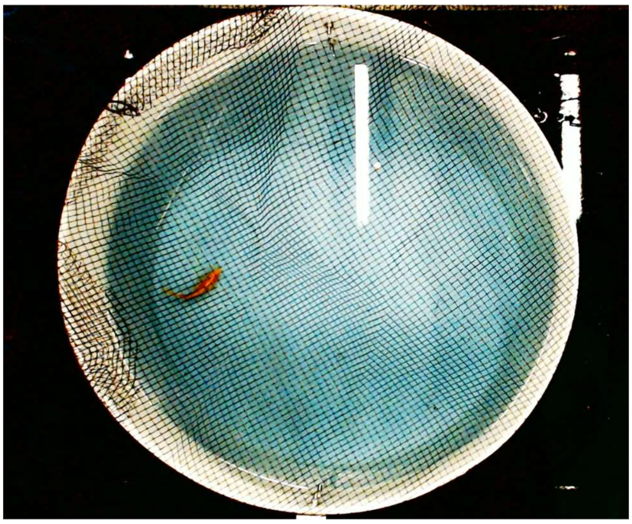


Figure 15 Still image from the video footage of a goldfish startling to a tone.

3.6 Statistical Analysis

Statistical analysis was conducted using R (version 3.6.3), and mostly consisted of GLM and GLMMs. The majority of the data followed a binomial distribution, however in cases where data was normal, it was validated by the Shapiro-Wilks test. Other cases considered count data and thus residuals followed a Poisson distribution. The GLMMs were used, with the individual as a random effect since in all experiments each individual received multiple stimuli. However, exposure (when multiple stimulus presentations were used) was also tested. The Akaike Information Criterion (AIC) was used to determine a parsimonious model fit, and in cases where the fixed effect model was more appropriate, a GLM was used.

The proceeding chapter (Chapter 4) will consider a methodological study that tested the effectiveness of reducing the internal reflectiveness of the arena walls. This in turn will establish the methodology used to fulfil Objective 1 (determine the startle response threshold in goldfish to pure tone acoustic stimuli) in Chapter 5 and for Objective 2 (quantify innate responses of goldfish responding to a 120 ms pure tone acoustic stimulus in presence and absence of band-limited (100 – 2500 Hz) random noise) in Chapter 6.

Chapter 4 Methodological Study: A comparison of sound fields in small experimental test arenas

4.1 Abstract

Laboratory-based bioacoustics experiments on fish enable the control of confounding factors, yet these experiments often use small tanks that are spatially complex in terms of particle motion and SPL. One solution is to submerge a tank in water to reduce the reverberation resultant of impedance differences between air and water as described in Chapter 3. Consequently, to establish a methodology to fulfil PhD Objectives 1 and 2, this experiment answered the following: (1) can the sound pressure homogeneity in small tanks be improved? (2) can the PA levels in small tanks be reduced? (3) does submerging small tanks allow the sound field to be reliably described by progressive plane waves? Three experimental setups were used, with the first being a rectangular in-air tank; the second being a cylindrical in-air tank and the third a cylindrical tank submerged in a large water body. Measurements of a 1.0 s, 125 dB tone at 250 Hz, 400 Hz, 600 Hz, 800 Hz, 1000 Hz and 2000 Hz were taken using a hydrophone and mapped to produce a 3D representation of the sound pressure and PA fields. The submerged arena possessed less heterogeneity in SPL and lower levels of PA than the in-air tank. The predicted PA (calculated to fulfil research question three) was a better approximation to the submerged arena than the in-air tank. This study demonstrates that the submerged arena gave greater control over the stimulus that a fish experiences in laboratory-based experiments. The submerged cylindrical arena was therefore used for subsequent experiments.

4.2 Introduction

Bioacoustics experiments may be undertaken *in situ* or in laboratory settings. There are benefits to conducting experiments both indoors and outdoors, with outdoor experiments, either fully *in situ* or in a pen, having high behavioural and acoustic validity but low experimental control (Slabbekoorn, 2016). Conversely, indoor tank experiments lack acoustic validity due to heterogeneous SPLs and high levels of particle motion. Whilst experiments *in situ* may be more favourable in terms of acoustic validity, indoor tank experiments have a much higher degree of experimental control (Akamatsu *et al.,* 2002). This is advantageous for behavioural studies in which external factors, such as water temperature and ambient noise, may compromise the behaviour more so *in situ* than in the laboratory (Akamatsu *et al.,* 2002; Johnsson and Näslund, 2018).

Small tanks have complex soundscapes due to their small size, the elasticity of the tank walls, and the large impedance differences between water and air at the tank boundaries (Rogers *et al.,* 2016). The largest problem is that of reverberation in which the 3D map of the acoustic field becomes increasingly inhomogeneous and the intensity becomes potentially anisotropic. The shape of the tank may also present challenges (Akamatsu *et al.,* 2002). For example, rectangular tanks constructed from glass or acrylic possess five hard surfaces (four sides and a bottom) in close proximity to each other. This introduces scattering from all the boundaries. The reverberation from this is increased by the impedance difference between the water in the tank and the air surrounding the tank. In this case, at very low frequencies and for thin-walled tanks, the tank walls can act as pressure release boundaries, meaning the sound pressure is zero but the particle motion is high (Popper and Hawkins, 2018) (although as frequency increases this rule breaks down; Birkin *et al.,* 2003). This encourages reverberation, which may introduce misleading particle motion data when using point pressure measurements (Gray *et al.,* 2016).

In fish biology, inhomogeneous sound fields mean the level received by the fish would vary according to its orientation and position. Thus, the SPL and particle motion would be unknown by the experimenter. A second issue would be that the degree of homogeneity may vary upon experiment replication by the experimenter or if another experimenter wishes to replicate the experiment and findings.

A practical way to improve sound pressure and particle motion fields whilst using readily available equipment is to alter experimental methodology. This may involve setups *in situ* (Debusschere *et al.,* 2014) or in a pen (Hubert *et al.,* 2020). However, the use of tanks allows control of environmental factors, and the constraint of fish in tanks provides an accurate determination of behaviour, which would be impossible in the field (Akamatsu *et al.,* 2002; Gray *et al.,* 2016). To increase the extent to which a tank is homogeneous, large impedance differences should be removed. Anechoic wedges may be applied to the walls for this purpose, however, for use in underwater bioacoustics studies they would be impractical and expensive. For frequencies of 250 – 2000 Hz, these wedges would be ~1.0 m in length (Kolaini and Crum, 1994), requiring a very large anechoic tank to provide a working space free of the niches provided by wedges in which the fish could be contained (e.g., by a net). Hence, this study tested a more practical method to homogenise the sound field.

The experiment aimed to answer the following research questions: (1) Can the sound pressure homogeneity in small tanks be improved? (2) Can the PA levels in small tanks be reduced? (3) Can small tanks be modified such that the sound field can be reliably described by plane waves? Three experimental setups were selected to answer these questions: a setup of a cylindrical (55.5 cm diameter) arena surrounded by air and placed on a concrete floor with a transducer situated in the arena; a setup of the same arena submerged in a large water tank with a speaker situated underneath; a rectangular acrylic tank surrounded by air and placed on concrete blocks, with two transducers situated at either end of an experimental arena.

4.3 **Methods**

4.3.1 Experimental Setup

The three setups for the experiment have been described in detail in Section 3.2.

4.3.2 Acoustic Stimuli & Sound Mapping

Two phases of experiments were undertaken to compare the sound fields of the three experimental setups. The first phase involved a comparison of the rectangular in-air tank (Figure 12) and the submerged arena (Figure 14), whilst the second considered the cylindrical in-air tank (Figure 13) and the submerged arena (Figure 14). The data for the submerged arena was collected on two separate occasions in November 2020 and July 2021 for phase one and phase two, respectively (Table 5).

Table 5 A summary of the three experimental setups used across two experimental phases for the methodological study. The sound field was calibrated such that the SPL was present in the centre of the experimental arena. The frequencies (Hz) generated, and the ambient SPLs (dB re 1 µPa) are described.

Setup	**SPL**	**Frequencies (Hz)**	**Ambient SPL**
Rectangular In-air Tank (Phase one)	125 dB re 1 µPa	400, 600, 800, 1000, 2000	<90 dB re 1 µPa
Submerged Arena (Phase one)	125 dB re 1 µPa	400, 600, 800, 1000, 2000	<109 dB re 1 µPa
Cylindrical In-air Tank (Phase two)	145 dB re 1 µPa	250, 400, 600, 800, 1000, 2000	<117 dB re 1 µPa
Submerged Arena (Phase two)	145 dB re 1 µPa	250, 400, 600, 800, 1000, 2000	<118 dB re 1 µPa

The SPLs of 1.0 s pure tones according to the frequencies outlined in Table 5 were measured and mapped using a calibrated hydrophone. The hydrophone was then attached to a manual slider (for the rectangular in-air tank: 80 measurements per depth, each 5.0 cm apart; for the cylindrical in-air tank and submerged arena: 76 measurements per depth, each 5.0 cm apart). Point measurements were recorded at three depths, measured from the water's surface (for the rectangular in-air tank: 7.0 cm, 13.5 cm, 20.0 cm; for the cylindrical in-air tank and submerged arena: 5.0 cm, 15.0 cm, 25.0 cm). The depths were chosen, as they represented the three depth quartiles (i.e., the middle, the bottom quarter and the upper quarter) for each tank, since they were filled to a different depth. The SPL and PA were calculated and mapped according to the methods set out in Section 3.3.

4.3.3 Data Analysis

All statistical analyses were performed in R, whilst acoustic maps were produced in MATLAB. The PA and SPL residuals followed a Gaussian distribution, determined by visual inspection of qq curves. Two-sided *F*-tests were conducted to compare the variance of PA and SPL data between the in-air tank and submerged arena setups for each frequency. Similarly, two-sided, Welch's *t*-tests were used to compare the means of PA and SPL between the submerged arena and in-air tank for each frequency.

To determine if small tanks can be modified so that the sound field can be described using a plane wave, an equation was used that allowed calculation of the PA had the sound propagated as such. The predicted PA could then be compared to the experimental PA to determine which setup better allowed the stimulus to propagate as a plane wave. If the plane wave assumption is satisfied, the gradient in acoustic pressure measured by paired hydrophone measurements in three orthogonal directions can be used to calculate the vector of acoustic particle velocity.

For a propagating plane wave, both PA (dB re 1 mm s^{-2}) and SPL (dB re 1 µPa) may be predicted by equations 9 and 10, respectively (Everest and Pohlmann, 2015):

$$SPL = 20\log_{10}\frac{p}{10^{-6}} \qquad \text{Equation 9}$$

$$PA = 20\log_{10}\frac{a}{10^{-3}} \qquad \text{Equation 10}$$

Equations 9 and 10 were used to calculate the PA at 15.0 cm depth, had the sound propagated as a plane wave. The predicted PA was then compared to the experimental PA:

$$PA_e - PA_p \qquad \text{Equation 11}$$

where PA_e (dB re 1 mm s^{-2}) was the experimental PA (using the hydrophone recordings and applying Equation 8), PA_p (dB re 1 mm s^{-2}) was the predicted PA (calculated by taking the SPL at each of the points measured across the middle plane, applying Equation 8 and Equation 9 followed by Equation 10).

Advantages and limitations of three experimental setups were previously identified by Slabbekoorn (2016). Factors considered were acoustic validity, behavioural validity and experimental control and were assigned a 'high', 'middle' or 'low' classification. Slabbekoorn (2016) assessed: captive indoor - indoor studies using fish tanks; captive outdoor - outdoor studies using captive fish that can move in a restricted area; free-range outdoor - outdoor studies on free-ranging fish that swim into the selected study area. The same process was applied to the submerged cylindrical arena setup used in this study and was presented alongside conclusions by Slabbekoorn (2016).

4.4 Results

4.4.1 Rectangular In-air Tank: Phase One

The SPL was heterogeneous across the horizontal plane for each frequency, with greatest variation observed at 1000 Hz and 2000 Hz since they had a shorter wavelength (Table 6). The SPL differed by ~6 dB between the top and bottom of the tank. The experimental PA was high, with 400 Hz exhibiting the highest levels of PA (Figure 16). Had the sound propagated as a plane wave, the PA was predicted to increase with frequency (Table 7; Appendix B); however, the experimental PA did not follow this trend. Hence, the two distributions were dissimilar (see Table 7).

Table 6 The mean SPL ± standard deviation of a 1.0 s pure tone calibrated at 125 dB re 1 µPa in the centre of a rectangular experimental arena within acrylic in-air tank at frequencies of: 400 Hz; 600 Hz; 800 Hz; 1000 Hz; 2000 Hz. Point measurements were taken at three depths (7.0 cm, 13.5 cm, 20.0 cm). Centre SPL refers to the SPL in the middle of the 13.5 cm layer.

Frequency (Hz)	*7.0 cm (dB re 1 µPa)*	*13.5 cm (dB re 1 µPa)*	*20.0 cm (dB re 1 µPa)*	*Centre SPL (dB re 1 µPa)*
400	124.3 ± 4.4	128.8 ± 3.4	131.4 ± 2.9	125.0 ± 0.5
600	128.5 ± 7.5	129.3 ± 7.4	134.8 ± 5.6	125.0 ± 1.4
800	134.6 ± 7.6	136.1 ± 9.2	138.6 ± 6.8	125.1 ± 2.8
1000	136.6 ± 8.2	137.7 ± 9.8	144.0 ± 6.2	125.1 ± 6.7
2000	136.5 ± 8.2	137.6 ± 9.8	143.9 ± 6.2	125.0 ± 6.7

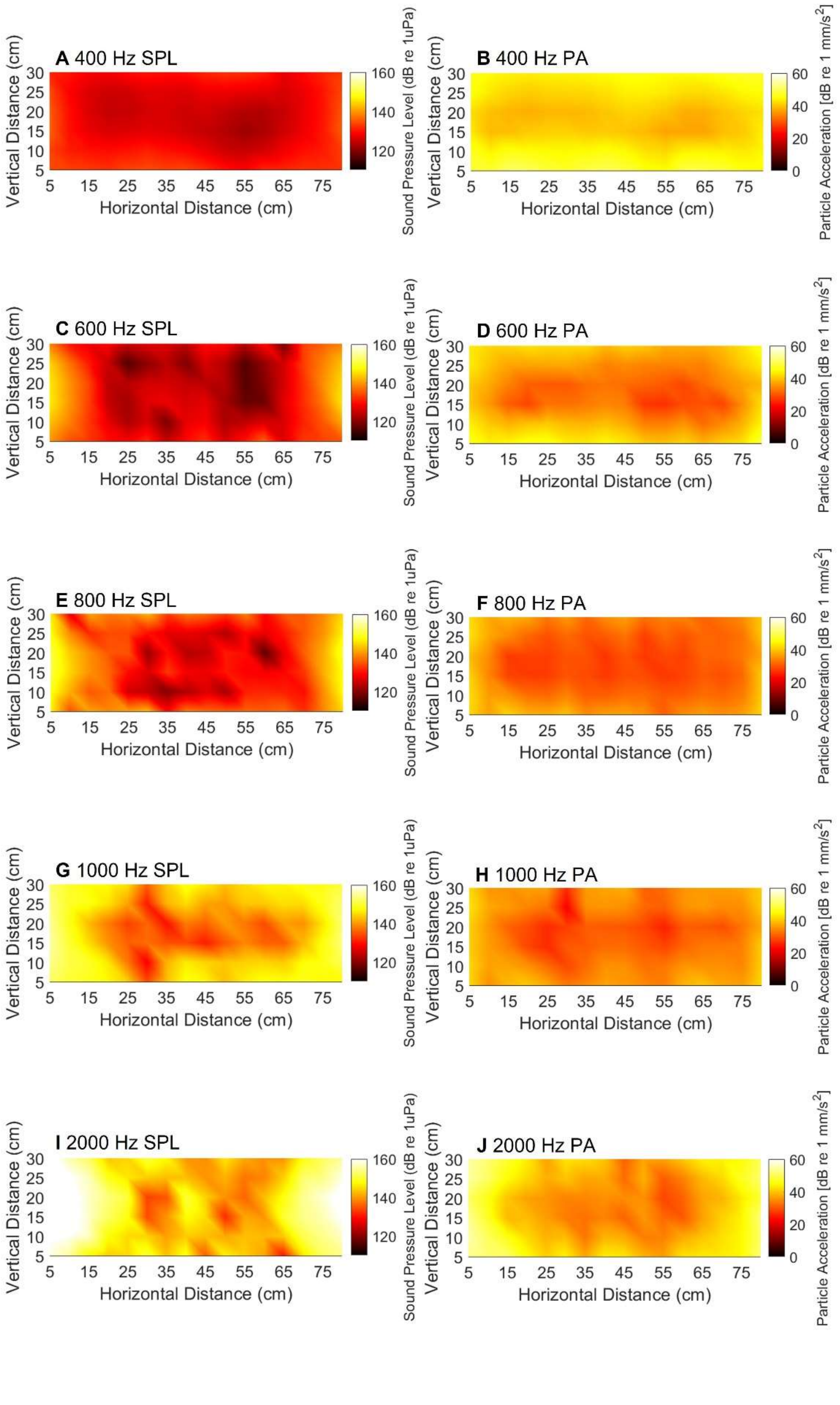


Figure 16 SPL maps (**A, C, E, G, I**) and PA maps (**B, D, F, H, J**) (13.5 cm depth) of a 1.0 s pure tone calibrated at 125 dB re 1 µPa in the centre of a rectangular experimental arena within acrylic in-air tank at frequencies of: 400 Hz, 600 Hz, 800 Hz, 1000 Hz, 2000 Hz. The vertical and horizontal distance were measured as per the description in Section 3.2.

Table 7 The mean PA ± standard deviation of a 1.0 s pure tones in the experimental arena within acrylic in-air tank at frequencies of: 400 Hz; 600 Hz; 800 Hz; 1000 Hz; 2000 Hz. Point SPL measurements were taken at three depths (7.0 cm, 13.5 cm, 20.0 cm) and PA (Experimental) was calculated from those values. PA (Predicted) was calculated using the plane wave approximation and the reduced *Experimental – Predicted* PA ($PA_e - PA_p$) was recorded.

Frequency (Hz)	***13.5 cm (dB re 1 mm s^{-2}) Experimental***	***13.5 cm (dB re 1 mm s^{-2})* Predicted**	**Experimental – Predicted *(dB)***
400	43.3 ± 3.4	12.9 ± 3.4	30.3 ± 2.4
600	37.5 ± 5.1	16.8 ± 7.4	20.7 ± 6.3
800	33.3 ± 4.3	19.3 ± 7.4	14.0 ± 5.4
1000	34.3 ± 4.2	29.7 ± 9.8	4.7 ± 8.2
2000	41.0 ± 6.6	35.6 ± 9.8	5.4 ± 6.8

4.4.2 Submerged Arena: Phase One

The SPL was relatively homogeneous across the horizontal plane for each frequency, with greatest variation observed at 2000 Hz because of the shorter wavelengths (Table 8). The SPL differed by ~11 dB between the top and bottom of the tank. The experimental PA was lower in value than the in-air tank (Figure 17). As with the in-air tank, had the sound propagated as a plane wave, the PA was predicted to increase with frequency (Table 9; Appendix B) and the experimental PA follow this trend (except for 400 Hz), resulting in smaller values of $PA_e - PA_p$ (Equation 11) for 400 – 1000 Hz compared to the in-air tank.

Table 8 The mean SPL ± standard deviation of a 1.0 s pure tone calibrated at 125 dB re 1 µPa in the centre of a cylindrical arena submerged in a large water-filled tank at frequencies of: 400 Hz, 600 Hz, 800 Hz, 1000 Hz, 2000 Hz. Point measurements were taken at three depths (5.0 cm, 15.0 cm, 25.0 cm). Centre SPL refers to the SPL in the centre of the tank.

Frequency (Hz)	***5.0 cm (dB re 1 µPa)***	***15.0 cm (dB re 1 µPa)***	***25.0 cm (dB re 1 µPa)***	***Centre SPL (dB re 1 µPa)***
400	113.8 ± 0.5	124.4 ± 0.4	128.5 ± 0.6	125.0 ± 0.3
600	113.4 ± 0.4	124.3 ± 0.3	128.0 ± 0.6	124.5 ± 0.1
800	114.7 ± 0.4	125.0 ± 0.2	128.4 ± 0.3	125.0 ± 0.1
1000	114.9 ± 0.6	124.9 ± 0.5	128.3 ± 0.5	125.0 ± 0.3
2000	114.9 ± 1.8	124.7 ± 2.4	124.0 ± 2.6	125.4 ± 0.6

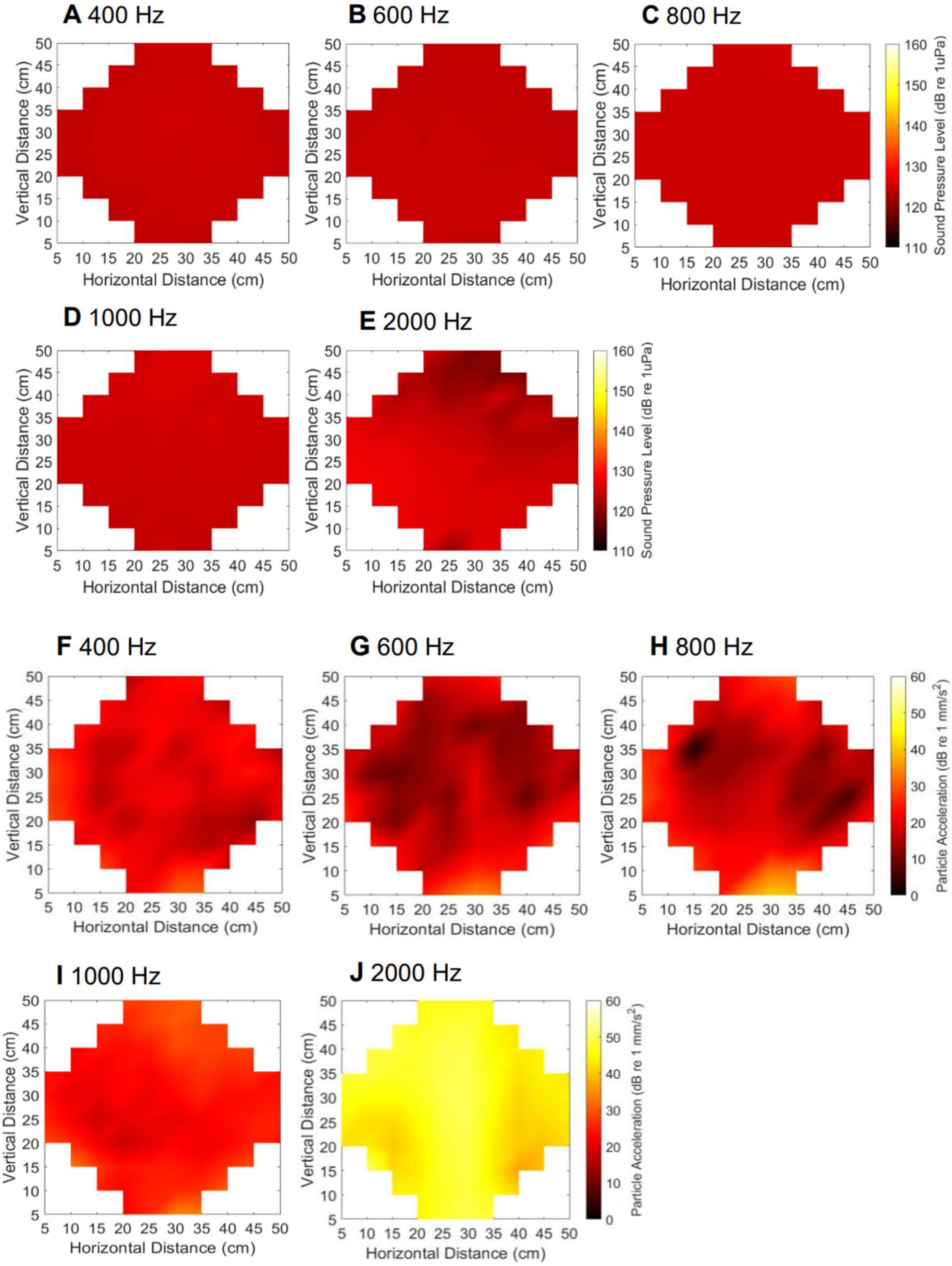


Figure 17 SPL maps (**A-E**) and PA maps (**F-J**) (15 cm depth) of a 1.0 s pure tone in the centre of a cylindrical arena submerged in a large water-filled tank at frequencies of 400 Hz, 600 Hz, 800 Hz, 1000 Hz, and 2000 Hz. The vertical and horizontal distance were measured as per the description in Section 3.2.

Table 9 The mean PA ± standard deviation of a 1.0 s pure tones in the cylindrical arena submerged in a large water-filled tank at frequencies of 400 Hz, 600 Hz, 800 Hz, 1000 Hz, 2000 Hz. Point SPL measurements were taken at three depths (5.0 cm, 15.0 cm, 25.0 cm) and PA (Experimental) was calculated from those values. PA (Predicted) was calculated using the plane wave approximation and the *Experimental – Predicted* PA ($PA_e - PA_p$) was recorded.

Frequency (Hz)	***15.0 cm (dB re 1 mm s^{-2}) Experimental***	***15.0 cm (dB re 1 mm s^{-2})* Predicted**	**Experimental – Predicted *(dB)***
400	21.1 ± 3.8	8.5 ± 0.4	12.6 ± 3.8
600	17.9 ± 5.6	11.9 ± 0.3	6.1 ± 5.6
800	20.3 ± 6.8	15.1 ± 0.2	5.2 ± 6.8
1000	24.8 ± 3.5	16.9 ± 0.5	7.9 ± 3.6
2000	45.3 ± 3.1	22.7 ± 2.4	22.6 ± 4.1

4.4.3 Phase One: Comparison of Setups

No difference was detected in the variance of experimental PA between the in-air tank and the submerged arena for frequencies of 400 Hz, 600 Hz and 1000 Hz (*F* = 1.45 – 0.79; *p* = 0.10 – 0.38, *df1* = 75, *df2* = 95) but a difference in variance was detected for 800 and 2000 Hz (*F* = 4.50 – 0.40; *p* = <0.001, *df1* = 75, *df2* = 95). There was a difference in the variance of SPL for all frequencies and depths (*F* = 5.53 – 2268.70; *p* = <0.001, *df1* = 75, *df2* = 95) between the in-air tank and the submerged arena. Therefore, these results suggest that the SPLs of the in-air setup were more heterogeneous than the submerged arena.

Next, Welch's *t*-tests were carried out, which detected the experimental (i.e., the PA calculated using the pressure data) PA to differ between the two setups, with PA being higher in the in-air tank than the submerged arena for 400 – 1000 Hz (*t* =14.61 – 40.53; *p* = <0.001, *df* = 170) and lower for 2000 Hz (*t* = -5.25, *p* = < 0.001, *df* = 170). Additionally, Welch's *t*-tests detected that the setup influenced the SPL at all frequencies and depths (*t* = 6.56 – 28.30; *p* = <0.001, *df* = 95.11 – 134.45). The in-air tank setup exhibited higher mean SPLs at all depths compared to the submerged arena setup.

The predicted PA was calculated for both the in-air tank and the submerged arena setup, which determined the PA had the sound propagated as a plane wave. The predicted PA was then compared to the experimental PA using Equation 11. For the in-air tank, the difference between the predicted PA and experimental PA was on average 15.0 ± 11.5 dB. The submerged arena had a smaller difference between the experimental and predicted PA at 10.9 ± 8.1 dB on average, depending on the frequency. This suggests the experimental PA and predicted PA are more similar for the submerged arena, meaning this setup provided a better approximation to the plane wave than the in-air tank.

4.4.4 Cylindrical In-air Tank: Phase Two

For each frequency, the SPL was heterogeneous across the horizontal plane (Figure 18). The most variation in this plane was observed at 800 Hz (Table 10). There was also a large difference between the centre SPL and the 15.0 cm depth SPL readings because the speaker was located in the centre of the arena, meaning higher values were recorded centrally. The SPL differed by ~14 dB between the top and bottom of the tank. Additionally, the PA was predicted to increase with frequency (Table 11; Appendix B) however, the experimental PA did not follow this trend. Hence, the difference between the experimental and predicted PA was large, with values of at least 25.9 dB.

Table 10 The mean SPL ± standard deviation of a 1.0 s pure tone calibrated at 145 dB re 1 µPa in the centre of a cylindrical arena at frequencies of 250 Hz, 400 Hz, 600 Hz, 800 Hz, 1000 Hz, and 2000 Hz. Point measurements were taken at three depths (5.0 cm, 15.0 cm, 25.0 cm). Centre SPL refers to the SPL in the centre of the tank.

Frequency (Hz)	*5.0 cm (dB re 1 µPa)*	*15.0 cm (dB re 1 µPa)*	*25.0 cm (dB re 1 µPa)*	*Centre SPL (dB re 1 µPa)*
250	119.1 ± 6.8	126.5 ± 11.2	135.7 ± 3.5	140.2 ± 4.4
400	120.1 ± 7.4	128.6 ± 11.1	138.6 ± 4.2	141.1 ± 4.7
600	119.2 ± 7.6	127.9 ± 10.3	131.0 ± 3.3	140.5 ± 5.0
800	119.0 ± 8.3	128.4 ± 10.0	128.2 ± 11.1	139.7 ± 4.6
1000	118.7 ± 7.8	128.6 ± 10.2	134.4 ± 4.4	140.9 ± 3.8
2000	126.7 ± 6.6	136.5 ± 7.2	141.0 ± 7.2	143.7 ± 1.9

Table 11 The mean PA ± standard deviation of a 1.0 s pure tones in the cylindrical arena at frequencies of 250 Hz, 400 Hz, 600 Hz, 800 Hz, 1000 Hz, and 2000 Hz. Point SPL measurements were taken at three depths (5.0 cm, 15.0 cm, 25.0 cm) and PA (Experimental) was calculated from those values. PA (Predicted) was calculated using the plane wave approximation and the *Experimental – Predicted* PA ($PA_e - PA_p$) was recorded.

Frequency (Hz)	*15.0 cm (dB re 1 mm s^{-2})* **Experimental**	*15.0 cm (dB re 1 mm s^{-2})* **Predicted**	**Experimental – Predicted** *(dB)*
250	52.9 ± 7.2	6.5 (s.d. 11.2)	46.7 ± 7.9
400	51.0 ± 6.8	12.6 ± 11.1	38.4 ± 7.8
600	50.1 ± 7.4	15.5 ± 10.3	34.6 ± 6.5
800	49.9 ± 7.1	18.5 ± 10.0	31.4 ± 6.2
1000	50.4 ± 6.0	20.6 ± 10.2	29.8 ± 6.8
2000	60.5 ± 5.0	34.5 ± 7.2	25.9 ± 7.9

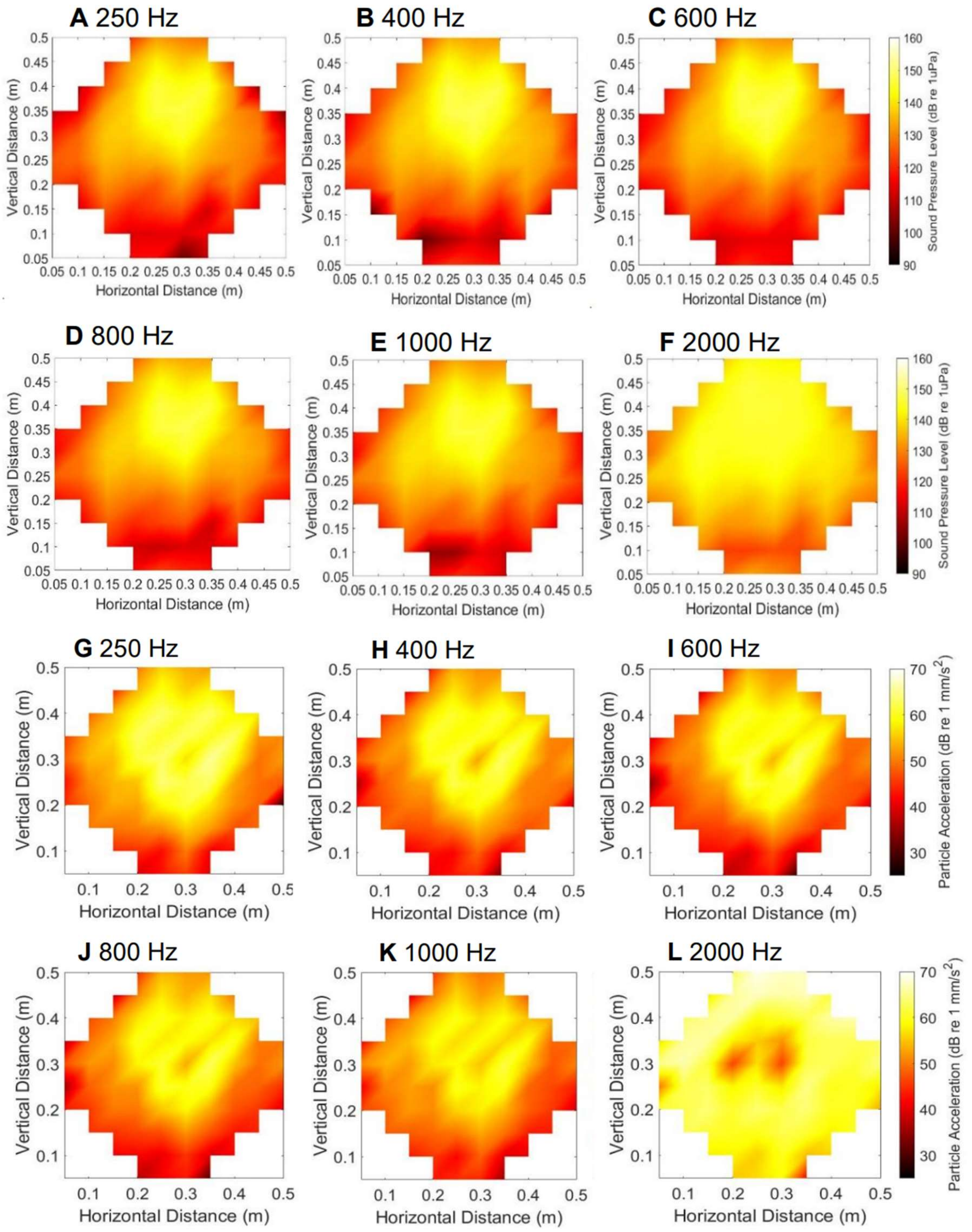


Figure 18 SPL maps (**A-F**) and PA maps (**G-L**) (15 cm depth) of a 1.0 s pure tone in the centre of a cylindrical arena situated on a concrete floor at frequencies of 400 Hz, 600 Hz, 800 Hz, 1000 Hz, and 2000 Hz. The vertical and horizontal distance were measured as per the description in Section 3.2.

4.4.5 Submerged Arena: Phase Two

The SPL was heterogeneous across the horizontal plane for each frequency (Figure 19 for the middle layer; Appendix B). Most of the variation in this plane was observed at 2000 Hz, which was as expected as it was the shortest wavelength (Table 12). The SPL differed by approximately 10 dB between the top and bottom of the tank. The PA was predicted to increase with frequency (Table 13; Appendix B) and, for the submerged tank, the experimental PA followed this trend. However, in these conditions, the predicted PA was higher than the experimental PA. Hence, $PA_e - PA_p$ (Equation 11) was less than the in-air tank, with a maximum difference of 14.8 dB.

Table 12 The mean SPL ± standard deviation of a 1.0 s pure tone calibrated at 145 dB re 1 µPa in the centre of a cylindrical arena submerged in a large water-filled tank at frequencies of 250 Hz, 400 Hz, 600 Hz, 800 Hz, 1000 Hz, and 2000 Hz. Point measurements were taken at three depths (5.0 cm, 15.0 cm, 25.0 cm). Centre SPL refers to the SPL in the centre of the tank.

Frequency (Hz)	*5.0 cm (dB re 1 µPa)*	*15.0 cm (dB re 1 µPa)*	*25.0 cm (dB re 1 µPa)*	*Centre SPL (dB re 1 µPa)*
250	136.3 ± 0.7	143.5 ± 0.6	146.9 ± 0.5	143.3 ± 0.4
400	137.9 ± 0.4	145.0 ± 0.5	148.3 ± 0.4	144.9 ± 0.3
600	137.5 ± 0.4	144.4 ± 0.4	147.6 ± 0.3	144.5 ± 0.3
800	137.2 ± 0.5	144.1 ± 0.5	147.8 ± 0.3	144.2 ± 0.3
1000	136.1 ± 0.6	143.2 ± 0.8	145.8 ± 0.3	143.4 ± 0.4
2000	139.9 ± 0.8	144.8 ± 0.6	141.0 ± 2.5	145.1 ± 0.1

Table 13 The mean PA ± standard deviation of a 1.0 s pure tones in the cylindrical arena submerged in a large water-filled tank at frequencies of 250 Hz, 400 Hz, 600 Hz, 800 Hz, 1000 Hz, and 2000 Hz. Point SPL measurements were taken at three depths (5.0 cm, 15.0 cm, 25.0 cm) and PA (Experimental) was calculated from those values. PA (Predicted) was calculated using the plane wave approximation and the *Experimental – Predicted* PA ($PA_e - PA_p$) was recorded.

Frequency (Hz)	*15.0 cm (dB re 1 mm s^{-2})* **Experimental**	*15.0 cm (dB re 1 mm s^{-2})* **Predicted**	**Experimental – Predicted** *(dB)*
250	15.5 ± 4.8	23.5 ± 0.6	-7.9 ± 4.7
400	16.0 ± 5.1	29.0 ± 0.5	-13.0 ± 5.1
600	17.2 ± 5.0	32.0 ± 0.4	-14.8 ± 5.0
800	19.8 ± 4.1	34.2 ± 0.5	-14.3 ± 4.2
1000	21.5 ± 3.7	35.2 ± 0.8	-13.6 ± 3.9
2000	45.6 ± 4.1	42.8 ± 0.6	2.8 ± 4.2

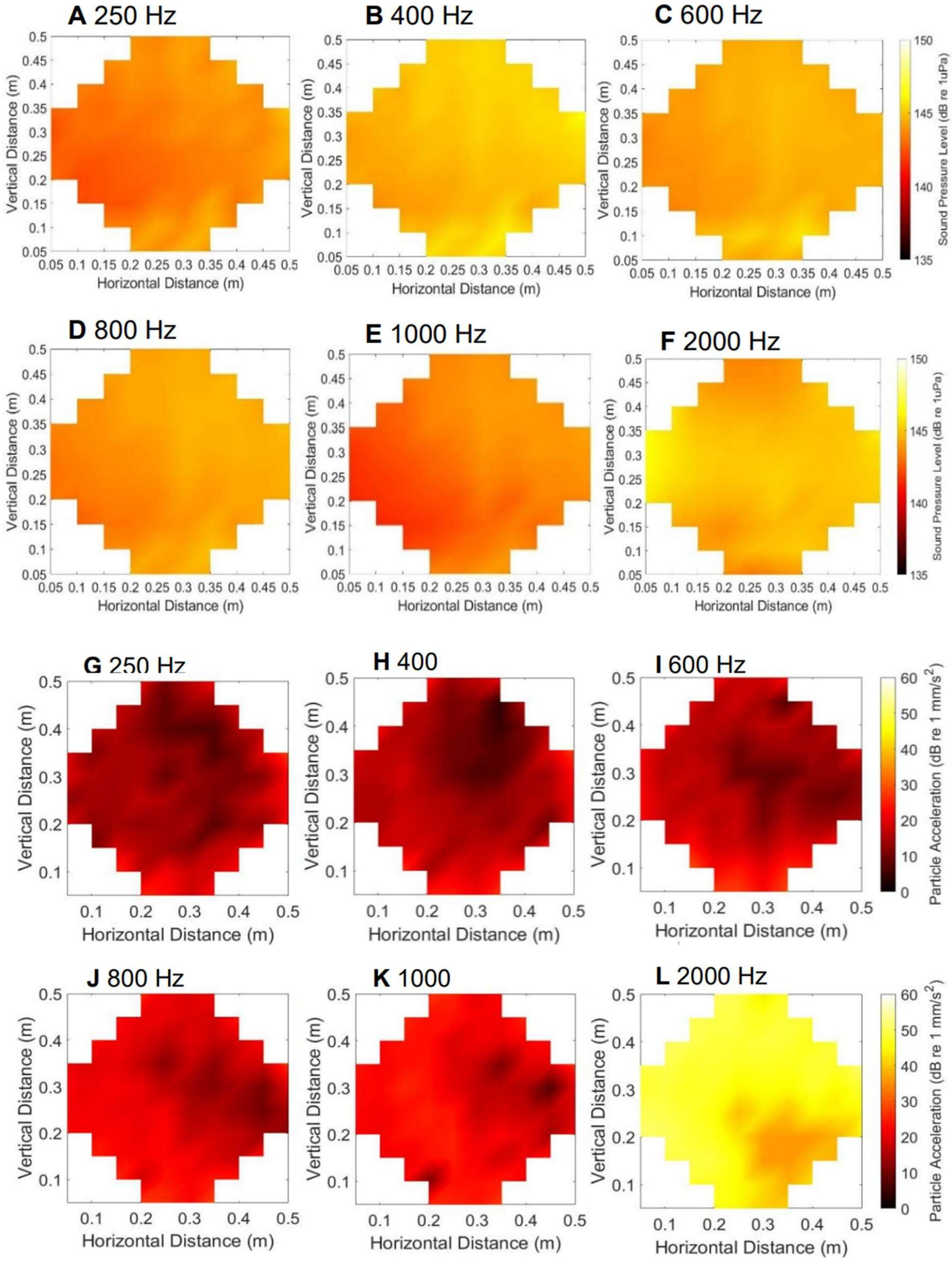


Figure 19 SPL maps (**A-F**) and PA maps (**G-L**) (15 cm depth) of a 1.0 s pure tone in the centre of a cylindrical arena submerged in a large water-filled tank at frequencies of 250 Hz, 400 Hz, 600 Hz, 800 Hz, 1000 Hz, and 2000 Hz. The vertical and horizontal distance were measured as per the description in Section 3.2.

4.4.6 Phase Two: Comparison of Setups

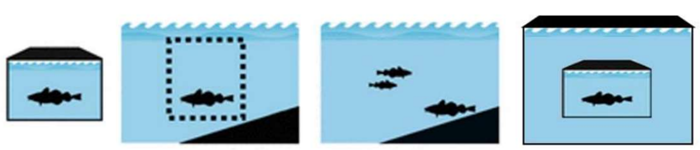
A difference in the variance of PA was detected between the in-air tank setup and the submerged arena setup for all frequencies (F = 1.75 – 3.06; p = <0.001 - 0.02, $df1$ = 75, $df2$ = 75) except 2000 Hz (F = 1.49, p = 0.09, $df1$ = 75, $df2$ = 75). The results indicated that the in-air tank exhibited higher variability in PA than the submerged arena. Similarly, a difference in the variance of SPL was detected between the two setups for all frequencies (F = 122.48 – 612.21; p = <0.001, $df1$ = 75, $df2$ = 75), with the in-air tank setup exhibiting higher variability in SPL than the submerged arena. Results suggested that the SPL and PA of the in-air setup were more heterogeneous than the submerged arena.

Welch's t-tests were carried out, showing PA was higher in the in-air tank setup than in the submerged arena setup (t = 19.90 – 37.59; p = <0.001, df = 119.30 – 150.0). The in-air tank setup exhibited lower mean SPLs at 15.0 cm (t =-13.92 – -9.94; p = <0.001, df = 75.25 – 76.23) and 25.0 cm (t =-23.03 – -6.91; p = <0.001, df = 75.08 – 81.00) than the submerged arena setup. At 5.0 cm depth, the setups possessed different SPLs at (p = <0.001 – 0.01), however SPLs were higher for 250 Hz (t = 35.34, df = 76.41) and 2000 Hz (t = 11.72, df = 77.42) in the in-air tank setup and lower for 400 – 1000 Hz (t = -3.70 – -2.61, df = 75.35 – 75.96).

The predicted PA was calculated for both the in-air tank and the submerged arena setup, which established the PA had the sound propagated as a plane wave. The predicted PA was then compared to the experimental PA by subtracting one from the other. For the in-air tank, the difference between the experimental PA and predicted PA was 25.9 – 46.7 dB. The submerged arena had a smaller difference between the experimental and predicted PA at -14.8 – 2.8 dB on average, depending on the frequency. Since the experimental PA was closer to the predicted PA for the submerged arena, it is suggested that this setup provides a better approximation to the plane wave than the in-air tank.

4.4.7 Overall Comparison of Setups

The in-air tanks from the phase one and phase two experiments were consistently more heterogeneous than the submerged equivalent, and both exhibited higher levels of PA. Using the in-air tank comparisons as guidance, the submerged arena setup used in this study was compared to three other setups (Figure 20) by considering acoustic validity, behavioural validity and experimental control (Slabbekoorn, 2016). This study improved the acoustic validity of the experimental arena compared to other indoor setups; however, it ranked lower than outdoor studies. As with other studies restricting fish movement, behavioural validity was low compared to *in situ* equivalents. Characteristically for *ex situ* studies, experimental control was high compared to outdoor experiments.



Acoustic Validity	Low	High	High	Medium
Behavioural Validity	Low	Low	High	Low
Experimental Control	High	Medium	Low	High

Figure 20 Comparison of indoor and outdoor experimental setups for fish behaviour studies. Acoustic validity, behavioural validity and the potential to control experimental design was assigned a 'high', 'medium' or 'low' classification. Slabbekoorn (2016) assessed (l-r): captive indoor - indoor studies using fish tanks; captive outdoor - outdoor studies using captive fish that can move in a restricted area; free-range outdoor - outdoor studies on free-ranging fish that swim into the selected study area. The setup added here was submerged indoor - indoor studies using fish tanks submerged in a larger tank.

4.5 Discussion

Small tanks have been a subject of debate amongst underwater bioacoustics researchers, due to their sound field complexity. This study quantified the sound field of three experimental tank setups and categorised a novel setup in terms of its acoustic and behavioural validity, as well as experimental control. The SPL heterogeneity was highest in the phase two in-air tank, followed by the phase one in-air tank and then the submerged arena, indicating that the submerged arena set up is an ideal substitute for creating a more homogeneous, replicable sound field. The PA was also higher in the two in-air tanks than the submerged arena, suggesting that the submerged arena tank walls were acoustically transparent, hence reducing boundary reflections. When the experimental PA was compared to a PA predicted using a plane wave equation, the submerged arena provided a better approximation. This study provided an alternative experimental setup for performing bioacoustics studies on fish that gave greater control over the stimulus that a fish experiences in laboratory-based experiments in terms of SPL and PA.

For open water fish species, experimental conditions should replicate far-field acoustics in which the PM and SPL increase proportionally (Slabbekoorn, 2016). However, if in-air tanks were used for open water species the PM would be disproportionally larger than SPLs compared to those open waters (Parvulescu, 1967; Rogers *et al.,* 2016). Therefore, the small in-air tanks would not be representative of an open-water habitat and may lead to misleading results (Popper and Hawkins, 2018). Nonetheless, fish species inhabiting shallow waters would encounter inhomogeneous sound fields due to turbulence (Tonolla *et al.,* 2009), close top and bottom boundaries, and volume reverberation (Hawkins and Myrberg, 1983; Lynch and Newhall, 2017). However, it is recommended that if non-uniform sound fields were required for a particular study, it would be more valid to modify a homogeneous sound field to the desired inhomogeneity. This approach would ensure the replicability of the sound field.

The results of this study are of particular importance to hearing experiments that were historically undertaken in small, in-air tanks. Whilst this has been discussed extensively elsewhere (see Section 2.2.1), the results from this study further suggest that some hearing experiments may be invalid due to the set up and the complexity of the sound field. In such conditions, the received level and source level may have been contradictory.

The submerged arena vastly improved the particle motion and SPL aspects of the sound field, primarily by reducing the average particle motion and reducing both SPL and particle motion variance. Submerging the tank in water removed air as a surrounding medium which meant the impedance and reverberation, factors that increase sound field complexity, were minimised (Rogers *et al.,* 2016). When comparing the submerged arena to other setups, the behavioural validity remains low compared to *in situ* experiments but retains high experimental control, practicality and feasibility (Slabbekoorn, 2016). Compared to *in situ* methodologies, the acoustic validity was lower, however there is a vast improvement to sound field homogeneity compared to small tank studies since a plane wave approximation was feasible. It is recommended that when cost, practicality and experimental control limit the use of *in situ* studies, a submerged tank would be a suitable alternative.

Whilst simply mapping the sound field may provide knowledge of the sound field, it does not account for the behavioural changes as a result of sound field inhomogeneity, nor does it account for the fact that complex sound fields often lack replicability. It is recommended, therefore, that consideration of the acoustic profile is made prior to conducting a study and that mapping is not a pretext for an unreliable sound field.

This study investigated two experimental setups: a ‘typical’ setup of a cylindrical (55.5 cm diameter) arena surrounded by air and placed on a concrete floor with a transducer situated in the arena, and a ‘novel’ setup of the same arena submerged in a large water tank with a speaker situated underneath. A submerged arena setup was chosen in order to reduce sound field inhomogeneity so that the level received by the fish is constant and known to the experimenter, as well as facilitating replicability. The in-air tank exhibited an inhomogeneous field with high levels of PA, whilst the submerged arena possessed a homogeneous sound field with PA measurements satisfying the plane wave approximation. Whilst the behavioural validity of the setup does not compare with *in situ* studies, submerging an experimental arena greatly improves the sound field homogeneity essential for acoustic and behavioural replicability in bioacoustics studies with fish.

Having, in Chapter 4, proven the effectiveness of reducing the internal reflectiveness of the arena walls, this will be used to provide the testing ground for Objective 1 (Table 1; determine the startle response threshold in goldfish to pure tone acoustic stimuli) and Research Question 1 (Which frequency (of a 120 ms pure tone) evokes an innate response in goldfish using the least acoustic energy?) in Chapter 5. It was also used to achieve Objective 2 (quantify innate responses of goldfish responding to a 120 ms pure tone acoustic stimulus in presence and absence of band-limited (100 – 2500 Hz) random noise) and Research Question 2 (Table 1; What effect does noise have on the startle responses of goldfish to a 120 ms pure tone?) in Chapter 6.

Chapter 5 Experiment 1: Applying appropriate frequency criteria to advance acoustic behavioural guidance systems for fish

5.1 Abstract

Using the submerged arena setup from Chapter 4, the next chapter focuses on an experiment using goldfish to fulfil Objective 1. Focusing on the broader context, the aforementioned deterrents that use acoustics to guide fish away from dangerous areas depend on the elicitation of avoidance in the target species (Section 2.6). Acoustic deterrents select the optimum frequency based on the assumption that the highest avoidance is likely to occur at the greatest sensitivity. However, such an assumption may be unfounded. Under laboratory conditions, the startle thresholds of individual goldfish exposed to 120 ms tones at six frequencies (250 Hz, 400 Hz, 600 Hz, 800 Hz, 1000 Hz, 2000 Hz) and SPLs (115, 125, 135, 145 dB re 1 µPa) were quantified. The startle threshold defined as the SPL at which 25.0% of the tested population that startled was calculated and compared to the hearing threshold obtained using AEP and PA threshold data. The optimum frequency to elicit a startle response was 250 Hz; different from the published hearing and PA sensitivities based on audiograms (~600 Hz). The difference between the startle threshold and published hearing threshold data varied from 47.1 dB at 250 Hz to 76.0 dB at 600 Hz. This study demonstrates that information obtained from audiograms may poorly predict the most suitable frequencies at which avoidance behaviours are elicited in fish.

5.2 Introduction

Having shown in Chapter 4 that the apparatus designed in this thesis can provide a more homogeneous soundfield compared to a typical rectangular in-air tank, it is now possible to address Objective 1 (determine the startle response threshold in goldfish to pure tone acoustic stimuli) and answer Research Question 1 (Which frequency (of a 120 ms pure tone) evokes an innate response in goldfish using the least acoustic energy?). Addressing this question is important because the efficacy of environmental impact mitigation technology can be highly variable with site, context, and species (e.g., Roscoe and Hinch, 2010), as illustrated for both fish passes (Brown *et al.* 2013) and physical screens, which themselves can be damaging if poorly designed (e.g., Swanson *et al.,* 2005; Black and Perry, 2014). Recently, efforts have been directed at improving the effectiveness of this technology through a process of returning to fundamental first principles to better understand the mechanisms that determine efficiency (e.g., for the influence of hydrodynamics Knapp *et al.,* 2019; for species Noonan *et al.,* 2012; for personality Mensinger *et al.,* 2021) and considering the combination of technologies to achieve synergistic effects. In particular, behavioural deterrents have been developed with the view to using them in combination with physical screens to enhance overall screening and guidance (e.g., in application of the marginal gains concept to fish screening; Deleau *et al.,* 2019; Miller *et al.,* 2022).

Behavioural guidance systems take advantage of the innate behaviours elicited by fish in response to a particular stimulus to modify the movement trajectories of a target species. Although cues that initiate either avoidance or attraction may in theory be used, in practice those that elicit an aversive reaction (e.g., akin to an anti-predator-like response, Short *et al.,* 2020; Currie *et al.,* 2021) are more commonly used. A wide variety of stimuli, mostly abiotic, have been employed as deterrents, including electricity (Miller *et al.,* 2021), strobe lights (Johnson *et al.,* 2005) and acoustics (e.g., experimentally Deleau *et al.,* 2019; 2020; and *in situ* Piper *et al.* 2019). Sound can be advantageous under some contexts because the stimulus is omnidirectional, and so can simultaneously reach a number of target individuals within a locality and is not affected by changes in illumination or turbidity (as are those that are mediated through vision). As a result, acoustic deterrents have been widely employed to reduce fish mortality at water abstraction points (Maes *et al.,* 2004), or to control the dispersal of invasive species e.g., bighead carp, in the Great Lakes, USA (Vetter *et al.,* 2017).

A limitation of acoustic deterrents is that their effectiveness can be highly variable (Vetter *et al.*, 2015; Jesus *et al.*, 2018; Putland and Mensinger, 2019). For example, deterrence efficiency (Appendix A) has been observed to range from 5.0% to 90.0% for juvenile Chinook salmon (*Oncorhynchus tshawytscha;* Mueller *et al.,* 1998 under experimental conditions) and from 11.0% (Turnpenny and Nedwell, 2003) to 87.9% (Maes et al., 2004) for European Sprat (*Sprattus sprattus*). There are many explanations proposed for such inconsistencies. The acoustic cues used may have been at frequencies outside the hearing range of the target species (Gregory and Clabburn, 2003), or the ambient sound levels were not accounted for (Putland and Mensinger, 2019). Alternatively, the results may reflect a lack of consideration of the relationship between hearing abilities (defined by the frequency range and hearing sensitivity) and the behavioural response of the target species (Putland and Mensinger, 2019). It had been previously assumed that, for different frequencies, there is a uniform difference between the hearing threshold and the level that elicits a behavioural response (Section 2.6); this difference may be expressed in dB_{ht} (Turnpenny and O'Keefe, 2005). This logic suggests that, for a fixed stimulus level, the frequency most likely to elicit a response is the one at which the animal's hearing is most sensitive (Fish Guidance Systems, 2023), i.e., where the sensory threshold is lowest. Such an assumption is not evidence-based and has been dismissed among some researchers (Sisneros *et al.,* 2016; Popper *et* *al.,* 2014). Nevertheless, some industry practitioners utilise the most sensitive hearing level to predict the behavioural response of fish when developing behavioural deterrents, including the use of audiograms in the design of deterrents for invasive carp (Fish Guidance Systems Ltd, 2023).

This experimental study fulfilled Objective 1 and examined the relationship between the frequency of hearing sensitivity and the startle response thresholds of fish. This study determined the: (1) presence and absence of startle responses to determine the proportion of the population that exhibited avoidance and, then, the relationship between the probability of startling and frequency (250 Hz, 400 Hz, 600 Hz, 800 Hz, 1000 Hz, 2000 Hz) and SPL (115, 125, 135, 145 dB re 1 µPa); (2) startle threshold for each frequency defined as the SPL at which at least 25.0% of the sampled population elicited a startle reaction; and (3) relationship between the startle threshold, the hearing threshold, and the PA threshold at each frequency based on existing data obtained from audiograms for the subject species.

5.3 Methods

5.3.1 Fish maintenance

Goldfish (n = 80; mean standard length [SD]: 64.0 [5.3] mm; mass: 10.2 [2.4] g) were transported from Hampshire Carp Hatcheries (UK) in oxygenated water to the ICER, University of Southampton, in November 2020. They were maintained in a holding tank (1.5 m long, 1.0 m wide, and 0.8 m deep, filled to 68.0 cm water depth) containing ~1200 L of aerated, filtered and dechlorinated water under an artificial photoperiod matching the light levels at the time of year (10:14 hr light:dark) and fed once daily (Tetra goldfish flakes; protein: 42.0%). Ammonia (0.1 [0.2] ppm), nitrites (0.0 [0.0] ppm), nitrates (40.0 [0.0] ppm), pH (pH 8.2 [0.0]) (API Freshwater Master Test Kit) and temperature (12.3 [1.2] °C) were monitored daily. Fish were acclimated in the holding tank for at least four days before 12 individuals were selected and moved to the experimental facility (<700 m) the night prior to the start of trials where they were maintained in a pre-test tank (84.0 cm long, 50.0 cm wide, and 65.0 cm deep, filled to 54.0 cm water depth) containing ~290 L of aerated and dechlorinated water for a further 13 hours to acclimate to the temperature of the experimental tank (temperature: 13.2 [0.5]°C). On completion of each trial, the subject fish (a single individual per trial) were placed in a post-test tank and returned to a separate holding tank at the ICER Facility at the end of the day.

5.3.2 Experimental setup

Trials were conducted in the submerged cylindrical tank described in Section 3.2. A black polyethylene mesh (6 mm mesh width) covered the tank to prevent escape of leaping fish. The test cylinder was filled to a depth of 30.0 cm with dechlorinated conditioned water that was replaced (~20 L water change) after each trial to maintain water quality. Acoustic stimuli were produced and mapped according to Section 3.3. Each trial was recorded and analysed at a later date.

5.3.3 Experimental design

The study consisted of 20 replicates of 24 treatments based on a combination of one of six frequencies (250 Hz, 400 Hz, 600 Hz, 800 Hz, 1000 Hz, 2000 Hz) and four SPLs (115, 125, 135, 145 dB re 1 µPa). These frequencies were selected, as previous studies had established a hearing threshold at these SPLs, which allowed for feasible comparison (Appendix C). Lower frequencies of 100 Hz or 150 Hz could not be facilitated due to the acoustic limitations of the equipment used. Steps of 5 dB re 1 µPa were selected to enable high-resolution analysis, whilst minimising the number of fish used in the study. If steps of 3 dB were selected, more trials (therefore more individuals) were needed to gain information across the SPL range. Conversely, if 6 dB steps were selected, this may have reduced the resolution of the data across the chosen SPL range.

Prior to the start of each trial, a single fish (N = 80) was acclimated in the experimental cylinder for 30 min. Fish experienced a total of six exposures (one at each test frequency selected at random) at one of the four randomly assigned test SPLs (see Table 14 for an example). Each exposure consisted of a sinusoidal 120 ms tone ramped with a 20 ms Hanning taper and was followed by 6 min of silence before the next exposure. Although latencies of Mauthner cell activation in goldfish is 5 – 10 ms, the tone was played at 120 ms so that it was sufficiently short to elicit a startle response but long enough to enable the frequency spectrum to be well defined at this lower signal duration (Eaton, 1977; Zeddies and Fay, 2005). Fish behaviour was continuously video recorded during the trial, and each fish was used in one trial only.

Table 14 An example of the selection of the treatments experienced by an individual fish. Trial (N = 80) represents the entire period in which an individual fish experienced the acclimation followed by six treatments. Treatment is each of the 24 combinations of SPL and frequency (n: treatment 1 - 24). Exposure represents the n^{th} treatment (1-6) experienced by an individual fish in one trial.

Trial	*Frequency (Hz)*	*SPL (dB re 1 µPa)*	*Order of Exposure*
1	600	115	1
1	800	145	2
1	400	115	3
1	1000	135	4
1	250	125	5
1	2000	145	6

5.3.4 Acoustic stimuli and sound mapping

The measured ambient SPL (TC4032, manufacturer-calibrated sensitivity -170 dB re: 1 V µPa; Teledyne Reson, USA) was on average less than 96 dB re 1 µPa, which was the electrical noise floor of the measurement system being used. The same soundfield data was used in Section 4.4.5. The SPL was relatively uniform across the horizontal plane for each frequency (Appendix B), with the greatest variation observed at the highest frequency (shortest wavelength) at 2000 Hz (Table 12). The SPL differed by ~10 dB between the top and bottom of the tank. The PA increased with frequency and varied up to 4.8 dB within the horizontal plane (Figure 19).

5.3.5 Behavioural and Data analysis

The startle responses were recorded (Section 3.5) and the video footage was reviewed blind of the treatment used and in a random order such that 99.5% of the recorded startles were consistent between the original data collection and the review.

To determine whether external factors may have confounded the results by influencing the probability of startling, a reductive model was developed. Factors included in the model were: tank days (minimum number of days in the holding tank); time (the beginning of the trial to the nearest hour); temperature difference between the experimental and holding tank (°C); and mass (g). The initial GLMM contained all predictor variables with exposure (order of stimulus exposure) and trial included as random effects, and manual backwards selection using variable significance (significance at $p < 0.05$) was undertaken as model simplification. No random effects were detected (Table 15) so fixed variable GLMs were used for further analysis. Exposure and trial were included in a GLM as fixed effects alongside the other external factors in logistic regression, however, none predicted that a startle would occur, and the null model (Intercept) had the optimum AIC (Table 16). Exposure was included since the individuals were subject to multiple stimuli; this identified that no tolerance offered during the duration of the trials.

Table 15 Random effects included in GLMMs developped to determine if external factors affect the presence of a startle response to 120 ms pure tones in goldfish.

Random Effect	***Std. dev***	***AIC***
Null (Intercept)	-	506.3
Exposure:Trial	<0.001	510.3
Trial	<0.001	508.3
Exposure	<0.001	508.3

Logistic regression was used to determine the influence of SPL and frequency on whether a startle response would occur. Logistic regression curves were, therefore, plotted with SPL against the probability of startle (the number of individuals that startled out of the total number tested) for each frequency and the significance of the relationship recorded. The logistic regression was then used to determine the 25.0% startle threshold. The 25.0% threshold was selected based on the observation that a maximum of 25.0% of the population startled at 600 Hz. To determine the SPL and PA at which 25.0% of the population startled at each frequency was predicted using the GLM. The output stated the probability that a startle occurred for a stated SPL (or PA). Both the SPL and PA were chosen and refined until the output was within 0.001.

Table 16 Variables included in GLMs developpped to determine if external factors affect the presence of a startle response to 120 ms pure tones in goldfish.

	Variables in Model[b]							
Model[a]	***Exposure***	***Mass***	***Tank Days***	***Temp Diff***	***Time***	***Trial***	***AIC***	***ΔAIC***
Null							506.3	0.00
1	x	x	x	x	x	x	514.8	8.5
2	x	x	x	x	x		512.8	6.5
3	x	x	x		x		511.2	4.9
4	x		x		x		509.6	3.3
5			x		x		508.1	1.8
6					x		507.3	1.0

[a] *The null model is shown without any predictor variables.*

[b] *Exposure (the nth stimulus played 1-6); mass (the mass of the individual); tank days (minimum number of days in the husbandry tank); temp diff (the difference between the experimental tank and the holding tank); time (the beginning of the trial to the nearest hour); trial (the trial number/individual).*

The proportions obtained by prediction using the GLM, quantified as startles per total number of individuals tested at each treatment, were represented on a plot of SPL against frequency and a plot of PA against frequency. Both 1000 Hz and 2000 Hz were omitted since extrapolation was unfeasible due to an insignificant logistic relationship (see Section 2.5.1). The 25.0% startle threshold was plotted on both figures alongside the hearing threshold for goldfish, obtained by averaging data from 23 studies (Appendix C). Mean values of hearing thresholds obtained via AEP were plotted with a 95.0% confidence interval to allow for comparison between the startle and hearing thresholds. The same analysis was completed for PA and compared to a single PA threshold (Radford *et al.,* 2012).

The difference between the startle and the hearing thresholds were calculated and followed a Gaussian distribution, determined by visual inspection of the qq curve. The *ΔThreshold* was defined as the difference between thresholds for hearing (Appendix C) and 25.0% startle response. The hearing threshold data was based on an average of 16 papers (a large sample size, allowing for comparison despite methodological differences), and a 95.0% confidence interval was also established. Notably, papers that qualified to be included in this data had underwater speakers, as opposed to in-air speakers. Although the tanks sizes may and responses may have varied, the use of a large number of papers The sound pressure *ΔThreshold* was calculated by subtracting published AEP hearing threshold values from the 25.0% startle threshold at each frequency. The same method was used for the PA *ΔThreshold* such that the published PA hearing threshold values were subtracted from the 25.0% startle threshold at each frequency. To assess the influence of frequency on threshold range, a GLM with Gaussian error structure was applied for both SPL and PA *ΔThreshold*. Planned *a priori* contrasts were used to determine whether the SPL *ΔThreshold* at 250 Hz, 400 Hz, 600 Hz and 800 Hz differed from each other. This was not undertaken for PA, as there was only a single data point for each frequency since the PA threshold was based on a single study.

Secondary behaviours were recorded and documented as a full turn (>90°), a half turn (45° – 90°) and a stop (stop within 1.0 s of the stimulus presentation). Each secondary behaviour was recorded as present or absent for each treatment, thus residuals were modelled using a binomial distribution. Bar plots were created showing the number of secondary behaviours exhibited at each SPL for every frequency tested. Startle responses were also shown on the plots for comparison. Following this, logistic regression was used to determine if there was a relationship between the secondary behaviours and increasing SPL for each frequency.

5.4 Results

Startles were observed in all frequency treatments. The probability (Figure 21) that an individual startled decreased with frequency ($z = 6.08$, $p = <0.001$), and within each frequency treatment increased with SPL for 250 Hz ($z = 4.89$, $p = <0.001$), 400 Hz ($z = 3.93$, $p = <0.001$) and 600 Hz ($z = 2.00$, $p = 0.045$), but not for 800 Hz ($z = 1.46$, $p = 0.14$), 1000 Hz ($z = 0.00$, $p = 1.00$) or 2000 Hz ($z = 0.38$, $p = 0.71$).

At least 25% of the test population startled at frequencies that ranged from 250 – 800 Hz. A higher SPL (Figure 22a) and PA (Figure 22b) was required to elicit a response for 25.0% of the population at 600 Hz and 800 Hz, compared to 250 Hz and 400 Hz. The published hearing sensitivity threshold for SPL had a minimum at ~600 Hz and at ~400 Hz for PA, after which the hearing threshold subsequently increased with frequency. The SPL eliciting a startle response for 25.0% of the population at 250 Hz, 400 Hz, 600 Hz, and 800 Hz was 123, 128, 145 and 145 dB re 1 µPa, respectively. The PA eliciting a startle response for 25.0% of the population at 250, 400, 600, and 800 Hz was -3, 2, 20 and 22 dB re 1 mm s^{-2}, respectively.

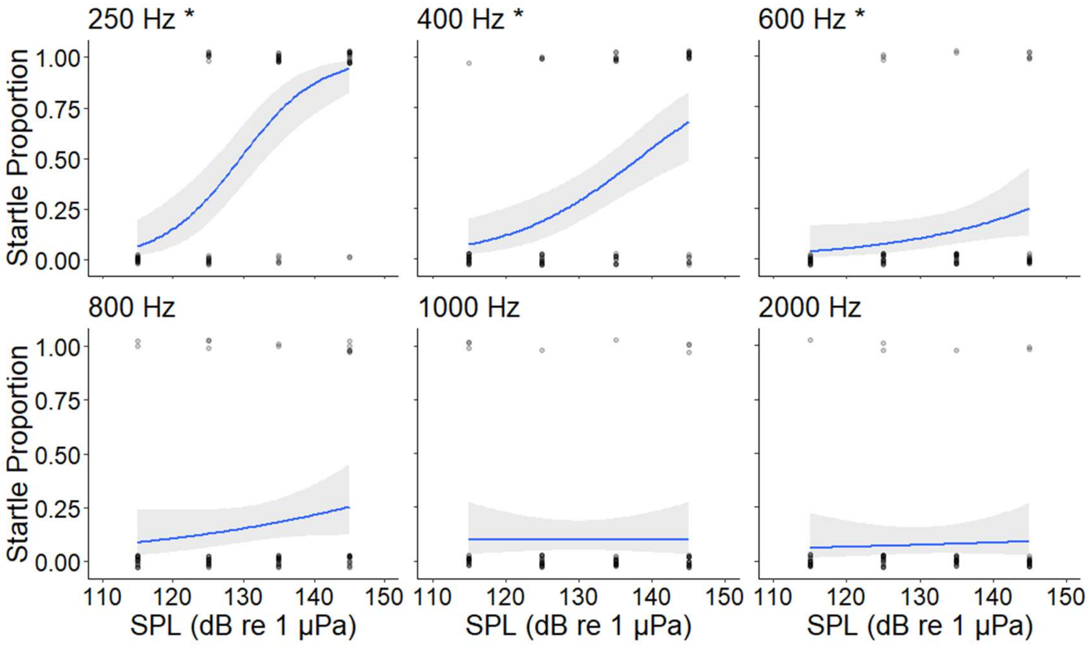


Figure 21 Logistic regression curves illustrating the proportion of goldfish that startled in response to a 120 ms pure tone at 115; 125; 135; 145 dB re 1 µPa. The asterisk (*) denotes significance (p < 0.05). Results were plotted for each frequency (250; 400; 600; 800; 1000; 2000 Hz). The grey regions indicate 95.0% confidence intervals.

The *ΔThreshold* for SPL increased with frequency, i.e., AEP (Figure23a; $t = 8.37$, $p = < 0.001$). The small sample size for the PA *ΔThreshold* meant only visual inspection was conducted. Visual inspection of the plot (Figure 23a) suggested the *ΔThreshold* increased with frequency up to

600 Hz but decreased at 800 Hz. The SPL *ΔThreshold* for 250, 400, 600 and 800 Hz was 43, 56, 74 and 73 dB, when comparing the startle threshold to the AEP hearing threshold. When comparing the startle threshold to the PA threshold (Figure 23b), the *ΔThreshold* was 52, 62, 80 and 76 dB for 250, 400, 600 and 800 Hz, respectively. *A priori* contrasts (Table 17) revealed the *ΔThreshold* at 250 Hz was less than all other frequencies ($p < 0.001$), and the *ΔThreshold* at 400 Hz was lower compared to 600 and 800 Hz ($p < 0.001$).

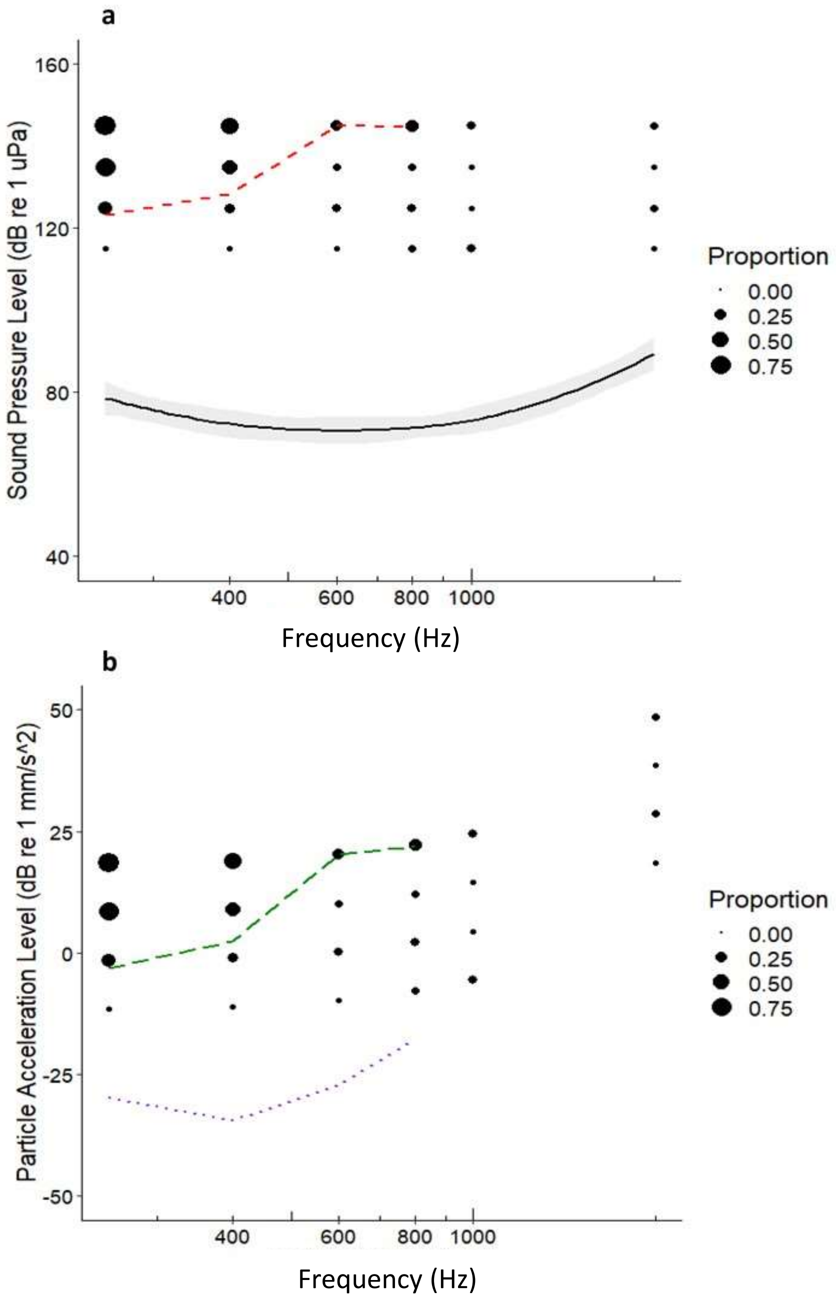


Figure 22 The startle threshold **a** (dashed line) indicating the SPL and **b** (long-dashed line) indicating the PA level for each frequency treatment at which 25.0% of the test population responded to a 120 ms pure tone stimulus. The solid circles indicate the proportion of the test population that startled. Hearing sensitivity thresholds based on the published literature are indicated by **a** AEP (solid line, Appendix C) and **b** the PA level (dotted line, Radford *et al.,* 2012). The shaded area indicates the 95.0% confidence interval.

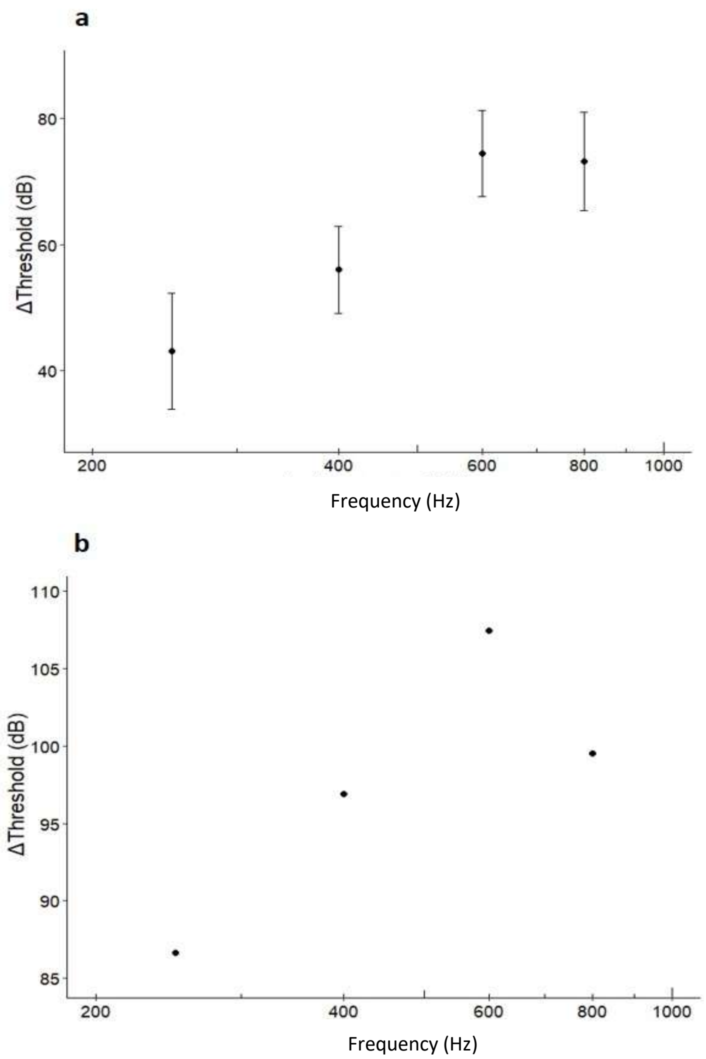


Figure 23 The SPL ΔThreshold between the 25.0% startle threshold and the **a** mean AEP hearing threshold (± SD) and **b** the PA threshold (N = 1, therefore SD was not included) from previously published data of goldfish at 250 Hz, 400 Hz, 600 Hz, 800 Hz.

Table 17 Planned *a priori* contrasts between ΔThreshold at four frequencies (250 Hz, 400 Hz, 600 Hz, 800 Hz). The ΔThreshold is the difference between the startle response threshold obtained in this study and existing published hearing threshold data for goldfish (Appendix C).

Contrast	*Effect of group*	
	z	*p*
250 Hz vs 400 Hz	-3.76	<0.001
250 Hz vs 600 Hz	-10.56	<0.001
250 Hz vs 800 Hz	-8.77	<0.001
400 Hz vs 600 Hz	-6.91	<0.001
400 Hz vs 800 Hz	-5.10	<0.001

The number of stops decreased with SPL (Figure 24) for 250 Hz (*p* = 0.045, *z* = -2.00), but increased with SPL at 600 Hz (*p* = 0.03, *z* = 2.13). However, there was no relationship between stops and SPL at 400 Hz (*p* = 0.51, *z* = -0.66), 800 Hz (*p* = 0.66, *z* = 0.44), 1000 Hz (*p* = 0.17, *z* = 1.39), or 2000 Hz (*p* = 0.17, *z* = 1.3). Additionally, the number of stop behaviours did not change over time, i.e., with each exposure (*p* = 0.06 – 0.91; *z* = -1.85 – 0.28). Increasing the SPL did not affect the outcome of a full turn for any frequency (*p* = 0.31 – 1.00; *z* = -1.01 – 0.90), nor did it change over time for any frequency (*p* = 0.28 – 0.98; *z* = -0.82 – 1.08). Similarly, increasing SPL did not affect the outcome of a half turn for any frequency (*p* = 0.38 – 0.87; *z* = 0.21 – 0.87), nor did it over time (*p* = 0.10 – 0.45; *z* = -1.66 – 1.67).

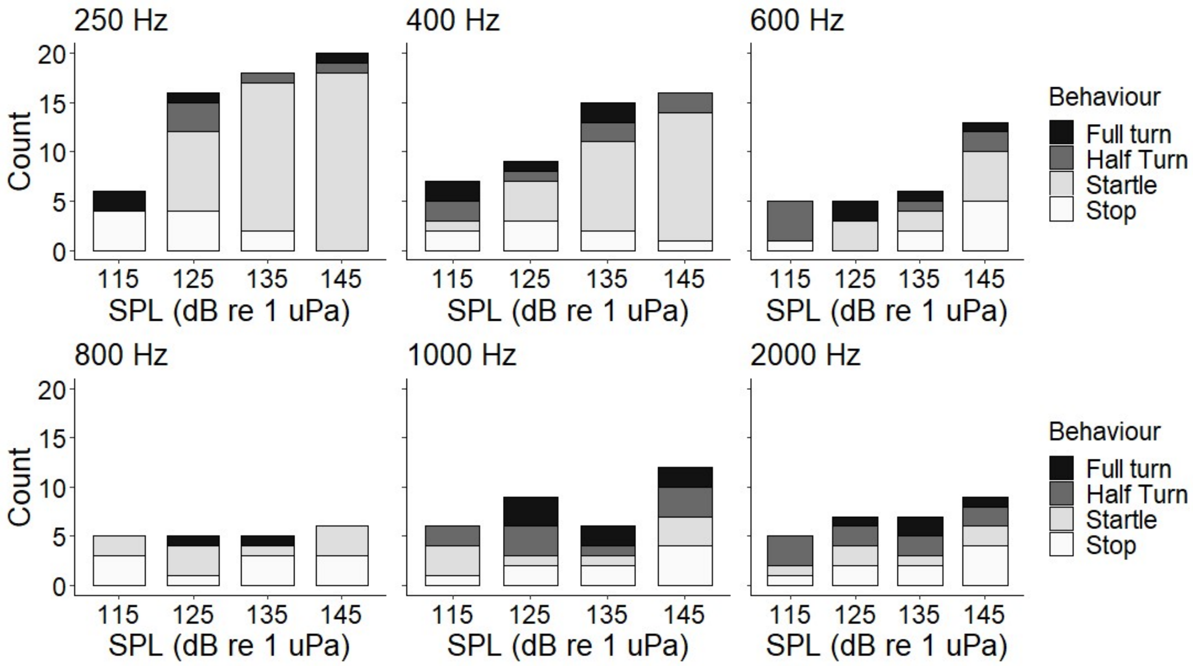


Figure 24 Bar plots showing the number of full turns (>90°), half turns (45° – 90°), startles (change in body tortuosity and direction) and stop (stop within 1.0 s) exhibited by goldfish responding to a 120 ms pure tone at six frequencies (250 Hz, 400 Hz, 600 Hz, 800 Hz, 1000 Hz, 2000 Hz) and four SPLs per frequency.

5.5 Discussion

A common assumption in the design of fish deterrents is that the frequency of greatest hearing sensitivity corresponds with that most likely to elicit an avoidance response in the species of interest (Fish Guidance Systems, 2023). The purpose of AEBR in this study was not to establish a hearing threshold, but to produce a behavioural threshold that can be used to identify the optimum frequency of avoidance for acoustic deterrents. Instead, one-quarter of all fish tested in the 250 Hz treatment startled in response to an acoustic stimulus of 123 dB re 1 µPa. This frequency is lower than that at which hearing is most sensitive, i.e., approximately 600 Hz; a frequency at which a higher SPL of 145 dB re 1 µPa was required to achieve an equivalent proportion of startles. Similarly, the number of stop behaviours decreased as the number of startles increased for 250 Hz and (subjectively) 400 Hz, meaning an individual may elicit a stop until it is sufficiently loud enough to elicit a startle response. Therefore, at 600 Hz, where the stop behaviour increased with frequency, the SPL was not sufficiently high enough to elicit a startle response, suggesting that at this frequency a much higher SPL that may be damaging to the ear would be required. These findings suggest that design criteria for behavioural deterrents should be reviewed and further advanced by returning to first principles to determine the characteristics of the sound field, including frequency and SPL, that are most likely to induce avoidance behaviour as required to meet efficiency targets.

Insight into the relationship between the frequency of minimum hearing threshold as indicated by audiograms and that which most effectively elicits a behavioural response may be informed by understanding of human audiology. Similar to the observations reported in this study for fish, in humans the thresholds of hearing and loudness discomfort, a measure of behavioural intolerance, do not always occur at the same frequencies (Sherlock and Formby, 2005). Loudness discomfort thresholds were 4 dB lower for 4000 Hz tones compared to lower frequencies, showing humans do not tolerate higher frequencies (Sherlock and Formby, 2005). In other cases, humans find noise irritating at frequencies lower than those at which hearing is most sensitive, such as hums ranging from about 10 Hz to 200 Hz (Leventhall, 2004). The fish in this study were more responsive at the lower frequencies within their hearing range.

Our findings complement those of another study that investigated the behavioural reaction threshold of fish *in situ*, focusing on marine species in the context of impacts of anthropogenic noise (Kastelein *et al.,* 2008). In agreement with our findings, these authors also observed that the difference between hearing and reaction thresholds varied with frequency. However, they found that the eight subject species they studied reacted very differently, making generalisations difficult, and perhaps unwise. In our study, we selected a freshwater species with specialised hearing and a high sensitivity to sound (Kenyon *et al.,* 1998; Ladich and Fay, 2013). Goldfish may be more reactive at the lower end of the hearing range because they are more sensitive to particle motion at 125 – 250 Hz (Radford *et al.,* 2012).

At frequencies below 400 Hz (Higgs and Radford, 2012), there may be functional overlap of the neuromast and the otolith (Braun and Sand, 2013). Both the otolith and the neuromast detect particle displacement, meaning differentiation between the contribution of the two to hearing is challenging since the inputs for auditory and lateral line nerves lie in close contact, meaning electrophysiological techniques to measure hearing are likely to detect both inputs (Coombs and

Montgomery, 1999; Higgs *et al.,* 2006). However, we would expect this same mechanism to be contributing to the electrophysical audiogram as well as the behavioural methods applied in this study. The importance of particle motion associated with low-frequency sound fields has previously been considered in the development of behavioural deterrents, particularly in respect to the protection of European eel (*Anguilla anguilla*; Sand *et al.,* 2000; Piper *et al.,* 2019).

As the current assumption about the relationship between detection of a sound and response to it was contradicted by the results reported here, the implications for future fish deterrent design should be considered. It is no longer valid to accept the premise that the frequency of highest probability of reaction corresponds with the greatest sensitive of hearing or that the difference (*ΔThreshold*) between the two remains constant independent of frequency. Our findings support the arguments of others (Hawkins and Popper, 2014; 2016; Popper and Hawkins, 2019) that the logic that underpins the use of dB_{ht} may be flawed, at least in the context described here, and may provide an explanation, at least in part, for why the efficiency of acoustic deterrents can be highly variable (Maes *et al.,* 2004; Putland and Mensinger, 2019).

This study highlights factors that should be further considered in advancing the design of acoustic fish deterrents. First, the importance of behavioural studies in understanding the response of fishes to sound (Popper and Hawkins, 2019) is reiterated, rather than developing design criteria based on data obtained from physiological methods alone. Quantification of thresholds of reaction is more appropriate from a fisheries management perspective, as avoidance is the often desired response in fish guidance system. Therefore, approaches such as those based on AEBR (Zeddies and Fay, 2005; Alderks and Sisneros, 2013) as used in this study, rather than AEP derived audiograms, are most appropriate because they determine the lowest SPLs over a range of frequencies at which a reaction is elicited. Second, once appropriate frequencies are identified there is a need to select SPLs that evoke the response desired accounting for ambient environmental conditions at the site of interest, i.e., considering appropriate SNRs and the effect of background noise (Objective 2). Furthermore, other acoustic parameters should be characterised, including spatial distribution and temporal patterns (Objective 3).

Based on this study, it recommended that future research is directed at quantifying variability as a result of abiotic (e.g., the hydrodynamic environment; Wysocki *et al.,* 2007a) and biotic factors, particularly between species and developmental stage or size (Kastelein *et al.,* 2008) with the view to identifying appropriate representatives' guilds of commercial and conservation concern. Likewise, greater understanding is needed of how response to acoustic signals may differ between species that are typically solitary and those that occupy positions within groups i.e., aggregations, shoals and schools (Short *et al.,* 2020; Currie *et al.,* 2021).

Chapter 5 used the submerged cylindrical arena of Chapter 4 to address Objective 1 (Table 1; Determine the startle response threshold in goldfish to pure tone acoustic stimuli) and Research Question 1 (Which frequency (of a 120 ms pure tone) evokes an innate response in goldfish using the least acoustic energy?). Given the frequency of a 120 ms pure tone evokes an innate response in goldfish at 250 Hz (i.e., a frequency other than that of best hearing), the foundation is present to address Objective 2 (To quantify innate responses of goldfish responding to a 120 ms pure tone acoustic stimulus in presence and absence of band-limited random noise) and Research Question 2 (What effect does noise have on the startle responses of goldfish to a 120 ms pure tone?).

Chapter 6 Experiments 2a and 2b: Using fine and coarse-scale analysis to quantify startle responses of fish in presence of noise to enhance acoustic deterrence

6.1 Abstract

One of the recommendations from Chapter 5 (addressing Objective 1) was that it is important to understand the effect of background noise on target individuals, as there are a huge variety of ambient soundscapes within waterways. This chapter combined two studies that tested the hypothesis that behavioural avoidance responses to a pure tone signal decrease with increasing background noise. Under laboratory conditions, the startle responses of individual goldfish exposed to 120 ms tones at 250 Hz (selected using the conclusions from the previous chapter) and four SPLs (115, 125, 135, 145 dB re 1 µPa) was quantified with four levels of band-limited random noise (ambient, 105, 115, 125 dB re 1 µPa). The proportion of fish that startled to the signal increased with increasing SPL. In the first experiment, no difference in the startle responses was detected between the ambient and 105 dB re 1 µPa background noise conditions. Hence, fine-scale analysis using Signal Detection Theory (SDT) showed that startle responses in the pre-signal period were more likely in presence of noise and that individuals were more likely to elicit a startle response over time. In the second experiment, more background noise levels were added to examine these results further. In this experiment, when compared to ambient noise, more startles occurred with 105 dB re 1 µPa background noise. The proportion of individuals that startled to the 135 and 145 dB re 1 µPa stimulus was scaled from 0 to 1 and a threshold level was added at 0.75, such that if the probability superseded that threshold, the startle was more likely to be elicited. For both stimulus levels, the standardised proportion superseded the 0.75 threshold at 105 dB re 1 µPa background noise, indicating presence of stochastic resonance in which the noise acts as a primer in eliciting an avoidance response. The results suggest that acoustic deterrents can be developed that are optimised based on the characteristics of the ambient soundscape, which would allow deterrents to use lower SPLs that deter fishes more efficiently, meaning the noise pollution associated with such devices would be minimised.

6.2 Introduction

The previous chapter (Chapter 5) identified the optimum frequency (250 Hz) of avoidance for individual goldfish reacting to a tone to address Objective 1 (Table 1; Determine the startle response threshold in goldfish to pure tone acoustic stimuli) and Research Question 1 (Which frequency (of a 120 ms pure tone) evokes an innate response in goldfish using the least acoustic energy?). Motives for this were that low efficacies of acoustic deterrents may have been because the acoustic stimulus was presented at frequencies outside the hearing range of the target species (e.g., see Gregory and Clabburn, 2003). In Chapter 5, it was recommended that the SNR was taken into account since ambient sound levels were not often accounted for in acoustic deterrence articles (Putland and Mensinger, 2019). Ambient noise levels are of particular interest since, when considered in a review, 86.0% of the literature did not record the background SPL (Putland and Mensinger, 2019). Of those that did, the SNR ranged from 33 dB (Harding *et al.,* 2016) to 75.0 dB (Turnpenny *et al.,* 1993), whilst the mean SNR was 59 ± 11 dB (see Putland and Mensinger, 2019). Hence, to create an acoustic deterrent that is suited for the real-world environment one must also consider background noise and determine its effect on avoidance. This will help to address Objective 2 (Table 1; To quantify innate responses of goldfish responding to a 120 ms pure tone acoustic stimulus in presence and absence of band-limited random noise) and Research Question 2 (What effect does noise have on the startle responses of goldfish to a 120 ms pure tone?).

The contribution of background noise to the effectiveness of acoustic deterrents is important since underwater noise from vessels may result in large sound differences between loud and quiet waterways (Section 2.5.1). Recording ambient noise levels when testing acoustic deterrents gives us information about the how loud the signal needs to be above the noise in order to elicit an avoidance response. As the SNR increases, the probability of an organism discriminating or discerning the signal will rise since the signal amplitude increased against the ambient noise. At a low SNR, the signal is not sufficiently loud enough to elicit a response, meaning the signal becomes masked. Clearly, signals are more likely to be masked at higher ambient noise levels when the SNR is low, as demonstrated elsewhere (e.g., Currie *et al.,* 2019). There is a growing number of studies observing the effects of noise on reproduction (e.g., de Jong *et al.,* 2020), predation (e.g., Simpson *et al.,* 2016) and foraging (e.g., Pieniazek *et al.,* 2020) success, however, far fewer studies have considered the SNR when developing acoustic deterrents for fish (see literature review: Putland and Mensinger, 2019). Consequently, this chapter considers pure tones played simultaneously with band-limited random noise to examine the relationship between ambient noise levels and the startle responses of goldfish.

To gather data to assess the effect of noise on the avoidance response of goldfish, whilst answering the research question: is an acoustic signal (pure tone) masked by background noise, inhibiting the startle response of the goldfish? To answer this question, two experiments were undertaken. Using the presence (treatment) and absence (ambient - control) of band-limited random noise (105 dB re 1 µPa), the first study (Experiment 2a) compared the startle response exhibited by goldfish between: (1) four signals of differing amplitude (SPL: 115, 125, 135, 145 dB re 1 uPa) within each of the two noise conditions, and (2) the treatment and control. We predicted that: (1) the proportion of startles exhibited would be positively related to SPL (signal strength) and (2) would be less likely under the noisy treatment during which there is greater probability that the signal would be masked. In addition to a coarse-scale quantification of the presence and absence of the exhibition of a startle response to the stimuli during each trial, for (2) a fine-scale analysis was conducted using SDT as the framework to determine the probability of fish exhibiting a response in the absence of the signal (false alarm) during the pre-signal baseline period in both the treatment and control tests. The SDT is regarded as fine-scale analysis since it is focused on the internal status of the fish, as opposed to 'coarse-scale' data analysis of behavioural (i.e., presence and absence of startle) responses.

Building on the first experiment, the second experiment (Experiment 2b) aimed to: (1) compare startle responses for four stimulus SPLs (115, 125, 135, 145 dB re 1 µPa) within three background noise conditions (105, 115, 125 dB re 1 µPa band-limited random noise); (2) compare the startle responses of goldfish to a 250 Hz stimulus between the four different background noise conditions (ambient [from the first study] and 105, 115, 125 dB re 1 µPa band-limited random noise) using stochastic resonance theory.

6.3 Experiment 2a Methods

6.3.1 Experiment 2a: Fish Husbandry

Goldfish (N = 160; mean standard length [SD]: 65.7 [6.8] mm; mass: 10.6 [3.1] g) were acquired in three batches from Hampshire Carp Hatcheries (UK) in oxygenated water to the ICER facility, University of Southampton, in April 2021. They were maintained in husbandry tanks described in Section 3.4. Fish were maintained under an artificial photoperiod (L:D 14:10) and fed once daily (Tetra goldfish flakes; protein: 42.0%). Ammonia (0.1 ppm; [0.1]), nitrites (0.0 [0.0] ppm) nitrates (40.0 [0.0] ppm), pH (pH 8.2 [0.04]) (API Freshwater Master Test Kit) and temperature (11.6 [1.1] °C) were monitored daily. The night before trials commenced, fish were transported to the experimental facility and kept in holding tanks (50.0 cm width × 84.0 cm length × 64.0 cm height, filled to 54.0 cm) containing a total of ~500 L of aerated, internally filtered and dechlorinated

(Aquasafe Water Conditioner; Tetra, Germany) water. Fish were acclimated for at least 4 days in the husbandry tanks and 14 hours in the holding tanks (temperature: 11.6 [0.7] °C) at the experimental facility (A. B. Wood Laboratory, Southampton) before trials commenced. On completion of each trial, the subject fish (a single individual per trial) were placed in a post-test tank and returned to the ICER husbandry facility at the end of the day.

6.3.2 Experiment 2a: Experimental Setup

Trials were conducted in the submerged cylindrical arena described in Section 3.2.

6.3.3 Experiment 2a: Experimental Design

The study consisted of 20 replicates of 8 treatments based on a combination of a 250 Hz, 120 ms signal played at one of four SPLs (115, 125, 135 or 145 dB re 1 µPa) and one of two background noise conditions (105 dB re 1 µPa band-limited 100-2500 Hz random noise or in ambient control conditions). Prior to the start of each trial, a single fish (N = 160) was acclimated in the experimental arena for 30 min. Fish experienced a total of four exposures (presentation of the same stimulus). Each exposure consisted of a sinusoidal 120 ms tone ramped with a 20 ms Hanning taper and was followed by 4 min of silence (pre-signal period) before the next exposure. Although the Mauthner cell activation latency in goldfish is 5-10 ms, the tone was played at 120 ms so that it was long enough to enable the frequency spectrum to be well defined at this lower signal duration (Eaton, 1977; Zeddies and Fay, 2005). Fish behaviour was continuously recorded during the trial and each fish was used once.

6.3.4 Experiment 2a: Acoustic Stimuli & Sound Mapping

Sound samples were produced as per the methods outlined in Section 3.3, then mapped to produce 3D plots of SPL and PA in the experimental arena (Figure 25). The SPL was uniform across the horizontal plane and the pure tone SPL differed by ~14.0 dB re 1 µPa between the top and the bottom of the tank, whilst the noise differed by ~8.8 dB re 1 µPa (Table 18). The PA was also calculated using point measurements and mapped (Figure 25).

Table 18 The mean ± standard deviation of the 145 dB re 1 µPa, 250 Hz tone and 105 dB re 1 µPa, 100 – 2500 Hz band-limited random noise across a cylindrical experimental tank submerged in a large water body taken at three different depths (5.0 cm; 15.0 cm; 25.0 cm, measured from the water surface). Centre SPL refers to the SPL in the centre of the tank.

Stimulus	***5.0 cm SPL (dB re 1 µPa)***	***15.0 cm SPL (dB re 1 µPa)***	***25.0 cm SPL (dB re 1 µPa)***	***Centre SPL (dB re 1 µPa)***	***15 cm (dB re 1 mm s^{-2})***
250 Hz	136.7 ± 0.7	145.0 ± 0.3	150.6 ± 0.5	144.9 ± 0.5	12.8 ± 4.3
Noise	95.4 ± 0.3	102.0 ± 0.5	104.2 ± 0.6	102.1 ± 0.2	

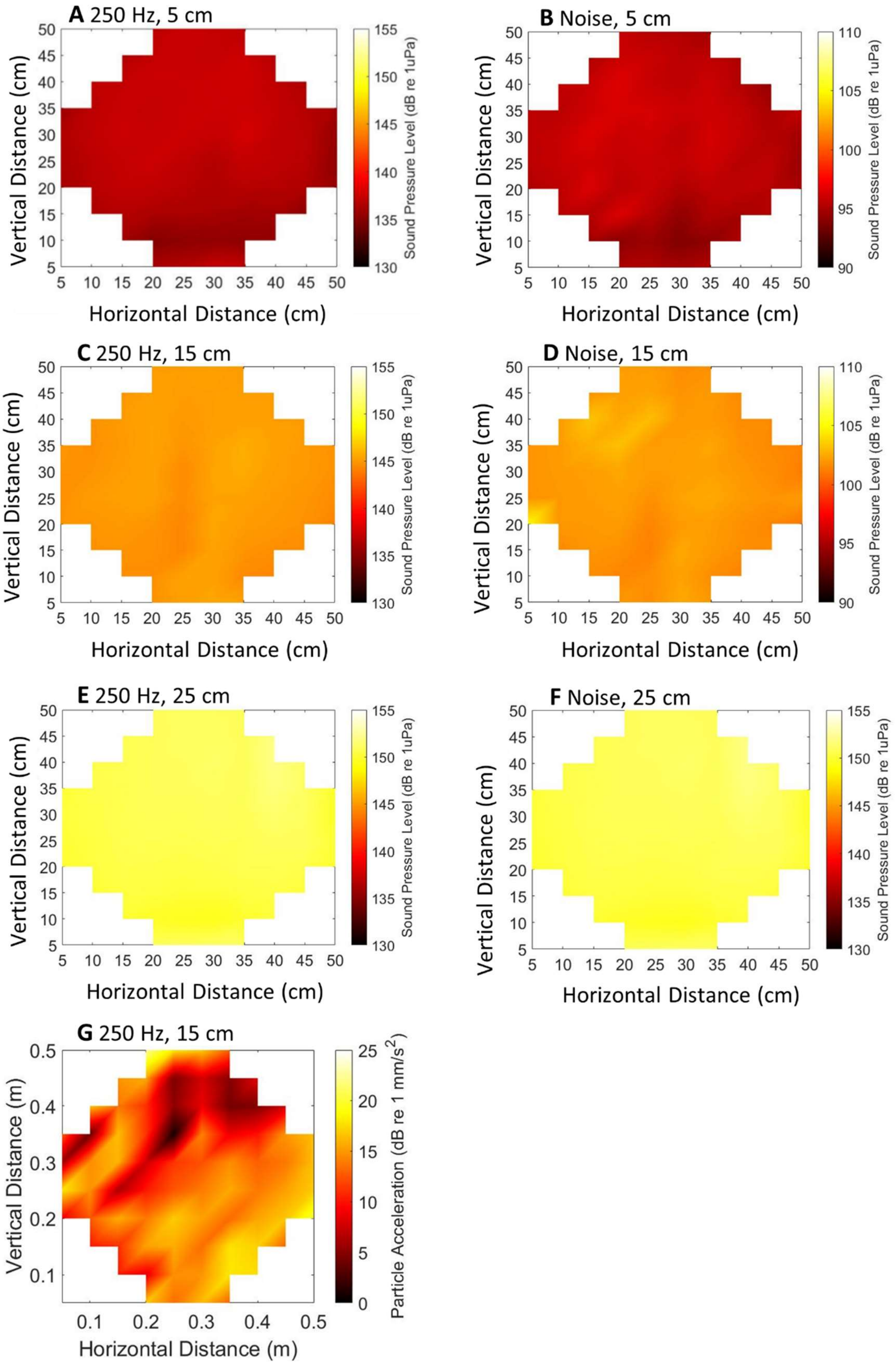


Figure 25 Maps showing SPL (**A-F**) and PA (**G**) of a 120 ms, 250 Hz stimulus (**A, C, E, G**) at 145 dB re 1 µPa in the centre of the arena and 100 – 2500 Hz band-limited random noise (**B, D, F**) at 105 dB re 1 µPa in the centre of the arena. Point measurements were taken at three depths (5.0 cm, 15.0 cm, 25.0 cm, measured from the water surface).

6.3.5 Experiment 2a: Behavioural and Data Analysis

Video recordings of fish behaviour obtained for each trial were analysed at a later date. Video footage was reviewed blind of the treatment used and in a random order such that 98.9% of the recorded startles were consistent between the original data recording and the review.

(i) Preliminary analyses

To determine whether external factors may have confounded the results by influencing the probability of startling, a reductive model was developed. Factors included in the model were: tank days (minimum number of days in the husbandry tank); time (the beginning of the trial to the nearest hour); difference between holding and experimental tank temperature (°C); mass (g). The initial GLMM contained all predictor variables with exposure (order of stimulus exposure), and/or trial included as random effects. Manual backwards selection using variable significance (significance at $p < 0.05$) was undertaken as model simplification. Trial was a random effect since the model produced the lowest AIC (Table 19). Exposure (the nth stimulus played, 1-4) was included in a GLMM as a fixed effect alongside the other external factors, however, none were recognised to predict startle responses and the null model (intercept) had the optimum AIC (Table 20).

Table 19 Random effects included in GLMMs developped to determine if external factors affect the presence of a startle response to 120 ms pure tones at 250 Hz and four SPLs (115, 125, 135, 145 dB re 1 µPa) in goldfish.

Random Effect	***SD***	***AIC***
Null (Intercept)	-	831.9
Exposure:Trial	0.03	833.9
Trial	2.77	669.7
Exposure	<0.001	833.9

Following this, the received noise and stimulus SPLs were calculated by estimating the individuals' depth using the video footage. To do this, the hydrophone-recorded SPLs were corrected using the data from the acoustic maps (Table 21).

The received stimulus level and received noise level were included in separate GLMs for each signal SPL, with trial as a random factor. The received noise level did not affect the occurrence of a startle response ($0.07 < p < 0.91$), however, the received stimulus level did for 135 dB re 1 µPa ($p = 0.049$) and 145 dB re 1 µPa ($p = 0.03$) stimuli but not for 115 dB re 1 µPa ($p = 0.28$) or 125 dB re 1 µPa ($p = 0.22$).

Table 20 Variables included in GLMMs developped to determine if external factors affect the presence of a startle response to 250 Hz 120 ms pure tones (SPLs of 115, 125, 135, 145 dB re 1 µPa) in goldfish in two acoustic environments (ambient and 105 dB re 1 µPa, 100-2500 Hz band-limited random noise).

	Variables in Model[b]						
Model[a]	***Exposure***	***Mass***	***Tank Days***	***Temp***	***Time***	***AIC***	***ΔAIC***
Null						663.2	0
1	x	x	x	x	x	671.6	8.4
2	x		x	x	x	669.7	6.5
3	x		x	x		667.8	4.6
4	x		x			666.3	3.1
5	x					664.6	1.4

[a] The null model is shown without any predictor variables.

[b] *Exposure (order of stimulus exposure); mass (g); tank days (minimum number of days in the husbandry tank); temp (difference between holding and experimental tank temperature, °C); time (the beginning of the trial to the nearest hour).*

Table 21 Corrections of SPL based on the depth of the goldfish in a cylindrical arena. Corrections were applied using average SPLs recorded during acoustic mapping of the 250 Hz pure tone and 100-2500 Hz band-limited random noise.

Position	***Stimulus Received Level Correction (dB re 1 µPa)***	***Noise Received Level Correction (dB re 1 µPa)***
Top (0-10 cm)	- 8.3	- 6.6
Middle (10-20 cm)	0	0
Bottom (20-30 cm)	+ 5.6	+ 2.2

(ii) Startle response within each noise condition

Logistic regression with binomial error structure was used to determine the influence of SPL on the presence of a startle response for both the treatment and ambient control noise conditions. Logistic regression curves were then represented on plots with SPL against the probability of a startle for each background noise condition and the significance of the relationship recorded.

(iii) Startle response between background noise treatments

Logistic regression with binomial error structure was also used to compare the startle responses between the ambient control and the treatment noise conditions. The distributions were compared according to the null hypothesis that there was no difference between the startle responses in the ambient control and the treatment.

(iv) Signal Detection Theory

For further analysis to determine the internal response of the fish, the startle responses in the 4 min pre-signal period for both the ambient control and treatment noise conditions were considered. In the pre-signal periods, there were some occasional external acoustic cues that were uncontrolled. These acoustic cues came from sources such as distant car door slamming. Additionally, in the pre-signal period, there were startles from individuals in the absence of the treatment stimulus. This prompted the researcher to investigate these further, as it may give an indication of the internal response of the fish to accompany the coarse-scale analysis. This fine-scale analysis can provide information not detected by traditional coarse-scale analysis and can therefore help to further understand how goldfish respond to tones in presence of noise.

Audio files, viewed in MATLAB, and video footage were used to identify whether the startling goldfish in the pre-signal period was responding to an external acoustic cue (AC determined) or not (AC undetermined). A high-pass Butterworth filter (6th order; cut-off frequency 120 Hz; sample frequency 25608 Hz) was applied to the audio signal and the filtered pressure values were then plotted, creating a series of peaks. If a peak occurred 0.5 dB re 1 µPa or more above the background noise level or if a group of peaks seemed periodic in nature (i.e. dropping water) these were recorded. If the peak in the audio file matched with a startle in the video footage, it was characterised as "AC determined"; if there was a startle and no peak identified it was recorded as "AC undetermined".

Three GLMs with Poisson error structure and a "log" link function determined whether the number of startles in the pre-signal periods (AC determined, AC undetermined, both ACs) affected the response to the 120 ms pure tone signal. Similarly, the number of startles for AC determined, AC undetermined, and for both cases were compared between noisy and quiet environments using a GLM with Poisson error structure. The GLM with Poisson error structure and a "log" link function determined that the number of startles in the pre-signal period did not affect the response to the 120 ms pure tone for any of the eight treatments (stimulus determined: $z = -0.79 – 1.82$, $p = 0.07 – 0.78$; stimulus undetermined: $z = -0.85 – 0.88$, $p = 0.17 – 1.00$; all stimuli: $z = -0.57 – 1.96$, $p = 0.05 – 0.84$). Therefore, the number of startles in the quiet and noisy pre-signal periods were compared and tested using a GLM with Poisson error structure.

The SDT was used to evaluate the fine-scale behaviour of individuals between the ambient control and treatment noise conditions in the 4 min pre-signal period. The advantage of using SDT to assess fish behaviour is that it considers response bias, which is the tendency for the individual to react as if the signal is present even if it is absent (Kerr *et al.,* 2019). If a peak in the audio file matched with a startle in the video footage, it was characterised as a "hit"; if there was a startle and no peak identified it was a “false alarm”; if there was a peak and no startle response it was a “miss” (Figure 26). A “non-response” was categorised as a 0.5 s interval in which there was neither an abnormal peak in the audio file or a startle in the video footage. The SDT discriminability, *d'*, and response criterion, *c'* are measures of how easily the stimulus is detected by an individual and the level that an internal response results in a behavioural response, respectively. The SDT discriminability, *d'*, and response criterion, *c',* are described as:

$$d' = Z_H - Z_{FA} \qquad \text{Equation 12}$$

$$c' = -\frac{(Z_H - Z_{FA})}{2} \qquad \text{Equation 13}$$

where Z_H and Z_{FA} are the standard deviation units (*Z* scores of the unit normal Gaussian distribution) of the probability of hit and false alarm assuming the data is normally distributed with similar variance (Kemp *et al.,* 2012; Kerr *et al.,* 2019).

The *d'* and *c'* were calculated using the percentage of fish that responded or did not respond to an AC in each 4 min pre-signal period. If *c'* is unbiased, it has a value of 0 and negative values of *c'* signify a bias toward responding whereas positive values signify a bias towards not responding. Values of *d'* at 1 and 2 are equivalent to one and two standard deviations, with higher values representing higher levels of signal discriminability. The discriminability and response criterion were calculated for all the pre-signal periods in the ambient control and the treatment noise conditions and plotted on a Receiver Operating Characteristic (ROC) curve. Since there were four signal exposures per trial, it was possible to observe the responses in the pre-signal periods prior to each exposure, hence, gaining an idea of the responses over time.

Figure 26 Four potential outcomes considered in SDT. In this study, the acoustic cue was either a determined (yes) or undetermined (no) cue in a 4-min pre-treatment period in presence or absence of noise. The response was the presence (yes) or absence (no) of a startle response.

		Response	
		Yes	No
Acoustic cue	Yes	Hit	Miss
	No	False Alarm	Correct non-response

6.4 Experiment 2b Methods

6.4.1 Experiment 2b: Fish Husbandry & Experimental Setup

Goldfish (N = 240; mean standard length [SD]: 65.6 [6.2] mm; mass: 11.0 [3.2] g) were acquired in five batches, from Hampshire Carp Hatcheries, UK, in February 2022. Fish were transported in oxygenated water to the A B Wood Laboratory, University of Southampton, where they were maintained in three husbandry tanks (two tanks: 50.0 cm width × 84.0 cm length × 64.0 cm height, filled to 54.0 cm; one tank: 37 cm diameter × 47.0 cm height) containing a total of ~500 L of aerated, internally filtered and dechlorinated (Aquasafe Water Conditioner; Tetra, Germany) water. Fish were maintained under an artificial photoperiod (L:D 10:14) and fed once daily (Goldfish flakes, 42.0% protein; Tetra, Germany). Ammonia (0.2 [0.1] ppm), nitrites (0.0 [0.1] ppm), nitrates (43.7 [10.2] ppm), pH (pH 8.2 [0.1]) (API Freshwater Master Test Kit) and temperature (11.3 [0.8] °C) were monitored daily. Fish were acclimated for at least 3 days in the husbandry tanks before trials commenced. On completion of each trial, the subject fish (a single individual per trial) were placed in a post-test tank. The setup of Experiment 2b was identical to that of Experiment 2a, described fully in Section 3.2.

6.4.2 Experiment 2b: Experimental Design

The study design consisted of 20 replicates of 12 treatments consisting of a pure tone stimulus of SPL 115, 125, 135 or 145 dB re 1 µPa played in presence 105, 115, or 125 dB re 1 µPa band-limited (100 – 2500 Hz) random noise. Prior to the start of each trial, a single fish (N = 240) was acclimated in the experimental arena for 30 min prior to each trial. As per experiment one, the fish experienced four exposures (the same stimulus presented four times) at one of the four randomly assigned signal SPLs and one of the three background noise conditions. Apart from the additional noise treatments described above, the experimental design and stimulus were identical to Experiment 2a.

6.4.3 Experiment 2b: Sound Mapping

Prior to conducting the trials, the sound field of the experimental arena was quantified. Using the same methodology as for Experiment 2a (outlined in Section 3.3), in which the SPL and PA of the experimental arena were determined. The SPL and PA were represented in maps (Figure 27). The SPL was uniform across the horizontal plane and the pure tone SPL differed by ~12.0 dB re 1 µPa between the top and the bottom of the tank, whilst the noise differed by ~9.0 dB re 1 µPa (Table 22).

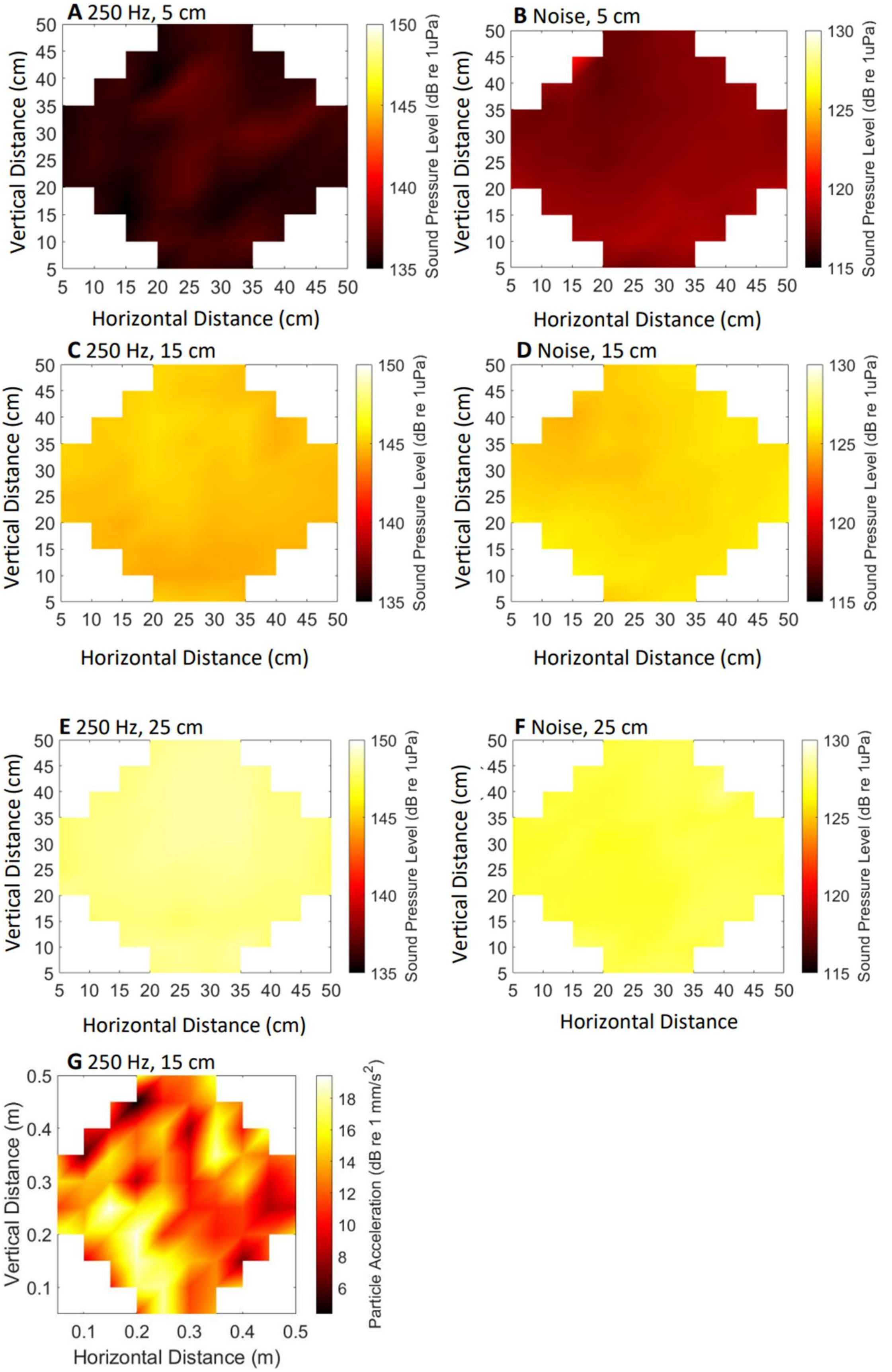


Figure 27 The mean ± standard deviation SPL (**A, C, E**) and PA (**G**) of the 145 dB re 1 µPa, 250 Hz tone and 105 dB re 1 µPa, 100 – 2500 Hz band-limited random noise (**B, D, F**) across a cylindrical experimental tank (55.5 cm diameter) taken at three different depths (5.0 cm; 15.0 cm; 25.0 cm). Centre SPL refers to the SPL in the centre of the tank.

Table 22 The mean ± standard deviation SPL and PA of the 145 dB re 1 µPa, 250 Hz tone and 105 dB re 1 µPa, 100-2500 Hz band-limited random noise across a cylindrical experimental tank submerged in a large water body taken at three different depths (5.0 cm; 15.0 cm; 25.0 cm). Centre SPL refers to the SPL in the centre of the tank.

Stimulus	***5.0 cm SPL (dB re 1 µPa)***	***15.0 cm SPL (dB re 1 µPa)***	***25.0 cm SPL (dB re 1 µPa)***	***Centre SPL (dB re 1 µPa)***	***15 cm (dB re 1 mm s^{-2})***
250 Hz	136.1 ± 0.5	144.9 ± 0.3	148.2 ± 0.3	145.1 ± 0.2	12.9 ± 3.2
Noise	118.0 ± 0.6	125.4 ± 0.3	127.2 ± 0.3	125.2 ± 0.2	

6.4.4 Experiment 2b: Behavioural and Data Analysis

For each trial, the startle responses were documented using video footage. The video footage was reviewed and rereviewed with a success rate of 98.6%.

As per Experiment 2a, a reductive model was developed to determine if the same external factors predicted the startle. The initial GLMM contained all predictor variables with exposure (order of stimulus exposure) and/or trial included as random effects. GLMMs with trial (i.e., each individual) as a random effect (Table 23) were used for further analysis. Exposure was included in a GLMM as a fixed effect alongside the other external factors however, none were recognised to predict startle responses and the null model (intercept) had the optimum AIC (Table 24).

Table 23 Random effects included in GLMMs developped to determine if external factors affect the presence of a startle response to 120 ms, 250 Hz pure tones at four SPLs (115, 125, 135, 145 dB re 1 µPa) in goldfish.

Random Effect	***Std. dev***	***AIC***
Null	-	1200.7
Exposure:Trial	<0.001	1202.7
Trial	3.38	902.2
Exposure	<0.001	1202.7

Table 24 Variables included in GLMMs developped to determine if external factors affect the presence of a startle response to 250 Hz, 120 ms pure tones (SPLs of 115, 125, 135, 145 dB re 1 µPa) in goldfish in three acoustic environments (105, 115, 125 dB re 1 µPa, 100-2500 Hz band-limited random noise).

	Variables in Model[b]						
Model[a]	***Exposure***	***Mass***	***Tank Days***	***Temp***	***Time***	***AIC***	***ΔAIC***
Null						902.2	0.0
1	x	x	x	x	x	910.3	8.1
2	x	x		x	x	908.3	6.1
3		x		x	x	906.4	4.2
4		x		x		904.7	2.5
5		x				903.4	1.2

[a] The null model is shown without any predictor variables.

[b] *Exposure (nth stimulus exposure 1-4); mass (g); tank days (minimum number of days in the husbandry tank); temp (difference between holding and experimental tank temperature, °C); time (the beginning of the trial to the nearest hour).*

A GLMM with trial as a random variable was used to determine the effect of signal SPL on the presence of a startle for each background noise level, and the significance of the relationship was recorded. *A priori* contrasts were also conducted to compare the startle responses between each of the background noise conditions for each of the stimulus SPLs.

The responses for the three background noise conditions were compared to responses in ambient noise obtained from Experiment 2a. Responses to the same signal stimuli in the 105 dB re 1 µPa background noise treatment ($p = 0.11$, $z = 1.62$) did not differ, which allowed for feasible comparison between the two datasets. After comparing the data to the ambient noise condition, the proportion of startles exhibited to the 135 dB re 1 µPa and 145 dB re 1 µPa signal were scaled from 0 to 1, with the latter being the highest probability of a startle. Then, plots were used to compare the background noise level and the standardised startle proportion. A chance line was plotted at a proportion of 0.5 and a threshold level was added at 0.75, such that if the probability superseded that threshold, the startle was more likely to be elicited (as per the methodology outlines by Sasaki *et al.,* 2008).

6.5 Experiment 2a Results

(i) Startle response within each noise condition

Startle responses were observed in each of the SPLs in each of the background noise conditions. The proportion of goldfish that startled (calculated by dividing the number of individuals that startles by the total number of replicates) increased with SPL in both the ambient control (z = 7.98, p = <0.001) and treatment (z = 9.29, p = <0.001) noise conditions (Figure 28).

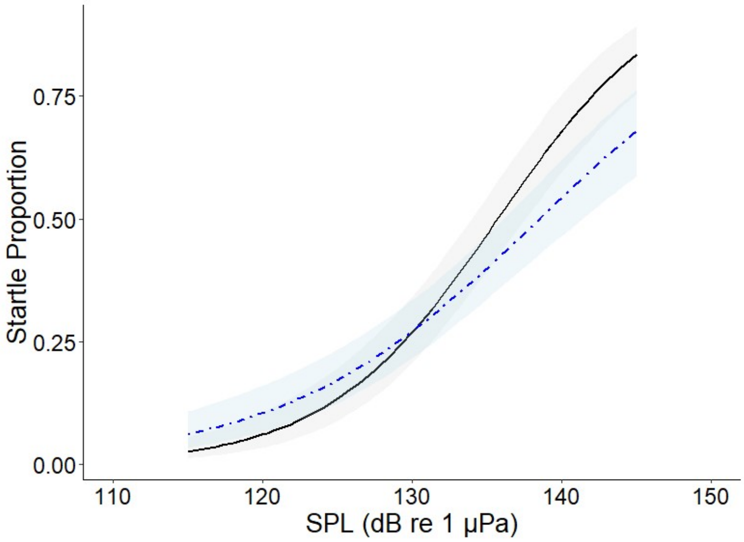


Figure 28 Logistic regression curves showing the proportion of goldfish that startled to a 120 ms, 250 Hz pure tone at 115, 125, 135, 145 dB re 1 µPa in two distinct acoustic environments: ambient background noise (blue dot dash line) and 105 dB re 1 µPa, 100-2500 Hz band-limited random noise (black solid line). The shaded regions indicate 95% confidence intervals.

(ii) Startle responses between the noise conditions

There was no difference in startle responses between the ambient control and the treatment noise condition (z = 1.00, p = 0.32). However, on visual inspection of the logistic regression curves, (Figure 28) a larger proportion of the population startled occurred in the quiet compared to the noisy condition when the SPL of the signal was 115 dB re 1 µPa and 125 re 1 µPa. Conversely, when the signal was 135 dB re 1 µPa and 145 dB re 1 µPa, a larger proportion of startles occurred in the noisy compared to the quiet background treatment.

(iii) Signal Detection Theory

The number of startles in the pre-signal periods for both AC determined (z = -2.30, p = 0.02) and AC undetermined (z = 7.72, p = <0.001) differed between the ambient control and the treatment background noise.

Using the SDT analytical framework (Figure 29) there was a difference in d' ($t = 6.66$, $p = 0.03$, $df = 3.95$) and c' ($t = -13.57$, $p = <0.001$, $df = 4.26$) between the ambient control and treatment background noise conditions for all the pre-signal periods, regardless of if they were played before the first signal exposure or the fourth. For the startle responses in the ambient control noise condition, both d' and c' did not differ between the pre-signal period. However, for the startle responses in the treatment noise condition, d' increased and c' decreased with each exposure, i.e., over time (Table 25). Therefore, the c' suggests that the individuals were more likely to respond in the treatment noise condition than the ambient control. Similarly, d' suggests that the goldfish were able to discriminate external stimuli in the treatment noise than in the ambient control. Interestingly, the individuals were also more likely to respond to AC determined (i.e., external stimuli) over time in the treatment noise condition than in the ambient control.

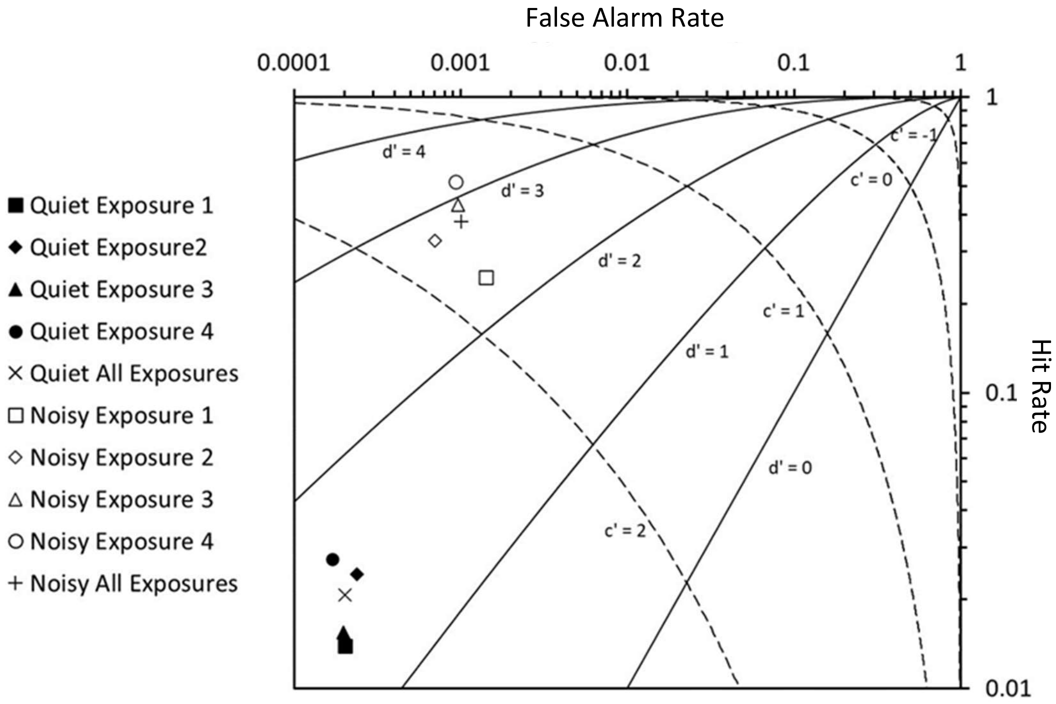


Figure 29 The ROC curve calculated as part of the use of SDT as a framework to investigate the response of goldfish to determined (external stimuli) and undetermined acoustic cues in a quiet (ambient noise) and noisy (105 dB re 1 µPa, 100 – 2500 Hz band-limited random noise) condition. Ten contexts were considered showing responses over time (exposures 1-4) and overall.

Table 25 Discriminability, d′, and response criterion, c′, calculated as part of SDT investigating response of goldfish to determined and undetermined acoustic cues in a quiet (ambient noise) and noisy (105 dB re 1 µPa, 100 – 2500 Hz band-limited random noise) condition. Ten contexts were considered showing responses over time (exposures 1 – 4) and overall.

Context	***Discriminability, d′***	***Response Criterion, c′***
Quiet Exposure 1	1.34	2.87
Quiet Exposure 2	1.52	2.73
Quiet Exposure 3	1.39	2.85
Quiet Exposure 4	1.66	2.75
Quiet All Exposures	1.50	2.79
Noisy Exposure 1	2.30	1.84
Noisy Exposure 2	2.75	1.82
Noisy Exposure 3	2.93	1.64
Noisy Exposure 4	3.15	1.54
Noisy All Exposures	2.78	1.70

6.6 Experiment 2b Results

Startle responses occurred at each of the 12 treatments, with a minimum of 1.1% to a maximum of 76.3% of the population startling to the stimulus in the three background noise conditions. The likelihood of an individual startling increased with increasing SPL for all three background noise conditions (z = 6.25 – 10.44; p = <0.001). Albeit a larger proportion of startles were generally observed in the 105 dB re 1 µPa background noise treatments, followed by 115 dB re 1 µPa then 125 dB re 1 µPa (Figure 30).

The *a priori* contrasts showed, for responses to the 145 dB re 1 µPa signal, startles in presence of 105 dB re 1 µPa occurred more frequently compared to the ambient noise (p = 0.02; z = 2.82) and the 125 dB re 1 µPa background noise (p = 0.03, z = -0.52). Thus, it was more likely for an individual to startle in the 105 dB re 1 µPa than to the equivalent signal presented in the ambient noise or 125 dB re 1 µPa condition. For responses to the 135 dB re 1 µPa signal, startles in presence of 105 dB re 1 µPa occurred more frequently compared to the 125 dB re 1 µPa noise (p = <0.001, z = -4.68), as did startles in the ambient noise (p = 0.004, z = -3.37) and the 115 dB re 1 µPa noise (p = 0.004, z = -3.35), compared to the 125 dB re 1 µPa noise.

The scaled startle responses showed that suprathreshold stochastic resonance was present for the 105 dB re 1 µPa background noise since the threshold was surpassed for individuals responding to both the 135 dB re 1 µPa and 145 dB re 1 µPa signals (Figure 31). Responses were higher than the chance level for the 135 dB re 1 µPa signal in the ambient and 115 dB re 1 µPa, but they did not reach the 0.75 (75.0%) threshold.

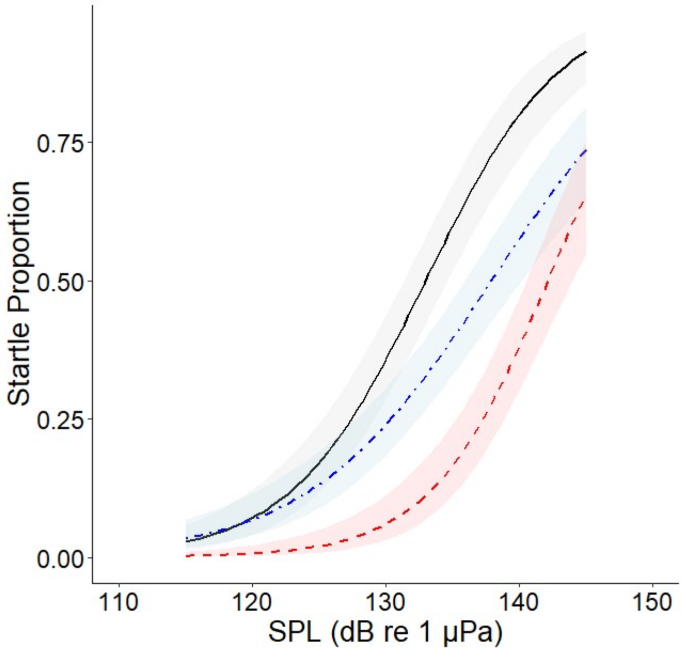


Figure 30 Logistic regression curves showing the proportion of goldfish that startled to a 120 ms, 250 Hz pure tone at 115, 125, 135, 145 dB re 1 µPa in three distinct acoustic environments: 105 dB re 1 µPa (black solid line), 115 dB re 1 µPa (blue dotdashed line), 125 dB re 1 µPa (red dashed line), 100-2500 Hz band-limited random noise (black solid line). The shaded regions indicate 95% confidence intervals.

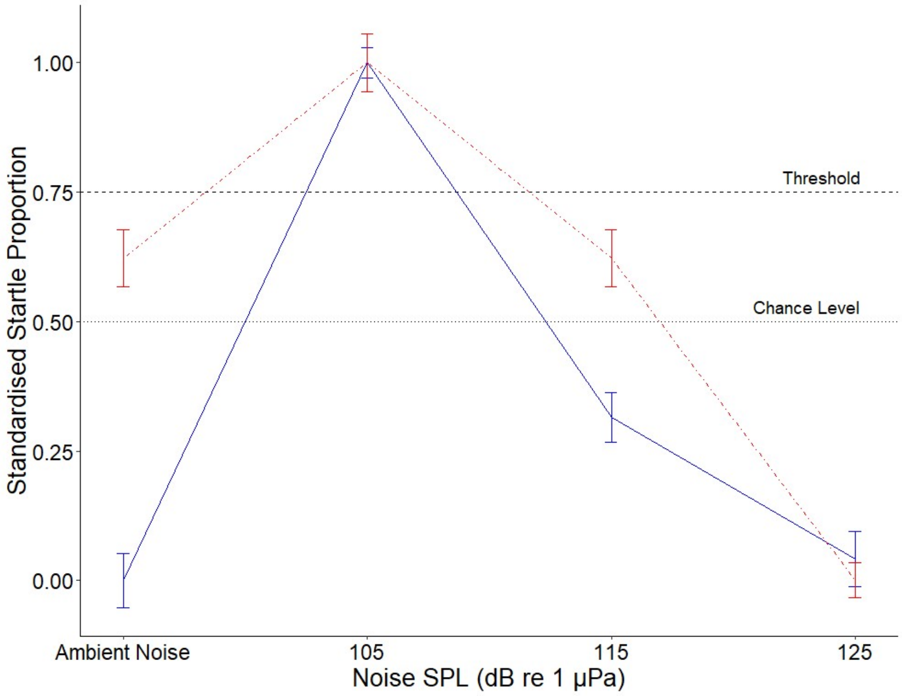


Figure 31 The proportion of goldfish (scaled between 0 and 1) that startled to a 120 ms, 250 Hz pure tone at 135 (red dot-dashed line), 145 dB re 1 µPa (blue solid line) in four distinct acoustic environments: ambient, 105 dB re 1 µPa, 115 dB re 1 µPa, 125 dB re 1 µPa, 100-2500 Hz band-limited random noise. The 95.0% confidence intervals are also represented.

6.7 Discussion

Using the presence (treatment) and absence (ambient control) of band-limited random noise (105 dB re 1 µPa), Experiment 2a compared the startle response exhibited by goldfish between: (1) four signals of differing amplitude (SPL: 115, 125, 134, 145 dB re 1 uPa) within each of the two noise conditions, and (2) the treatment and control. For (1), the proportion of startles exhibited was positively related to SPL. We predicted for (2) that startle responses would be less likely under the noisy treatment during which there is greater probability that the signal would be masked. In the coarse-scale analysis, there was no difference between the treatment and control, whilst in the fine-scale analysis it was found that there were more startle responses in the pre-treatment period for the treatment than the ambient background noise. Building on this, Experiment 2b tested more background noise levels (105, 115 and 125 dB re 1 µPa) to investigate the presence of stochastic resonance. It was found that the probability of a startle response to a stimulus was less likely with increasing background noise levels (105 – 125 dB re 1 µPa band-limited background noise). However, when comparing the responses with the ambient noise used in Experiment 2a, the responses were more frequent to a tone with 105 dB re 1 1 µPa band-limited background noise than in ambient noise conditions. Hence, this study showed that noise can act as a primer, influencing the response of goldfish reacting to a tone (Figure 31).

As expected, the presence of startle responses increased with increasing signal strength for both Experiment 2a and 2b, regardless of the background noise level. These results are consistent with other studies (Currie *et al.,* 2019; Holgate *et al.,* 2023). For Experiment 2a, when comparing the responses in the treatment and the ambient control, there was no statistical difference between the two (see Section 6.5 ii). Hence, the masking effect was not so great as to create a difference in the responses to the tone. This was also observed in Experiment 2b, where more startles were observed at low signal SPLs regardless of the background noise level. Perhaps for the chosen signals, there is a threshold for which the signal is masked and when it becomes distinguishable for the fish.

The SDT was a valuable tool to investigate startle responses in Experiment 2a to stimuli in higher resolution. The SDT provided an appropriate method to further investigate this since it provides a framework to better understand the effects of noise on fish response to environmental stimuli (e.g., hydrodynamic noise: Kemp *et al.,* 2012; Kerr and Kemp, 2018; acoustic noise: Currie *et al.,* 2021). The SDT represents a fine-scale approach in understanding the behaviour unlike binary response (or non-response) to a stimulus. Whilst the coarse-scale analyses in Experiment 2a showed startle responses to the treatment stimulus to be and the ambient control to be similar, the fine-scale analysis gave additional information that would otherwise have been unknown. It is demonstrated, therefore, that fine-scale analyses such as SDT is a useful tool in fish bioacoustics research.

Focusing on Experiment 2b, at higher signal SPLs (i.e., at an appropriate SNR) stochastic resonance was observed, since the standardised startle responses occurred above the 0.75 threshold for 105 dB re 1 µPa band-limited noise (Figure 31). Hence, the background noise acted as a primer to the startle response for signals at 135 and 145 dB re 1 µPa above the aforementioned background noise level. A limited number of studies have demonstrated that fishes may exhibit startle responses more frequently in noisy environments (Purser and Radford, 2011; Voellmy *et al.,* 2014; Shafiei Sabet *et al.,* 2015). Findings in European Minnow and Three-Spined Stickleback (*Gasterosteus aculeatus*) showed that startle responses were elicited more often during playback of additional noise than during ambient conditions (Purser and Radford, 2011; Voellmy *et al.* 2014b). In these studies, the individual is subject to noise only and not an additional stimulus. Therefore, the current study is the first, to our knowledge, that demonstrates the presence of suprathreshold stochastic resonance when using an acoustic signal played above background noise.

The notion of masking is not discounted by this study; rather we have demonstrated that, at least in goldfish, there is an SNR that is most effective at eliciting a startle response before masking effects take precedence. It is therefore recommended to act with caution when deploying acoustic deterrents in locations with high levels of ambient noise. In these conditions, the deterrent would become ineffective except when the stimulus has a very high SPL. Potential complications in this circumstance are twofold. The first is that the stimulus may contribute to an already noisy soundscape. The second is that the stimulus may become loud enough to induce TTS or PTS in the target species, or heterospecifics. For example, 0.1 – 10.0 kHz of white noise at 170 dB re 1 µPa induced a threshold shift of 5 dB after 10 min of exposure (Smith *et al.,* 2004a). After 48 hr of exposure to the same stimulus, goldfish had significant hair cell damage up to 8 days after exposure (Smith *et al.,* 2006). Hence, in such locations other behavioural and/or mechanical methods would be more appropriate.

Habituation is another topic of caution within acoustic deterrent research, as the most effective deterrent is that which continues to work well over time. In this study, the likelihood of a startle response did not change over multiple stimulus presentations, which suggests four minutes was a sufficient gap such that no tolerance was observed. However, it is recommended that longer-term studies are undertaken, since habituation may be likely under longer periods (Vetter *et al.,* 2015 for habituation of silver carp to pure tones; Neo *et al.,* 2018 for habituation of sea bass to noise). Additionally, there are limitations of behaviour exhibited by individuals in experimental studies, meaning that further investigation is required for groups as well as *in situ*. Alternatively, habituation may not have been observed as there may be increased sensitivity, i.e., heightened stress, in presence of noise, as seen in larval zebrafish (Bhandiwad *et al.,* 2018).

Using the methodology demonstrated in this study, acoustic deterrents can be developed that are optimised based on the characteristics of the ambient soundscape. This would allow deterrents to use lower SPLs that deter fishes more efficiently, meaning the noise pollution associated with such devices would be minimised. Such deterrents would be useful for fish guidance or for conservation purposes. These deterrents may be employed at cooling water intake systems (Maes *et al.,* 2004; Sonny *et al.,* 2006) or to guide fish towards a fish pass (Schilt, 2007). Another use for this acoustic deterrent is for trapping systems for non-native species, such as common carp in Canada (Bzonek *et al.,* 2021) and silver carp in the USA (Murchy *et al.,* 2017). Yet, we recommend testing whether behavioural stochastic resonance is present in other fish species, ranging from other Otophysans (e.g., *Cyprinidae* and *Siluridae*) to those with less specialised hearing (e.g., *Salmonidae*).

Chapter 6 used the submerged cylindrical arena of Chapter 4 to address Objective 2 (Table 1; To quantify innate responses of goldfish responding to a 120 ms pure tone acoustic stimulus in presence and absence of band-limited random noise) and Research Question 2 (What effect does noise have on the startle responses of goldfish to a 120 ms pure tone?). Experiment 2a and 2b showed that low SPL signals are masked by background noise, but signals in presence of background noise evoke stochastic resonance. The next step to achieve the thesis aim and to inform acoustic deterrence was to fulfil Objective 3 (Table 1; Utilise the temporal characteristics of fish sounds to inform acoustic deterrence and identify the optimal temporal sound characteristics to elicit an avoidance response) and Research Question 3 (Do all fishes respond to a particular set of temporal sound characteristics?).

Chapter 7 A systematic literature review and meta-analysis of fish sounds to inform acoustic deterrence

7.1 Abstract

Understanding and employing fish sounds, as well as determining the optimum frequency and SNR, can be useful in identifying the temporal characteristics needed for acoustic deterrence. In the wider animal kingdom, alarm calls may be interpreted by both con and heterospecifics; this may be useful for acoustic deterrence. However, alarm calls in fish are unproven and further understanding of the temporal characteristics of the sounds is required to inform acoustic deterrence. Hence, to fulfil Objective 3, a systematic review and meta-analysis determined: (1) whether temporal characteristics (pulse duration [PD], pulse period [PP], pulses per sound [PPS], sound duration [SD]) of sound production in fishes are consistent under a variety of contexts (e.g., courtship, disturbance, territorial aggression, amongst others); (2) whether sound production mechanisms and habitat-specific factors influence the sound production parameters. The Centre for Environmental Evidence (CEE) guidelines were used to search, identify and screen eligible peer-reviewed studies obtained from scholarly search engine databases. The sounds differed between the temporal characteristics (PD, PP, PPS, SD) however, they also differed within each context. Additionally, there was variation in the sound production parameters even within the same mechanism. Species inhabiting the pelagic zone consistently had the lowest PP, PD and PPS. Overall, there is little evidence of a common structure in the sounds produced by fish. Though it was not possible to generalise the temporal characteristics that would be ideal for acoustic deterrents, further research, additional meta-analyses, and standardisation of methodology are necessary to determine the conditions in which best to deter fishes. Alternatively, it may be more adequate to use sound production from the species of interest, rather than seek a general solution for all species.

7.2 Introduction

Chapter 6 fulfilled Objective 2 (Table 1; To quantify innate responses of goldfish responding to a 120 ms pure tone acoustic stimulus in presence and absence of band-limited random noise) and Research Question 2 (What effect does noise have on the startle responses of goldfish to a 120 ms pure tone?) by evaluating the effect of noise on the behaviour of goldfish responding to a tone, thus, contributing to a growing field of research determining how to develop acoustic deterrents that are better suited for the real-world environment. Following this (and the preceding chapter determining the optimum frequency), this chapter achieved Objective 3 (Table 1; Utilise the temporal characteristics of fish sounds to inform acoustic deterrence and identify the optimal temporal sound characteristics to elicit an avoidance response) and research Question 3 (Do all fishes respond to a particular set of temporal sound characteristics?). To do this, utilising and understanding the characteristics of fish sounds in specific contexts can be useful in identifying the temporal characteristics needed for acoustic deterrence.

As discussed in Section 2.5, acoustic stimuli have a pivotal role in information acquisition and communication in fishes (Ladich, 2014; Putland *et al.,* 2018). Sound production allows fish to communicate in various contexts such as for agonistic interactions, courtship and conspecific communication to manipulate school and shoal cohesion (Lugli and Fine, 2003; Ladich and Schleinzer, 2015; Radford *et al.,* 2015). Consequently, fishes may display negative (e.g. tu-fish, *Schizopygopsis younghusbandi*, for heterospesific sound production; Qin et al., 2019) or positive (e.g. round goby, *Neogobius melanostomus*, to conspesific sound production; Isabella-Valenzi and Higgs, 2013) phonotaxis to both hetero and conspesific sound production, suggesting that it may be a useful metric to inform acoustic deterrence.

Considering acoustic deterrence in the other animalia, it is known that alarm calls may be produced by mammals, birds and amphibians. Such alarm calls may be produced to identify an incoming threat or predator. An example of alarm calls are those of blue tits (*Parus caeruleus*) produding '*seeet'* alarm calls when identifying sparrow hawks (*Accipiter nisus*; Carlson *et al.,* 2017). As well as informing conspecifics, many species can be alerted, invoking a learned or unlearned response. Unlearned responses to alarm calls may occur when heterospecific calls have acoustic features similar to that used to recognise conspecific calls (e.g., fairy-wrens; *Malurus cyaneus*), or distinct sounds (Fallow *et al.,* 2011; Magrath *et al.,* 2015). Therefore these alarm calls can, in some instances, be interpreted by many species. Consequently, this suggests that that there might be a sound recognised by a range of species. In such conditions, this may be useful for acoustic deterrence.

For some species, alarm calls have been used to develop acoustic deterrents. For example, a deterrent using the alarm calls of deer (Cervidae sp.) has been used to prevent deer-train collisions in Japan (Shimura *et al.,* 2021). Similarly, alarm calls from crimson rosellas (*Platycercus elegans*), a parrot native to eastern and south-eastern Australia, have been effective in deterring conspecifics in orchards, with no difference between the use of local and non-local alarm calls (Ribot *et al.,* 2011).

Concerning fishes, most sounds produced by fishes are categorised according to the corresponding behaviour, such as aggression (e.g., Mann, 2012; Radford *et al.,* 2018), agonistic (e.g., Almada *et al.,* 1996; Lagardère *et al.,* 2005), courtship (e.g., Malavasi *et al.,* 2004; Amorim and Neves, 2007) and disturbance (e.g., Schärer *et al.,* 2012; Rountree and Juanes, 2018). Aggression, agonistic and courtship calls have been identified through behavioural observations whilst disturbance sounds, also known as distress calls, are typically produced when an individual is hand-held (Parmentier *et al.,* 2017a). The anthropocentric methodology in regards to disturbance calls may not extrapolate to real-world situations and thus certain fish sounds such as alarm, startling, warning, distress and disturbance are unproven (Ladich, 2021).

To establish how the sounds produced by fishes may be used to inform acoustic deterrence, a meta-analysis and literature review was conducted. Objectives were to (1) determine whether temporal characteristics (PD, PP, PPS, SD) of sound production in fishes are consistent under a variety of contexts (e.g., courtship, disturbance, territorial aggression, amongst others); (2) determine whether sound production mechanisms and habitat-specific factors influence the sound production parameters. Biases in taxonomy and methodology of the studies were also identified to highlight literature gaps and inform future studies.

7.3 Methods

7.3.1 Literature search and data extraction

Standard systematic review methods were followed (CEE, 2013) to identify and retrieve data from empirical studies. To identify suitable peer-reviewed articles, literature searches were undertaken on Google Scholar (n = 75), Web of Science Core Collection (n = 961), Scopus (n = 1093) and Google (n = 17). The search term "(fish*) AND ((("alarm" OR "defenc*" OR "aggress*" OR "defenc*" OR "distress" OR "stridulat*" OR "courtship") AND ("sounds" OR "calls" OR "vocali*")) OR "vocali*" OR "sound production")" was used in the literature databases and was adapted for use in Google (removal of asterisks). Research outputs were limited to peer-reviewed articles, peer-reviewed conference papers and theses. There were no restrictions for the year of publication. Of all the papers identified through search engines, 31.0% were replicates. Additionally, five literature reviews concerning sound production of fishes were randomly selected to identify additional literature through 'snowballing' in which the bibliography of each literature review was screened and studies not included in the initial literature search were identified.

The titles of 1,806 and abstracts of 1,257 papers were screened manually to determined which papers directly or potentially addressed sound production of fishes (Figure 32). Only titles in the English language were considered. Subsequently, 687 texts were scanned manually to omit papers that did not directly address sound production. For example, many papers considered passive acoustic monitoring in which multiple sound production were heard (e.g., Straight *et al.,* 2014; Locascio and Burton, 2016). Following that, 382 full texts were read and selected (Figure 32) based on planned eligibility criteria. Relevant studies were that of individual, adult life stage, teleost fishes with at least one temporal characteristic of a sound production produced at least 10% of the time in a known context. This was sufficient for the literature review, however, for the meta-data, the mean, standard deviation (or standard error) and the sample size were necessary for the text to be included in further analysis. Data were extracted from the text, whilst tables and figures were interpreted using MATLAB.

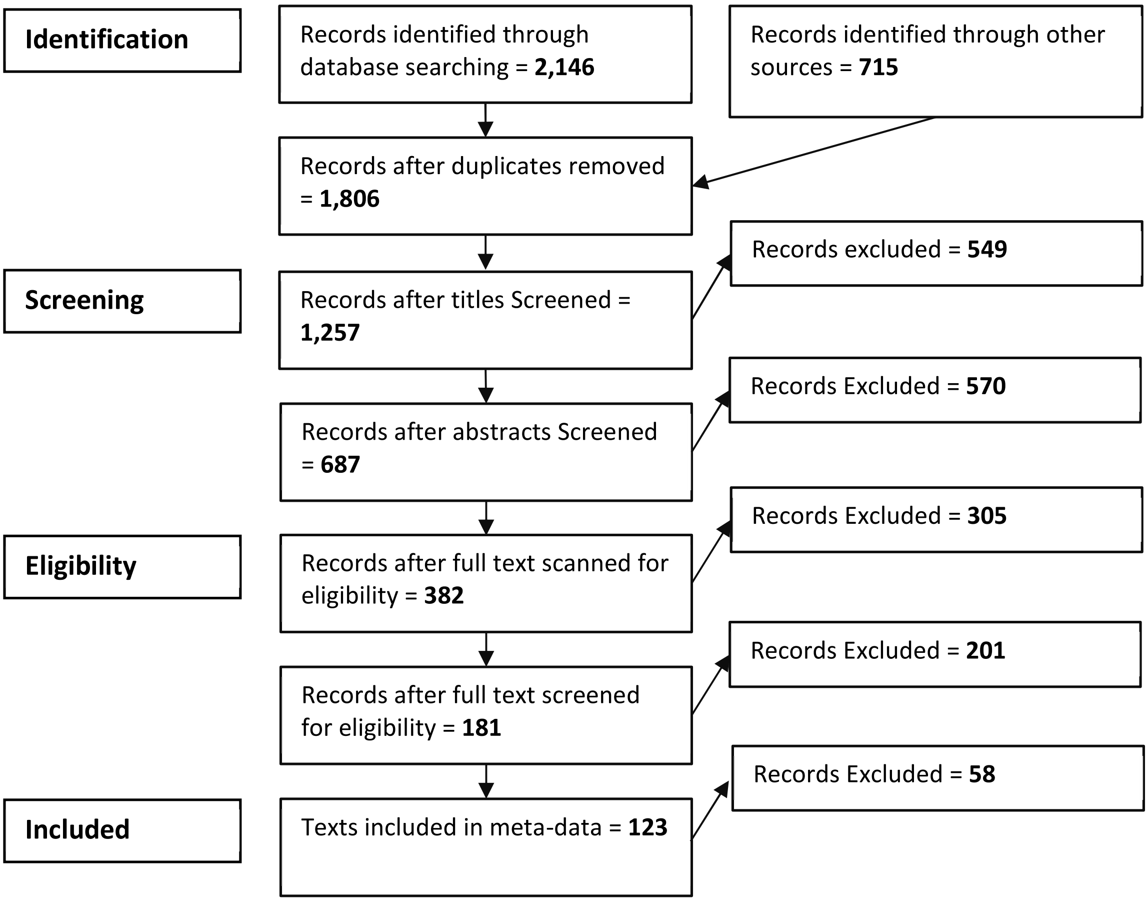


Figure 32 The number of texts and records identified and screened for a meta-analysis. Screening was conducted manually. Relevant studies of adult life stage fishes included at least one temporal characteristic of a sound production produced at least 10% of the time in a known context.

The methodological variables collected were: lead author of the article; publication year; study location; *in situ* or laboratory recordings; fish origin (captive or wild); season of recording (spawning or non-spawning); recording duration; number of replicates. Variables regarding the sound-producing individual were species; taxonomic order; sex; marine or freshwater; zone of habitation (e.g., pelagic, demersal); standard length (tip of the snout to the end of the body excluding the caudal fin); total length (tip of the snout to the tip of the longest part of the caudal fin); sound production mechanism; sound production behaviour (context). Temporal characteristics recorded were PP (peak to peak time between the onset of two successive pulses, ms); PD (duration of a single pulse, ms); PPS (number of pulses in one sound); SD (duration of a sound that may be regarded as a particular timbre, such as a croak or chirp, ms).

7.3.2 Methodology for Literature Review

Of the 181 records selected (Appendix D), there were 100 lead authors with literature published from 1958 to 2020. There was a total of 624 sound production (i.e., 624 data rows) of 205 species, recorded from 15 taxonomic orders. There were 11 described behaviours and six mechanisms of sound production. To identify potential biases in taxonomy, a pie chart was created to determine the spread of the data amongst the 15 taxonomic orders. Additionally, line plots were used to show the number of research outputs per year for each taxonomic order. As for identifying methodological biases, a pie chart observing the continent in which the study took place was created. Further, consideration of other methodological parameters such as the recording duration, the origin of the fish, whether the recordings took place *in situ* or in a tank, and whether the recordings were made in spawning season or not were considered.

7.3.3 Methodology for Meta-Analysis

For the meta-analysis (Appendix E), only papers considering agonistic, courtship, disturbance, spawning and territorial aggression were considered, since the feeding mechanism may have been a circumstantial sound from snapping teeth, and the other five behaviours concerned only a small sample size (1 - 15). This meant 3 courtship and spawning, 10 feeding, 1 nest building, 1 oral incubation, and 2 postspawning papers were omitted. Other papers were excluded because they did not record the number of individuals used or state mean and standard deviation (or standard error) - the majority of whom recorded the median and the range. In total, 58 papers were excluded from the literature review data, meaning 123 papers with 73 lead authors and literature published from 1972 – 2020. Overall, 428 sound production from 155 species (14 orders) were considered. There were four described behaviours and six mechanisms of sound production. The data were inspected initially, by creating bar blots of count data against behaviour (Figure 33), order (Figure 34) and sonic mechanism (Figure 35) for each predictor variable (PD, PP, PPS, SD). In all cases, the data was skewed, which meant that the most robust analysis was that of data visualisation using the mean and standard deviation. If the standard error was not stated and a standard deviation, σ, was given, the formula $SE = \frac{\sigma}{\sqrt{n}}$ was used, where *n* is the sample size. For each parameter recorded (PD, PP, PPS, SD) a small-sample size correction was applied (Doncaster and Spakes, 2018):

$$S^2 = \frac{(\sum_{i=1}^{k} s_i^2)/k}{n} \quad \text{Equation 14}$$

where S^2 is the corrected variance, s^2 is the sample variance, *n* is the study sample size, and *k* is the number of studies in the meta-analysis.

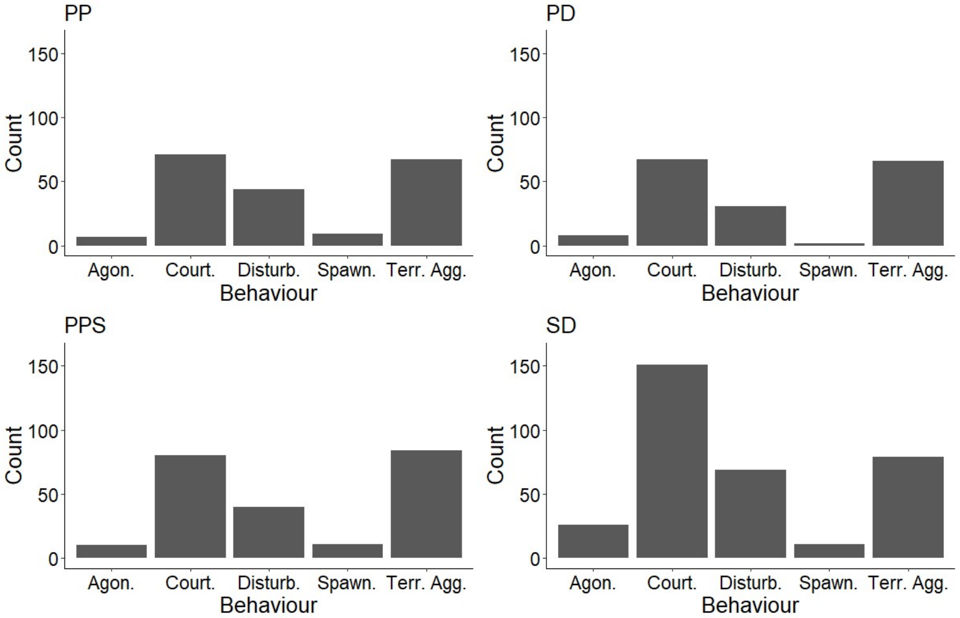


Figure 33 Number (count) of data points for each sound production behaviour: agonistic (agon.); courtship (court.); disturbance (disturb.); spawning (spawn.); territorial aggression (Terr. Agg.). Count data was recorded (and titled) for each temporal sound characteristic (pulse period – PP; pulse duration – PD; pulses per sound – PPS; sound duration – SD).

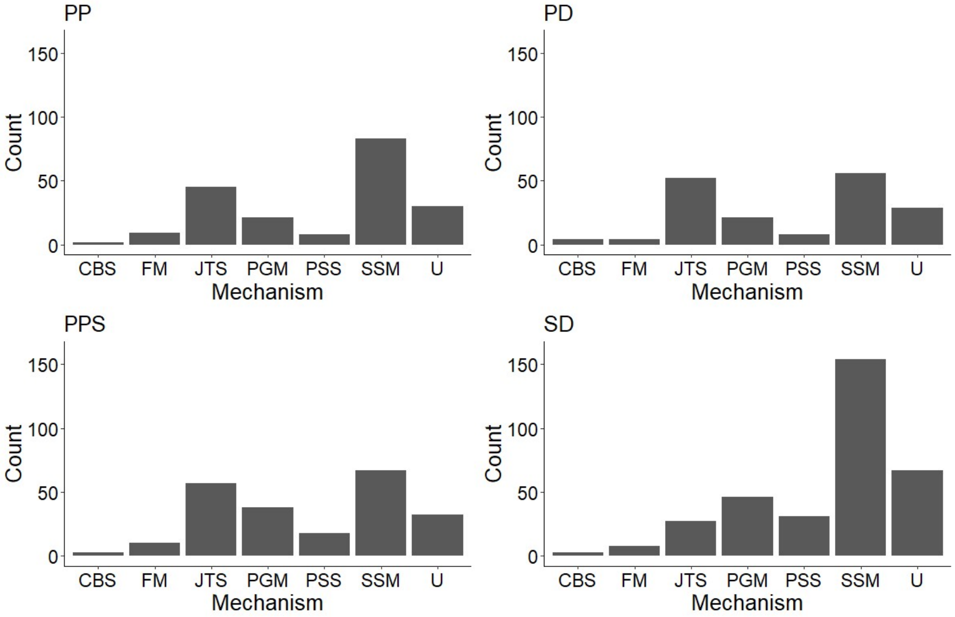


Figure 34 Number (count) of data points for each sound production mechanism: cranial bone stridulation (CBS); fin movement (FM); jaw or teeth stridulation (JTS); pectoral girdle muscle (PGM); swimbladder sonic muscle (SSM); unknown (U). Count data was recorded (and titled) for each temporal sound characteristic (pulse period – PP; pulse duration – PD; pulses per sound – PPS; sound duration – SD).

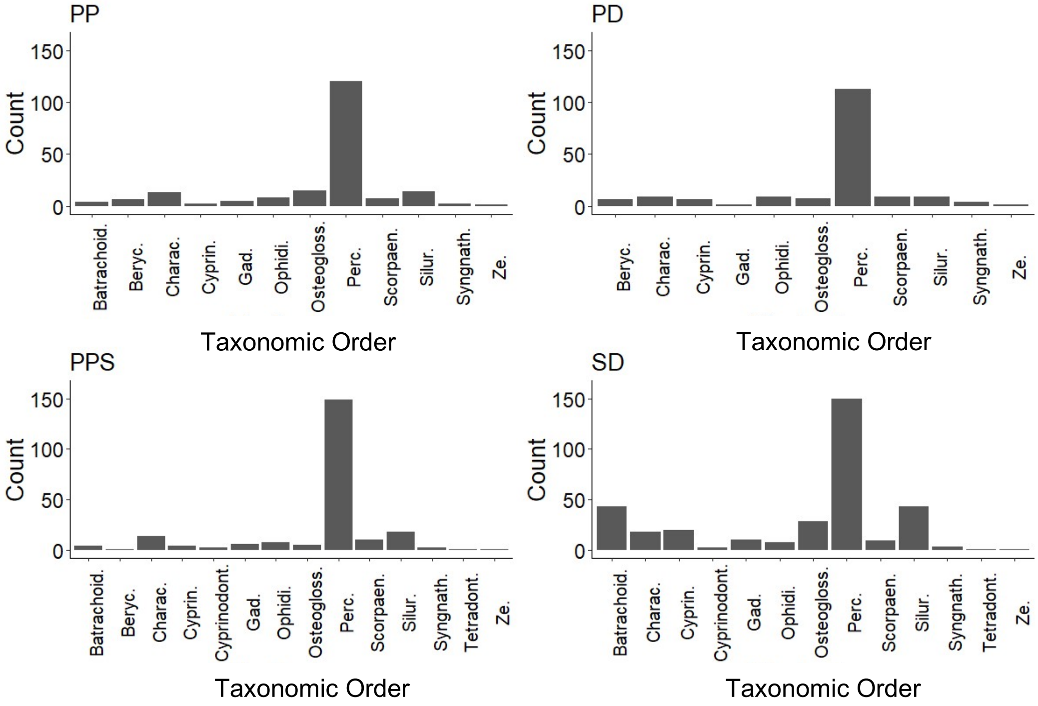


Figure 35 Number (count) of data points for each taxonomic order (all titled without the 'iformes' suffix). Count data was recorded (and titled) for each temporal sound characteristic (pulse period – PP; pulse duration – PD; pulses per sound – PPS; sound duration – SD).

Orchard plots were created for each predictor variable (PD, PP, PPS, SD), showing overall mean effects, 95% confidence and prediction intervals, and the individual effect sizes scaled by their precision (Lagisz *et al.,* 2020). Consequently, for each predictor variable, using the 'escalc' function in R, the raw mean, corrected standard deviation (*S*) and sample size were used to quantify the sampling variance. Following this, the raw mean and sampling variance were used in a multivariate linear mixed model with the study as a random variable.

To determine whether the temporal characteristics were consistent under a variety of contexts, the sound production were categorised according to the context (e.g., for behaviour: Agonistic, Courtship, Disturbance and Territorial Aggression). For each context, a subgroup GLM was formulated with the to determine the *Q*-value (the test statistic for residual heterogeneity) and the p-value and Z-value were obtained to determine whether the sound production differed within each behaviour. Similarly, subgroup differences were tested, obtaining a value for Q_M (test statistic for the omnibus test of moderators). This was carried out for each of the four temporal characteristics. To determine whether sound production mechanisms and habitat-specific factors influence the sound production parameters, the same methodology was used with the sonic mechanism and habitation zone as the subgroup, respectively. This information was also shown in orchard plots following the methodology found in Lagisz *et al.* (2020).

7.4 Results

7.4.1 Literature Review

The most common taxonomic order recorded in the data was Perciformes, whilst the other 14 taxonomic orders constituted 0.2% – 9.0% of the total data (Figure 36). From 1995 onwards, there was a greater variety of research on different taxonomic orders (Figure 37), although the greatest number of articles investigated Perciformes, with large increases in publication rate from 2006 to 2020. Overall, the majority of the research into sound production of teleost fishes has occurred after 2000.

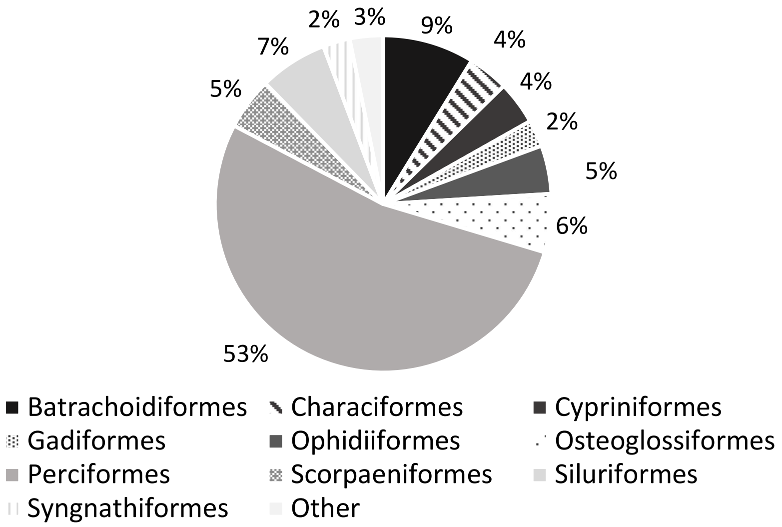


Figure 36 A pie chart showing the distribution of the fish sound production data across 15 taxonomic orders. Other constitutes of: Acipenseriformes (0.16%); Beryciformes (0.96%); Cyprinodontiformes (0.48%); Tetradontiformes (1.28%); Zeiformes (0.32%).

The majority of the research was located in Europe and North America, both of which are predominantly northern hemisphere continents (Figure 38). Not all studies recorded the location, with 4.0% lacking a description. Of all the sounds produced, 4.0% were recorded in a concrete tank, 31.0% *in situ* and 65.0% in a tank. The water temperature was recorded in 80.0% of cases. The tanks varied in volume, recording depth and material. The recording time was documented in 62.0% of cases. Of those that did, the majority of recordings were less than 30 min, with 21.0% in the interval $0 < x \leq 10$ min and 22.0% in the interval 10 min $< x \leq 30$ min. Approximately 10% of the data was recorded in intervals between 30 min and 2 hr, with the remaining data recorded for longer durations, and some surpassing 24 hr.

Of all the sounds produced, 71.0% of the data points documented when the recordings took place. Of these, 76.0% of the sound production took place in the spawning season, 3.0% occurred outside this period and 22.0% did not specify if the recordings were in the spawning season or not. Since courtship and spawning behaviours evidently took place in the spawning season, these values were recalculated on behaviours that weren't labelled as "courtship" or "spawning". Of those behaviours, 56.0% stated when the recordings took place. Of those that did, 40.0% occurred during the spawning season, 7.0% outside this period and 53.0% did not specify if the recordings were in the spawning season or not. The length of the individuals was recorded 59.0% of the time, whilst the sex was documented in 72.0% of cases.

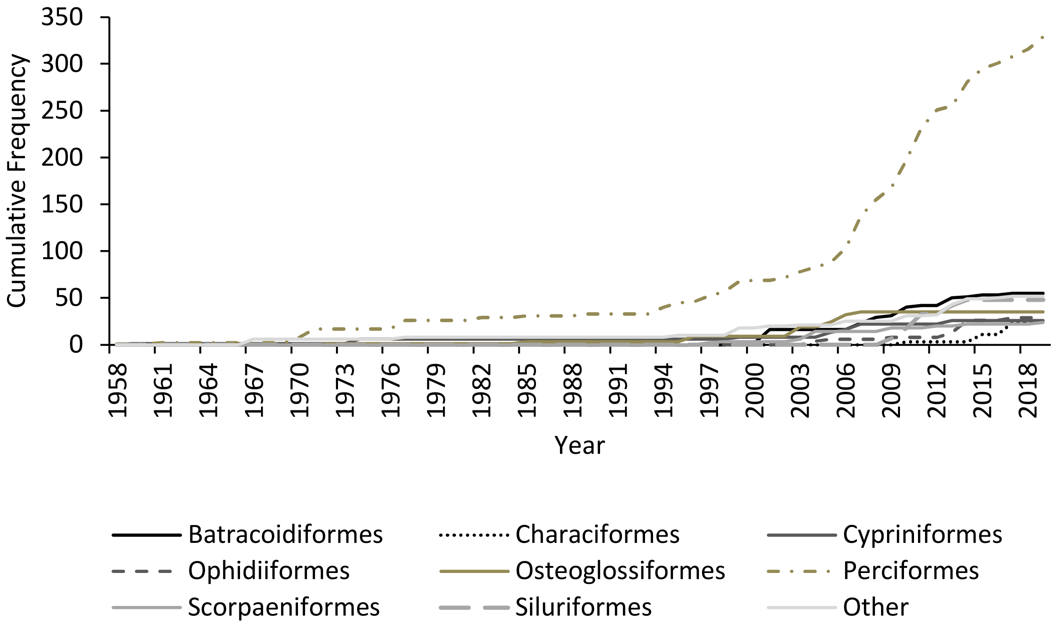


Figure 37 A line graph showing the cumulative frequency of the fish sound production publications across 15 taxonomic orders. Other constitutes of: Acipenseriformes; Beryciformes; Cyprinodontiformes; Gadiformes; Syngnathiformes; Tetradontiformes; Zeiformes.

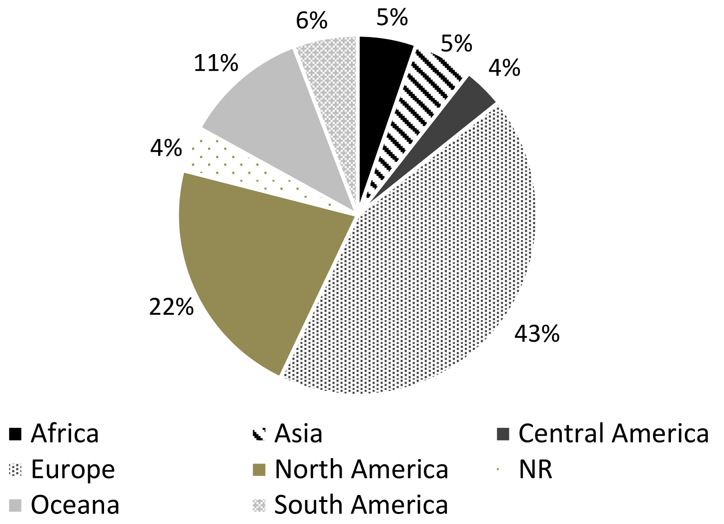


Figure 38 A pie chart showing the study location of literature investigating teleost fish sound production. NR – Not recorded.

7.4.2 Meta-Analysis

7.4.2.1 Behavioural Context

The territorial aggression calls had the largest range of values for the PD, PP and PPS compared to the other behavioural contexts (Figure 39). For the SD data, courtship exhibited the largest range due to an outlier at 80 s. Nevertheless, significant differences were recorded within all the contexts for every temporal characteristic (except spawning: SD and PD; disturbance: SD). Similarly, differences between each context were found for every temporal characteristic (Table 26), meaning there was a difference in sound production between behaviours. Upon subjective inspection of the mean values, the disturbance calls had more consistently low values for PD, PP, PPS and SD compared to the other contexts, whereas courtship calls exhibited higher values.

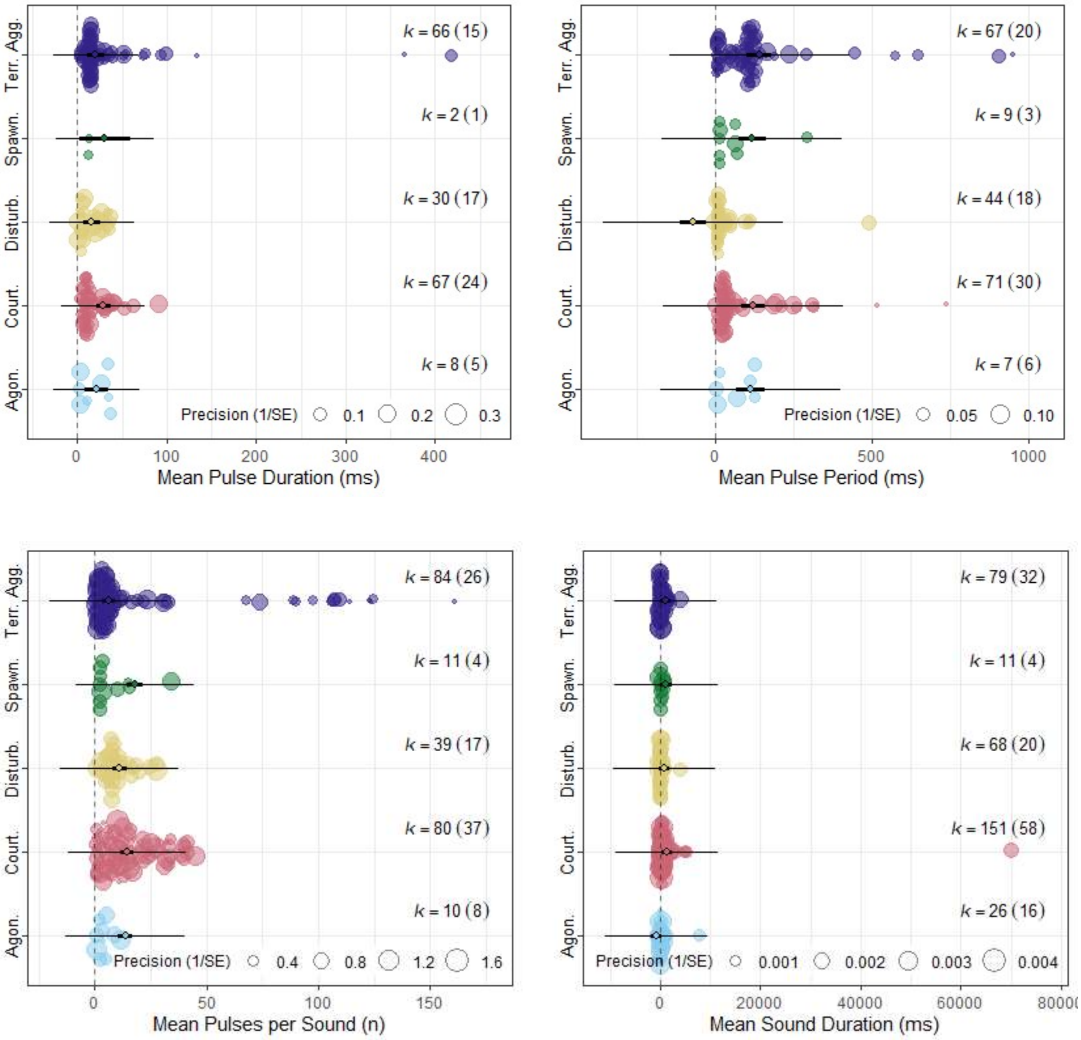


Figure 39 Orchard plots for each temporal characteristic showing the point estimate (centre of the bar), 95% confidence interval (thick line), 95% prediction interval (thin line) and individual effect sized (bubbles with the scale at the bottom of each plot) for five recorded behaviours: agonistic (agon.); courtship (court.); disturbance (disturb.); spawning (spawn.); territorial aggression (terr. agg.). The k value is the number of data points and the number in brackets is the number of studies the data points come from.

Table 26 The behavioural context for each predictor variable in a meta-analysis comparing sound production of fishes. PD – Pulse Duration; PP – Pulse Deriod; PPS – Pulses Per Sound; SD – Sound Duration. Statistical tests were conducted within each context, between all the data and between each context. The asterisk denotes statistical significance ($p < 0.05$). All values are to 3 significant figures.

Predictor Variable	**Context**	**Mean [95% CI]**	**Q/Qm**	**df**	**z**	**p**
PD	Agonistic	19.1 [4.58, 33.7]	22.2	7	2.58	0.00*
	Courtship	22.7 [15.7, 30.0]	241	66	6.30	0.00*
	Disturbance	16.9 [10.7, 23.1]	51.7	29	5.36	0.01*
	Spawning	12.7 [-12.9, 38.2]	0.00	1	0.97	0.97
	Territorial Aggression	32.5 [13.7, 51.3]	1410	65	3.39	0.00*
	All		1750	172	6.43	0.00*
	Subgroup Differences		12.5	4		0.01*
PP	Agonistic	55.4 [10.9, 100]	50.5	6	2.44	0.00*
	Courtship	94.8 [52.2, 137]	967	70	4.36	0.00*
	Disturbance	38.7 [5.1, 72.3]	873	43	2.62	0.00*
	Spawning	50.6 [13.9, 87.2]	67.9	8	2.70	0.00*
	Territorial Aggression	118 [25.5, 210]	2670	66	2.50	0.00*
	All		5000	197	4.57	0.00*
	Subgroup Differences		216	4		0.00*
PPS	Agonistic	4.46 [1.8, 7.2]	101	9	3.23	0.00*
	Courtship	14.6 [11.0, 18.1]	6120	79	8.08	0.00*
	Disturbance	9.3 [6.3, 12.3]	1260	38	6.02	0.00*
	Spawning	10.7 [0.9, 20.5]	787	10	2.14	0.00*
	Territorial Aggression	10.5 [3.0, 18.1]	23300	83	2.74	0.00*
	All		32900	223	7.33	0.00*
	Subgroup Differences		364	4		0.00*
SD	Agonistic	516 [-37.7, 1070]	111	25	1.83	0.00*
	Courtship	1760 [-593, 4110]	16300	150	1.47	0.00*
	Disturbance	199 [55.8, 343]	36.9	67	2.72	1.00
	Spawning	300 [-36.5, 636]	2.78	10	1.75	0.99
	Territorial Aggression	467 [257, 678]	103	78	4.35	0.03*
	All		16700	334	1.92	0.00*
	Subgroup Differences		116	4		0.00*

7.4.2.2 Sound Mechanism

The recorded sonic mechanisms were: Cranial Bone Stridulation (CBS); Fin Movement (FM); Jaw or Teeth Stridulation (JTS); Pectoral Girdle Muscle (PGM); Swimbladder Sonic Muscle (SSM); Unknown (U). The species that used pectoral spine stridulation had a lower PP and PD than the other sound production mechanisms (Figure 40). The FM produced signals with a large PD and limited PPS. Differences were recorded within all the sound production mechanisms for every temporal characteristic (Table 27), except those that had a low number of data points and/or were from a small number of studies. Similarly, differences between each sound production mechanism were found for PD, PP and PPS, meaning there was a difference in sound production between the mechanism of sound production. However, there was no difference between each sound production mechanism for the sound duration data, indicating that the length of the sound production did not differ with the mechanism.

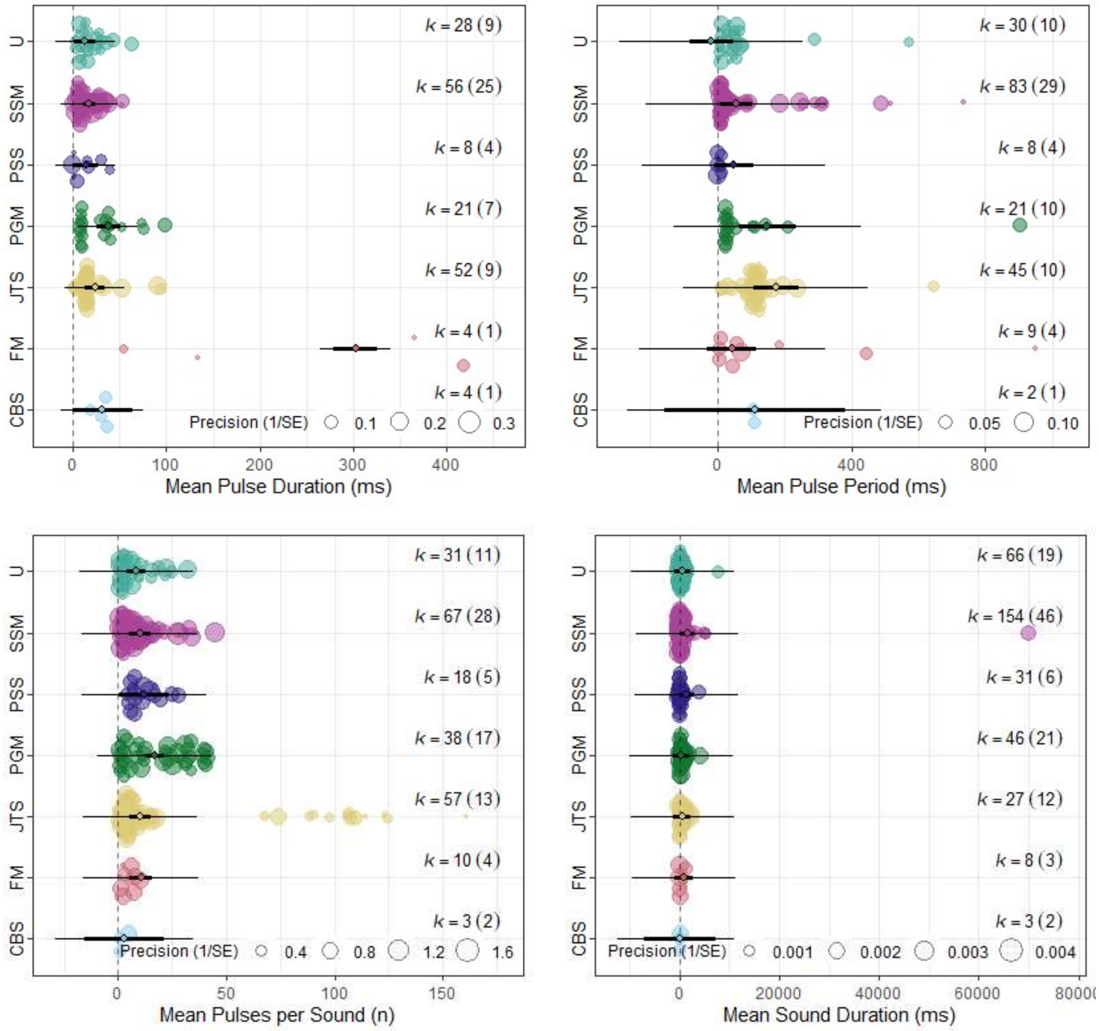


Figure 40 Orchard plots for each temporal sound characteristic showing the point estimate (centre of the bar), 95% confidence interval (thick line), 95.0% prediction interval (thin line) and individual effect sized (bubbles with the scale at the bottom of each plot) for six recorded sound production mechanisms: Cranial Bone Stridulation (CBS); Fin Movement (FM); Jaw or Teeth Stridulation (JTS); Pectoral Girdle Muscle (PGM); Swimbladder Sonic Muscle (SSM); Unknown (U). The k value is the number of data points and the number in brackets is the number of studies the data points come from.

Table 27 The sound production mechanism context for each predictor variable in a meta-analysis comparing sound production of fishes. PD – Pulse Duration; PP – Pulse Period; PPS – Pulses Per Sound; SD – Sound Duration; CBS – Cranial Bone Stridulation; FM – Fin Movement; JTS – Jaw or Teeth Stridulation; PGM – Pectoral Girdle Muscle; SSM – Swimbladder Sonic Muscle; U – Unknown. The asterisk denotes statistical significance (p < 0.05). All values are to 3 significant figures.

Predictor Variable	**Context**	**Mean [95% CI]**	**Q/Qm**	**df**	**z**	**p**
PD	CBS	31.3 [19.0, 43.6]	1.07	3	4.99	0.78
	FM	321 [302, 340]	240	3	33.3	0.00*
	JTS	21.7 [7.9, 35.6]	237	51	3.08	0.00*
	PGM	40.6 [17.8, 63.4]	116	20	3.49	0.00*
	PSS	8.66 [-5.03, 22.3]	8.28	7	1.24	0.31
	SSM	17.7 [13, 22.4]	98.7	55	7.39	0.00*
	U	17.7 [7.9, 27.6]	43.5	27	3.53	0.00*
	All		1750	172	6.43	0.00*
	Subgroup Differences		621.6	6		0.00*
PP	CBS	111 [76.1, 146]	0.02	1	6.21	0.90
	FM	142 [-55.1, 339]	372	8	1.41	0.00*
	JTS	130 [13.7, 246]	521	44	2.19	0.00*
	PGM	149 [-18.1, 316]	1670	20	1.75	0.00*
	PSS	4.17 [-10, 18.4]	0.45	7	0.58	1.00
	SSM	58.8 [31.7, 86]	1720	82	4.25	0.00*
	U	75.4 [43.1, 108]	279	29	1.82	0.00*
	All		5000	197	4.57	0.00*
	Subgroup Differences		43.9	6		0.00*
PPS	CBS	2.94 [-0.79, 6.66]	4.58	2	1.55	0.10
	FM	5.48 [1.59, 9.37]	47.0	9	2.77	0.00*
	JTS	14.4 [0.39, 28.3]	21400	56	2.02	0.00*
	PGM	14.8 [8.91, 20.7]	3600	37	4.92	0.00*
	PSS	11.8 [10.4, 13.4]	346	17	15.5	0.00*
	SSM	10.0 [6.94, 13.1]	4630	66	6.35	0.00*
	U	7.69 [3.98, 11.4]	1320	30	4.07	0.00*
	All		32900	223	7.33	0.00*
	Subgroup Differences		57.3	6		0.00*
SD	CBS	35.2 [-649, 719]	0.00	2	0.10	1.00
	FM	209 [-199, 616]	2.82	7	1.00	0.90
	JTS	521 [217, 825]	49.2	26	3.36	0.00*
	PGM	570 [283, 858]	80.0	45	3.89	0.00*
	PSS	241 [-81, 564]	35.3	30	1.47	0.23
	SSM	1620 [-613, 3890]	16300	153	1.42	0.00*
	U	510 [206, 815]	121	65	3.29	0.00*
	All		16700	354	1.91	0.00*
	Subgroup Differences		1.73	6		0.94

7.4.2.3 Zone of Habitation

The PD only differed within the benthopelagic and demersal zones (Table 28). However, differences were detected between each zone, with reef dwelling fishes producing sound production with a long PD and pelagic fishes producing calls roughly 10 times shorter PD. Additionally for the SD, differences were detected within each zone for benthopelagic and demersal fishes, however, there were no subgroup differences. Upon inspection of the raw mean data (Figure 41), species inhabiting the pelagic zone had the lowest PD, PP, and PPS. For the other sound characteristics, there were differences both within each subgroup and between each subgroup except for the bathydemersal species as there was a sample size of one.

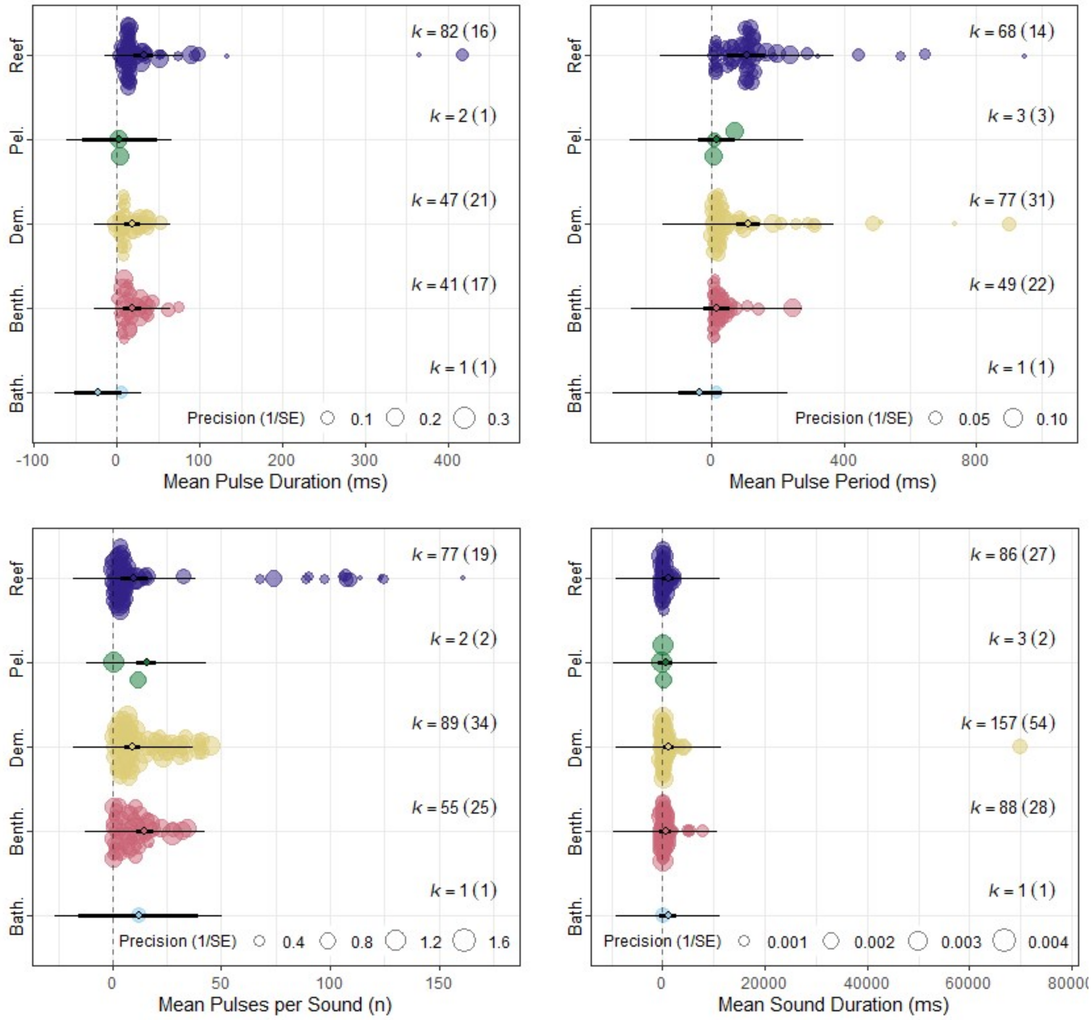


Figure 41 Orchard plots showing the point estimate (centre of the bar), 95% confidence interval (thick line), 95% prediction interval (thin line) and individual effect sized (bubbles with the scale at the bottom of each plot) for five zones of habitation: bathydemersal (bath.); benthopelagic (benth.); demersal (dem.); pelagic (pel.); reef. The k value is the number of data points and the number in brackets is the number of studies the data points come from. Data was recorded for each temporal sound characteristic (pulse period – PP; pulse duration – PD; pulses per sound – PPS; sound duration – SD).

Table 28 The zone of habitation context for each predictor variable in a meta-analysis comparing sound production of fishes. PD – Pulse Duration; PP – Pulse Period; PPS – Pulses Per Sound; SD – Sound Duration. The asterisk denotes statistical significance ($p < 0.05$). Values are to 3 significant figures.

Predictor Variable	**Context**	**Mean [95% CI]**	**Q/Qm**	**df**	**z**	**p**
PD	Bathydemersal	6.00 [-14.9, 26.9]	0.00	0	0.56	1.00
	Benthopelagic	19.9 [12.9, 27]	87.4	40	5.53	0.00*
	Demersal	18.4 [11.8, 15]	86.3	46	5.46	0.00*
	Pelagic	3.50 [-4.6, 11.6]	0.01	1	0.85	0.90
	Reef	32.1[14, 50.3]	1530	81	3.48	0.90
	All			172	6.43	0.00*
	Subgroup Differences			4		0.01*
PP	Bathydemersal	14 [-32.8, 60.8]	0.00	0	0.56	1.00
	Benthopelagic	40.4 [23.5, 57.2]	323	48	4.70	0.00*
	Demersal	88.7 [29.6, 148]	3150	76	2.94	0.00*
	Pelagic	30.3 [-13.2, 73.9]	15.2	2	1.37	0.00*
	Reef	99.5 [31.8, 167]	1140	67	2.88	0.00*
	All		5000	197	4.57	0.00*
	Subgroup Differences		71.4	4		0.00*
PPS	Bathydemersal	14 [-32.8, 60.8]	0.00	0	8.68	1.00
	Benthopelagic	9.93 [7.24, 12.6]	2910	54	7.23	0.00*
	Demersal	13.5 [10.2, 16.9]	6880	88	7.91	0.00*
	Pelagic	6.31 [-4.18, 16.8]	57	1	1.18	0.00*
	Reef	9.96 [0.15, 19.8]	22400	76	1.99	0.00*
	All		32900	223	7.33	0.00*
	Subgroup Differences		39.8	4		0.00*
SD	Bathydemersal	221 [-848, 1290]	0.00	0	0.41	1.00
	Benthopelagic	528 [265, 791]	204	87	3.93	0.00*
	Demersal	1510 [-388, 3410]	16300	156	1.56	0.00*
	Pelagic	74.0 [-304, 452]	0.11	2	0.38	0.95
	Reef	469 [338, 600]	79.3	85	7.02	0.65
	All		16700	334	1.92	0.00*
	Subgroup Differences		4.22	4		0.38

7.5 Discussion

Given the growing urgency to develop efficient acoustic deterrents, this study reviewed sound production of fishes to inform the temporal characteristics (PD, PP, PPS, SD) of such devices. The studies included freshwater, estuarine, and marine teleost fishes and were conducted in field and laboratory settings. A total of 123 studies were analysed, consisting of 428 sound production from 14 taxonomic orders. The sound production was used to develop models to determine whether temporal characteristics of sound production in fishes are similar under a variety of behavioural contexts, mechanisms and habitat-specific factors.

The advantage of classifying species according to their taxonomic order is that they often share taxonomic similarities. Hence, some orders possess the same sound production mechanism (e.g. Batrachoidiformes used the swimbladder sonic muscle). However, individuals in taxonomic orders use different sounds for different behavioural contexts (Kaatz et al., 2017), whilst some taxonomic orders exhibit a variety of calls and mechanisms (e.g., Perciformes). Classifying by behaviour is useful for understanding the calls of similar species, but when extrapolating it to others, it is limited by the mechanism, e.g., swimbladder muscles have a shorter pulse period, or the habitat in which the fish lives, e.g., reef dwelling fishes don't need sound to traverse long distances. Alternatively, the zone of habitation was useful for fishes living in a similar habitat (according to the aforementioned reasons), however, this doesn't account for the physiological differences between species and orders or between behavioural differences in sound production.

The temporal characteristics (PD, PP, PPS, SD) differed between each of the sounds produced and they also differed within each context. The territorial aggression calls were generally the most variable, however, a possible reason for this is that these calls were made both within and outside of the courtship period. Upon subjective inspection of the mean values, the disturbance calls had generally lower PD, PP, PPS and SD compared to the other behavioural contexts. To test this further, it is recommended that disturbance sound production is recorded on a wider variety of species, e.g., exploring a wider range of taxonomic orders, such as Cypriniformes (the taxonomic order largely focused on within this thesis), since the data was largely for Perciformes. Additionally, it is recommended that larger sample sizes/replicates are used (more than 10), since the majority of data had sample sizes <10. Differences in sound production within each context may be a result of the sound production mechanism, species or experimental methodology. It was not possible to test this further in this study since the data was largely biased and had small sample sizes.

The pectoral spine stridulation sound production had a lower PP and PD, most likely due to the nature of the mechanism as it is a result of friction of skeletal elements spine abduction or adduction (Parmentier *et al.,* 2010a). Conversely, FM produced sounds with large PD and low PPS. The FM has lower latency compared to the other sound production mechanisms. Swimbladder sonic muscles are often associated with the production of long-duration sounds, which was reflected in the results (Fine *et al.,* 2009; Fine and Parmentier, 2015). The swimbladder sonic muscles are attached to the swimbladder wall, which rapidly contract and vibrate (widely recognised as fast, intermediate and slow vibrations). This produces sounds (Smith, 1905; Ladich *et al.,* 2006) that with fast (e.g. red-bellied piranha; Millot *et al.,* 2011), slow (e.g. pearlfish, *Carapus boraborensis;* Parmentier *et al.,* 2008) or intermediate (e.g. pearl perch, *Glaucosoma* *buergeri*; Mok *et al.,* 2011) vibrations. Thus, there is variation in the sound production parameters even within the same mechanism.

Species inhabiting the pelagic zone consistently had the lowest PP, PD and PPS perhaps because the signal needed to traverse over a greater distance. The benthopelagic and demersal inhabiting fishes produced sounds that differed within each group for the SD and PD, whereas fish inhabiting reefs, bathydemersal and pelagic zones did not. Reasons for this may be that the data had species with a large variety of sound production mechanisms. Collinearity may be a factor that affected the outcome, and thus further investigation is required. Unfortunately, to subset the data enough to eliminate collinearity would have left sample sizes that were too small to analyse. Thus, more data on fish sound production is required. Additionally, to avoid confounding factors, it is suggested that researchers adopt a systematic methodology. For example, recording sound production for the same duration and using standardised metrics for the sound production parameters. Whilst pragmatics and cost of equipment may make it difficult to do so, some changes in methodology for both field and lab-based studies such as documenting if the sound production took place in the spawning season, the study location, recording duration and fish length would enable the identification of confounding factors and create more sophisticated statistical models. For lab-based experiments, standardisation of the tank size and material, whilst being sympathetic to the constraints of lab-based experiments would be of benefit to researchers. Focusing on pragmatics, it is recommended that researchers in the field collaborate, such as at workshops or conferences, and establish definitions of particular metrics and methodology standardisation for field and lab-based experiments. Following this, new guidelines may be outlined for researchers within the field.

Although there is little evidence of a common structure in the sounds produced by fish, this may not be entirely surprising across all fish in all circumstances. Even fish using the same sound production mechanisms do not share common sound structures. According to the acoustic niche hypothesis (Krause, 1987), animals tend to vocalise in different frequency bands, as to reduce competition. For most call types, an individual would intend to communicate with conspecifics, at least, i.e., if all fish exhibited the same call, then these sounds would be ineffective. For this study, one might expect *a priori*, that the sounds would all be different except for the alarm call. However, there is currently no evidence of such in fish (Ladich, 2021), which is further supported by this study.

Though it was not possible to determine the temporal characteristics that would be ideal for acoustic deterrents, it is recommended that further research and meta-analyses are necessary to determine the conditions in which best to deter fish. Alternatively, it may be more adequate to use sound production from the species of interest, rather than seek a general solution for all species. The most appropriate call to use may be the disturbance call since it is not produced solely in the spawning season.

Chapter 8 Thesis Discussion

As the most threatened ecosystems on the planet (He *et al.,* 2019), and facing greater environmental pressures than any other (Reid *et al.,* 2018), fresh waters are experiencing a 'biodiversity crisis' (Darwall *et al.,* 2018). Preserving these ecosystems is a necessity since freshwater species make up 48.0% of all fish species and 25.0% of all vertebrates (Eschmeyer and Fong, 2013). Compared to marine environments that cover 71.0% of the Earth's surface, freshwaters cover <1.0% and host an abundance of biota (Dawson, 2012). In freshwaters, there are around 13,000 fish species and in marine ecosystems <15,000 which covers a much larger area (Dawson, 2012).

Land-system change, freshwater use, biogeochemical flows, amongst others, all contribute to the interactions between physical, chemical, and biological processes, the effects of which are likely to be exacerbated by feedback loops (Steffen *et al.*, 2015). Global change and anthropogenic stressors thus contribute to biodiversity loss and, inevitably, loss of ecosystem functions and services (Oliver *et al.,* 2015). This will, therefore, have detrimental impacts on the world's biota (Diaz *et al.,* 2006). Anthropogenic stressors have been widely reported to affect marine and terrestrial species (Ávila *et al.,* 2018; Gamelon *et al.,* 2019; amongst others), however, freshwater species remain largely underrepresented within the current literature (Flitcroft *et al.,* 2019). Populations of freshwater species have declined 83.0% since 1970 and efforts from the scientific community are essential in preventing further deterioration (WWF, 2018). For freshwater fish, this means conserving the 13,000 extant species (IUCN, 2019).

When considering this research and its wider applications, one must consider the ecosystem services that freshwater dwelling species provide. Provisioning services are yielded through aquatic organisms that can be used for medicines or food (Aylward, 2005). Similarly, freshwater biota contribute to supporting services via nutrient cycling, predator-prey relationships and ecosystem resilience (Aylward, 2005). Aquatic organisms may even provide cultural ecosystem services through tourism and existence values (Aylward, 2005). Nevertheless, ecosystem services have been greatly impacted by humans and it has been suggested that the potential of these services across the globe has been diminished (Dodds *et al.,* 2013).

There are various explanations for the pervasive (Darwall *et al.,* 2018) deterioration of freshwater environments, such as wetland drainage (Kobza *et al.,* 2004); channelization (Latli *et al.,* 2019); invasive species (Daniels and Kemp, 2022); climate change (Poff *et al.,* 2012); increased agricultural production (Van Soesbergen *et al.,* 2019); reduced river flows (Grill *et al.,* 2019); declining water quality (Klimaszyk *et al.,* 2020). There are also novel pollutants, such as microplastics (Birkenhead *et al.,* 2020), anthropogenic noise (Currie *et al.,* 2021) and artificial light at night (Vowles and Kemp, 2021). The cumulative effects of multiple stressors may also exacerbate the response of the ecosystem (Reid *et al.,* 2018; Bayramoglu *et al.,* 2019).

To tackle the effects of environmental stressors on the ecosystem, there are a number of initiatives and regulations. For example, the Water Framework Directive (2000/60/EC), EIA Directive (2011/92/EU), the UK Environment Act (2021), and the Salmon and Freshwater Fisheries Act (1975). Some laws may limit the impacts of environmental stressors such as prohibiting the discharge of oil or hazardous substances (e.g., the Clean Water Act 1972 in the USA), release of invasive species (e.g., Fisheries Management Act 2007 in Australia), or the construction of infrastructure, such as dams and weirs, without appropriate mitigation (e.g., Salmon and Freshwater Fisheries Act 1975 in the UK). However, the legislation predominantly considers marine, coastal and estuarine environments above freshwater ecosystems, such as with the Marine Strategy Framework Directive (MSFD 2008/56/EC) and Goal 14 (life under water) of the Sustainable Development Goals. As such, whilst the methodology in this research is applicable to marine and freshwater species, the focus was predominantly on the latter.

Species of particular need of research focus are those listed in the International Union for Conservation of Nature (IUCN) database as endangered or critically endangered. As for UK freshwater fish species, this involves species such as the European eel. Not only do species experiencing population decline require protection, invasive species such as topmouth gudgeon (*Pseudorasbora parva*) in the UK require control. Increased connectivity, commerce and escape of ornamental fish have all led to the prevalence of invasive fishes in waterways globally (Keller et al., 2011). Introduction of goldfish, for example, in Australia and the US has caused extensive ecological damage, such as parasite dispersal and increased water turbidity from bottom feeding (see Lorenzoni *et al.,* 2010; Beatty *et al.,* 2016; Trujillo-González *et al.,* 2018). Both control of invasive species and protection of endangered species is a global issue that requires a number of integrative solutions.

Restoration of ecosystems, including freshwater environments, involves a multimodal approach in which fiscal policy, legislation, societal change and technology all play a key part. Focusing on technology, ‘green infrastructure’ is an essential aspect in the regeneration of ecosystems and the services they provide (Semeraro *et al.,* 2017). This technology may include alternative turbine designs to reduce injury and mortality at hydropower (Piper *et al.,* 2019), fish passes that allow migratory species to access their spawning grounds more easily (Montali-Ashworth *et al.,* 2021), and guidance (or deterrent) systems that allow safe passage of fishes at infrastructure and prevent entrainment.

In terms of protecting freshwater fishes, behavioural or physical deterrents may be used to guide fish away from harm. Physical screens are designed to prevent fishes from swimming into cooling water intakes, dams or any other unwanted locations. Typically, these screens consist of metal bars or mesh in various shapes and sizes (Ebenwaldner, 2018). Whilst physical screens have been more widely installed and with greater success, these devices may cause physical injury or mortality (Swanson *et al.,* 2005). Behavioural deterrents, however, are useful in that they take advantage of the natural response of an individual to a stimulus. These deterrents have the potential to minimise entrainment of fish at hydropower plants and water intake systems and may be useful in augmenting physical screens (Deleau *et al.,* 2019). As aforementioned, there are a variety of behavioural deterrents such as strobe lights (Kim *et al.,* 2017), bubble curtains (Zielinski and Sorensen, 2016; Flores-Martin *et al.,* 2021), electricity (Miller *et al.,* 2022) and acoustics (Deleau *et al.,* 2019; Currie *et al.,* 2021). The advantage of an acoustic stimulus is that it does not rely on light availability or eyesight of the target species, as every fish species has some form of hearing, be it via particle motion or sound pressure. Additionally, it is lower-cost and lower health and safety risk than other approaches such as electrical barriers (Noatch & Suski 2012).

Putland and Mensinger (2019) highlighted the methodological shortcomings in the design of acoustic deterrents. Shortcomings of acoustic deterrents were that studies may have played the stimulus outside of the range of hearing and may not have considered the role of noise in the behavioural response of the target individuals. Additionally, consideration of the effect of noise on the response of the target species has largely been lacking, since few studies have measured the ambient noise when testing acoustic deterrents (Putland and Mensinger, 2019). Finally, the temporal characteristics of the stimuli presented in the acoustic deterrents differed greatly (see Appendix A), with efficacies varying greatly within (e.g., Atlantic salmon; Knudsen *et al.,* 1994), or between studies (e.g., chinook salmon; Mueller *et al.,* 1998; Ploskey *et al.,* 2000), meaning the selection of the stimulus can be *ad hoc*. Collectively, these reasons have contributed to the fallibility of acoustic deterrents.

Building on the work of Matheus Deleau (2018) and Helen Currie (2021), this thesis returned to first principles to create a set of methodologies that move away from *ad hoc* selection of acoustic parameters when designing behavioural deterrents. The first objective was to select the optimum frequency (Chapter 5), then to understand the contribution of noise (Chapter 6), followed by understanding how fish vocalisations can inform the temporal characteristics of the deterrent (Chapter 7). This thesis has highlighted the importance and value of understanding fundamental fish behaviour in application to acoustic deterrence. Additionally, this thesis has also stressed that there are perhaps areas of fish behaviour that have been overlooked or understudied. It is proposed that for a target species, the startle threshold (Chapter 5) is undertaken to identify the optimum frequency, followed by the introduction of noise (Chapter 6) to determine the most suitable SNR, and finally selecting the temporal characteristics of the stimulus (Chapter 7) based on vocalisations (if they are available). The methodology presented in this study is a useful tool in optimising acoustic deterrents, so they produce a heightened response of the target individuals. Additionally, presenting the stimulus at the lowest SPL possible whilst maintaining a good response of the target individuals is useful in limiting noise pollution. Finally, the methodology used considers stimuli that use the least amount of energy, and thus lends itself to an environmentally conscious deterrent design.

A major theme of this thesis is that there is continued perceived wisdom concerning acoustic deterrence. There are very few studies that consider the concept of noise priming the response of fishes, with most considering masking effects. The study undertaken in this thesis (Chapter 6) was the first, to our knowledge, that demonstrated the presence of suprathreshold stochastic resonance when using an acoustic signal played above background noise. Furthermore, those in industry may present an acoustic stimulus according to the ‘best hearing’ of the target species (Fish Guidance Systems, 2023), something discredited by the scientific community (Popper *et al.,* 2014, amongst others). Although this concept is recognised in the scientific community, the work presented in this thesis acts to support that case, whilst addressing the limitations of commercially available acoustic deterrents and how to overcome those challenges. Considering the disconnect between science and industry, as well as the difficulties in comparing methodology for both the acoustic deterrent efficacies (Section 2.6) and for the fish sounds (Chapter 7), it is suggested that there is a requirement for standardisation of testing methodology for bioacoustics experiments. This is not a novel suggestion, since key players in the field (Halvorsen *et al.,* 2019; Ainslie *et al.,* 2022a; 2022b; Popper *et al.,* 2022) have proposed standardisation of methodology to facilitate replicability, to allow comparisons between studies, and to streamline cross-disciplinary research.

Throughout this thesis, all the studies used an improved small tank set-up in which the experimental arena was submerged in a larger tank filled with water. The walls of the arena were, thus, acoustically transparent, reducing reverberation as a result of reflections at the tank boundary. This allowed for greater acoustic replicability and behavioural validity. Moreover, a cylindrical tank was selected over a rectangular tank to again reduce scattering to produce an isotropic sound field, thus improving validity. Similarly, a cylindrical arena was more appropriate for behavioural measurements on fish as typically fish would dwell in corners when using a rectangular tank. Still-water conditions were used throughout each of the experiments, as hydrodynamic cues may also affect the behaviour of the individuals (Ericsson *et al.,* in prep).

Future studies may consider the role of both acoustic and hydrodynamic cues to determine whether it would be appropriate to use acoustic deterrents in lentic environments.

Each experiment used individual goldfish as the response of aggregations, groups or shoals to an acoustic stimulus may differ (Short *et al.,* 2020; Currie *et al.,* 2022). Most significantly, if an individual in a group elicits a startle response, it may encourage others to mimic the reaction (Short *et al.,* 2020). Thus, to determine the startle threshold and to quantify the role of noise on this response, it was necessary to use individuals. Nevertheless, there is a lack of understanding of how groups respond to acoustic stimuli (Neo *et al.,* 2015). To determine how collective behaviour may influence the responses to the stimuli discussed throughout this thesis, it is recommended that future studies test the stimulus, developed by using the proposed methodology, on groups as well as individuals.

Hatchery fish were used for all the experiments, and thus responses of wild fishes may vary. Goldfish were selected due to their hearing specialisations and a wealth of literature concerning their SPL and PA audiograms. Whilst it was possible to use wild or released goldfish in the UK, this would have introduced a large range of sizes, ages and life history, potentially introducing confounding variables and collinearity. In terms of life history, it would be impossible to determine the previous noise exposure of wild fish, and thus the contribution of this to the response of the individual would be unknown. Now a clear set of methodological principles has been established, there is potential to extend the study to consider the differences, if any, between hatchery and wild fish. This is of particular importance for application such as controlling invasive goldfish and applying the methodology to conserve populations of threatened fish species.

An interesting avenue to explore would be how the responses of goldfish change with size and life-history. The goldfish used throughout this PhD were small, young but sexually mature individuals purchased from local hatcheries. They were therefore limited in terms of noise exposure and stress. Considering age (and therefore size), it is likely that responses may be a result of previous noise exposure (Fakan and McCormick, 2019) or stressful experiences (Jonsson and Jonsson, 2014) that may influence boldness and risk-taking, or physiology (Jonsson and Jonsson, 2014). Bold and shy individuals may exhibit differing responses to acoustic cues. To our knowledge, there are no studies considering personality type and response to acoustic stimuli, however studies have considered the role of boldness on exploration (e.g., brook trout; *Salvelinus fontinalis*; White *et al.,* 2017) and fish passage (e.g., for American eel; *Anguilla rostrata*; Mensinger *et al.,* 2021). For example, the tendency of three-spined sticklebacks to explore an open arena from cover was observed (Price-Whelan *et al.,* 2019). Shy individuals exhibited greater variability in their reactions and were less predictable in their responses. Hence, future research may consider whether certain acoustic characteristics are more efficient for deterring bold individuals or *vice versa*. Additionally, individuals may experience a contribution of the swim bladder by transferring sound pressure to the ear via the Weberian ossicles (e.g., goldfish; Yan *et al.,* 2000). Further, resonance of the swim bladder, such as in crucian carp (*Carassius carassius*), may enhance hearing sensitivity (Li *et al.,* 2022), meaning a greater understanding of the contribution of the swim bladder is required. When considering all the points aforementioned, one must assess whether trade-offs are required to deter the maximum proportion of the population *in situ*.

Field testing of the methodology set out throughout this thesis is necessary, especially considering the contribution of ambient noise and frequency distribution at the site of deployment. Perhaps this would help identify sites that would be most appropriate for acoustic deterrents. The author hypothesises that sites with lentic waters and minimal to moderate ambient noise would be most appropriate. Additionally, cost-benefit analysis would be useful since the methodology proposed here requires more time than conventional strategies such as selecting a loud stimulus.

It is recommended that this methodology is tested on other species. Recommended species for testing are those that have one or more of the following: (1) possess specialised hearing such as Weberian ossicles; (2) are threatened and lack successful deterrence methods, such as the European eel (Deleau *et al.,* 2019; Piper *et al.,* 2019;); (3) are invasive, such as goldfish, silver carp and bighead carp; (4) have well understood sound production to determine the most appropriate temporal characteristics for the stimulus.

Chapter 9 Conclusions and contributions to existing knowledge

9.1 Conclusions

The research undertaken in this thesis was to fulfil the following aim: to inform acoustic deterrence through quantification of innate behavioural responses of fish to short-duration pure tones. To achieve this aim, three research objectives were devised (Section 1.2.4). Conclusions in relation to each objective are outlined below.

9.1.1 Research Objective 1: Determine the startle response threshold in goldfish to pure tone acoustic stimuli.

In Chapter 5, startle responses of goldfish were used to determine the optimum frequency for anti-predator avoidance in relation to a pure tone acoustic stimulus (Objective 1). The startle threshold (the SPL at which 25.0% of the tested population that startled) was calculated and compared to the AEP and PA hearing threshold. The optimum frequency to elicit a startle response was 250 Hz; different from the published hearing and PA sensitivities based on audiograms, and those used in industry. Additionally, the difference between the startle threshold and published hearing threshold data was not uniform. This study demonstrates that information obtained from audiograms may inadequately determine the most suitable frequencies at which avoidance behaviours are elicited in fish.

9.1.2 Research Objective 2: To quantify innate responses of goldfish responding to a 120 ms pure tone acoustic stimulus in presence and absence of band-limited (100 – 2500 Hz) random noise.

Chapter 6 combined two studies that tested behavioural avoidance responses to a pure tone signal decrease with increasing background noise (Objective 2). The proportion of fish that startled to the signal increased with increasing SPL. In the first experiment, no difference in the startle responses was detected between the ambient and 105 dB re 1 µPa background noise conditions. Hence, fine-scale analysis using SDT showed that startle responses in the pre-signal period were more likely in presence of noise and that individuals were more likely to elicit a startle response over time. In the second experiment, more background noise levels were added to examine these results further. In this experiment, when compared to ambient noise, more startles occurred with 105 dB re 1 µPa background noise, indicating presence of stochastic resonance in which the noise acts as a primer in eliciting an avoidance response. The results suggest that acoustic deterrents can be developed that are optimised based on the characteristics of the ambient soundscape, which would allow deterrents to use lower SPLs that deter fishes more efficiently, meaning the noise pollution associated with such devices would be minimised.

9.1.3 Research Objective 3: Utilise the temporal characteristics of fish sounds to inform acoustic deterrence and identify the optimal temporal sound characteristics to elicit an avoidance response.

In Chapter 7, a systematic review and meta-analysis (Objective 3) showed that sounds produced by fishes differed between the temporal characteristics (PD, PP, PPS, SD) however, they also differed within each context. Additionally, there was variation in the sound production parameters even within the same mechanism. Overall, there is little evidence of a common structure in the sounds produced by fish. Further research and standardisation of methodology are necessary to determine the conditions in which best to deter fishes. Alternatively, it may be more adequate to use sound production from the species of interest, rather than seek a general solution for all species.

9.2 Contributions to existing knowledge

Numerous contributions have been made to existing knowledge throughout this PhD. They have been outlined below.

- The literature review in Chapter 2 established that some industry players select frequencies for acoustic deterrents based on their frequency of best hearing obtained by AEP or behavioural audiograms. Similarly, as highlighted in (Putland and Mensinger, 2019), the efficacy of acoustic deterrents can be very low as acoustic deterrents may be played outside the hearing range of the target fish and the SNR may be neglected. Through the literature review and an additional literature search, it was identified that the selection of acoustic parameters is somewhat *ad hoc* and requires returning to first principles to design a set of methodologies to ameliorate this issue.

- Prior to commencing experiments using fish, a methodological study was designed to improve the sound field within the experimental arena. The study demonstrated that submerging a cylindrical experimental arena in a large water body produced a homogeneous and replicable soundfield. This study was presented at the Aquatic Noise Conference 2022 in Berlin and is in submission as a conference paper: Holgate, A., White, P. R., Leighton, T. G., and Kemp, P. S. (In Submission). A comparison of sound fields in two small experimental test arenas. In: Popper, A., Hawkins, A. (eds) The Effects of Noise on Aquatic Life III. Journal of the Acoustical Society of America. Springer, New York, NY.

- This thesis used a set of methodologies to address the *ad hoc* selection of acoustic parameters for deterrence of fish. The first experiment identified the optimum frequency of deterrence by using the startle response, akin to an anti-predator response. This work has been presented in a poster at the British Ecological Society Symposium 2021, as well as other University-based conferences such as the CDT conference 2020. The experiment has also been published as: Holgate, A., White, P. R., Leighton, T. G., and Kemp, P. S. (2023). Applying appropriate frequency criteria to advance acoustic behavioural guidance systems for fish. *Scientific Reports*, 13(1). doi:10.1038/s41598-023-33423-5.

- Experiment 2a (Chapter 6) used SDT to analyse fine-scale behaviour of goldfish in pre-signal periods, identifying that noise may influence the reaction of individuals to acoustic stimuli. The SDT is not often used within the context of acoustic deterrence but provided a useful tool to identify future avenues for research. This is being prepared for submission to the first issue of the Freshwater Science journal as: Holgate, A., White, P. R., Leighton, T. G., and Kemp, P. S. (In prep.). Advancing acoustic deterrents for fish conservation: accounting for the influence of background noise. Freshwater Science, 1.

- Experiment 2b (Chapter 6) found the presence of stochastic resonance, i.e., that noise acts as a primer to the response of goldfish to a pure tone stimulus. To our knowledge, this is the first study that demonstrates the presence of suprathreshold stochastic resonance when using an acoustic signal played above background noise.

- Following the PhD objectives, a meta-analysis was undertaken to inform acoustic deterrence using sounds produced by fishes. Whilst it was not possible to generalise the temporal characteristics that would be ideal for acoustic deterrents, further research, additional meta-analyses, and standardisation of methodology are necessary to determine the conditions in which best to deter fishes. To our knowledge this is the first study of its kind to analyse fish sounds in relation to acoustic deterrence.

- Throughout the PhD candidature I was able to collaborate on other projects, such as an article based on a keynote speech delivered at the Aquatic Noise 2018 conference in Den Haag, delivered by Prof. Timothy G. Leighton. The aim of this paper was to provide a comparison between ultrasound and its impacts on humans, as well as sound and its impact on fish. The article discussed the difficulties with progression of ultrasound and its impacts and its relevancy to aquatic bioacoustics. This paper was published as Leighton, T., Currie, H. A. L., Holgate, A., Dolder, C., Lloyd Jones, S., White, P. and Kemp, P. (2019). Analogies in contextualizing human response to airborne ultrasound and fish response to acoustic noise and deterrents. Proceedings of Meetings on Acoustics, 37, pp. 010014. doi: 10.1121/2.0001260.

- Similarly, the opportunity was provided to work in collaboration with Universidade Federal de São João del-Rei, Brazil, in 2019. The research projected aimed to investigate barotrauma in two dual-chambered physostomous Neotropical fish (pacu, *Piaractus mesopotamicus*, and piracanjuba, *Brycon orbignyanus*) exposed to rapid (< 1 second) decompression at different ratios of pressure change, using a hypo-hyperbaric chamber in relation to hydropower development taking place in Neotropical regions. The collaboration involved working in Brazil for a month investigating the injuries to piracanjuba related to pressure changes. This research is currently in submission to Science of the Total Environment as Castro, A., Melo, N., Daniels, J., Holgate, A., Dolman, L., Silva, L., Kemp, P. (In submission). The effects of rapid decompression on two Neotropical fish species and implications for hydropower turbine passage. Science of the total environment.

Appendix A Acoustic Deterrent Studies

A summary of acoustic deterrent studies. Variables considered are author (the main author on the paper); year; Latin name; common name; order; source (wild or hatchery); country (country of the study); study location (Tank, in situ, or artificial pond); pure or broadband; stimulus type (continuous, chirp, pulse, or crescendo); Freq. (frequency); One frequency (whether only one frequency was presented to the subject); Source SPL; ambient noise; SNR (signal to noise ratio); Best hearing (the most sensitive frequencies from the hearing threshold); total duration (total trial time); pulse duration; pulse rate; other pulse (for non-pulsed stimuli presented in an on-off style but long enough to be considered continuous); other pulse rate (for non-pulsed stimuli presented in an on-off style but long enough to be considered continuous); deterrence (percentage deterrence). NR – nor recorded; NA – not applicable.

Author	Year	Latin name	Common name	Order	Source	Country	Study Location	Pure or broadband?	Stimulus type	Freq. (Hz)	One frequency?	Source SPL (mean dB re 1 µPa)	Ambient Noise (mean dB re 1 µPa)	SNR	Best Hearing (Hz)	Total Duration	Pulse Duration (ms)	Pulse Rate (min^{-1})	Other Pulse	Other Pulse Rate	Deterrence (%)
Deleau	2019	*Anguilla anguilla*	Silver eel	Anguilliformes	Wild	UK	Artificial Pond	Broadband	Continuous	60-1000	N	150	112	1.339286	10–300[a]	21 days	NA	NA	≤60 min	NA	NR
Deleau	2019	*Anguilla anguilla*	Yellow eel	Anguilliformes	Wild	UK	Artificial Pond	Broadband	Continuous	60-1000	N	150	112	1.339286	10–300[a]	21 days	NA	NA	≤60 min	NA	NR
Deleau	2019	*Lampetra fluviatilis*	European River lamprey	Petromyzontiformes	Wild	UK	Artificial Pond	Broadband	Continuous	60-1000	N	150	112	1.339286		21 days	NA	NA	≤60 min	NA	NR
EPRI	1990	*Alosa pseudoharengus*	Alewife	Clupeiformes	Wild	Canada	Tank	Pure	Continuous	20-1000	N	190	NR	NR	200–4000, 10,000–100,000[b,c]	NR	NA	NA	30 min	NA	NR
EPRI	1990	*Salmo Salar*	Atlantic Salmon	Salmoniformes	Hatchery	Canada	Tank	Pure	Continuous	20-1000	N	190	NR	NR	10–1000[d,e]	NR	NA	NA	30 min	NA	NR
EPRI	1990	*Oncorhynchus tshawytscha*	Chinook salmon	Salmoniformes	Wild	Canada	Tank	Pure	Continuous	20-1000	N	190	NR	NR	10–1000[d,e]	NR	NA	NA	30 min	NA	NR
EPRI	1990	*Oncorhynchus mykiss*	Rainbow trout	Salmoniformes	Hatchery	Canada	Tank	Pure	Continuous	20-1000	N	190	NR	NR	10–1000[d,e]	NR	NA	NA	30 min	NA	NR
Gregory	2003	*Alosa fallax*	Twait shad	Clupeiformes	Wild	UK	In situ	Pure	Pulse	420000	Y	202	NR	NR	200–4000, 10,000–100,000[b,c]	4 mnth	0.2	20	NA	NA	NR
Gregory	2003	*Alosa fallax*	Twait shad	Clupeiformes	Wild	UK	In situ	Pure	Pulse	200000	Y	218	NR	NR	200–4000, 10,000–100,000[b,c]	4 mnth	0.2	20	30 min	every 30 min	NR
Jesus	2018	*Pseudochondrostoma duriense*	Northern Straight-Mouth Nase	Cypriniformes	Wild	Portugal	Tank	Pure	Chirp	2000	Y	140	NR	NR	100–7000[f,g]	NR	5000	12	NA	NA	87.9
Jesus	2018	*Salmo Trutta*	Brown trout	Salmoniformes	Wild	Portugal	Tank	Pure	Chirp	2000	Y	140	NR	NR	10–1000[d,e]	NR	5000	12	NA	NA	8.7
Jesus	2018	*Luciobarbus bocagei*	Iberian Barbel	Cypriniformes	Wild	Portugal	Tank	Pure	Chirp	2000	Y	140	NR	NR	100–7000[f,g]	NR	5000	12	NA	NA	95.9
Jesus	2018	*Luciobarbus bocagei*	Iberian Barbel	Cypriniformes	Wild	Portugal	Tank	Pure	Pulse	140	Y	140	NR	NR	100–7000[f,g]	NR	50	195	NA	NA	15.9
Jesus	2018	*Pseudochondrostoma duriense*	Northern Straight-Mouth Nase	Cypriniformes	Wild	Portugal	Tank	Pure	Pulse	140	Y	140	NR	NR	100–7000[f,g]	NR	50	195	NA	NA	30.7
Jesus	2018	*Salmo Trutta*	Brown trout	Salmoniformes	Wild	Portugal	Tank	Pure	Pulse	140	Y	140	NR	NR	10–1000[d,e]	NR	50	195	NA	NA	14.7
Knudsen	1992	*Salmo Salar*	Atlantic Salmon	Salmoniformes	Wild	Norway	Artificial Pond	Broadband	Pulse	10	N	NR	NR	NR	10–1000[d,e]	3-4 hr	NA	NA	2-5 sec	every 35 sec	NR
Knudsen	1992	*Salmo Salar*	Atlantic Salmon	Salmoniformes	Hatchery	Norway	Artificial Pond	Broadband	Pulse	10	N	NR	NR	NR	10–1000[d,e]	3-4 hr	NA	NA	2-5 sec	every 35 sec	NR

Knudsen	1992	*Salmo Salar*	Atlantic Salmon	Salmoniformes	Wild	Norway	Artificial Pond	Pure	Pulse	150	Y	NR	NR	NR	10–1000[d,e]	3-4 hr	NA	NA	2-5 sec	every 35 sec	NR
Knudsen	1992	*Salmo Salar*	Atlantic Salmon	Salmoniformes	Hatchery	Norway	Artificial Pond	Pure	Pulse	150	Y	NR	NR	NR	10–1000[d,e]	3-4 hr	NA	NA	2-5 sec	every 35 sec	NR
Knudsen	1994	*Salmo Salar*	Atlantic Salmon	Salmoniformes	Wild	Norway	In situ	Broadband	Pulse	10	N	NR	NR	NR	10–1000[d,e]	14 dys	10000	NR	NA	NR	98.2
Knudsen	1994	*Salmo Salar*	Atlantic Salmon	Salmoniformes	Wild	Norway	In situ	Pure	Pulse	150	Y	NR	NR	NR	10–1000[d,e]	14 dys	10000	NR	NA	NR	-11.5
Knudsen	1997	*Oncorhynchus tshawytscha*	Chinook salmon	Salmoniformes	Hatchery	USA	Tank	Broadband	Pulse	10	N	NR	NR	NR	10–1000[d,e]	3 mnth	5000	NR	NA	NR	NR
Knudsen	1997	*Oncorhynchus mykiss*	Rainbow trout	Salmoniformes	Hatchery	USA	Tank	Broadband	Pulse	10	N	NR	NR	NR	10–1000[d,e]	3 mnth	5000	NR	NA	NR	NR
Kynard	1990	*Alosa sapidissima*	American Shad	Clupeiformes	Wild	USA	In situ	Pure	Pulse	161900	Y	NR	NR	NR	200–4000, 10,000–100,000[b,c]	10 dys	NR	NR	NA	NA	NR
MacNamara	2012	*Anguilla anguilla*	Silver Eel	Anguilliformes	Wild	Ireland	In situ	Pure	Pulse	12.5	Y	NR	NR	NR	10–300[a]	5 hr	NA	NA	10 min	every 10 min	NR
MacNamara	2012	*Anguilla anguilla*	Silver Eel	Anguilliformes	Wild	Ireland	In situ	Pure	Pulse	16	Y	NR	NR	NR	10–300[a]	5 hr	NA	NA	10 min	every 10 min	NR
Maes	2004	*Anguilla Anguilla*	European eel	Anguilliformes	Wild	Belgium	In situ	Pure	Pulse	20-600	N	174	NR	NR	10–300[a]	48 hr	200	300	NA	NA	37.3
Maes	2004	*Clupea harengus*	Atlantic Herring	Clupeiformes	Wild	Belgium	In situ	Pure	Pulse	20-600	N	174	NR	NR	200–4000, 10,000–100,000[b,c]	48 hr	200	300	NA	NA	94.7
Maes	2004	*Sprattus sprattus*	European Sprat	Clupeiformes	Wild	Belgium	In situ	Pure	Pulse	20-600	N	174	NR	NR	200–4000, 10,000–100,000[b,c]	48 hr	200	300	NA	NA	87.9
Maes	2004	*Abramis bjoerkna*	Silver Bream	Cypriniformes	Wild	Belgium	In situ	Pure	Pulse	20-600	N	174	NR	NR	100–7000[f,g]	48 hr	200	300	NA	NA	40.1
Maes	2004	*Pungitius pungitius*	Ninespine Stickleback	Gasterosteiformes	Wild	Belgium	In situ	Pure	Pulse	20-600	N	174	NR	NR		48 hr	200	300	NA	NA	7.1
Maes	2004	*Gasterosteus aculeatus*	Three Spined Stickleback	Gasterosteiformes	Wild	Belgium	In situ	Pure	Pulse	20-600	N	174	NR	NR		48 hr	200	300	NA	NA	1.4
Maes	2004	*Liza ramada*	Thinlip Mullet	Mugiliformes	Wild	Belgium	In situ	Pure	Pulse	20-600	N	174	NR	NR		48 hr	200	300	NA	NA	75.8
Maes	2004	*Osmerus eperlanus*	European Smelt	Osmeriformes	Wild	Belgium	In situ	Pure	Pulse	20-600	N	174	NR	NR		48 hr	200	300	NA	NA	53.5
Maes	2004	*Dicentrarchus labrax*	European Bass	Perciformes	Wild	Belgium	In situ	Pure	Pulse	20-600	N	174	NR	NR	10–500[h]	48 hr	200	300	NA	NA	75.6
Maes	2004	*Perca fluviatilis*	European Perch	Perciformes	Wild	Belgium	In situ	Pure	Pulse	20-600	N	174	NR	NR	10–500 [h]	48 hr	200	300	NA	NA	51.2
Maes	2004	*Pomatoschistus*	Goby	Perciformes	Wild	Belgium	In situ	Pure	Pulse	20-600	N	174	NR	NR	10–500 [h]	48 hr	200	300	NA	NA	46.1
Maes	2004	*Stizostedion lucioperca*	Zander	Perciformes	Wild	Belgium	In situ	Pure	Pulse	20-600	N	174	NR	NR	10–500 [h]	48 hr	200	300	NA	NA	96.8
Maes	2004	*Lampetra fluviatilis*	European River Lamprey	Petromyzontiformes	Wild	Belgium	In situ	Pure	Pulse	20-600	N	174	NR	NR		48 hr	200	300	NA	NA	5.9
Maes	2004	*Limanda Limanda*	Common dab	Pleuronectiformes	Wild	Belgium	In situ	Pure	Pulse	20-600	N	174	NR	NR	10–300[a]	48 hr	200	300	NA	NA	0
Maes	2004	*Solea Solea*	Common Sole	Pleuronectiformes	Wild	Belgium	In situ	Pure	Pulse	20-600	N	174	NR	NR	10–300[a]	48 hr	200	300	NA	NA	46.6
Maes	2004	*Platichthys flesus*	European Flounder	Pleuronectiformes	Wild	Belgium	In situ	Pure	Pulse	20-600	N	174	NR	NR	10–300[a]	48 hr	200	300	NA	NA	37.7
Maniwa	1973		Mackerel	Scombridae	Wild	Japan	UN	UN	UN	UN	UN	96	NR	NR		NR	NR	NR	NR	NR	NR
Maniwa	1973		Yellowtail		Wild	Japan	UN	UN	UN	UN	UN	85	NR	NR		NR	NR	NR	NR	NR	NR
Maniwa	1973	*Trachurus symmetricus*	Jack Mackerel	Carangiformes	Wild	Japan	NR	NR	NR	NR	UN	96	NR	NR		NR	NR	NR	NR	NR	NR

Mueller	1998	*Oncorhynchus tshawytscha*	Chinook salmon	Salmoniformes	Wild	USA	Tank	Pure	Continuous	150	Y	162	NR	NR	10–1000^{d,e}	48 hr	NA	NA	15 sec	NR	47.5
Mueller	1998	*Oncorhynchus tshawytscha*	Chinook salmon	Salmoniformes	Wild	USA	Tank	Pure	Continuous	180	Y	162	NR	NR	10–1000^{d,e}	48 hr	NA	NA	15 sec	NR	30
Mueller	1998	*Oncorhynchus tshawytscha*	Chinook salmon	Salmoniformes	Wild	USA	Tank	Pure	Continuous	200	Y	162	NR	NR	10–1000^{d,e}	48 hr	NA	NA	15 sec	NR	22.5
Mueller	1998	*Oncorhynchus tshawytscha*	Chinook salmon	Salmoniformes	Hatchery	USA	Tank	Pure	Continuous	150	Y	162	NR	NR	10–1000^{d,e}	48 hr	NA	NA	15 sec	NR	5
Mueller	1998	*Oncorhynchus tshawytscha*	Chinook salmon	Salmoniformes	Hatchery	USA	Tank	Pure	Continuous	180	Y	162	NR	NR	10–1000^{d,e}	48 hr	NA	NA	15 sec	NR	10
Mueller	1998	*Oncorhynchus tshawytscha*	Chinook salmon	Salmoniformes	Hatchery	USA	Tank	Pure	Continuous	200	Y	162	NR	NR	10–1000^{d,e}	48 hr	NA	NA	15 sec	NR	5
Mueller	1998	*Oncorhynchus tshawytscha*	Chinook salmon	Salmoniformes	Wild	USA	Tank	Pure	Continuous	7	Y	155	NR	NR	10–1000^{d,e}	NR	NA	NA	5 - 15 sec	Every 5 - 10 min	35
Mueller	1998	*Oncorhynchus tshawytscha*	Chinook salmon	Salmoniformes	Hatchery	USA	Tank	Pure	Continuous	7	Y	155	NR	NR	10–1000^{d,e}	NR	NA	NA	5 - 15 sec	Every 5 - 10 min	7
Mueller	1998	*Oncorhynchus tshawytscha*	Chinook salmon	Salmoniformes	Wild	USA	Tank	Pure	Continuous	10 to 14	Y	NR	NR	NR	10–1000^{d,e}	NR	NA	NA	5 - 15 sec	Every 5 - 10 min	90
Mueller	1998	*Oncorhynchus tshawytscha*	Chinook salmon	Salmoniformes	Hatchery	USA	Tank	Pure	Continuous	10 to 14	Y	NR	NR	NR	10–1000^{d,e}	NR	NA	NA	5 - 15 sec	Every 5 - 10 min	70
Mueller	1998	*Oncorhynchus mykiss*	Rainbow trout	Salmoniformes	Hatchery	USA	Tank	Pure	Continuous	150	Y	162	NR	NR	10–1000^{d,e}	48 hr	NA	NA	15 sec	NR	25
Mueller	1998	*Oncorhynchus mykiss*	Rainbow trout	Salmoniformes	Hatchery	USA	Tank	Pure	Continuous	180	Y	162	NR	NR	10–1000^{d,e}	48 hr	NA	NA	15 sec	NR	30
Mueller	1998	*Oncorhynchus mykiss*	Rainbow trout	Salmoniformes	Hatchery	USA	Tank	Pure	Continuous	200	Y	162	NR	NR	10–1000^{d,e}	48 hr	NA	NA	15 sec	NR	20
Mueller	1998	*Oncorhynchus mykiss*	Rainbow trout	Salmoniformes	Hatchery	USA	Tank	Pure	Continuous	7	Y	155	NR	NR	10–1000^{d,e}	NR	NA	NA	5 - 15 sec	Every 5 - 10 min	8
Mueller	1998	*Oncorhynchus mykiss*	Rainbow trout	Salmoniformes	Hatchery	USA	Tank	Pure	Continuous	10 to 14	Y	NR	NR	NR	10–1000^{d,e}	NR	NA	NA	5 - 15 sec	Every 5 - 10 min	70
Murchy	2016	*Acipenser fulvescens*	Lake sturgeon	Acipenseriformes	NR	USA	Tank	Broadband	Continuous	60-10,000	N	145	NR	NR		10 min	NA	NA	NA	NA	0
Murchy	2016	*Polyodon spathula*	Paddlefish	Acipenseriformes	NR	USA	Tank	Broadband	Continuous	60-10,000	N	145	NR	NR		10 min	NA	NA	NA	NA	0
Murchy	2016	*Ictiobus cyprinellus*	Bigmouth buffalo	Cypriniformes	NR	USA	Artificial Pond	Broadband	Continuous	60-10,000	N	150	NR	NR	100–7000^{f,g}	10 min	NA	NA	NA	NA	NR
Murchy	2016	*Cyprinus carpio*	Common carp	Cypriniformes	NR	USA	Artificial Pond	Broadband	Continuous	60-10,000	N	150	NR	NR	100–7000^{f,g}	10 min	NA	NA	NA	NA	NR
Murchy	2016	*Pimephales promelas*	Fathead minnow	Cypriniformes	NR	USA	Tank	Broadband	Continuous	60-10,000	N	145	NR	NR	100–7000^{f,g}	10 min	NA	NA	NA	NA	0
Murchy	2016	*Ctenopharyngodon idella*	Grass carp	Cypriniformes	NR	USA	Artificial Pond	Broadband	Continuous	60-10,000	N	150	NR	NR	100–7000^{f,g}	10 min	NA	NA	NA	NA	NR
Murchy	2016	*Ictalurus punctatus*	Channel catfish	Ictaluriformes	NR	USA	Tank	Broadband	Continuous	60-10,000	N	145	NR	NR		10 min	NA	NA	NA	NA	0
Murchy	2016	*Dorosoma cepedianum*	Gizzard shad	Ictaluriformes	NR	USA	Tank	Broadband	Continuous	60-10,000	N	145	NR	NR		10 min	NA	NA	NA	NA	NR
Murchy	2016	*Lepomis macrochirus*	Bluegill	Perciformes	NR	USA	Artificial Pond	Broadband	Continuous	60-10,000	N	150	NR	NR	10–500^{h}	10 min	NA	NA	NA	NA	NR
Murchy	2016	*Sander vitreus*	Walleye	Perciformes	NR	USA	Artificial Pond	Broadband	Continuous	60-10,000	N	150	NR	NR	10–500^{h}	10 min	NA	NA	NA	NA	NR
Murchy	2016	*Oncorhynchus mykiss*	Rainbow trout	Salmoniformes	NR	USA	Artificial Pond	Broadband	Continuous	60-10,000	N	150	NR	NR	10–1000^{d,e}	10 min	NA	NA	NA	NA	NR
Murchy	2017	*Hypopthalmichtys nobilis*	Bighead carp	Cypriniformes	NR	USA	Artificial Pond	Broadband	Continuous	60-10,000	N	155	NR	NR	100–7000^{f,g}	30 min	NA	NA	NA	NA	93.7
Murchy	2017	*Hypophthalmichthys molitrix*	Silver carp	Cypriniformes	NR	USA	Artificial Pond	Broadband	Continuous	60-10,000	N	155	NR	NR	100–7000^{f,g}	30 min	NA	NA	NA	NA	82.4
Nestler	1992	*Alosa aestivalis*	blueback herring	Clupeiformes	Wild	USA	In situ	Pure	Continuous	80000-150000	N	199.5	NR	NR	200–4000, 10,000–100,000^{b,c}	1-1.15 min	NA	NA	NA	NA	NR

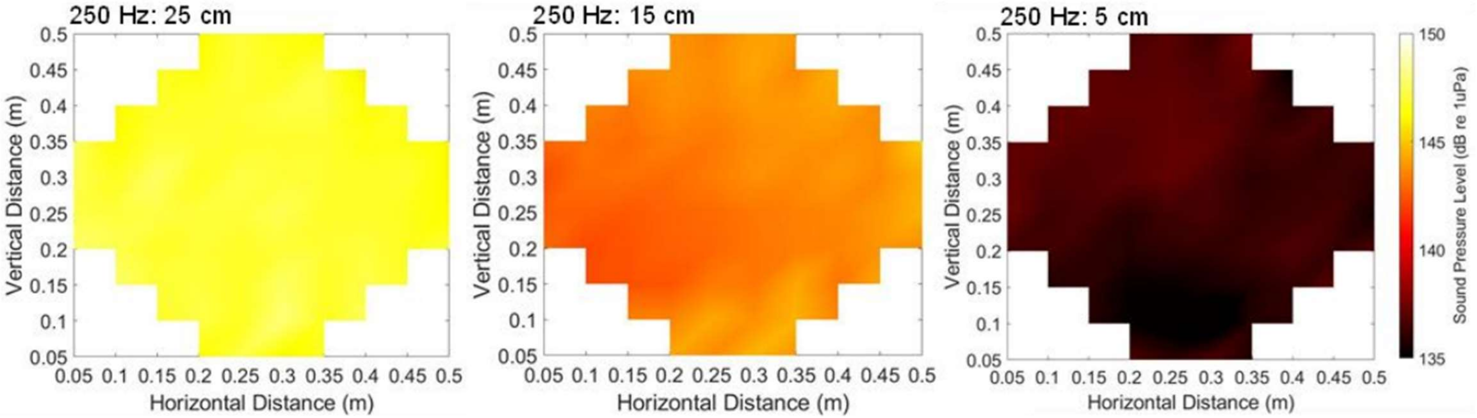
Nestler	1992	*Alosa aestivalis*	blueback herring	Clupeiformes	Wild	USA	In situ	Pure	Continuous	420000	Y	NR	NR	NR	200–4000, 10,000–100,000^{b,c}	1 min	NA	NA	NA	NA	NR
Nestler	1992	*Alosa aestivalis*	blueback herring	Clupeiformes	Wild	USA	In situ	Pure	Pulse	100-1000	N	170	NR	NR	200–4000, 10,000–100,000^{b,c}	15 min	200	NA	NA	Every 1 sec	NR
Nestler	1992	*Alosa aestivalis*	blueback herring	Clupeiformes	Wild	USA	In situ	Pure	Pulse	100-500	N	160	NR	NR	200–4000, 10,000–100,000^{b,c}	15 min	500	NA	NA	Every 10 sec	NR
Nestler	1992	*Alosa aestivalis*	blueback herring	Clupeiformes	Wild	USA	In situ	Pure	Pulse	80000-150000	N	199.5	NR	NR	200–4000, 10,000–100,000^{b,c}	1-1.15 min	200	NA	NA	Every 1 sec	NR
O'Keefe	2009	*Alosa fallax*	Twaite shad	Clupeiformes	Wild	UK	Tank	Pure	Continuous	45000	Y	172.5	NR	NR	200–4000, 10,000–100,000^{b,c}	NR	NA	NA	NA	NA	NR
O'Keefe	2009	*Alosa fallax*	Twaite shad	Clupeiformes	Wild	UK	Tank	Pure	Continuous	45000	Y	172.5	NR	NR	200–4000, 10,000–100,000^{b,c}	NR	NA	NA	NA	NA	NR
Piper	2019	*Anguilla anguilla*	European eel	Anguilliformes	Wild	UK	In situ	Pure	Continuous	11.9	Y	192	139	1.381295	10–300^{a}	10 dys	NA	NA	NR	NR	22
Ploskey	2000	*Oncorhynchus tshawytscha*	Chinook salmon	Salmoniformes	NR	USA	In situ	Broadband	Crescendo	300 - 400	N	170	127.5	1.333333	10–1000^{d,e}	NR	2000	30	1 min	30 sec	13.2
Ploskey	2000	*Oncorhynchus kisutch*	Coho salmon	Salmoniformes	Hatchery	USA	In situ	Broadband	Crescendo	300 - 400	N	170	127.5	1.333333	10–1000^{d,e}	NR	2000	30	1 min	30 sec	NR
Ploskey	2000	*Oncorhynchus nerka*	Sockeye salmon	Salmoniformes	NR	USA	In situ	Broadband	Crescendo	300 - 400	N	170	127.5	1.333333	10–1000^{d,e}	NR	2000	30	1 min	30 sec	NR
Ploskey	2000			Salmoniformes	Wild	USA	In situ	Broadband	Crescendo	300 - 400	N	160	93.5	1.71123	10–1000^{d,e}	20 dys	2000	30	4 hour	every 4 hour	NR
Ploskey	2000			Salmoniformes	Wild	USA	In situ	Broadband	Crescendo	300 - 400	N	160	93.5	1.71123	10–1000^{d,e}	10 dys	2000	30	24 hr	every 24 hr	NR
Ruggerone	2008	*Oncorhynchus kisutch*	Coho salmon	Salmoniformes	Hatchery	USA	In situ	Broadband	Pulse	NR	N	189	140	1.35	10–1000^{d,e}	4.3 hr	NR	NA	2.6 min	Every 1.3 sec	NR
Sand	2000	*Anguilla Anguilla*	Silver Eel	Anguilliformes	Wild	Norway	In situ	Pure	Continuous	11.8	Y	NR	NR	NR	10–300^{a}	7 dys	NA	NA	NA	NA	43
Sand	2000	*Anguilla Anguilla*	Silver Eel	Anguilliformes	Wild	Norway	Tank	Pure	Continuous	11.8	Y	NR	NR	NR	10–300^{a}	2 dys	NA	NA	NA	NA	NR
Schack	2008	*Gadus morhua*	Atlantic cod	Gadiformes	Wild	Denmark	Tank	Pure	Pulse	50000	Y	214	NR	NR	50–300^{i,j}	10 mnth	10	600	1 sec	NA	NR
Sonny	2006	*Anguilla Anguilla*	Silver Eel	Anguilliformes	Wild	Belgium	In situ	Pure	Continuous	16	Y	NR	NR	NR	10–300^{a}	7 dys	NA	NA	20 min	every 20 min	NR
Sonny	2006	*Leuciscus cephalus*	Chub	Cypriniformes	Wild	Belgium	In situ	Pure	Continuous	16	Y	NR	NR	NR	100–7000^{f,g}	7 dys	NA	NA	20 min	every 20 min	NR
Sonny	2006	*Alburnus alburnus*	common bleak	Cypriniformes	Wild	Belgium	In situ	Pure	Continuous	16	Y	NR	NR	NR	100–7000^{f,g}	7 dys	NA	NA	20 min	every 20 min	NR
Sonny	2006	*Abramis brama*	common bream	Cypriniformes	Wild	Belgium	In situ	Pure	Continuous	16	Y	NR	NR	NR	100–7000^{f,g}	7 dys	NA	NA	20 min	every 20 min	NR
Sonny	2006	*Rutilis rutilus*	Roach	Cypriniformes	Wild	Belgium	In situ	Pure	Continuous	16	Y	NR	NR	NR	100–7000^{f,g}	7 dys	NA	NA	20 min	every 20 min	NR
Teague	2011	*Alosa fallax*	Twaite shad	Clupeiformes	Wild	UK	Tank	Pure	Continuous	45,000	Y	NR	NR	NR	200–4000, 10,000–100,000^{b,c}	3 dys	NA	NA	6 hour	every 6 hour	76.6
Teague	2011	*Alosa fallax*	Twaite shad	Clupeiformes	Wild	UK	In situ	Pure	NR	45000 - 90,000	N	NR	NR	NR	200–4000, 10,000–100,000^{b,c}	3 dys	NR	NR	6 hour	every 6 hour	29
Turnpenny	2003	*Clupea harengus*	Atlantic herring	Clupeiformes	Wild	UK	In situ	NA	Chirp	100-600	N	172	NR	NR	200–4000, 10,000–100,000^{b,c}	24 dys	NA	NA	24 hr	24 hr	NR
Turnpenny	2003	*Clupea harengus*	Atlantic herring	Clupeiformes	Wild	UK	In situ	NA	Chirp	20-600	N	172	NR	NR	200–4000, 10,000–100,000^{b,c}	18 dys	NA	NA	24 hr	24 hr	NR
Turnpenny	2003	*Sprattus sprattus*	European sprat	Clupeiformes	Wild	UK	In situ	NA	Chirp	150-1,000	N	158	NR	NR	200–4000, 10,000–100,000^{b,c}	14 dys	NA	NA	24 hr	24 hr	11

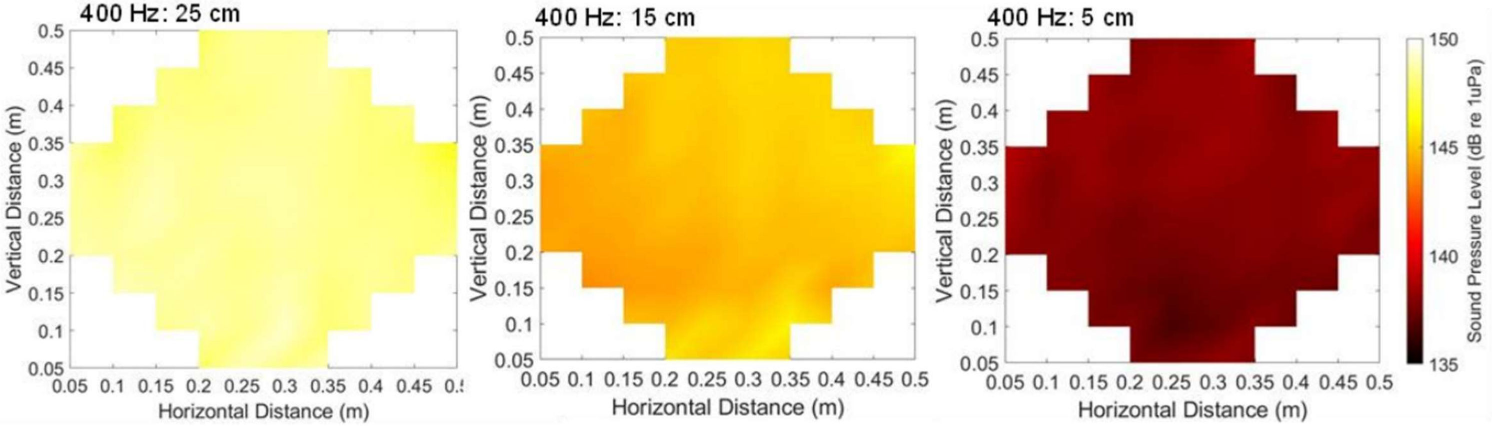
Turnpenny	2003	*Sprattus sprattus*	European sprat	Clupeiformes	Wild	UK	In situ	NA	Chirp	100-600	N	172	NR	NR	200–4000, 10,000–100,000[b,c]	24 dys	NA	NA	24 hr	24 hr	NR
Turnpenny	2003	*Sprattus sprattus*	European sprat	Clupeiformes	Wild	UK	In situ	NA	Chirp	20-600	N	172	NR	NR	200–4000, 10,000–100,000[b,c]	18 dys	NA	NA	24 hr	24 hr	NR
Turnpenny	2003			Clupeiformes	Wild	UK	In situ	NA	Chirp	120-600	N	172	NR	NR	200–4000, 10,000–100,000[b,c]	42 dys	NA	NA	24 hr	24 hr	-43
Turnpenny	2003	*Merlangius merlangus*	whiting	Gadiformes	Wild	UK	In situ	NA	Chirp	150-1,000	N	158	NR	NR	50–300[i,j]	14 dys	NA	NA	24 hr	24 hr	6
Turnpenny	2003	*Merlangius merlangus*	whiting	Gadiformes	Wild	UK	In situ	NA	Chirp	100-600	N	172	NR	NR	50–300[i,j]	24 dys	NA	NA	24 hr	24 hr	NR
Turnpenny	2003	*Merlangius merlangus*	whiting	Gadiformes	Wild	UK	In situ	NA	Chirp	20-600	N	172	NR	NR	50–300[i,j]	18 dys	NA	NA	24 hr	24 hr	NR
Turnpenny	2003			Gadiformes	Wild	UK	In situ	NA	Chirp	120-600	N	172	NR	NR	50–300[i,j]	42 dys	NA	NA	24 hr	24 hr	-25
Turnpenny	2003	*Dicentrarchus labrax*	European bass	Perciformes	Wild	UK	In situ	NA	Chirp	150-1,000	N	158	NR	NR	10–500[h]	14 dys	NA	NA	24 hr	24 hr	39
Turnpenny	2003		Benthic Fish		Wild	UK	In situ	NA	Chirp	20-600	N	172	NR	NR		24 dys	NA	NA	24 hr	24 hr	NR
Turnpenny	2003		Benthic Fish		Wild	UK	In situ	NA	Chirp	20-600	N	172	NR	NR		18 dys	NA	NA	24 hr	24 hr	NR
Turnpenny	2003		Demersal Fish		Wild	UK	In situ	NA	Chirp	20-600	N	172	NR	NR		24 dys	NA	NA	24 hr	24 hr	NR
Turnpenny	2003		Demersal Fish		Wild	UK	In situ	NA	Chirp	20-600	N	172	NR	NR		18 dys	NA	NA	24 hr	24 hr	NR
Turnpenny	2003		Pelagic Fish		Wild	UK	In situ	NA	Chirp	20-600	N	172	NR	NR		24 dys	NA	NA	24 hr	24 hr	NR
Turnpenny	2003		Pelagic Fish		Wild	UK	In situ	NA	Chirp	20-600	N	172	NR	NR		18 dys	NA	NA	24 hr	24 hr	NR
Van Der Walker	1967	*Oncorhynchus tshawytscha*	Chinook salmon	Salmoniformes	NR	USA	Tank	Pure	Continuous	10-500	N	156	NR	NR	10–1000[d,e]	NR	NA	NA	1 min	NA	NR
Vetter	2015	*Hypophthalmichthys molitrix*	Silver carp	Cypriniformes	NR	USA	Artificial Pond	Broadband	Continuous	0-10000	N	150	NR	NR	100–7000[f,g]	48 hr	NA	NA	30 sec	NA	100
Vetter	2015	*Hypophthalmichthys molitrix*	Silver carp	Cypriniformes	NR	USA	Artificial Pond	Pure	Continuous	500-2000	N	150	NR	NR	100–7000[f,g]	48 hr	NA	NA	30 sec	NA	12
Vetter	2017	*Hypophthalmichthys nobilis*	Bighead carp	Cypriniformes	Hatchery	USA	Artificial Pond	Broadband	Continuous	60-10000	N	155	NR	NR	100–7000[f,g]	48 hr	NA	NA	30 sec	NA	100
Vetter	2017	*Hypophthalmichthys nobilis*	Bighead carp	Cypriniformes	Hatchery	USA	Artificial Pond	Pure	Continuous	500-2000	N	155	NR	NR	100–7000[f,g]	48 hr	NA	NA	30 sec	NA	53

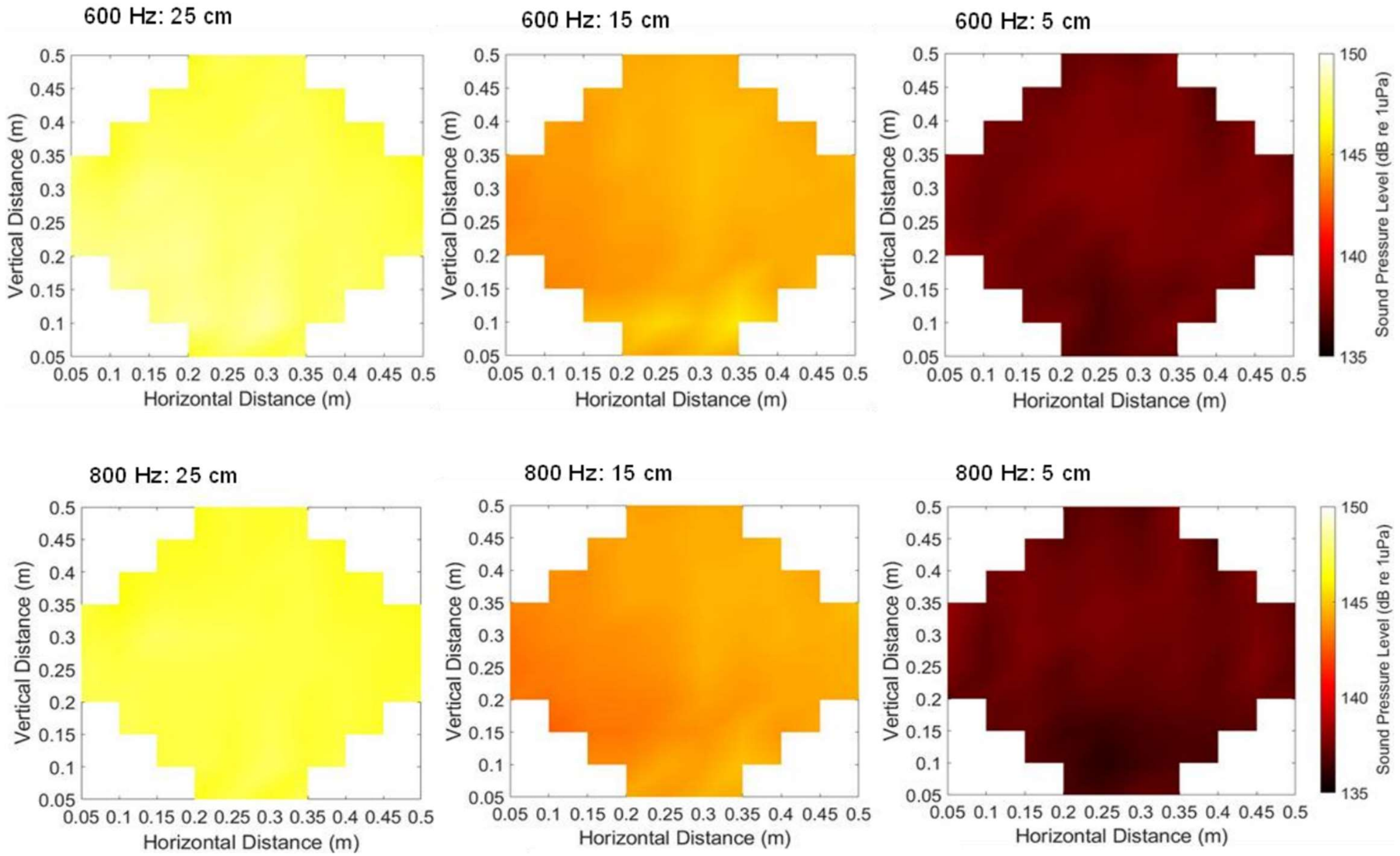
a)Jerkø, 1989; b) Mann et al., 1997, c) Mann et al., 2001; d) Van der Walker, 1966; e) Hawkins and Johnstone, 1978; f) Lovell et al., 2006; g) Vetter et al., 2018; h) Karlsen, 1992; i) Buerkle, 1968; j) Chapman and Hawkins, 1973.

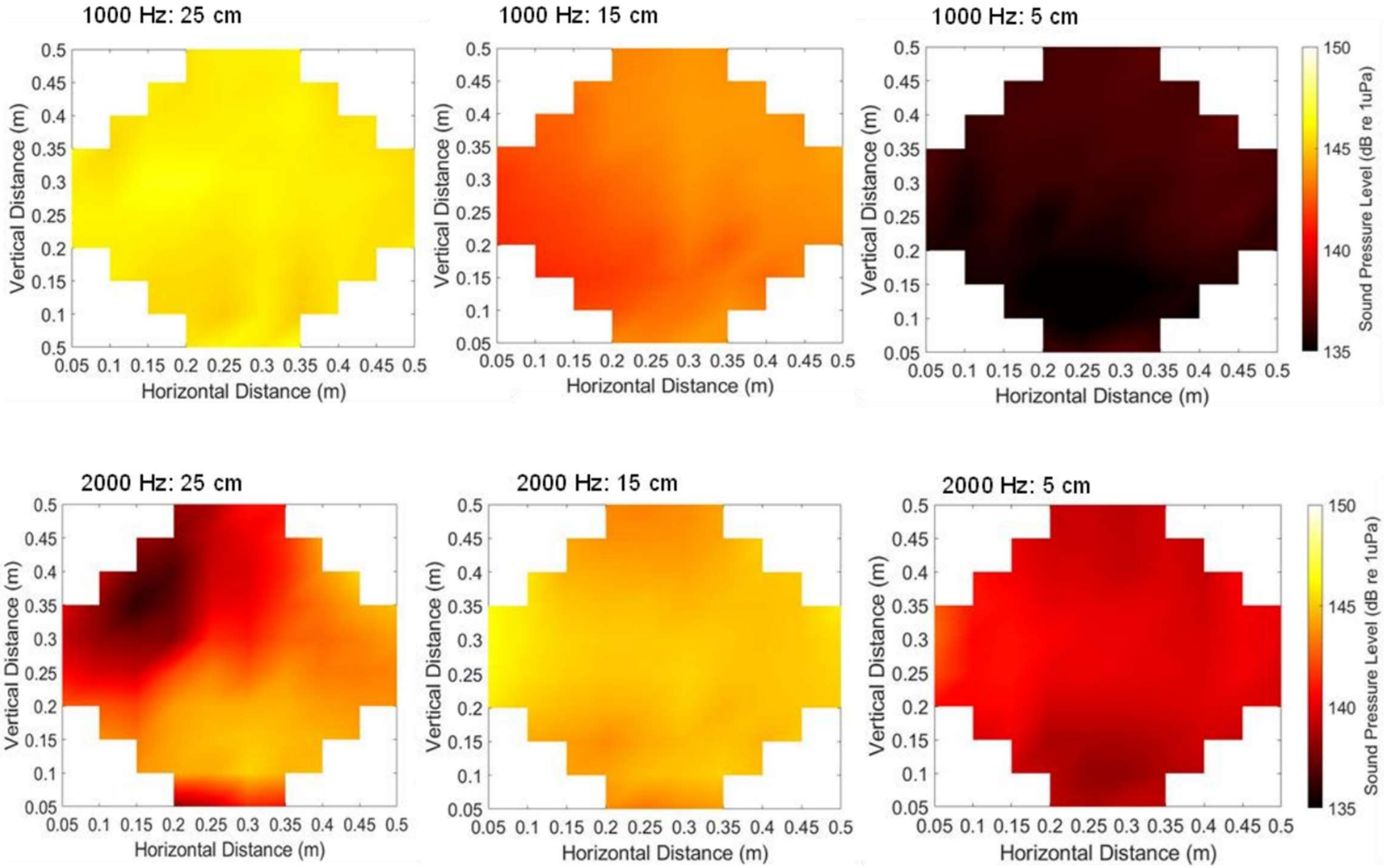
Appendix B Methodological Study and Objective 1 Data

SPL and PA Maps - The SPL maps of the submerged arena. The speaker was placed 70 cm below the tank and played at 250 Hz, 400 Hz, 600 Hz, 800 Hz, 1,000 Hz, 2,000 Hz. The SPL was mapped, and the SPL was calibrated at 145 dB re 1 µPa in the centre of the arena. Each figure is titled by the frequency played and the depth of recording.

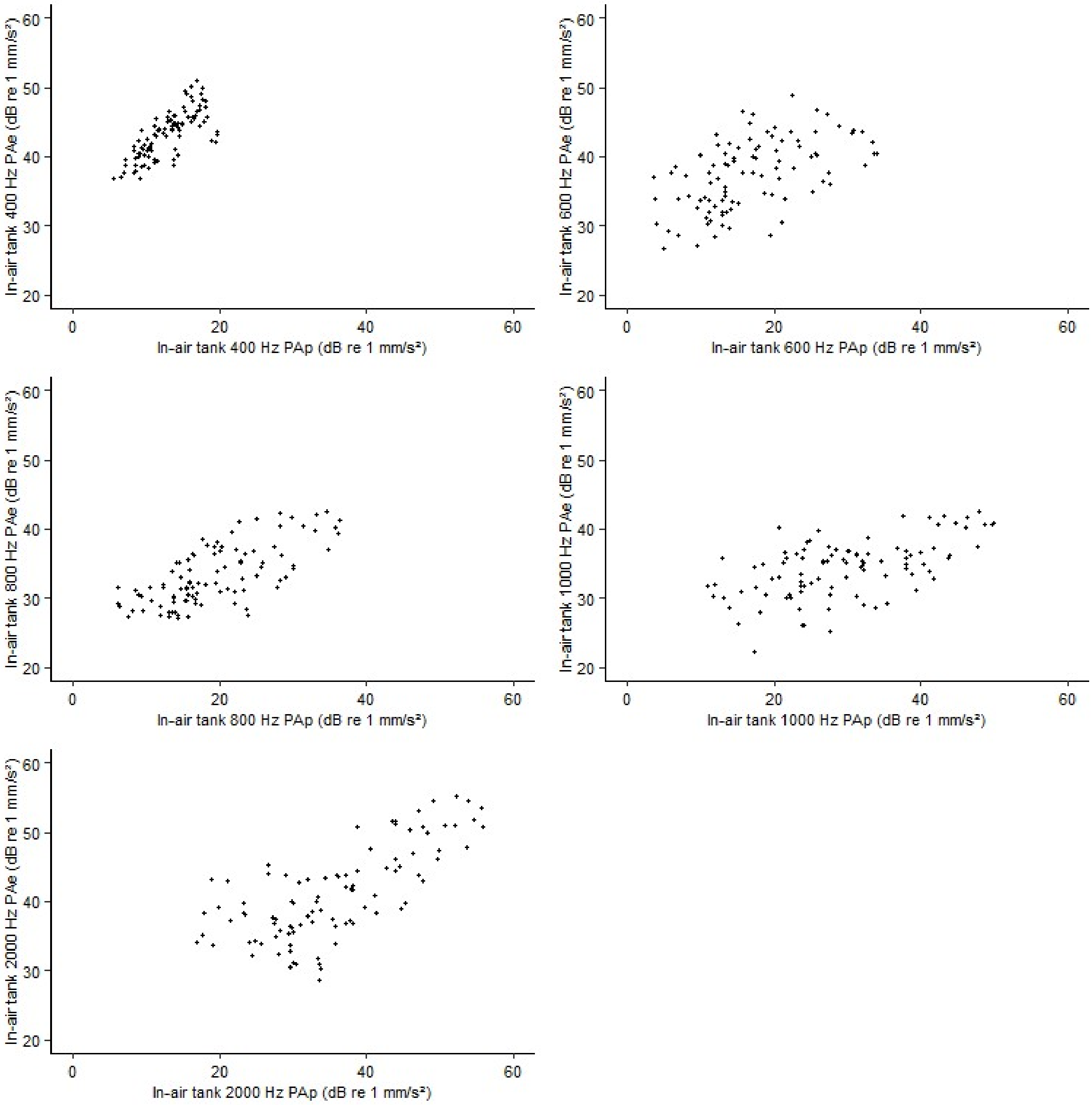




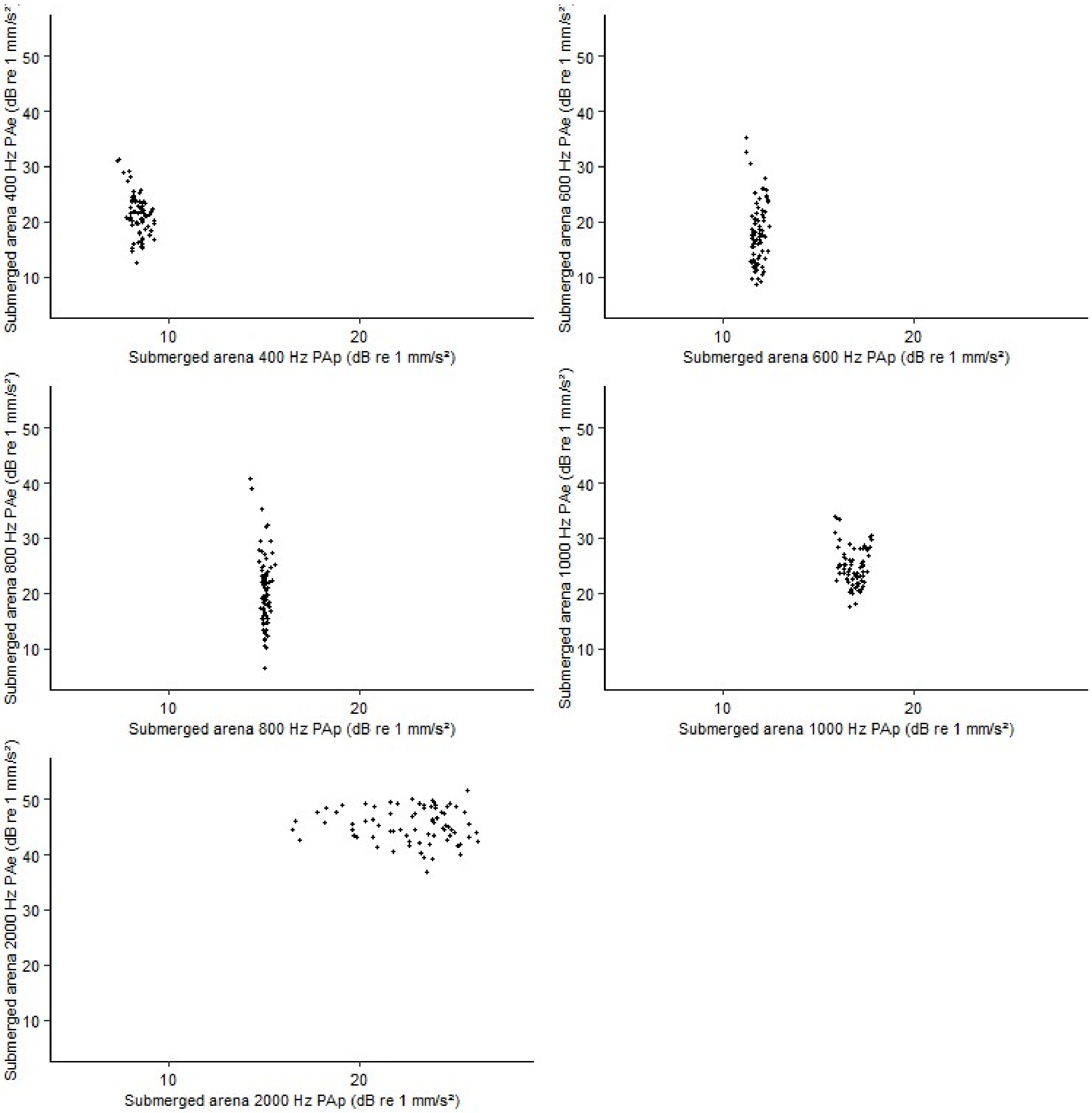

600 Hz: 25 cm
600 Hz: 15 cm
600 Hz: 5 cm
800 Hz: 25 cm
800 Hz: 15 cm
800 Hz: 5 cm
Vertical Distance (m)
Horizontal Distance (m)
0.05 0.1 0.15 0.2 0.25 0.3 0.35 0.4 0.45 0.5
Sound Pressure Level (dB re 1uPa)
150
145
140
135


1000 Hz: 25 cm
1000 Hz: 15 cm
1000 Hz: 5 cm
2000 Hz: 25 cm
2000 Hz: 15 cm
2000 Hz: 5 cm
Vertical Distance (m)
Horizontal Distance (m)
0.05
0.1
0.15
0.2
0.25
0.3
0.35
0.4
0.45
0.5
Sound Pressure Level (dB re 1uPa)
135
140
145
150

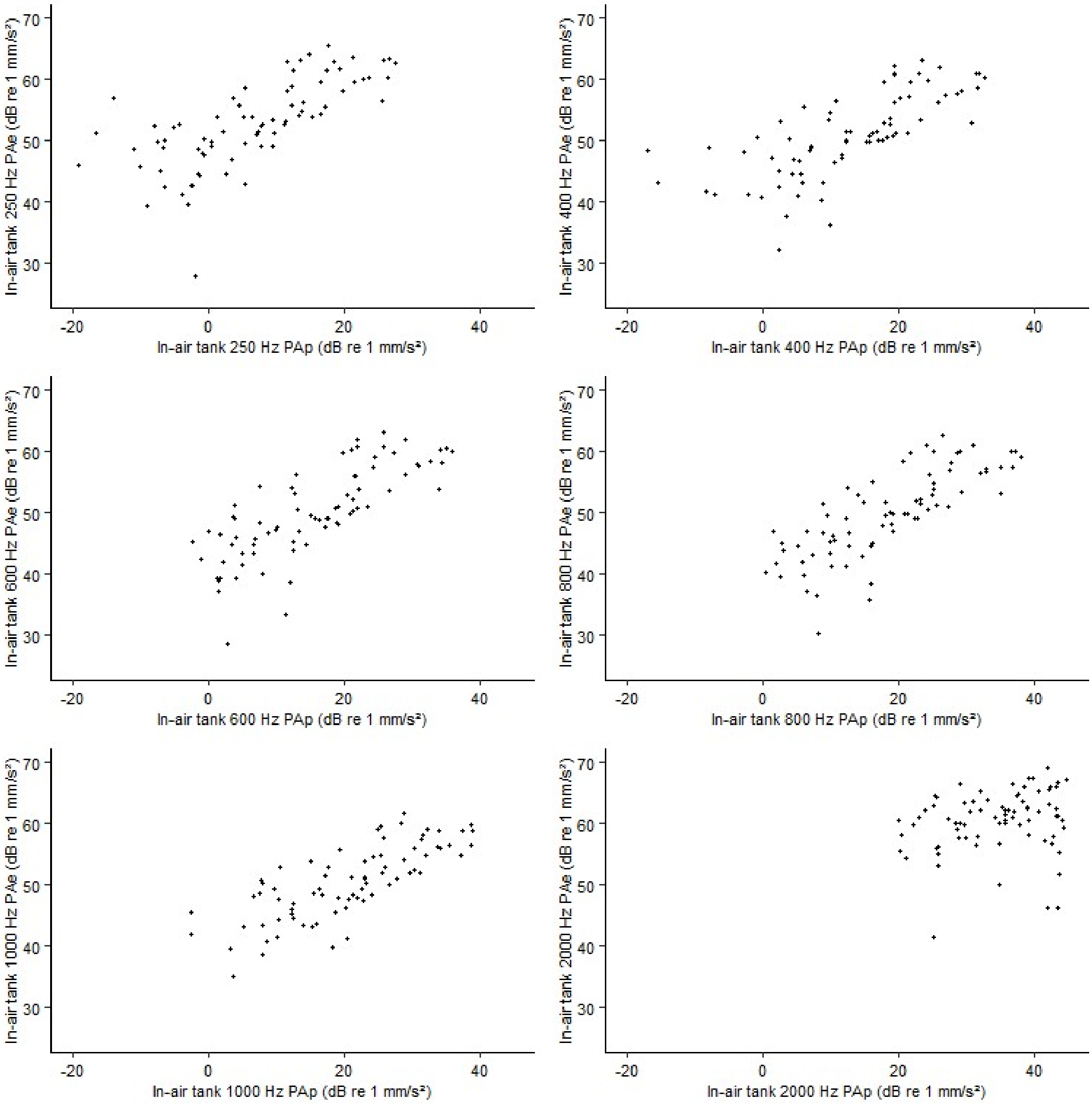
Phase 1 Data In-air Tank - Data used for the methodological study for the rectangular in air tank. Each plot is for each frequency tested (400 Hz; 600 Hz; 800 Hz; 800 Hz; 1000 Hz; 2000 Hz). Plots show experimental particle acceleration (PA_e) in dB re 1 mm s^{-2} vs predicted particle acceleration (PA_p) in dB re 1 mm s^{-2}.



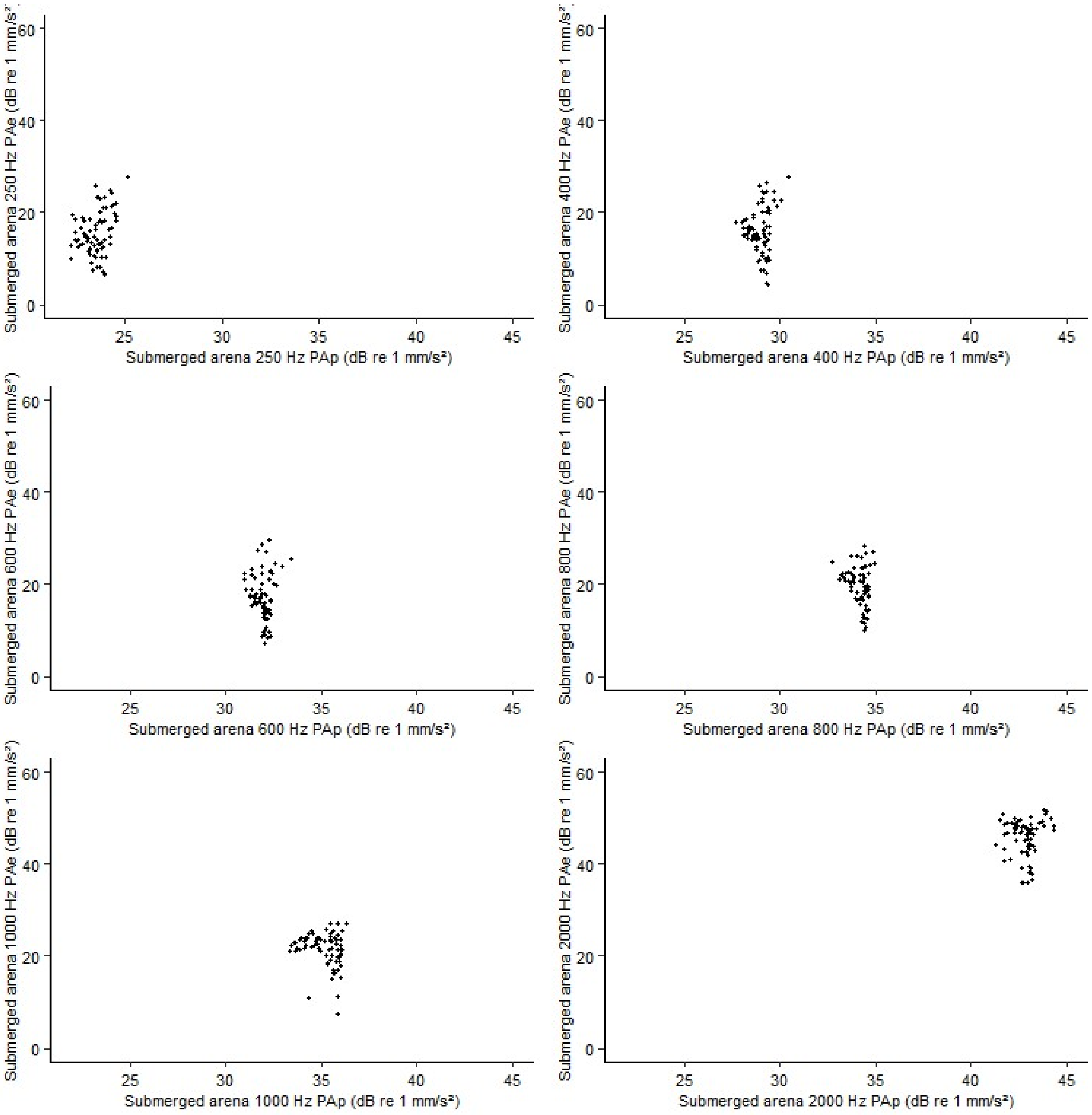
Phase 1 Data Submerged Arena - Data used for the methodological study for the cylindrical submerged arena. Each plot is for each frequency tested (400 Hz; 600 Hz; 800 Hz; 800 Hz; 1000 Hz; 2000 Hz). Plots show experimental particle acceleration (PA_e) in dB re 1 mm s^{-2} vs predicted particle acceleration (PA_p) in dB re 1 mm s^{-2}.



Phase 2 Data In-air Tank - Data used for the methodological study for the cylindrical in air tank. Each plot is for each frequency tested (250 Hz; 400 Hz; 600 Hz; 800 Hz; 800 Hz; 1000 Hz; 2000 Hz). Plots show experimental particle acceleration (PA_e) in dB re 1 mm s^{-2} vs predicted particle acceleration (PA_p) in dB re 1 mm s^{-2}.



Phase 2 Data Submerged Arena - Data used for the methodological study for submerged cylindrical arena. Each plot is for each frequency tested (250 Hz; 400 Hz; 600 Hz; 800 Hz; 800 Hz; 1000 Hz; 2000 Hz). Plots show experimental particle acceleration (PA_e) in dB re 1 mm s^{-2} vs predicted particle acceleration (PA_p) in dB re 1 mm s^{-2}.



Appendix C Hearing threshold data

Hearing threshold (SPL) data (dB re 1 µPa) for goldfish using the AEP hearing method at 12 frequencies (200; 250; 300; 400; 500; 600; 700; 800; 900; 1,000; 1,500; 2,000 Hz). Author: Lead author; Year: publishing year; AEP avg: The average hearing level at each frequency (dB); AEP sd: The standard deviation at each frequency (dB); AEP med: The median hearing level at each frequency (dB). Values in bold were calculated by averaging and scaling the hearing level at the two closed frequencies.

Author	Year	200 Hz	250 Hz	300 Hz	400 Hz	500 Hz	600 Hz	700 Hz	800 Hz	900 Hz	1000 Hz	1500 Hz	2000 Hz
Amoser	2003	74.5	**71.4**	68.3	**65.55**	62.8	**63.413**		64.7		66.1		81.3
Cordova	2007	90.3	**88.375**	**86.45**	82.6		80.9		81.3		76.5	90.1	**93.7**
Gutscher	2011	**81.25**	**77.62**	75.2	**71.6**	68	**66.313**		63		69.2		97.7
Kenyon	1998	73.3	**71.05**	68.8	63.9	64	64.1		64		64.6	71.5	80
Kojima	2005	72.7	**70.55**	68.4	63.6	63.5	63.5		63.6		64.2	70.7	79.3
Ladich	1999	71.9	**69.925**		64		**64.147**		**64.337**		64.5		78.3
Lu	2002	83.8	**82.4**		**79.147**	76.8	**77.4**		**78.6**		79.8		106
Ramcharitar	2006	84	**82.5**	81	73	71.5	67.5	70.4	67.6	68.5	74.4		77.9
Ramcharitar	2010	63.4	**62.4**	61.4	71.1	77.2	75.5	86.9	81.7	92.4	85.1		85.9
Smith	2004a	89.1	**83.85**		68.1		74.7		74.4		79.8		97.2
Smith	2004b	79.4	**78.3**		75		75.3		78.4		79.2		90.3
Smith	2006	101.6	**97.1**		83.6		79		80		79.3		104.1
Smith	2011	**84.027**	82.7		76.8	75.9	65.4		65.9		64	72.6	93
Suga	2005		87.4		**84.1**	81.9	**82.88**		**84.84**		86.8		93.4
Wysocki	2005	76.3	**73.98**		**68.553**	64.7	65.14		**66.02**		66.9		85.9
Yan	2000			69.1	**66.8**	64.5	**64.4**		64.2		**66.414**	71.8	**86**
AEP avg		75.29153	77.2048	71.07	70.05938	70	69.26831	79.35	71.46813	83.06667	73.6125	82.3125	90.81456
AEP sd		8.051397	11.12149	10.29867	9.056757	9.904544	9.311813	6.808451	10.3274	10.4353	9.424826	15.48188	14.75259
AEP Med		74.5	76.14	68.6	68.9265	68.1	67.0265	80.75	66.81	88.3	75.4	81.85	89.65

Appendix D Literature review data

Data used for the literature review of fish sounds to inform acoustic deterrence considering: paper number; lead author; year; continent of study; fish sound recording time; season of data collection (spring – March, April, May; summer – June, July, August; Autumn – September, October, November; Winter – December, January, February); whether it was a tank study or in situ; number of replicates; Latin name; zone of habitation (retrieved from fishbase); sex; standard length (SL; mm; standard deviation; min-max); total length (TL; mm; standard deviation; min-max); sonic mechanism (CBS – cranial bone stridulation; FM – fin movement; JTS – jaw/teeth stridulation; PGM – pectoral girdle muscle; PSS – pectoral spine stridulation; SSM – Sonic swimbladder mechanism); spawning season (as per UK seasons aforementioned); sound number (if the fish sounds were distinctly different they were labelled as sound number 1, 2 etc to avoid repeats in the table). NR – Not recorded.

Paper number	Lead Author	Year	Continent of Study	Recording Time	Season (as per UK seasons)	Tank/in situ	Number of replicates	Latin name	Zone of habitation	Sex	Length SL	Length TL	Sonic mechanism	Spawning season (as per UK seasons)	Behaviour	Sound timbre	Sound Number (if repeats are in the table)
1	Aalbers	2008	North America	3 min every 30 min	Spring-Summer	in situ	15	*Atractoscion nobilis*	Demersal	Male	NR	(830-1260)	SSM	Spring-Summer	Courtship	pulse	
1	Aalbers	2008	North America	3 min every 30 min	Spring-Summer	in situ	15	*Atractoscion nobilis*	Demersal	Male	NR	(830-1260)	SSM	Spring-Summer	Courtship	thud	
1	Aalbers	2008	North America	3 min every 30 min	Spring-Summer	in situ	15	*Atractoscion nobilis*	Demersal	Male	NR	(830-1260)	SSM	Spring-Summer	Courtship	drum	
1	Aalbers	2008	North America	3 min every 30 min	Spring-Summer	in situ	15	*Atractoscion nobilis*	Demersal	Male	NR	(830-1260)	SSM	Spring-Summer	Courtship	chant	
1	Aalbers	2008	North America	3 min every 30 min	Spring-Summer	in situ	15	*Atractoscion nobilis*	Demersal	Male	NR	(830-1260)	SSM	Spring-Summer	Courtship	pulse	
1	Aalbers	2008	North America	3 min every 30 min	Spring-Summer	in situ	15	*Atractoscion nobilis*	Demersal	Male	NR	(830-1260)	SSM	Spring-Summer	Postspawn	pulse	1
1	Aalbers	2008	North America	3 min every 30 min	Spring-Summer	in situ	15	*Atractoscion nobilis*	Demersal	Male	NR	(830-1260)	SSM	Spring-Summer	Postspawn	pulse	2
1	Aalbers	2008	North America	3 min every 30 min	Spring-Summer	in situ	15	*Atractoscion nobilis*	Demersal	Male	NR	(830-1260)	SSM	Spring-Summer	Spawning	pulse	
1	Aalbers	2008	North America	3 min every 30 min	Spring-Summer	in situ	15	*Atractoscion nobilis*	Demersal	Male	NR	(830-1260)	SSM	Spring-Summer	Spawning	thud	
1	Aalbers	2008	North America	3 min every 30 min	Spring-Summer	in situ	15	*Atractoscion nobilis*	Demersal	Male	NR	(830-1260)	SSM	Spring-Summer	Spawning	drum	
1	Aalbers	2008	North America	3 min every 30 min	Spring-Summer	in situ	15	*Atractoscion nobilis*	Demersal	Male	NR	(830-1260)	SSM	Spring-Summer	Spawning	chant	
1	Aalbers	2008	North America	3 min every 30 min	Spring-Summer	in situ	15	*Atractoscion nobilis*	Demersal	Male	NR	(830-1260)	SSM	Spring-Summer	Spawning	pulse	
2	Almada	1996	Europe	5 x 30 min	Winter	tank	2	*Gaidropsarus mediterraneus*	Demersal	NR	169(138-200)	NR	Unknown	NR	Territorial Aggression	thump	
3	Bischof	1996	Europe	NR	NR	tank	34	*Macropodus opercularis*	Pelagic	Male	NR	NR	FM	NR	Agonistic	pulse	
4	Picciulin	2020	Europe	5 min	Summer	in situ	NR	*Sciaena umbra*	Demersal	Male	NR	NR	SSM	Summer	Courtship	pulse	
5	Tellechea	2011	South America	NR	Autumn-Winter	tank	6	*Pogonias cromis*	Demersal	Male	NR	62.16(11.03)	SSM	Autumn	Courtship	pulse	
5	Tellechea	2011	South America	NR	Winter	tank	12	*Pogonias cromis*	Demersal	Female	NR	53.95(7.65)	SSM	Autumn	Disturbance	pulse	
5	Tellechea	2011	South America	NR	Winter	tank	6	*Pogonias cromis*	Demersal	Male	NR	62.49(11.19)	SSM	Autumn	Disturbance	pulse	

6	Kever	2014	Europe	10 min every 30 min	Summer	tank	1	*Ophidion rochei*	Demersal	Male	NR	133	SSM	Summer	Courtship	pulse	
6	Kever	2014	Europe	10 min every 30 min	Summer	tank	1	*Ophidion rochei*	Demersal	Male	NR	169	SSM	Summer	Courtship	pulse	
6	Kever	2014	Europe	10 min every 30 min	Summer	tank	1	*Ophidion rochei*	Demersal	Male	NR	166.8	SSM	Summer	Courtship	pulse	
6	Kever	2014	Europe	10 min every 30 min	Summer	tank	1	*Ophidion rochei*	Demersal	Male	NR	169.3	SSM	Summer	Courtship	pulse	
6	Kever	2014	Europe	10 min every 30 min	Summer	tank	1	*Ophidion rochei*	Demersal	Male	NR	153.3	SSM	Summer	Courtship	pulse	
7	Parmentier	2016	Asia	NR	Spring-Autumn	tank	3	*Terapon jarbua*	Demersal	NR	NR	159.33(8.99;148-170)	SSM	NR	Disturbance	tonal	
7	Parmentier	2016	Asia	NR	Spring-Autumn	tank	6	*Pelates quadrilineatus*	Reef	NR	NR	122(22.62;70-144)	SSM	NR	Disturbance	tonal	
7	Parmentier	2016	Asia	NR	Spring-Autumn	tank	3	*Pempheris oualensis*	Reef	NR	NR	(120-131)	SSM	NR	Disturbance	tonal	
8	Lugli	1995	Europe	NR	NR	tank	5	*Knipowitschia punctatissima*	Demersal	Male	NR	40(32-54)	JTS	NR	Courtship & Spawning	pulse	
8	Lugli	1995	Europe	NR	NR	tank	15	*Padogobius martensii*	Demersal	Male	NR	74.9(62-87)	PGS	NR	Courtship & Spawning	tonal	
8	Lugli	1995	Europe	NR	NR	tank	15	*Padogobius martensii*	Demersal	Male	NR	75.1(62-87)	PGM	NR	Courtship & Spawning	pulse	
8	Lugli	1995	Europe	NR	NR	tank	15	*Padogobius martensii*	Demersal	Male	NR	74.9(62-87)	PGM	NR	Courtship & Spawning	pulse	
8	Lugli	1995	Europe	NR	NR	tank	15	*Padogobius martensii*	Demersal	Male	NR	74.9(62-87)	PGM	NR	Courtship & Spawning	tonal	
9	Crawford	1986	NR	NR	NR	tank	2	*Pollimyrus isidori*	Demersal	Male	84(83-85)	NR	SSM	Spring-summer	Courtship	growl	
9	Crawford	1986	North America	NR	NR	tank	2	*Pollimyrus isidori*	Demersal	Male	84(83-85)	NR	SSM	Spring-summer	Courtship	grunt	
10	Staaterman	2018	Central America	12-20 hr	Winter-Spring	in situ		*Amphichthys cryptocentrus*	Reef	Male	NR	NR	SSM	All year	Courtship	grunt	
10	Staaterman	2018	Central America	12-20 hr	Winter-Spring	in situ		*Amphichthys cryptocentrus*	Reef	Male	NR	NR	SSM	All year	Courtship	boop	
11	Parmentier	2010	Oceana	24 hr	Winter-Spring	in situ	NR	*Dascyllus flavicaudus*	Reef	Both	NR	NR	Unknown	Winter-Spring	Agonistic	pulse	1
11	Parmentier	2010	Oceana	24 hr	Winter-Spring	in situ	NR	*Dascyllus flavicaudus*	Reef	Both	NR	NR	Unknown	Winter-Spring	Agonistic	pulse	2
11	Parmentier	2010	Oceana	24 hr	Winter-Spring	in situ	NR	*Dascyllus flavicaudus*	Reef	Male	NR	NR	Unknown	Winter-Spring	Courtship	pulse	
11	Parmentier	2010	Oceana	24 hr	Winter-Spring	in situ	NR	*Dascyllus flavicaudus*	Reef	Male	NR	NR	Unknown	Winter-Spring	Spawning	pulse	
11	Parmentier	2010	Oceana	24 hr	Winter-Spring	in situ	NR	*Dascyllus flavicaudus*	Reef	Male	NR	NR	Unknown	Winter-Spring	Territorial Aggression	pulse	1
11	Parmentier	2010	Oceana	24 hr	Winter-Spring	in situ	NR	*Dascyllus flavicaudus*	Reef	Male	NR	NR	Unknown	Winter-Spring	Territorial Aggression	pulse	2
12	Lamml	2007	Europe	1-2 hr	Summer	tank	3	*Marcusenius macrolepidotus*	Demersal	Male	121-159	NR	Unknown	NR	Territorial Aggression	hoot	
12	Lamml	2007	Europe	1-2 hr	Winter-Spring	tank	5	*Marcusenius macrolepidotus*	Demersal	Both	93-210	NR	Unknown	NR	Territorial Aggression	hoot	
12	Lamml	2007	Europe	1-2 hr	Autumn	tank	1	*Marcusenius macrolepidotus*	Demersal	Male	97	NR	Unknown	NR	Territorial Aggression	hoot	
12	Lamml	2007	Europe	1-2 hr	Autumn	tank	1	*Marcusenius macrolepidotus*	Demersal	Female	88	NR	Unknown	NR	Territorial Aggression	hoot	
12	Lamml	2007	Europe	1-2 hr	Winter-Spring	tank	6	*Marcusenius macrolepidotus*	Demersal	Both	93-210	NR	Unknown	NR	Territorial Aggression	growl	

12	Lamml	2007	Europe	1-2 hr	Summer	tank	6	*Marcusenius macrolepidotus*	Demersal	Male	121-159	NR	Unknown	NR	Territorial Aggression	growl	
12	Lamml	2007	Europe	1-2 hr	Autumn	tank	1	*Marcusenius macrolepidotus*	Demersal	Male	97	NR	Unknown	NR	Territorial Aggression	growl	
12	Lamml	2007	Europe	1-2 hr	Autumn	tank	1	*Marcusenius macrolepidotus*	Demersal	Male	130	NR	Unknown	NR	Territorial Aggression	growl	
13	Amorim	2011	Europe	8 days	Summer	in situ	13	*Halobatrachus didactylus*	Demersal	Male	NR	429(379-477)	SSM	Summer	Courtship	boatwhistle	
13	Amorim	2011	Europe	10 min	Summer	in situ	13	*Halobatrachus didactylus*	Demersal	Male	NR	429(379-477)	SSM	Summer	Courtship	boatwhistle	
14	Lugli	2003	Europe	NR	Spring-Summer	tank	6	*Padogobius martensii*	Demersal	Male	NR	50-75	PGM	Spring-Summer	Courtship	tonal	
14	Lugli	2003	Europe	NR	Spring-Summer	tank	6	*Padogobius martensii*	Demersal	Male	NR	50-75	PGM	Spring-Summer	Courtship	pulse train	
15	Ladich	1998	Europe	NR	NR	tank	10	*Trichopsis pumila*	Benthopelagic	NR	NR	NR	FM	NR	Territorial Aggression	croak	
15	Ladich	1998	Europe	NR	NR	tank	10	*Trichopsis vittata*	Demersal	NR	NR	NR	FM	NR	Territorial Aggression	croak	
16	Sebastianutto	2008	Europe	10 min	NOT spring	tank	8	*Gobius cruentatus*	Demersal	Both	NR	131.6(14.4)	Unknown	Spring	Territorial Aggression	noisy	
16	Sebastianutto	2008	Europe	10 min	NOT spring	tank	9	*Gobius cruentatus*	Demersal	Both	NR	131.6(14.4)	Unknown	Spring	Territorial Aggression	tonal	
16	Sebastianutto	2008	Europe	10 min	NOT spring	tank	7	*Gobius cruentatus*	Demersal	Both	NR	131.6(14.4)	Unknown	Spring	Territorial Aggression	tonal	
16	Sebastianutto	2008	Europe	10 min	NOT spring	tank	7	*Gobius cruentatus*	Demersal	Both	NR	131.6(14.4)	Unknown	Spring	Territorial Aggression	pulse	
16	Sebastianutto	2008	Europe	10 min	NOT spring	tank	7	*Gobius cruentatus*	Demersal	Both	NR	131.6(14.4)	Unknown	Spring	Territorial Aggression	pulse train	
17	Johnston	2007	Central America	30-60 min	Spring	tank	5	*Codoma ornata*	Benthopelagic	Male	48.7(3.6)	NR	Unknown	Spring	Agonistic	pulse	
17	Johnston	2007	Central America	30-60 min	Spring	tank	5	*Codoma ornata*	Benthopelagic	Male	48.7(3.6)	NR	Unknown	Spring	Agonistic	pulse	
17	Johnston	2007	Central America	30-60 min	Spring	tank	5	*Codoma ornata*	Benthopelagic	Male	48.7(3.6)	NR	Unknown	Spring	Courtship	pulse	
18	Johnston	2008	North America	30-60 min	Summer	tank	8	*Micropterus coosae*	Demersal	Both	NR	194(41;130-370)	Unknown	NR	Territorial Aggression	pulse	
19	Maruska	2009	North America	121 days	Summer	concrete tank	14	*Opsanus tau*	Reef	Both	26.7 (4.3; 22-33)	NR	SSM	Summer	Courtship	boatwhistle	
19	Maruska	2009	North America	121 days	Summer	concrete tank	14	*Opsanus tau*	Reef	Both	26.7 (4.3; 22-33)	NR	SSM	Summer	Disturbance	grunt	
20	Tellechea	2010	South America	NR	Autumn-Spring	tank	1	*Micropogonias furnieri*	Demersal	Male	NR	280	SSM	Autumn-Spring	Courtship	pulse	
20	Tellechea	2010	South America	NR	Autumn-Spring	tank	1	*Micropogonias furnieri*	Demersal	Male	NR	305	SSM	Autumn-Spring	Courtship	pulse	
20	Tellechea	2010	South America	NR	Autumn-Spring	tank	112	*Micropogonias furnieri*	Demersal	Both	NR	(100-560)	SSM	Autumn-Spring	Disturbance	pulse	
21	Speares	2011	North America	30 min	Spring	tank	12	*Etheostoma oophylax*	Benthopelagic	Male	(590-750)	NR	Unknown	Spring	Courtship	drum	
21	Speares	2011	North America	30 min	Spring	tank	12	*Etheostoma oophylax*	Benthopelagic	Male	(590-750)	NR	Unknown	Spring	Courtship	knock	
21	Speares	2011	North America	30 min	Spring	tank	12	*Etheostoma oophylax*	Benthopelagic	Male	(590-750)	NR	Unknown	Spring	Courtship	purr	
21	Speares	2011	North America	30 min	Spring	tank	12	*Etheostoma oophylax*	Benthopelagic	Male	(590-750)	NR	Unknown	Spring	Territorial Aggression	drum	
21	Speares	2011	North America	30 min	Spring	tank	12	*Etheostoma oophylax*	Benthopelagic	Male	(590-750)	NR	Unknown	Spring	Territorial Aggression	knock	

21	Speares	2011	North America	30 min	Spring	tank	12	*Etheostoma oophylax*	Benthopelagic	Male	(590-750)	NR	Unknown	Spring	Territorial Aggression	purr	
22	Danley	2012	Africa	3.5 hr	NR	in situ	1	*Cynotilapia afra*	Benthopelagic	Male	NR	NR	Unknown	NR	Courtship	trill	
22	Danley	2012	Africa	3.5 hr	NR	in situ	1	*Labeotropheus fuelleborni*	Benthopelagic	Male	NR	NR	Unknown	NR	Courtship	trill	
22	Danley	2012	Africa	3.5 hr	NR	in situ	1	*Maylandia aurora*	Demersal	Male	NR	NR	Unknown	NR	Courtship	trill	
22	Danley	2012	Africa	3.5 hr	NR	in situ	1	*Maylandia callainos*	Demersal	Male	NR	NR	Unknown	NR	Courtship	trill	
22	Danley	2012	Africa	3.5 hr	NR	in situ	1	*Maylandia zebra*	Demersal	Male	NR	NR	JTS	NR	Courtship	trill	
22	Danley	2012	Africa	3.5 hr	NR	in situ	1	*Petrotilapia nigra*	Demersal	Male	NR	NR	Unknown	NR	Courtship	trill	
23	Mosharo	2012	Central America	35.5(16;15-57)	Winter	in situ	6	*Batrachoides gilberti*	Demersal	Male	NR	NR	SSM	Winter	Courtship	boatwhistle	
23	Mosharo	2012	Central America	45-48 min	Winter	in situ	NR	*Sanopus astrifer*	Reef	Male	NR	NR	SSM	Winter	Courtship	boatwhistle	
24	Blom	2016	Europe	60 min	Spring	tank	5	*Pomatoschistus microps*	Demersal	Male	NR	33.7(2.5)	PGM	Spring	Courtship	pulse	
24	Blom	2016	Europe	60 min	Spring	tank	5	*Pomatoschistus minutus*	Demersal	Male	NR	53.8(3.2)	PGM	Spring	Courtship	pulse	
25	Smith	2018	South America	45 min	Winter	tank	3	*Prochilodus argenteus*	Benthopelagic	Male	30.8(3.7;27.5-36)	NR	SSM	Winter	Courtship	pulse train	
25	Smith	2018	South America	188-192 min	Winter	tank	3	*Prochilodus argenteus*	Benthopelagic	Male	32.17(2.25;29.5-35)	NR	SSM	Winter	Courtship	pulse train	
25	Smith	2018	South America	188-192 min	Winter	tank	3	*Prochilodus argenteus*	Benthopelagic	Male	32.17(2.25;29.5-35)	NR	SSM	Winter	Courtship	pulse	
25	Smith	2018	South America	224-247 min	Winter	tank	3	*Prochilodus costatus*	Benthopelagic	Male	30.83(1.31;29-32)	NR	SSM	Winter	Courtship	pulse train	
25	Smith	2018	South America	224-247 min	Winter	tank	3	*Prochilodus costatus*	Benthopelagic	Male	30.83(1.31;29-32)	NR	SSM	Winter	Courtship	pulse	
25	Smith	2018	South America	191-192 min	Autumn	tank	3	*Prochilodus lineatus*	Benthopelagic	Male	40(0.81;39-41)	NR	SSM	Autumn	Courtship	pulse train	
25	Smith	2018	South America	191-192 min	Autumn	tank	3	*Prochilodus lineatus*	Benthopelagic	Male	40(0.81;39-41)	NR	SSM	Autumn	Courtship	pulse	
26	Tellechea	2019	South America	NR	Spring	in situ	NR	*Macrodon atricauda*	Demersal	Males	NR	NR	SSM	Spring	Courtship	pulse	
26	Tellechea	2019	South America	3 hr	Spring	tank	5	*Macrodon atricauda*	Demersal	Males	NR	(260-289)	SSM	Spring	Courtship	pulse	
26	Tellechea	2019	South America	NR	Spring	tank	5	*Macrodon atricauda*	Demersal	Males	NR	(260-289)	SSM	Spring	Disturbance	pulse	
27	Holt	2020	North America	NR	Spring	tank	5	*Cottus carolinae*	Demersal	NR	81.8(12.8;65-95)	NR	PGM	Winter-Spring	Territorial Aggression	tonal	
27	Holt	2020	North America	NR	Spring	tank	12	*Cottus carolinae*	Demersal	NR	65.42(8.86;53-80)	NR	PGM	Winter-Spring	Territorial Aggression	pulse	
28	Spinks	2017	Africa	8 min	Summer	concrete tank	7	*Neolamprologus pulcher*	Benthopelagic	Both	NR	NR	JTS	NR	Agonistic	click	
28	Spinks	2017	Africa	8 min	Spring	concrete tank	4	*Neolamprologus pulcher*	Benthopelagic	Both	NR	NR	JTS	NR	Agonistic	click	
29	Ladich	2006	Europe	NR	NR	tank	15	*Trichopsis vittata*	Demersal	Female	36-41	NR	FM	NR	Courtship	purr	
29	Ladich	2006	Europe	NR	NR	tank	10	*Trichopsis vittata*	Demersal	Male	37-44	NR	FM	NR	Territorial Aggression	croak	
29	Ladich	2006	Europe	NR	NR	tank	15	*Trichopsis vittata*	Demersal	Female	37-42	NR	FM	NR	Territorial Aggression	croak	

30	de Jong	2007	Europe	>10 min	Summer	in situ	15	*Parablennius parvicornis*	Demersal	Male	NR	NR	Unknown	Summer	Courtship	NR	
30	de Jong	2007	Europe	>10 min	Summer	in situ	16	*Parablennius parvicornis*	Demersal	Male	NR	141.4(11.9; 125-160)	Unknown	Summer	Courtship	grunt	
30	de Jong	2007	Europe	>10 min	Summer	in situ	10	*Parablennius parvicornis*	Demersal	Male	NR	NR	Unknown	Summer	Courtship	NR	
31	Philips	2008	North America	30 min	Spring-Summer	tank	33	*Cyprinella galactura*	Benthopelagic	Male	NR	NR	SSM	Spring-Summer	Agonistic	knock	
31	Philips	2008	North America	30 min	Spring-Summer	tank	28	*Cyprinella galactura*	Benthopelagic	Male	NR	NR	SSM	Spring-Summer	Agonistic	knock	
31	Philips	2008	North America	30 min	Spring-Summer	tank	33	*Cyprinella galactura*	Benthopelagic	Male	NR	NR	SSM	Spring-Summer	Agonistic	pulse	
31	Philips	2008	North America	30 min	Spring-Summer	tank	15	*Cyprinella galactura*	Benthopelagic	Male	NR	NR	SSM	Spring-Summer	Courtship	knock	
31	Philips	2008	North America	30 min	Spring-Summer	tank	13	*Cyprinella galactura*	Benthopelagic	Male	NR	NR	SSM	Spring-Summer	Courtship	knock	
31	Philips	2008	North America	30 min	Spring-Summer	tank	15	*Cyprinella galactura*	Benthopelagic	Male	NR	NR	SSM	Spring-Summer	Courtship	pulse	
32	Bolgan	2020	Europe	300s every 900 s	Spring	concrete tank	17	*Argyrosomus regius*	Benthopelagic	NR	NR	NR	SSM	Spring	Courtship	pulse	
32	Bolgan	2020	Europe	300s every 900 s	Spring	concrete tank	17	*Argyrosomus regius*	Benthopelagic	NR	NR	NR	SSM	Spring	Spawning	pulse	
32	Bolgan	2020	Europe	90s every 1710s	Summer	concrete tank		*Sciaenops ocellatus*	Demersal	Male	NR	NR	SSM	Summer	Spawning	pulse	
32	Bolgan	2020	Europe	300s every 900 s	Spring	concrete tank	5	*Umbrina cirrosa*	Demersal	NR	NR	NR	SSM	Spring	Courtship	pulse	
32	Bolgan	2020	Europe	300s every 900 s	Spring	concrete tank	5	*Umbrina cirrosa*	Demersal	NR	NR	NR	SSM	Spring	Spawning	pulse	
33	Ladich	2015	Europe	NR	NR	tank	11	*Trichopsis vittata*	Demersal	Male	NR	NR	FM	NR	Territorial Aggression	croak	1
33	Ladich	2015	Europe	NR	NR	tank	11	*Trichopsis vittata*	Demersal	Male	NR	NR	FM	NR	Territorial Aggression	croak	2
33	Ladich	2015	Europe	NR	NR	tank	11	*Trichopsis vittata*	Demersal	Male	NR	NR	FM	NR	Territorial Aggression	croak	3
34	Feng	2016	North America	24 x 1 hr	Spring	tank	6	*Porichthys notatus*	Demersal	Male	202.5 (6.7)	NR	SSM	Spring	Courtship	hum	
34	Feng	2016	North America	24 x 1 hr	Spring	tank	6	*Porichthys notatus*	Demersal	Male	236.5 (4.6)	NR	SSM	Spring	Courtship	hum	
35	Parmentier	2018	South America	8 min every 30 min	Autumn	tank	9	*Genypterus chilensis*	Bathydemersal	NR	NR	NR	SSM	Autumn	Courtship	pulse	
35	Parmentier	2018	South America	8 min every 30 min	Autumn	tank	11	*Genypterus maculatus*	Demersal	NR	NR	NR	SSM	Autumn	Courtship	growl	
35	Parmentier	2018	South America	8 min every 30 min	Autumn	tank	11	*Genypterus maculatus*	Demersal	NR	NR	NR	SSM	Autumn	Courtship	pulse	
36	Casaretto	2014	Europe	>15 min	Spring	in situ	NR	*Melanogrammus aeglefinus*	Demersal	Male	NR	NR	SSM	Spring	Courtship & Spawning	knock	1
36	Casaretto	2014	Europe	>15 min	Spring	in situ	NR	*Melanogrammus aeglefinus*	Demersal	Male	NR	NR	SSM	Spring	Courtship & Spawning	knock	2
36	Casaretto	2014	Europe	>15 min	Spring	in situ	NR	*Melanogrammus aeglefinus*	Demersal	Male	NR	NR	SSM	Spring	Courtship & Spawning	knock	3
36	Casaretto	2014	Europe	>15 min	Spring	tank	NR	*Melanogrammus aeglefinus*	Demersal	Male	NR	NR	SSM	Spring	Courtship & Spawning	knock	4
37	Vicente	2015	Europe	10-30 min	Winter-Spring	tank	3	*Pomatoschistus pictus*	Demersal	Male	NR	NR	PGM	Winter-Spring	Courtship	drum	
37	Vicente	2015	Europe	10-30 min	Winter-Spring	tank	6	*Pomatoschistus pictus*	Demersal	Male	NR	NR	PGM	Winter-Spring	Courtship	drum	

37	Vicente	2015	Europe	10-30 min	Winter-Spring	tank	6	*Pomatoschistus pictus*	Demersal	Male	NR	NR	PGM	Winter-Spring	Courtship	drum	1
37	Vicente	2015	Europe	10-30 min	Winter-Spring	tank	6	*Pomatoschistus pictus*	Demersal	Male	NR	NR	PGM	Winter-Spring	Courtship	drum	2
37	Vicente	2015	Europe	10-30 min	Winter-Spring	tank	6	*Pomatoschistus pictus*	Demersal	Male	NR	NR	PGM	Winter-Spring	Courtship	drum	3
37	Vicente	2015	Europe	10-30 min	Winter-Spring	tank	7	*Pomatoschistus pictus*	Demersal	Male	NR	NR	PGM	Winter-Spring	Courtship	drum	
37	Vicente	2015	Europe	10-30 min	Winter-Spring	tank	8	*Pomatoschistus pictus*	Demersal	Male	NR	NR	PGM	Winter-Spring	Courtship	drum	1
37	Vicente	2015	Europe	10-30 min	Winter-Spring	tank	8	*Pomatoschistus pictus*	Demersal	Male	NR	NR	PGM	Winter-Spring	Courtship	drum	2
37	Vicente	2015	Europe	10-30 min	Winter-Spring	tank	8	*Pomatoschistus pictus*	Demersal	Male	NR	NR	PGM	Winter-Spring	Courtship	drum	3
38	Ripley	2007	North America	16 min	Spring-Autumn	tank	10	*Syngnathus fuscus*	Demersal	Male	(138-167)	NR	Unknown	NR	Feeding	click	
38	Ripley	2007	North America	16 min	Spring-Autumn	tank	10	*Syngnathus fuscus*	Demersal	Female	(129-164)	NR	Unknown	NR	Feeding	click	
38	Ripley	2007	North America	16 min	Spring-Autumn	tank	10	*Syngnathus louisianae*	Reef	Male	(131-185)	NR	Unknown	NR	Feeding	click	
38	Ripley	2007	North America	16 min	Spring-Autumn	tank	10	*Syngnathus louisianae*	Reef	Female	(171-230)	NR	Unknown	NR	Feeding	click	
39	Amorim	2015	Europe	1hr	Spring-summer	tank	13	*Halobatrachus didactylus*	Demersal	Male	NR	419(18;393-460)	SSM	Spring-summer	Territorial Aggression	boatwhistle	
39	Amorim	2007	Europe	20 min	Spring	tank	20	*Pomatoschistus pictus*	Demersal	Male	29.2(3.1; 25-37)	NR	PGM	Spring	Courtship	thump	
40	Pruzsinsky	1998	Europe	NR	spawning season	tank	21	*Corydoras paleatus*	Demersal	Male	NR	NR	PSS	NR	Agonistic	abduction	
40	Pruzsinsky	1998	Europe	NR	spawning season	tank	21	*Corydoras paleatus*	Demersal	Male	NR	NR	PSS	NR	Courtship	abduction	
41	Lobel	1998	Africa	30-45 min	NR	in situ	5	*Copadichromis conophorus*	Benthopelagic	Male	NR	NR	Unknown	NR	Courtship	pulse	
41	Lobel	1998	Africa	30-45 min	NR	in situ	2	*Tramitichromis intermedius*	Demersal	Male	NR	NR	Unknown	NR	Courtship	pulse	
42	Hawkins	2000	Europe	30 min every 3 hr	Winter-Spring	tank	6	*Melanogrammus aeglefinus*	Demersal	Male	NR	315(15.8;290-340)	SSM	Winter-spring	Agonistic	knock	
42	Hawkins	2000	Europe	30 min every 3 hr	Winter-Spring	tank	6	*Melanogrammus aeglefinus*	Demersal	Male	NR	315(15.8;290-340)	SSM	Winter-spring	Spawning	hum	
42	Hawkins	2000	Europe	30 min every 3 hr	Winter-Spring	tank	6	*Melanogrammus aeglefinus*	Demersal	Male	NR	315(15.8;290-340)	SSM	Winter-spring	Spawning	knock	1
42	Hawkins	2000	Europe	30 min every 3 hr	Winter-Spring	tank	6	*Melanogrammus aeglefinus*	Demersal	Male	NR	315(15.8;290-340)	SSM	Winter-spring	Spawning	knock	2
42	Hawkins	2000	Europe	30 min every 3 hr	Winter-Spring	tank	6	*Melanogrammus aeglefinus*	Demersal	Male	NR	315(15.8;290-340)	SSM	Winter-spring	Spawning	knock	3
43	Johnson	2000	Central America	5 min	Spring-summer	in situ	5	*Cyprinodon bifasciatus*	Benthopelagic	Male	NR	NR	Unknown	Spring-Summer	Courtship	pulse	
43	Johnson	2000	Central America	5 min	Spring-summer	in situ	5	*Cyprinodon bifasciatus*	Benthopelagic	Male	NR	NR	Unknown	Spring-Summer	Postspawn	pulse	
43	Johnson	2000	Central America	5 min	Spring-summer	in situ	15	*Cyprinodon bifasciatus*	Benthopelagic	Male	NR	NR	Unknown	Spring-Summer	Territorial Aggression	pulse	
44	Lindstrom	2000	Europe	NR	Spring	tank	8	*Pomatoschistus minutus*	Demersal	Male	NR	50.25 (2.54; 45-53)	PGM	Spring	Courtship	pulse	
45	Thorson	2002	North America	17:00-19:30	Spring	in situ	5	*Opsanus beta*	Demersal	Male	NR	NR	SSM	Spring	Courtship	grunt	
45	Thorson	2002	North America	17:00-19:30	Spring	in situ	5	*Opsanus beta*	Demersal	Male	NR	NR	SSM	Spring	Courtship	boop	

46	Bremner	2002	North America	3 hr	Spring-Summer	tank	1	*Melanogrammus aeglefinus*	Demersal	Male	NR	(450-600)	SSM	Spring-Summer	Courtship	knock	1
46	Bremner	2002	North America	3 hr	Spring-Summer	tank	1	*Melanogrammus aeglefinus*	Demersal	Male	NR	(450-600)	SSM	Spring-Summer	Courtship	knock	2
47	Malavasi	2003	Europe	30 min	Spring	concrete tank	5	*Zosterisessor ophiocephalus*	Demersal	Male	NR	(112-130)	Unknown	Spring	Courtship	grunt	
47	Malavasi	2003	Europe	30 min	Spring	concrete tank	9	*Zosterisessor ophiocephalus*	Demersal	Male	NR	(140-196)	Unknown	Spring	Courtship	grunt	
48	Finstad	2004	Europe	9 x	Spring	tank	29	*Gadus morhua*	Benthopelagic	Male	NR	760(123; 510-1040)	SSM	Spring	Courtship	grunt	
49	Melotte	2016	Europe	NR	NR	tank	7	*Serrasalmus compressus*	Benthopelagic	NR	75(6)	NR	SSM	NR	Disturbance	tonal	
49	Melotte	2016	South America	NR	Spring	tank	10	*Serrasalmus eigenmanni*	Benthopelagic	NR	116(15)	NR	SSM	NR	Disturbance	tonal	
49	Melotte	2016	Europe	NR	NR	tank	9	*Serrasalmus elongatus*	Benthopelagic	NR	77(19)	NR	SSM	NR	Disturbance	tonal	
49	Melotte	2016	Europe	NR	NR	tank	4	*Serrasalmus manueli*	Benthopelagic	NR	125(6)	NR	SSM	NR	Disturbance	tonal	
49	Melotte	2016	Europe	NR	NR	tank	6	*Serrasalmus marginatus*	Benthopelagic	NR	58(7)	NR	SSM	NR	Disturbance	tonal	
49	Melotte	2016	South America	NR	Spring	tank	8	*Serrasalmus rhombeus*	Benthopelagic	NR	112(21)	NR	SSM	NR	Disturbance	tonal	
49	Melotte	2016	Europe	NR	NR	tank	7	*Serrasalmus spilopleura*	Benthopelagic	NR	79(4)	NR	SSM	NR	Disturbance	tonal	
49	Melotte	2016	Europe	NR	NR	tank	12	*Pygocentrus nattereri*	Pelagic	NR	59(14)	NR	SSM	NR	Disturbance	tonal	
50	Amorim	2003	Europe	20 min	NR	tank	19	*Oreochromis mossambicus*	Benthopelagic	Male	106(14;84-129)	NR	JTS	NR	Courtship	pulse	
51	Lobel	1995	Oceana	NR	Spring	in situ	6	*Dascyllus albisella*	Reef	Male	NR	NR	Unknown	Spring	Courtship	pulse	
51	Lobel	1995	Oceana	NR	Spring	in situ	6	*Dascyllus albisella*	Reef	Male	NR	NR	Unknown	Spring	Spawning	pulse	
52	Amorim	1996	Europe	60 min	NR	tank	5	*Chromis viridis*	Reef	Both	NR	(80-90)	Unknown	NR	Territorial Aggression	click	
53	Dos Santos	2000	Europe	15-60 min	Summer	in situ	21	*Halobatrachus didactylus*	Demersal	Male	NR	NR	SSM	Summer	Courtship	boatwhistle	
53	Dos Santos	2000	Europe	NR	NR	tank	19	*Halobatrachus didactylus*	Demersal	Both	(170-228)	NR	SSM	Summer	Disturbance	knock	
54	Edds-Walton	2002	North America	15 min	Summer	in situ	1	*Opsanus tau*	Reef	Male	NR	NR	SSM	Spring-Summer	Courtship	boatwhistle	1
54	Edds-Walton	2002	North America	15 min	Summer	in situ	1	*Opsanus tau*	Reef	Male	NR	NR	SSM	Spring-Summer	Courtship	boatwhistle	2
54	Edds-Walton	2002	North America	15 min	Summer	in situ	1	*Opsanus tau*	Reef	Male	NR	NR	SSM	Spring-Summer	Courtship	boatwhistle	3
54	Edds-Walton	2002	North America	15 min	Summer	in situ	1	*Opsanus tau*	Reef	Male	NR	NR	SSM	Spring-Summer	Courtship	boatwhistle	4
54	Edds-Walton	2002	North America	15 min	Summer	in situ	1	*Opsanus tau*	Reef	Male	NR	NR	SSM	Spring-Summer	Courtship	boatwhistle	5
54	Edds-Walton	2002	North America	15 min	Summer	in situ	1	*Opsanus tau*	Reef	Male	NR	NR	SSM	Spring-Summer	Courtship	boatwhistle	6
54	Edds-Walton	2002	North America	15 min	Summer	in situ	1	*Opsanus tau*	Reef	Male	NR	NR	SSM	Spring-Summer	Courtship	boatwhistle	7
54	Edds-Walton	2002	North America	15 min	Summer	in situ	1	*Opsanus tau*	Reef	Male	NR	NR	SSM	Spring-Summer	Courtship	boatwhistle	8
54	Edds-Walton	2002	North America	15 min	Spring	in situ	1	*Opsanus tau*	Reef	Male	NR	NR	SSM	Spring-Summer	Courtship	boatwhistle	9

54	Edds-Walton	2002	North America	15 min	Spring	in situ	1	*Opsanus tau*	Reef	Male	NR	NR	SSM	Spring-Summer	Courtship	boatwhistle	10
54	Edds-Walton	2002	North America	15 min	Spring	in situ	1	*Opsanus tau*	Reef	Male	NR	NR	SSM	Spring-Summer	Courtship	boatwhistle	11
54	Edds-Walton	2002	North America	15 min	Spring	in situ	1	*Opsanus tau*	Reef	Male	NR	NR	SSM	Spring-Summer	Courtship	boatwhistle	12
55	Lamml	2005	Europe	30 min	Summer	tank	1	*Pollimyrus marianne*	Benthopelagic	Male	62	NR	SSM	Summer	Courtship	moan	1
55	Lamml	2005	Europe	30 min	Summer	tank	1	*Pollimyrus marianne*	Benthopelagic	Male	62	NR	SSM	Summer	Courtship	moan	2
55	Lamml	2005	Europe	30 min	Summer	tank	1	*Pollimyrus marianne*	Benthopelagic	Male	64	NR	SSM	Summer	Courtship	moan	
55	Lamml	2005	Europe	30 min	Summer	tank	1	*Pollimyrus marianne*	Benthopelagic	Male	55	NR	SSM	Summer	Courtship	moan	
55	Lamml	2005	Europe	30 min	Summer	tank	1	*Pollimyrus marianne*	Benthopelagic	Male	62	NR	SSM	Summer	Courtship	grunt	1
55	Lamml	2005	Europe	30 min	Summer	tank	1	*Pollimyrus marianne*	Benthopelagic	Male	62	NR	SSM	Summer	Courtship	grunt	2
55	Lamml	2005	Europe	30 min	Summer	tank	1	*Pollimyrus marianne*	Benthopelagic	Male	64	NR	SSM	Summer	Courtship	grunt	
55	Lamml	2005	Europe	30 min	Summer	tank	1	*Pollimyrus marianne*	Benthopelagic	Male	55	NR	SSM	Summer	Courtship	grunt	
55	Lamml	2005	Europe	30 min	Summer	tank	1	*Pollimyrus marianne*	Benthopelagic	Male	62	NR	SSM	Summer	Territorial Aggression	moan	
55	Lamml	2005	Europe	30 min	Summer	tank	1	*Pollimyrus marianne*	Benthopelagic	Male	55	NR	SSM	Summer	Territorial Aggression	moan	
56	Lamml	2008	Europe	NR	Summer	tank	3	*Petrocephalus catostoma*	Demersal	Both	100.33(3.3;96-104)	NR	SSM	NR	Territorial Aggression	hoot	
56	Lamml	2008	Europe	NR	Summer	tank	2	*Petrocephalus catostoma*	Demersal	Male	95(3;92-98)	NR	SSM	NR	Territorial Aggression	hoot	
56	Lamml	2008	Europe	NR	Summer	tank	2	*Petrocephalus catostoma*	Demersal	Male	92(1;91-93)	NR	SSM	NR	Territorial Aggression	hoot	
57	Picciulin	2013	Europe	12 hr	Summer	in situ	NR	*Sciaena umbra*	Demersal	Male	NR	NR	SSM	Summer	Courtship	pulse	1
57	Picciulin	2013	Europe	12 hr	Summer	in situ	NR	*Sciaena umbra*	Demersal	Male	NR	NR	SSM	Summer	Courtship	pulse	2
57	Picciulin	2013	Europe	12 hr	Summer	in situ	NR	*Sciaena umbra*	Demersal	Male	NR	NR	SSM	Summer	Courtship	pulse	3
58	Ladich	2020	Europe	20 sounds	NR	tank	20	*Trichopsis schalleri*	Benthopelagic	Female	NR	NR	FM	NR	Territorial Aggression	croak	
59	Holt	2014	North America	17 min - 2.5 hr	NR	tank	18	*Cyprinella venusta*	Benthopelagic	Male	NR	NR	Unknown	NR	Courtship	growl	1
59	Holt	2014	North America	17 min - 2.5 hr	NR	tank	18	*Cyprinella venusta*	Benthopelagic	Male	NR	NR	Unknown	NR	Courtship	growl	2
59	Holt	2014	North America	17 min - 2.5 hr	NR	tank	14	*Cyprinella venusta*	Benthopelagic	Male	NR	NR	Unknown	NR	Territorial Aggression	knock	1
59	Holt	2014	North America	17 min - 2.5 hr	NR	tank	14	*Cyprinella venusta*	Benthopelagic	Male	NR	NR	Unknown	NR	Territorial Aggression	knock	2
60	Hernandez	2013	North America	24 hr for 75 days	Spring	in situ	NR	*Gadus morhua*	Benthopelagic	Male	NR	NR	SSM	Spring	Courtship	grunt	
61	Erisman	2017	Central America	60 sec	Spring	in situ	NR	*Cynoscion othonopterus*	Benthopelagic	Male	NR	NR	SSM	Spring	Courtship	pulse	
62	Parmentier	2005	Europe	NR	NR	tank	12	*Amphiprion akallopisos*	Reef	Female	NR	NR	JTS	NR	Territorial Aggression	pop	1
62	Parmentier	2005	Europe	NR	NR	tank	12	*Amphiprion akallopisos*	Reef	Female	NR	NR	JTS	NR	Territorial Aggression	pop	2

62	Parmentier	2005	Africa	15 min	NR	tank	10	*Amphiprion akallopisos*	Reef	Female	NR	62-74	JTS	NR	Territorial Aggression	pop	1
62	Parmentier	2005	Africa	15 min	NR	tank	10	*Amphiprion akallopisos*	Reef	Female	NR	62-74	JTS	NR	Territorial Aggression	pop	2
62	Parmentier	2005	Africa	15 min	NR	tank	10	*Amphiprion akallopisos*	Reef	Female	NR	62-74	JTS	NR	Territorial Aggression	chirp	
63	Boyle	2014	Europe	5 min	NR	tank	3	*Synodontis angelica*	Benthopelagic	NR	NR	NR	PSS	NR	Disturbance	growl	
63	Boyle	2014	Europe	5 min	NR	tank	3	*Synodontis angelica*	Benthopelagic	NR	NR	NR	PSS	NR	Disturbance	pulse	
63	Boyle	2014	Europe	5 min	NR	tank	4	*Synodontis euptera*	Benthopelagic	NR	NR	NR	PSS	NR	Disturbance	growl	
63	Boyle	2014	Europe	5 min	NR	tank	4	*Synodontis euptera*	Benthopelagic	NR	NR	NR	PSS	NR	Disturbance	pulse	
63	Boyle	2014	Europe	5 min	NR	tank	7	*Synodontis marmorata*	Benthopelagic	NR	NR	NR	PSS	NR	Disturbance	growl	
63	Boyle	2014	Europe	5 min	NR	tank	7	*Synodontis marmorata*	Benthopelagic	NR	NR	NR	PSS	NR	Disturbance	pulse	
63	Boyle	2014	Europe	5 min	NR	tank	6	*Synodontis grandiops*	Demersal	NR	NR	NR	PSS	NR	Disturbance	growl	
63	Boyle	2014	Europe	5 min	NR	tank	6	*Synodontis grandiops*	Demersal	NR	NR	NR	PSS	NR	Disturbance	pulse	
64	Malavasi	2009	Europe	NR	Spring	tank	10	*Pomatoschistus canestrinii*	Demersal	Male	(42-52)	NR	Unknown	Spring	Courtship	thump	
65	Kever	2015	Europe	10 min every 30 min	Spring	in situ	NR	*Ophidion rochei*	Demersal	Male	NR	NR	SSM	Summer-Autumn	Courtship	pulse	1
65	Kever	2015	Europe	10 min every 30 min	Autumn	in situ	NR	*Ophidion rochei*	Demersal	Male	NR	NR	SSM	Summer-Autumn	Courtship	pulse	2
65	Kever	2015	Europe	10 min every 30 min	Autumn	in situ	NR	*Ophidion rochei*	Demersal	Male	NR	NR	SSM	Summer-Autumn	Courtship	pulse	3
65	Kever	2015	Europe	10 min every 30 min	Summer	in situ	NR	*Ophidion rochei*	Demersal	Male	NR	NR	SSM	Summer-Autumn	Courtship	pulse	4
65	Kever	2015	Europe	10 min every 30 min	Autumn	in situ	NR	*Ophidion rochei*	Demersal	Female	NR	NR	SSM	Summer-Autumn	Courtship	pulse	5
65	Kever	2015	Europe	10 min every 30 min	Autumn	in situ	NR	*Ophidion rochei*	Demersal	Female	NR	NR	SSM	Summer-Autumn	Courtship	pulse	6
65	Kever	2015	Europe	10 min every 30 min	Summer	in situ	NR	*Ophidion rochei*	Demersal	Female	NR	NR	SSM	Summer-Autumn	Courtship	pulse	7
65	Kever	2015	Europe	10 min every 30 min	Spring	in situ	NR	*Ophidion rochei*	Demersal	Female	NR	NR	SSM	Summer-Autumn	Courtship	pulse	8
65	Kever	2015	Europe	10 min every 30 min	Summer	in situ	NR	*Ophidion rochei*	Demersal	Male	NR	NR	SSM	Summer-Autumn	Courtship	pulse	9
66	Amorim	2013	Europe	20 min	Winter-Spring	tank	19	*Pomatoschistus pictus*	Demersal	Male	36.9(4.2;30-46)	NR	PGM	Winter-Spring	Courtship	thump	
66	Amorim	2013	Europe	20 min	Winter-Spring	tank	19	*Pomatoschistus pictus*	Demersal	Male	36.9(4.2;30-46)	NR	PGM	Winter-Spring	Courtship	drum	
67	Zhang	2015	Asia	NR	Summer	tank	20	*Sebastiscus marmoratus*	Demersal	NR	NR	(125-155)	SSM	NR	Disturbance	pulse	1
67	Zhang	2015	Asia	NR	Summer	tank	20	*Sebastiscus marmoratus*	Demersal	NR	NR	(125-155)	SSM	NR	Disturbance	pulse	2
68	Horvatic	2016	Europe	30 min	Spring-Summer	tank	8	*Neogobius fluviatilis*	Benthopelagic	Male	128.5(11.2)	NR	PGM	Spring-Summer	Courtship	pulse	
68	Horvatic	2016	Europe	30 min	Spring-Summer	tank	5	*Neogobius fluviatilis*	Benthopelagic	Female	116.2(11.8)	NR	PGM	Spring-Summer	Territorial Aggression	pulse	
68	Horvatic	2016	Europe	30 min	Spring-Summer	tank	8	*Neogobius fluviatilis*	Benthopelagic	Male	132.7(8.3)	NR	PGM	Spring-Summer	Territorial Aggression	pulse	

69	Rountree	2018	South America	NR	Summer	in situ	1	*Serrasalmus compressus*	Benthopelagic	NR	NR	NR	SSM	NR	Disturbance	bark	
69	Rountree	2018	South America	NR	Summer	in situ	1	*Serrasalmus eigenmanni*	Benthopelagic	NR	20	NR	SSM	NR	Disturbance	bark	
69	Rountree	2018	South America	NR	Summer	in situ	3	*Serrasalmus sanchezi*	Benthopelagic	NR	127(60;115-135)	NR	Unknown	NR	Disturbance	bark	
69	Rountree	2018	South America	NR	Summer	in situ	27	*Serrasalmus spp.*	NA	NR	94.38(19.22;55-125)	NR	Unknown	NR	Disturbance	bark	
69	Rountree	2018	South America	NR	Summer	in situ	39	*Pygocentrus nattereri*	Pelagic	NR	111.25(23.37;65-175)	NR	SSM	NR	Disturbance	bark	
69	Rountree	2018	South America	NR	Summer	in situ	12	*Serrasalmus maculatus*	Pelagic	NR	95.45(21.37;70-10)	NR	Unknown	NR	Disturbance	bark	
70	Malavasi	2007	Europe	NR	Spring-summer	tank	6	*Gobius cobitis*	Demersal	Male	NR	147(37)	Unknown	Spring-Summer	Territorial Aggression	grunt	
70	Malavasi	2007	Europe	NR	Spring-summer	tank	3	*Gobius niger*	Demersal	Male	NR	126(12)	Unknown	Spring-Summer	Courtship	grunt	
70	Malavasi	2007	Europe	NR	Spring-summer	tank	5	*Gobius niger*	Demersal	Male	NR	121(12)	Unknown	Spring-Summer	Territorial Aggression	grunt	
70	Malavasi	2007	Europe	NR	Spring-summer	tank	11	*Gobius paganellus*	Demersal	Male	NR	112(7)	PGM	Spring-Summer	Courtship	grunt	
70	Malavasi	2007	Europe	NR	Spring-summer	tank	6	*Gobius paganellus*	Demersal	Male	NR	118(27)	PGM	Spring-Summer	Territorial Aggression	grunt	
70	Malavasi	2007	Europe	NR	Spring-summer	tank	5	*Pomatoschistus canestrinii*	Demersal	Male	NR	49(3)	Unknown	Spring-Summer	Courtship	grunt	
70	Malavasi	2007	Europe	NR	Spring-summer	tank	4	*Pomatoschistus canestrinii*	Demersal	Male	NR	49(3)	Unknown	Spring-Summer	Territorial Aggression	grunt	
71	Parmentier	2009	Oceana	NR	Spring	in situ	6	*Dascyllus albisella*	Reef	Male	NR	NR	Unknown	Spring	Courtship	pulse	
71	Parmentier	2009	Oceana	1-4 hr	Summer	in situ	4	*Dascyllus aruanus*	Reef	Male	NR	NR	Unknown	Summer	Courtship	pulse	
71	Parmentier	2009	Africa	2 hr	Autumn	in situ	3	*Dascyllus aruanus*	Reef	Male	NR	NR	Unknown	Autumn	Courtship	pulse	
71	Parmentier	2009	Oceana	1-4 hr	Summer	in situ	5	*Dascyllus trimaculatus*	Reef	Male	NR	NR	Unknown	Summer	Courtship	pulse	
71	Parmentier	2009	Africa	2 hr	Autumn	in situ	6	*Dascyllus trimaculatus*	Reef	Male	NR	NR	Unknown	Autumn	Courtship	pulse	
71	Parmentier	2009	Oceana	1-4 hr	Summer	in situ	4	*Dascyllus flavicaudus*	Reef	Male	NR	NR	Unknown	Summer	Courtship	pulse	
71	Parmentier	2009	Oceana	1-4 hr	Summer	in situ	5	*Dascyllus flavicaudus*	Reef	Male	NR	NR	Unknown	Summer	Courtship	pulse	
72	Lugli	1996	Europe	NR		tank	2	*Padogobius martensii*	Demersal	Male	NR	89-140	PGM	NR	Courtship	tonal	1
72	Lugli	1996	Europe	NR		tank	2	*Padogobius martensii*	Demersal	Male	NR	89-140	PGM	NR	Courtship	tonal	2
72	Lugli	1996	Europe	NR		tank	1	*Padogobius martensii*	Demersal	Male	NR	89-140	PGM	NR	Courtship	tonal	
73	Lugli	1999	Europe	NR	Spring-summer	tank	4	*Knipowitschia panizzae*	Demersal	Male	NR	(33-37)	Unknown	Spring-Summer	Courtship	pulse	
73	Lugli	1999	Europe	NR	Spring-summer	tank	1	*Pomatoschistus canestrinii*	Demersal	Male	NR	50	Unknown	Spring-Summer	Courtship	pulse	
73	Lugli	1999	Europe	NR	Spring-summer	tank	5	*Pomatoschistus marmoratus*	Demersal	Male	NR	(49-63)	Unknown	Spring-Summer	Courtship	pulse	
74	Amorim	2004	Europe	15 min	Not spawning	tank	NR	*Eutrigla gurnardus*	Demersal	Both	NR	(100-400)	SSM	NR	Feeding	growl	
74	Amorim	2004	Europe	15 min	Not spawning	tank	NR	*Eutrigla gurnardus*	Demersal	Both	NR	(100-400)	SSM	NR	Feeding	grunt	

74	Amorim	2004	Europe	15 min	Not spawning	tank	NR	*Eutrigla gurnardus*	Demersal	Both	NR	(100-400)	SSM	NR	Feeding	knock	
75	Amorim	2004	NR	20 min		tank	8	*Maylandia callainos*	Benthopelagic	Male	98.3(2.8;86.8-110.8)	NR	Unknown	NR	Courtship	pulse	
75	Amorim	2004	NR	20 min		tank	6	*Maylandia zebra*	Demersal	Male	99.9(2.3;96-106.5)	NR	JTS	NR	Courtship	pulse	
75	Amorim	2004	NR	20 min		tank	9	*Maylandia zebra gold*	Demersal	Male	105.3(0.9;100.7-109.6)	NR	JTS	NR	Courtship	pulse	
76	Scholz	2006	Europe	10-45 min	NR	tank	16	*Pseudorasbora parva*	Benthopelagic	NR	(53-72.5)	NR	JTS	NR	Feeding	strike	
76	Scholz	2006	Europe	10-45 min	NR	tank	17	*Pseudorasbora parva*	Benthopelagic	NR	(53-72.5)	NR	JTS	NR	Feeding	grind	
76	Scholz	2006	Europe	10-45 min	NR	tank	15	*Pseudorasbora parva*	Benthopelagic	NR	(53-72.5)	NR	JTS	NR	Feeding	grind	
76	Scholz	2006	Europe	10-45 min	NR	tank	16	*Pseudorasbora parva*	Benthopelagic	NR	(53-72.5)	NR	JTS	NR	Feeding	strike	
76	Scholz	2006	Europe	10-45 min	NR	tank	17	*Pseudorasbora parva*	Benthopelagic	NR	(53-72.5)	NR	JTS	NR	Feeding	strike	
77	Amorim	2008	Europe	20 min	NR	tank	13	*Maylandia callainos*	Benthopelagic	Male	97.7(86.8-115)	NR	Unknown	NR	Courtship	pulse	
77	Amorim	2008	Europe	20 min	NR	tank	14	*Maylandia emmiltos*	Demersal	Male	126.3(116-139)	NR	Unknown	NR	Courtship	pulse	
77	Amorim	2008	Europe	20 min	NR	tank	13	*Maylandia fainzilberi*	Demersal	Male	118.7(109-128)	NR	Unknown	NR	Courtship	pulse	
77	Amorim	2008	Europe	20 min	NR	tank	12	*Maylandia zebra*	Demersal	Male	107.7(88-122)	NR	JTS	NR	Courtship	pulse	
77	Amorim	2008	Europe	20 min	NR	tank	12	*Maylandia zebra gold*	Demersal	Male	107.3(89-123)	NR	JTS	NR	Courtship	pulse	
78	Amorim	2008	Europe	5-10 min	Summer	in situ	NR	*Halobatrachus didactylus*	Demersal	Male	NR	NR	SSM	Spring-Summer	Courtship	boatwhistle	1
78	Amorim	2008	Europe	5-10 min	Summer	in situ	NR	*Halobatrachus didactylus*	Demersal	Male	NR	NR	SSM	Spring-Summer	Courtship	boatwhistle	2
78	Amorim	2008	Europe	5-10 min	Summer	in situ	NR	*Halobatrachus didactylus*	Demersal	Male	NR	NR	SSM	Spring-Summer	Courtship	boatwhistle	3
79	Colleye	2009	Africa	30 min	Autumn	tank	6	*Amphiprion akallopisos*	Reef	Male	28-90	NR	JTS	NR	Territorial Aggression	pulse	
79	Colleye	2009	Africa	30 min	Autumn	tank	6	*Amphiprion akallopisos*	Reef	Female	28-90	NR	JTS	NR	Territorial Aggression	pulse	
80	Boyle	2009	Oceana	16 s - 11 min	Summer	in situ	16	*Gomphosus varius*	Reef	Male	NR	NR	JTS	Summer	Courtship	pulse	1
80	Boyle	2009	Oceana	16 s - 11 min	Summer	in situ	16	*Gomphosus varius*	Reef	Male	NR	NR	JTS	Summer	Courtship	pulse	2
80	Boyle	2009	Oceana	16 s - 11 min	Summer	in situ	4	*Gomphosus varius*	Reef	Male	NR	NR	JTS	Summer	Spawning	pulse	
80	Boyle	2009	Oceana	16 s - 11 min	Summer	in situ	7	*Thalassoma duperrey*	Reef	Male	NR	NR	JTS	Summer	Courtship	pulse	
80	Boyle	2009	Oceana	16 s - 11 min	Summer	in situ	2	*Thalassoma duperrey*	Reef	Male	NR	NR	JTS	Summer	Spawning	pulse	
81	Kierl	2010	North America	60 min	Spring-Summer	in situ	9	*Cottus paulus*	Demersal	Male	29.32(1.91;26.22-32.41)	NR	PGM	Spring-Summer	Agonistic	knock	1
81	Kierl	2010	North America	60 min	Spring-Summer	in situ	9	*Cottus paulus*	Demersal	Male	29.32(1.91;26.22-32.41)	NR	PGM	Spring-Summer	Agonistic	knock	2
81	Kierl	2010	North America	60 min	Spring-Summer	in situ	9	*Cottus paulus*	Demersal	Male	29.32(1.91;26.22-32.41)	NR	PGM	Spring-Summer	Courtship	knock	1
81	Kierl	2010	North America	60 min	Spring-Summer	in situ	9	*Cottus paulus*	Demersal	Male	29.32(1.91;26.22-32.41)	NR	PGM	Spring-Summer	Courtship	knock	2

82	Bertucci	2012	Europe	20 min	NR	tank	17	*Metriaclima zebra*	Demersal	Male	64.57(1.36)	77.86(1.91)	SSM	NR	Territorial Aggression	pulse	
82	Bertucci	2012	Europe	20 min	NR	tank	20	*Metriaclima zebra*	Demersal	Male	104.5(1.26)	121.25(2.09)	SSM	NR	Territorial Aggression	pulse	
83	Amorim	2005	Europe	5 min	Summer	tank	NR	*Eutrigla gurnardus*	Demersal	NR	NR	(100-150)	SSM	NR	Feeding	knock	
83	Amorim	2005	Europe	5 min	Summer	tank	NR	*Eutrigla gurnardus*	Demersal	NR	NR	(100-150)	SSM	NR	Feeding	grunt	
83	Amorim	2005	Europe	5 min	Spring-Winter	tank	NR	*Eutrigla gurnardus*	Demersal	NR	NR	(150-200)	SSM	NR	Feeding	knock	
83	Amorim	2005	Europe	5 min	Spring-Winter	tank	NR	*Eutrigla gurnardus*	Demersal	NR	NR	(150-200)	SSM	NR	Feeding	grunt	
83	Amorim	2005	Europe	5 min	Spring	tank	NR	*Eutrigla gurnardus*	Demersal	NR	NR	(250-300)	SSM	NR	Feeding	knock	
83	Amorim	2005	Europe	5 min	Spring	tank	NR	*Eutrigla gurnardus*	Demersal	NR	NR	(250-300)	SSM	NR	Feeding	grunt	
83	Amorim	2005	Europe	5 min	Autumn	tank	NR	*Eutrigla gurnardus*	Demersal	NR	NR	(300-400)	SSM	NR	Feeding	knock	
83	Amorim	2005	Europe	5 min	Autumn	tank	NR	*Eutrigla gurnardus*	Demersal	NR	NR	(300-400)	SSM	NR	Feeding	grunt	
84	Vasconcelos	2009	Europe	11-56 hr	Summer	in situ	16	*Holobatrachus didactylus*	Demersal	Male	NR	(350-480)	SSM	Spring-Summer	Territorial Aggression	boatwhistle	
84	Vasconcelos	2009	Europe	60 min	Spring-Summer	tank	15	*Holobatrachus didactylus*	Demersal	Male	NR	(380-520)	SSM	Spring-Summer	Territorial Aggression	boatwhistle	
85	Longrie	2008	NR	NR	Autumn	tank	8	*Oreochromis niloticus*	Benthopelagic	Male	NR	300(160)	PGM	Autumn	Territorial Aggression	pulse	
86	Bocast	2014	North America	NR	Spring	in situ	NR	*Acipenser fulvescens*	Demersal	Male	NR	NR	Unknown	Spring	Spawning	drum	
87	Bertucci	2015	Europe	5 min every 60 min	Summer-Autumn	in situ	NR	*Epinephelus marginatus*	Reef	NR	NR	NR	SSM	Spring-Summer	Courtship	boom	
87	Bertucci	2015	Europe	6 min every 60 min	Summer-Autumn	in situ	NR	*Epinephelus marginatus*	Reef	NR	NR	NR	SSM	Spring-Summer	Courtship	boom	1
87	Bertucci	2015	Europe	6 min every 60 min	Summer-Autumn	in situ	NR	*Epinephelus marginatus*	Reef	NR	NR	NR	SSM	Spring-Summer	Courtship	boom	2
87	Bertucci	2015	Europe	10 min	Summer	tank	2	*Epinephelus marginatus*	Reef	NR	NR	(700-900)	SSM	Spring-Summer	Courtship	boom	
87	Bertucci	2015	Europe	10 min	Spring	tank	1	*Epinephelus marginatus*	Reef	Male	NR	(750-800)	SSM	Spring-Summer	Courtship	boom	
88	Picciulin	2016	Europe	12 hr	Spring	in situ	NR	*Sciaena umbra*	Demersal	NR	NR	NR	SSM	Summer	Courtship	pulse	
88	Picciulin	2016	Europe	continuous	Spring	tank	30	*Umbrina cirrosa*	Demersal	NR	NR	NR	SSM	Summer	Courtship	pulse	
89	Montie	2016	North America	2 min every 20 min	Autumn	tank	2	*Sciaenops ocellatus*	Demersal	Male	NR	903(36;939-867)	SSM	Autumn	Courtship	drum	
89	Montie	2016	North America	2 min every 20 min	Autumn	tank	2	*Sciaenops ocellatus*	Demersal	Male	NR	1057.5(19.5;1038-1077)	SSM	Autumn	Courtship	drum	
89	Montie	2016	North America	2 min every 20 min	Autumn	tank	1	*Sciaenops ocellatus*	Demersal	Male	NR	930(0)	SSM	Autumn	Courtship	drum	
89	Montie	2016	North America	2 min every 20 min	Autumn	tank	1	*Sciaenops ocellatus*	Demersal	Male	NR	912(0)	SSM	Autumn	Courtship	drum	
90	Rowell	2018	Central America	1 min every 5 min	Spring	in situ	5	*Mycteroperca jordani*	Reef	Male	NR	1404(64;1337-1495)	SSM	Spring	Courtship & Spawning	tonal	1
90	Rowell	2018	Central America	1 min every 5 min	Spring	in situ	5	*Mycteroperca jordani*	Reef	Male	NR	1404(64;1337-1495)	SSM	Spring	Courtship & Spawning	tonal	2
90	Rowell	2018	Central America	1 min every 5 min	Spring	in situ	5	*Mycteroperca jordani*	Reef	Male	NR	1404(64;1337-1495)	SSM	Spring	Courtship & Spawning	pulse	1

90	Rowell	2018	Central America	1 min every 5 min	Spring	in situ	5	*Mycteroperca jordani*	Reef	Male	NR	1404(64;1337-1495)	SSM	Spring	Courtship & Spawning	pulse	2
90	Rowell	2018	Central America	1 min every 5 min	Spring	in situ	5	*Mycteroperca jordani*	Reef	Male	NR	1404(64;1337-1495)	SSM	Spring	Courtship & Spawning	pulse	3
90	Rowell	2018	Central America	1 min every 5 min	Spring	in situ	5	*Mycteroperca jordani*	Reef	Male	NR	1404(64;1337-1495)	SSM	Spring	Courtship & Spawning	pulse	4
91	Tellechea	2017	South America	2 hr	Summer-Winter	in situ	NR	*Umbrina canosai*	Demersal	Male	NR	NR	SSM	Summer-Winter	Courtship	pulse	
91	Tellechea	2017	South America	NR	Summer-Winter	tank	34	*Umbrina canosai*	Demersal	Male	23.69(5.2;15-35)	NR	SSM	Summer-Winter	Disturbance	pulse	
92	Oliviera	2014	Europe	1-4.3 min	NR	tank	5	*Hippocampus reidi*	Reef	Male	NR	(109-173)	CBS	NR	Courtship	click	
92	Oliviera	2014	Europe	1-4.3 min	NR	tank	5	*Hippocampus reidi*	Reef	Female	NR	(116-170)	CBS	NR	Courtship	click	
92	Oliviera	2014	Europe	1 hr	NR	tank	8	*Hippocampus reidi*	Reef	Female	NR	(116-170)	CBS	NR	Disturbance	growl	
92	Oliviera	2014	Europe	1 hr	NR	tank	8	*Hippocampus reidi*	Reef	Male	NR	(109-173)	CBS	NR	Disturbance	growl	
92	Oliviera	2014	Europe	15-36 min	NR	tank	7	*Hippocampus reidi*	Reef	Male	NR	(109-173)	CBS	NR	Feeding	click	
92	Oliviera	2014	Europe	15-36 min	NR	tank	6	*Hippocampus reidi*	Reef	Female	NR	(116-170)	CBS	NR	Feeding	click	
93	Horvatic	2019	Europe	17 x 30 min	Spring	tank	6	*Perccottus glenii*	Demersal	Male	84-96	NR	PGM	Spring	Courtship	thump	1
93	Horvatic	2019	Europe	17 x 30 min	Spring	tank	6	*Perccottus glenii*	Demersal	Male	84-96	NR	PGM	Spring	Courtship	thump	2
93	Horvatic	2019	Europe	17 x 30 min	Spring	tank	3	*Perccottus glenii*	Demersal	Male	84-96	NR	PGM	Spring	Courtship	tonal	
94	Kever	2015	Europe	5 min per hr	Summer	in situ	NR	*Ophidion rochei*	Demersal	Male	NR	NR	SSM	Summer	Courtship	pulse	1
94	Kever	2015	Europe	5 min per hr	Summer	in situ	NR	*Ophidion rochei*	Demersal	Male	NR	NR	SSM	Summer	Courtship	pulse	2
94	Kever	2015	Europe	5 min per hr	Summer	in situ	NR	*Ophidion rochei*	Demersal	Male	NR	NR	SSM	Summer	Courtship	pulse	3
94	Kever	2015	Europe	5 min per hr	Summer	in situ	NR	*Ophidion rochei*	Demersal	Male	NR	NR	SSM	Summer	Courtship	pulse	4
95	Fine	2004	North America	NR	NR	tank	5	*Micropogonias undulatus*	Demersal	NR	NR	NR	SSM	NR	Disturbance	pulse	
96	Fish	1972	North America	NR	Spring	tank	1	*Cynoscion xanthulu*	Benthopelagic	NR	NR	NR	SSM	Spring	Courtship	knock	
97	Lin	2006	Asia	NR	NR	tank	NR	*Johnius macrorhynus*	Benthopelagic	Male	NR	NR	SSM	Spring-Summer	Disturbance	purr	
98	Simoes	2008	Europe	NR	Winter-Summer	tank	5	*Maylandia zebra*	Demersal	Female	103.6(0.002;100-106.5)	NR	JTS	Winter-Summer	Agonistic	pulse	
98	Simoes	2008	Europe	NR	Winter-Summer	tank	12	*Maylandia zebra*	Demersal	Male	107.1(11.8;88-122)	NR	JTS	Winter-Summer	Agonistic	pulse	
98	Simoes	2008	Europe	NR	Winter-Summer	tank	12	*Maylandia zebra*	Demersal	Male	107.1(11.8;88-122)	NR	JTS	Winter-Summer	Courtship	pulse	
99	Mann	1997	Oceana	NR	Spring	in situ	4	*Dascyllus albisella*	Reef	Male	NR	NR	Unknown	Spring	Courtship	pulse	
100	Crawford	1997	NR	NR	Summer	tank	NR	*Pollimyrus adspersus*	Demersal	Male	NR	NR	SSM	Summer	Courtship	moan	
100	Crawford	1997	NR	NR	Summer	tank	NR	*Pollimyrus adspersus*	Demersal	Male	NR	NR	SSM	Summer	Courtship	grunt	
100	Crawford	1997	Africa	NR	Summer	in situ	NR	*Pollimyrus isidori*	Demersal	Male	NR	NR	SSM	Summer	Courtship	moan	

100	Crawford	1997	Africa	NR	Summer	in situ	NR	*Pollimyrus isidori*	Demersal	Male	NR	NR	SSM	Summer	Courtship	grunt	
101	Parsons	2012	Oceana	every 30 min	NR	in situ	NR	*Argyrosomus japonicus*	Benthopelagic	NR	NR	NR	SSM	NR	Spawning	pulse	1
101	Parsons	2012	Oceana	every 30 min	NR	in situ	NR	*Argyrosomus japonicus*	Benthopelagic	NR	NR	NR	SSM	NR	Spawning	pulse	2
102	Parsons	2013	Oceana	5 in every 7 min	Winter	in situ	1	*Glaucosoma hebraicum*	Reef	Male	NR	450	SSM	NR	Disturbance	pulse	
102	Parsons	2013	Oceana	5 in every 7 min	Winter	in situ	1	*Glaucosoma hebraicum*	Reef	Male	NR	320	SSM	NR	Disturbance	pulse	
103	Lim	2015	Asia	NR	NR	tank	5	*Hippocampus comes*	Reef	Both	NR	116(107;99-129)	PGM	NR	Disturbance	growl	
103	Lim	2015	Asia	NR	NR	tank	6	*Hippocampus comes*	Reef	Both	NR	116(107;99-129)	PGM	NR	Feeding	click	
104	Parmentier	2007	Europe	NR	NR	tank	4	*Amphiprion clarkii*	Reef	Both	NR	NR	JTS	NR	Territorial Aggression	pop	
105	Winn	1960	NR	5 min	Summer	tank	NR	*Notropis analostanus*	Benthopelagic	Male	NR	NR	Unknown	Summer	Agonistic	knock	
106	Barimo	2011	North America	NR	Summer	in situ	1	*Opsanus tau*	Reef	Male	NR	NR	SSM	Summer	Agonistic	grunt	1
106	Barimo	2011	North America	NR	Summer	in situ	1	*Opsanus tau*	Reef	Male	NR	NR	SSM	Summer	Agonistic	grunt	2
106	Barimo	2011	North America	NR	Summer	in situ	1	*Opsanus tau*	Reef	Male	NR	NR	SSM	Summer	Courtship	boatwhistle	1
106	Barimo	2011	North America	NR	Summer	in situ	1	*Opsanus tau*	Reef	Male	NR	NR	SSM	Summer	Courtship	boatwhistle	2
106	Barimo	2011	North America	NR	Summer	in situ	1	*Opsanus tau*	Reef	Male	NR	NR	SSM	Summer	Courtship	boatwhistle	3
106	Barimo	2011	North America	NR	Summer	in situ	1	*Opsanus tau*	Reef	Male	NR	NR	SSM	Summer	Courtship	boatwhistle	4
106	Barimo	2011	North America	NR	Summer	in situ	1	*Opsanus tau*	Reef	Male	NR	NR	SSM	Summer	Courtship	boatwhistle	5
107	Amorim	2008	Europe	20 min	Winter-Spring	tank	20	*Pomatoschistus pictus*	Demersal	Male	29(3.1;25-36)	NR	PGM	Winter-Summer	Territorial Aggression	thump	
108	Bolgan	2013	Europe	20 min	Winter-Spring	tank	1	*Pomatoschistus microps*	Demersal	Male	32.3(1.4;30-34)	NR	PGM	Winter-Spring	Territorial Aggression	drum	
108	Bolgan	2013	Europe	20 min	Winter-Spring	tank	5	*Pomatoschistus pictus*	Demersal	Male	38.6(0.9;38-40)	NR	PGM	Winter-Spring	Courtship	drum	
108	Bolgan	2013	Europe	20 min	Winter-Spring	tank	6	*Pomatoschistus pictus*	Demersal	Male	35.5(3.21;31-40)	NR	PGM	Winter-Spring	Territorial Aggression	drum	
109	Colleye	2011	NR	NR	NR	tank	11	*Amphiprion akallopisos*	Reef	NR	64.88	NR	JTS	NR	Territorial Aggression	pulse	
109	Colleye	2011	NR	NR	NR	tank	2	*Amphiprion akindynos*	Reef	NR	73.56	NR	JTS	NR	Territorial Aggression	pulse	
109	Colleye	2011	NR	NR	NR	tank	1	*Amphiprion chrysogaster*	Reef	NR	93.01	NR	JTS	NR	Territorial Aggression	pulse	
109	Colleye	2011	NR	NR	NR	tank	1	*Amphiprion chrysopterus*	Reef	NR	100.14	NR	JTS	NR	Territorial Aggression	pulse	
109	Colleye	2011	NR	NR	NR	tank	6	*Amphiprion clarkii*	Reef	NR	83.31	NR	JTS	NR	Territorial Aggression	pulse	
109	Colleye	2011	NR	NR	NR	tank	6	*Amphiprion frenatus*	Reef	NR	78.54	NR	JTS	NR	Territorial Aggression	pulse	
109	Colleye	2011	NR	NR	NR	tank	1	*Amphiprion latifasciatus*	Reef	NR	53.97	NR	JTS	NR	Territorial Aggression	pulse	
109	Colleye	2011	NR	NR	NR	tank	2	*Amphiprion melanopus*	Reef	NR	65.62	NR	JTS	NR	Territorial Aggression	pulse	

109	Colleye	2011	NR	NR	NR	tank	2	*Amphiprion nigripes*	Reef	NR	49.32	NR	JTS	NR	Territorial Aggression	pulse	
109	Colleye	2011	NR	NR	NR	tank	4	*Amphiprion ocellaris*	Reef	NR	51.61	NR	JTS	NR	Territorial Aggression	pulse	
109	Colleye	2011	NR	NR	NR	tank	2	*Amphiprion percula*	Reef	NR	44.93	NR	JTS	NR	Territorial Aggression	pulse	
109	Colleye	2011	NR	NR	NR	tank	2	*Amphiprion perideraion*	Reef	NR	62.26	NR	JTS	NR	Territorial Aggression	pulse	
109	Colleye	2011	NR	NR	NR	tank	2	*Amphiprion polymnus*	Reef	NR	69.04	NR	JTS	NR	Territorial Aggression	pulse	
109	Colleye	2011	NR	NR	NR	tank	1	*Premnas biaculeatus*	Reef	NR	110	NR	JTS	NR	Territorial Aggression	pulse	
110	Lechner	2010	Africa	10 sounds per individual	NR	tank	4	*Synodontis schoutedeni*	Benthopelagic	NR	NR	NR	SSM	NR	Disturbance	stridulation	
110	Lechner	2010	Africa	10 sounds per individual	NR	tank	6	*Synodontis schoutedeni*	Benthopelagic	NR	NR	NR	SSM	NR	Disturbance	stridulation	1
110	Lechner	2010	Europe	10 sounds per individual	NR	tank	6	*Synodontis schoutedeni*	Benthopelagic	NR	NR	NR	SSM	NR	Disturbance	stridulation	2
110	Lechner	2010	Europe	10 sounds per individual	NR	tank	6	*Synodontis schoutedeni*	Benthopelagic	NR	NR	NR	SSM	NR	Disturbance	stridulation	3
110	Lechner	2010	Europe	10 sounds per individual	NR	tank	5	*Synodontis schoutedeni*	Benthopelagic	NR	NR	NR	SSM	NR	Disturbance	stridulation	
111	Colleye	2013	Europe	30 min every 2 hr	Autumn	tank	9	*Cottus perifretum*	Benthopelagic	NR	98.67(15.1;80-125)	(80-125)	PGM	NR	Territorial Aggression	pulse	
111	Colleye	2013	Europe	30 min every 2 hr	Autumn	tank	9	*Cottus rhenanus*	Benthopelagic	NR	93.76(9.1;78-105)	(78-105)	PGM	NR	Territorial Aggression	pulse	
112	Parmentier	2011	Europe	NR	Spring	tank	2	*Holocentrus rufus*	Reef	NR	NR	NR	SSM	NR	Disturbance	pulse	
112	Parmentier	2011	Africa	NR	Autumn	tank	5	*Myripristis kuntee*	Reef	NR	NR	NR	SSM	NR	Disturbance	pulse	1
112	Parmentier	2011	Oceana	NR	Spring	tank	5	*Myripristis violacea*	Reef	NR	NR	NR	SSM	NR	Disturbance	pulse	2
112	Parmentier	2011	Oceana	NR	Spring	tank	11	*Nenoniphon samara*	Reef	NR	NR	NR	SSM	NR	Disturbance	pulse	1
112	Parmentier	2011	Africa	NR	Autumn	tank	11	*Neoniphon sammara*	Reef	NR	NR	NR	SSM	NR	Disturbance	pulse	2
112	Parmentier	2011	Africa	NR	Autumn	tank	5	*Sargocentron diadema*	Reef	NR	NR	NR	SSM	NR	Disturbance	grunt	
113	Maruska	2007	Oceana	NR	Spring-Summer	in situ	30	*Abudefduf abdominalis*	Reef	NR	NR	NR	JTS	Spring-Summer	Courtship	pulse	1
113	Maruska	2007	Oceana	NR	Spring-Summer	in situ	30	*Abudefduf abdominalis*	Reef	NR	NR	NR	JTS	Spring-Summer	Courtship	pulse	2
113	Maruska	2007	Oceana	NR	Spring-Summer	in situ	30	*Abudefduf abdominalis*	Reef	Male	NR	NR	JTS	Spring-Summer	Nest Building	pulse	
113	Maruska	2007	Oceana	NR	Spring-Summer	in situ	30	*Abudefduf abdominalis*	Reef	Male	NR	NR	JTS	Spring-Summer	Territorial Aggression	pulse	1
113	Maruska	2007	Oceana	NR	Spring-Summer	in situ	30	*Abudefduf abdominalis*	Reef	Male	NR	NR	JTS	Spring-Summer	Territorial Aggression	pulse	2
114	Vasconcelos	2007	Europe	1-4 min		tank	22	*Halobatrachus didactylus*	Demersal	NR	71(19;37.5-85.7)	NR	SSM	NR	Territorial Aggression	grunt	
114	Vasconcelos	2007	Europe	1-4 min		tank	22	*Halobatrachus didactylus*	Demersal	NR	174.5(57.7;96.4-270.5)	NR	SSM	NR	Territorial Aggression	grunt	
115	Rice	2009	North America	12-15hr	Winter-Summer	tank	NR	*Batrachomoeus trispinosus*	Reef	Male	NR	NR	SSM	NR	Courtship	hoot	
115	Rice	2009	North America	12-15hr	Winter-Summer	tank	NR	*Batrachomoeus trispinosus*	Reef	Both	NR	NR	SSM	NR	Territorial Aggression	grunt	

115	Rice	2009	North America	12-15hr	Winter-Summer	tank	NR	*Batrachomoeus trispinosus*	Reef	Both	NR	NR	SSM	NR	Territorial Aggression	grunt	
116	Rubow	2009	North America	NR	Spring-Summer	in situ	5	*Porichthys notatus*	Demersal	Male	(120-200)	NR	SSM	Spring-Summer	Agonistic	grunt	
117	Longrie	2009	Europe	NR	spawning season	tank	4	*Oreochromis niloticus*	Benthopelagic	Male	150	NR	PGM	NR	Territorial Aggression	pulse	1
117	Longrie	2009	Europe	NR	spawning season	tank	4	*Oreochromis niloticus*	Benthopelagic	Male	150	NR	PGM	NR	Territorial Aggression	pulse	2
118	Parmentier	2010	Europe	NR	NR	tank	1	*Synodontis decorus*	Benthopelagic	NR	94.2(0)	NR	PSS	NR	Disturbance	abduction	1
118	Parmentier	2010	Europe	NR	NR	tank	1	*Synodontis decorus*	Benthopelagic	NR	94.2(0)	NR	PSS	NR	Disturbance	adduction	2
119	Parmentier	2010	Europe	10 min every 30 min	Autumn	in situ	NR	*Ophidion rochei*	Demersal	NR	NR	NR	SSM	Autumn	Courtship	pulse	1
119	Parmentier	2010	Europe	10 min every 30 min	Autumn	in situ	NR	*Ophidion rochei*	Demersal	NR	NR	NR	SSM	Autumn	Courtship	pulse	2
120	Boyle	2010	Oceana	NR	Summer	in situ	2	*Hemitaurichthys polylepis*	Reef	NR	NR	NR	SSM	Summer	Agonistic	pulse	
120	Boyle	2010	Oceana	NR	Summer	in situ	4	*Hemitaurichthys polylepis*	Reef	NR	NR	NR	SSM	Summer	Disturbance	pulse	
121	Parmentier	2011	Oceana	10 min	Spring	in situ	NR	*Heniochus chrysostomus*	Reef	NR	NR	NR	SSM	NR	Agonistic	pulse	
121	Parmentier	2011	Oceana	NR	Spring	tank	5	*Heniochus chrysostomus*	Reef	NR	(112-134)	NR	SSM	NR	Disturbance	pulse	
121	Parmentier	2011	Oceana	NR	Spring	tank	5	*Heniochus chrysostomus*	Reef	NR	(112-134)	NR	SSM	NR	Disturbance	pulse	
122	Millot	2011	Europe	2hr	NR	tank	30	*Pygocentrus nattereri*	Pelagic	NR	90(10)	NR	SSM	NR	Agonistic	pulse	
122	Millot	2011	Europe	2hr	NR	tank	30	*Pygocentrus nattereri*	Pelagic	NR	90(10)	NR	SSM	NR	Agonistic	bark	
122	Millot	2011	Europe	2hr	NR	tank	30	*Pygocentrus nattereri*	Pelagic	NR	90(10)	NR	SSM	NR	Feeding	pulse	
123	Boyle	2011	Oceana	NR	NR	tank	4	*Forcipiger flavissimus*	Reef	NR	NR	NR	PGM	NR	Territorial Aggression	pulse	
123	Boyle	2011	Oceana	NR	NR	tank	14	*Forcipiger longirostris*	Reef	NR	110.71(21.53; 72-148)	NR	PGM	NR	Territorial Aggression	pulse	
124	Colleye	2012	Asia	15 min	Spring-Summer	tank	18	*Amphiprion clarkii*	Reef	NR	82	NR	JTS	NR	Territorial Aggression	pulse	
124	Colleye	2012	Asia	15 min	Spring-Summer	tank	18	*Amphiprion clarkii*	Reef	NR	83	NR	JTS	NR	Territorial Aggression	pulse	
124	Colleye	2012	Asia	15 min	Spring-Summer	tank	18	*Amphiprion clarkii*	Reef	NR	83	NR	JTS	NR	Territorial Aggression	pulse	
124	Colleye	2012	Asia	15 min	Spring-Summer	tank	18	*Amphiprion clarkii*	Reef	NR	72	NR	JTS	NR	Territorial Aggression	pulse	
124	Colleye	2012	Asia	15 min	Spring-Summer	tank	18	*Amphiprion clarkii*	Reef	NR	95	NR	JTS	NR	Territorial Aggression	pulse	
124	Colleye	2012	Asia	15 min	Spring-Summer	tank	18	*Amphiprion clarkii*	Reef	NR	87	NR	JTS	NR	Territorial Aggression	pulse	
124	Colleye	2012	Asia	15 min	Spring-Summer	tank	18	*Amphiprion clarkii*	Reef	NR	76	NR	JTS	NR	Territorial Aggression	pulse	
124	Colleye	2012	Asia	15 min	Spring-Summer	tank	18	*Amphiprion clarkii*	Reef	NR	55	NR	JTS	NR	Territorial Aggression	pulse	
124	Colleye	2012	Asia	15 min	Spring-Summer	tank	18	*Amphiprion clarkii*	Reef	NR	94	NR	JTS	NR	Territorial Aggression	pulse	
124	Colleye	2012	Asia	15 min	Spring-Summer	tank	18	*Amphiprion clarkii*	Reef	NR	85	NR	JTS	NR	Territorial Aggression	pulse	

124	Colleye	2012	Asia	15 min	Spring-Summer	tank	18	*Amphiprion clarkii*	Reef	NR	108	NR	JTS	NR	Territorial Aggression	pulse	
124	Colleye	2012	Asia	15 min	Spring-Summer	tank	18	*Amphiprion clarkii*	Reef	NR	97	NR	JTS	NR	Territorial Aggression	pulse	
124	Colleye	2012	Asia	15 min	Spring-Summer	tank	18	*Amphiprion clarkii*	Reef	NR	75	NR	JTS	NR	Territorial Aggression	pulse	
124	Colleye	2012	Asia	15 min	Spring-Summer	tank	18	*Amphiprion clarkii*	Reef	NR	85	NR	JTS	NR	Territorial Aggression	pulse	
124	Colleye	2012	Asia	15 min	Spring-Summer	tank	18	*Amphiprion clarkii*	Reef	NR	90	NR	JTS	NR	Territorial Aggression	pulse	
124	Colleye	2012	Asia	15 min	Spring-Summer	tank	18	*Amphiprion clarkii*	Reef	NR	90	NR	JTS	NR	Territorial Aggression	pulse	
124	Colleye	2012	Asia	15 min	Spring-Summer	tank	18	*Amphiprion clarkii*	Reef	NR	81	NR	JTS	NR	Territorial Aggression	pulse	
124	Colleye	2012	Asia	15 min	Spring-Summer	tank	18	*Amphiprion clarkii*	Reef	NR	76	NR	JTS	NR	Territorial Aggression	pulse	
125	Parmentier	2013	Europe	NR	Autumn-Winter	tank	15	*Gobius paganellus*	Demersal	NR	NR	(58-150)	PGM	NR	Territorial Aggression	pulse	
125	Parmentier	2013	Europe	NR	Winter-Spring	tank	18	*Gobius paganellus*	Demersal	NR	NR	(56-105)	PGM	NR	Territorial Aggression	pulse	
126	Mensinger	2014	North America	NR	Spring-Summer	concrete tank	1	*Opsanus tau*	Reef	Male	NR	NR	SSM	Spring-Summer	Courtship	boatwhistle	1
126	Mensinger	2014	North America	NR	Spring-Summer	concrete tank	1	*Opsanus tau*	Reef	Male	NR	NR	SSM	Spring-Summer	Courtship	boatwhistle	2
126	Mensinger	2014	North America	NR	Spring-Summer	concrete tank	1	*Opsanus tau*	Reef	Male	NR	NR	SSM	Spring-Summer	Courtship	boatwhistle	3
126	Mensinger	2014	North America	NR	Spring-Summer	concrete tank	1	*Opsanus tau*	Reef	Male	NR	NR	SSM	Spring-Summer	Courtship	boatwhistle	4
126	Mensinger	2014	North America	NR	Spring-Summer	concrete tank	1	*Opsanus tau*	Reef	Male	NR	NR	SSM	Spring-Summer	Courtship	boatwhistle	5
127	McIver	2014	North America	NR	Summer	in situ	NR	*Porichthys notatus*	Demersal	Male	NR	NR	SSM	Summer	Agonistic	growl	
127	McIver	2014	North America	NR	Summer	in situ	3	*Porichthys notatus*	Demersal	Male	NR	NR	SSM	Summer	Agonistic	grunt	
127	McIver	2014	North America	NR	Summer	in situ	9	*Porichthys notatus*	Demersal	Male	NR	NR	SSM	Summer	Courtship	hum	
128	Bertucci	2014	Europe	NR	NR	tank	9	*Haemulon flavolineatum*	Reef	NR	NR	105.78(24.16; 75-140)	JTS	NR	Disturbance	grunt	
128	Bertucci	2014	Europe	NR	NR	tank	3	*Haemulon flavolineatum*	Reef	NR	NR	NR	JTS	NR	Feeding	grunt	
129	Knight	2012	Europe	1 min	NR	tank	7	*Agamyxis pectinifrons*	Demersal	Both	(59-66)	NR	PSS	NR	Disturbance	adduction	
129	Knight	2012	Europe	1 min	NR	tank	7	*Agamyxis pectinifrons*	Demersal	Both	(59-66)	NR	PSS	NR	Disturbance	abduction	
129	Knight	2012	Europe	1 min	NR	tank	7	*Agamyxis pectinifrons*	Demersal	Both	(59-66)	NR	SSM	NR	Disturbance	drum	
129	Knight	2012	Europe	1 min	NR	tank	5	*Amblydoras affinis*	Demersal	Both	(65-75)	NR	PSS	NR	Disturbance	adduction	
129	Knight	2012	Europe	1 min	NR	tank	5	*Amblydoras affinis*	Demersal	Both	(65-75)	NR	PSS	NR	Disturbance	abduction	
129	Knight	2012	Europe	1 min	NR	tank	5	*Amblydoras affinis*	Demersal	Both	(65-75)	NR	SSM	NR	Disturbance	drum	
129	Knight	2012	Europe	1 min	NR	tank	12	*Hemidoras morrisi*	Demersal	Both	(84-138)	NR	PSS	NR	Disturbance	adduction	
129	Knight	2012	Europe	1 min	NR	tank	12	*Hemidoras morrisi*	Demersal	Both	(84-138)	NR	PSS	NR	Disturbance	abduction	

129	Knight	2012	Europe	1 min	NR	tank	12	*Hemidoras morrisi*	Demersal	Both	(84-138)	NR	SSM	NR	Disturbance	drum	
129	Knight	2012	Europe	1 min	NR	tank	10	*Megalodoras uranoscopus*	Demersal	Both	(118-160)	NR	PSS	NR	Disturbance	adduction	
129	Knight	2012	Europe	1 min	NR	tank	10	*Megalodoras uranoscpous*	Demersal	Both	(118-160)	NR	PSS	NR	Disturbance	abduction	
129	Knight	2012	Europe	1 min	NR	tank	10	*Megalodoras uranoscpous*	Demersal	Both	(118-160)	NR	SSM	NR	Disturbance	drum	
129	Knight	2012	Europe	1 min	NR	tank	3	*Oxydoras niger*	Demersal	Both	(217-237)	NR	PSS	NR	Disturbance	adduction	
129	Knight	2012	Europe	1 min	NR	tank	3	*Oxydoras niger*	Demersal	Both	(217-237)	NR	PSS	NR	Disturbance	abduction	
129	Knight	2012	Europe	1 min	NR	tank	3	*Oxydoras niger*	Demersal	Both	(217-237)	NR	SSM	NR	Disturbance	drum	
130	Ghahramani	2014	North America	8 sounds		in situ	10	*Ictalurus furcatus*	Demersal	NR	NR	(160-325)	PSS	NR	Disturbance	Sweep	
131	Tricas	2015	Oceana	15-30 min	NR	tank	5	*Chaetodon auriga*	Reef	NR	111(7)	NR	JTS	NR	Territorial Aggression	pulse	
131	Tricas	2015	Oceana	15-30 min	NR	tank	3	*Chaetodon kleinii*	Reef	NR	78(4.6)	NR	JTS	NR	Territorial Aggression	pulse	
131	Tricas	2015	Oceana	15-30 min	NR	tank	7	*Chaetodon multicinctus*	Reef	Both	71.2(14.2)	NR	FM	NR	Territorial Aggression	pulse	
131	Tricas	2015	Oceana	15-30 min	NR	tank	9	*Chaetodon multicinctus*	Reef	Both	71.2(14.2)	NR	Unknown	NR	Territorial Aggression	pulse	
131	Tricas	2015	Oceana	15-30 min	NR	tank	1	*Chaetodon ornatissimus*	Reef	Both	78.7(5.9)	NR	FM	NR	Territorial Aggression	pulse	
131	Tricas	2015	Oceana	15-30 min	NR	tank	1	*Chaetodon ornatissimus*	Reef	Both	78.7(5.9)	NR	FM	NR	Territorial Aggression	pulse	
131	Tricas	2015	Oceana	15-30 min	NR	tank	3	*Chaetodon unimaculatus*	Reef	NR	122(29.2)	NR	PGM	NR	Territorial Aggression	pulse	
131	Tricas	2015	Oceana	15-30 min	NR	tank	2	*Forcipiger flavissimus*	Reef	NR	99.7(12.1)	NR	FM	NR	Territorial Aggression	pulse	
131	Tricas	2015	Oceana	15-30 min	NR	tank	3	*Forcipiger flavissimus*	Reef	NR	99.7(12.1)	NR	Unknown	NR	Territorial Aggression	pulse	
132	Boyle	2015	Europe	NR	NR	tank	3	*Acanthodoras cataphractus*	Demersal	NR	88(7.2)	NR	SSM	NR	Disturbance	drum	1
132	Boyle	2015	Europe	NR	NR	tank	3	*Acanthodoras cataphractus*	Demersal	NR	88(7.2)	NR	SSM	NR	Disturbance	drum	2
132	Boyle	2015	Europe	NR	NR	tank	3	*Agamyxis pectinifrons*	Demersal	NR	99(6)	NR	SSM	NR	Disturbance	drum	1
132	Boyle	2015	Europe	NR	NR	tank	3	*Agamyxis pectinifrons*	Demersal	NR	99(6)	NR	SSM	NR	Disturbance	drum	2
132	Boyle	2015	Europe	NR	NR	tank	7	*Platydoras hancockii*	Demersal	NR	56(3.1)	NR	SSM	NR	Disturbance	drum	1
132	Boyle	2015	Europe	NR	NR	tank	7	*Platydoras hancockii*	Demersal	NR	56(3.1)	NR	SSM	NR	Disturbance	drum	2
133	Parmentier	2017	Oceana	NR	Spring	tank	11	*Rhinecanthus aculeatus*	Reef	NR	NR	(159-206)	FM	NR	Disturbance	pulse	
134	Parmentier	2017	Europe	NR	Winter-Spring	tank	17	*Pomatoschistus pictus*	Demersal	Male	NR	42.8(2.5)	PGM	NR	Courtship	drum	
135	Amorim	2018	Europe	20 min	Spring	tank	3	*Pomatoschistus marmoratus*	Demersal	Male	37(33-40)	NR	PGM	Spring	Courtship	drum	
136	Liesch	2020	Europe	NR	NR	tank	13	*Trichopsis pumila*	Benthopelagic	Female	NR	NR	FM	NR	Territorial Aggression	croak	
136	Liesch	2020	Europe	NR	NR	tank	12	*Trichopsis pumila*	Benthopelagic	Male	NR	NR	FM	NR	Territorial Aggression	croak	

137	Longrie	2013	Europe	3 10 min	NR	tank	5	*Oreochromis niloticus*	Benthopelagic	Female	121(10)	NR	PGM	NR	Oral incubation	pulse	
137	Longrie	2013	Europe	3 10 min	NR	tank	5	*Oreochromis niloticus*	Benthopelagic	Female	121(10)	NR	PGM	NR	Territorial Aggression	pulse	
138	Papes	2011	Europe	NR	NR	tank	8	*Platydoras armatulus*	Demersal	NR	(108.6-121.1)	(126.2-142.5)	PSS	NR	Disturbance	abduction	1
138	Papes	2011	Europe	NR	NR	tank	8	*Platydoras armatulus*	Demersal	NR	(108.6-121.1)	(126.2-142.5)	PSS	NR	Disturbance	abduction	2
138	Papes	2011	Europe	NR	NR	tank	8	*Platydoras armatulus*	Demersal	NR	(108.6-121.1)	(126.2-142.5)	PSS	NR	Disturbance	abduction	3
138	Papes	2011	Europe	NR	NR	tank	8	*Platydoras armatulus*	Demersal	NR	(108.6-121.1)	(126.2-142.5)	PSS	NR	Disturbance	adduction	1
138	Papes	2011	Europe	NR	NR	tank	8	*Platydoras armatulus*	Demersal	NR	(108.6-121.1)	(126.2-142.5)	PSS	NR	Disturbance	adduction	2
138	Papes	2011	Europe	NR	NR	tank	8	*Platydoras armatulus*	Demersal	NR	(108.6-121.1)	(126.2-142.5)	PSS	NR	Disturbance	adduction	3
138	Papes	2011	Europe	NR	NR	tank	8	*Platydoras armatulus*	Demersal	NR	(108.6-121.1)	(126.2-142.5)	PSS	NR	Disturbance	drum	1
138	Papes	2011	Europe	NR	NR	tank	8	*Platydoras armatulus*	Demersal	NR	(108.6-121.1)	(126.2-142.5)	PSS	NR	Disturbance	drum	2
138	Papes	2011	Europe	NR	NR	tank	8	*Platydoras armatulus*	Demersal	NR	(108.6-121.1)	(126.2-142.5)	PSS	NR	Disturbance	drum	3
139	Maruska	2012	North America	20-30 min	NR	tank	22	*Astatotilapia burtoni*	Benthopelagic	Males	(47-87)	NR	JTS	NR	Courtship	pulse	
140	Colleye	2012	Asia	20 x 40 min	Spring-Summer	tank	9	*Amphiprion frenatus*	Reef	NR	76.42(22.1;44-112)	NR	JTS	summer	Territorial Aggression	pulse	
141	Pedroso	2013	Europe	20 min	Spring-Summer	tank	21	*Pomatoschistus minutus*	Demersal	Male	44(3.2;39-49)	NR	PGM	Spring-summer	Courtship	drum	
141	Pedroso	2013	Europe	20 min	Spring-Summer	tank	16	*Pomatoschistus pictus*	Demersal	Male	40(2.8;36-45)	NR	PGM	Spring-summer	Courtship	drum	
142	Borie	2014	South America	30-120 min	Autumn-Winter	in situ	NR	*Plagioscion squamosissimus*	Benthopelagic	Male	NR	NR	SSM	Autumn-Winter	Courtship	pulse	
142	Borie	2014	South America	15-60 min	Autumn-Winter	in situ	NR	*Plagioscion squamosissimus*	Benthopelagic	Male	(200-340)	NR	SSM	Autumn-Winter	Courtship	pulse	
143	Radford	2018	Oceana	NR	Winter-Spring	in situ	NR	*Zeus faber*	Benthopelagic	NR	NR	NR	SSM	NR	Territorial Aggression	pulse	
143	Radford	2018	Oceana	NR	Winter	tank	10	*Zeus faber*	Benthopelagic	NR	300-500	NR	SSM	NR	Disturbance	pulse	
144	Fine	2008	North America	NR	Spring	in situ	1	*Opsanus tau*	Reef	Male	NR	NR	SSM	Summer	Courtship	boatwhistle	1
144	Fine	2008	North America	NR	Spring	in situ	1	*Opsanus tau*	Reef	Male	NR	NR	SSM	Summer	Courtship	boatwhistle	2
145	Tellechea	2011	South America	NR	Spring	tank	30	*Iheringichthys labrosus*	Demersal	Both	NR	(50-550)	PSS	Winter-Spring	Disturbance	abduction	
145	Tellechea	2011	South America	NR	Spring	tank	30	*Iheringichthys labrosus*	Demersal	Both	NR	(50-550)	SSM	Winter-Spring	Disturbance	drum	
146	Rigley	1973	NR	NR	NR	tank	NR	*Gnathonemus petersi*	Demersal	NR	NR	(110-177)	Unknown	NR	Agonistic	click	
147	Perkins	2001	North America	NR	Spring-summer	in situ	NR	*Cynoscion regalis*	Demersal	Male	NR	NR	SSM	Spring-summer	Courtship	drum	
148	Scharer	2012	Central America	20 s every 5 min	Spring-Summer	in situ	NR	*Mycteroperca venenosa*	Reef	Male	NR	NR	Unknown	Spring	Courtship	pulse	
148	Scharer	2012	Central America	20 s every 5 min	Spring-Summer	in situ	NR	*Mycteroperca venenosa*	Reef	Male	NR	NR	Unknown	Spring	Courtship	tonal	
149	Mann	2010	Central America	20 s every 5 min	Winter-Spring	in situ	NR	*Epinephelus guttatus*	Reef	Male	NR	NR	Unknown	Winter-Spring	Territorial Aggression	pulse	

149	Mann	2010	Central America	20 s every 5 min	Winter-Spring	in situ	NR	*Epinephelus guttatus*	Reef	Male	NR	NR	Unknown	Winter-Spring	Territorial Aggression	pulse	
150	Nelson	2011	North America	24 hr	Spring	in situ	10	*Epinephelus morio*	Reef	Male	NR	NR	SSM	Spring	Courtship	growl	1
150	Nelson	2011	North America	24 hr	Spring	in situ	10	*Epinephelus morio*	Reef	Male	NR	NR	SSM	Spring	Courtship	growl	2
150	Nelson	2011	North America	24 hr	Spring	in situ	10	*Epinephelus morio*	Reef	Male	NR	NR	SSM	Spring	Courtship	pulse	1
150	Nelson	2011	North America	24 hr	Spring	in situ	10	*Epinephelus morio*	Reef	Male	NR	NR	SSM	Spring	Courtship	pulse	2
150	Nelson	2011	North America	24 hr	Spring	in situ	10	*Epinephelus morio*	Reef	Male	NR	NR	SSM	Spring	Courtship	pulse	3
151	Scharer	2012	Central America	15 min	Winter	in situ	12	*Epinephelus striatus*	Reef	NR	NR	NR	SSM	Winter-Spring	Courtship	tonal	
151	Scharer	2012	Central America	continuous	Winter	in situ	NR	*Epinephelus striatus*	Reef	NR	NR	NR	SSM	Winter	Disturbance	pulse	
152	Vieira	2019	Europe	24 hr	Spring	concrete tank	10	*Argyrosomus regius*	Benthopelagic	Male	NR	870(690-1020)	SSM	Spring-Summer	Courtship	grunt	1
152	Vieira	2019	Europe	24 hr	Spring	concrete tank	10	*Argyrosomus regius*	Benthopelagic	Male	NR	870(690-1020)	SSM	Spring-Summer	Courtship	grunt	2
153	Lim	2015	Asia	NR	NR	tank	3	*Doryichthys deokhatoides*	Benthopelagic	NR	NR	109(85)	CBS	NR	Feeding	click	
153	Lim	2015	Asia	NR	NR	tank	3	*Doryichthys deokhatoides*	Benthopelagic	NR	NR	109(85)	CBS	NR	Feeding	click	
153	Lim	2015	Asia	NR	NR	tank	4	*Doryichthys martensii*	Benthopelagic	NR	NR	125(20)	CBS	NR	Feeding	click	
153	Lim	2015	Asia	NR	NR	tank	6	*Syngnathoides biaculeatus*	Reef	NR	NR	194(10)	CBS	NR	Feeding	click	
154	Pereira	2020	Europe	5 day	Spring-Summer	in situ	NR	*Argyrosomus regius*	Benthopelagic	NR	NR	NR	SSM	Spring-Summer	Courtship	pulse	
154	Pereira	2020	Europe	2 hr	Summer	tank	10	*Argyrosomus regius*	Benthopelagic	NR	NR	87(69-102)	SSM	Spring-Summer	Courtship	pulse	
154	Pereira	2020	Europe	3 min	Summer	tank	4	*Argyrosomus regius*	Benthopelagic	Female	NR	NR	SSM	Spring-Summer	Disturbance	pulse	
154	Pereira	2020	Europe	3 min	Summer	tank	6	*Argyrosomus regius*	Benthopelagic	Male	NR	NR	SSM	Spring-Summer	Disturbance	pulse	
155	Parsons	2006	Oceana	5-8 min	Winter	in situ	NR	*Argyrosomus japonicus*	Benthopelagic	Male	NR	NR	SSM	Winter-Spring	Spawning	baarp	
155	Parsons	2006	Oceana	5-8 min	Winter	in situ	NR	*Argyrosomus japonicus*	Benthopelagic	Male	NR	NR	SSM	Winter-Spring	Spawning	ba-barp	
155	Parsons	2006	Oceana	5-8 min	Winter	in situ	NR	*Argyrosomus japonicus*	Benthopelagic	Male	NR	NR	SSM	Winter-Spring	Spawning	bup	1
155	Parsons	2006	Oceana	5-8 min	Winter	in situ	NR	*Argyrosomus japonicus*	Benthopelagic	Male	NR	NR	SSM	Winter-Spring	Spawning	bup	2
156	Johnston	2000	North America	30-60 min	Spring	tank	11	*Etheostoma crossopterum*	Benthopelagic	Male	75.8(5.8;66-82)	NR	Unknown	Spring	Alone in nest	drum	
156	Johnston	2000	North America	30-60 min	Spring	tank	11	*Etheostoma crossopterum*	Benthopelagic	Male	75.8(5.8;66-82)	NR	Unknown	Spring	Alone in nest	knock	
156	Johnston	2000	North America	30-60 min	Spring	tank	11	*Etheostoma crossopterum*	Benthopelagic	Male	75.8(5.8;66-82)	NR	Unknown	Spring	Courtship	drum	
156	Johnston	2000	North America	30-60 min	Spring	tank	11	*Etheostoma crossopterum*	Benthopelagic	Male	75.8(5.8;66-82)	NR	Unknown	Spring	Courtship	knock	
156	Johnston	2000	North America	30-60 min	Spring	tank	11	*Etheostoma crossopterum*	Benthopelagic	Male	75.8(5.8;66-82)	NR	Unknown	Spring	Territorial Aggression	drum	
156	Johnston	2000	North America	30-60 min	Spring	tank	11	*Etheostoma crossopterum*	Benthopelagic	Male	75.8(5.8;66-82)	NR	Unknown	Spring	Territorial Aggression	knock	

156	Johnston	2000	North America	30-60 min	Spring	tank	11	*Etheostoma nigripinne*	Benthopelagic	Male	56.1(3.8;50-60.7)	NR	Unknown	Spring	Courtship	drum	
156	Johnston	2000	North America	30-60 min	Spring	tank	11	*Etheostoma nigripinne*	Benthopelagic	Male	56.1(3.8;50-60.7)	NR	Unknown	Spring	Territorial Aggression	drum	
157	Johnston	2000	North America	30-60 min	Spring	tank	8	*Pimephales notatus*	Demersal	Male	NR	NR	Unknown	NR	Territorial Aggression	pulse	1
157	Johnston	2000	North America	30-60 min	Spring	tank	8	*Pimephales notatus*	Demersal	Male	NR	NR	Unknown	NR	Territorial Aggression	pulse	2
158	Gerald	1971	North America	NR	NR	in situ	NR	*Lepomis cyanellus*	Benthopelagic	Male	NR	NR	Unknown	NR	Courtship	grunt	
158	Gerald	1971	North America	NR	NR	in situ	NR	*Lepomis humilis*	Benthopelagic	Male	NR	NR	Unknown	NR	Courtship	grunt	
158	Gerald	1971	North America	NR	NR	in situ	NR	*Lepomis macrochirus*	Benthopelagic	Male	NR	NR	Unknown	NR	Courtship	grunt	
158	Gerald	1971	North America	NR	NR	in situ	NR	*Lepomis megalotis*	Benthopelagic	Male	NR	NR	Unknown	NR	Courtship	grunt	
158	Gerald	1971	North America	NR	NR	in situ	NR	*Lepomis microlophus*	Demersal	Male	NR	NR	JTS	NR	Courtship	grunt	
158	Gerald	1971	North America	NR	NR	in situ	NR	*Lepomis punctatus*	Demersal	Male	NR	NR	Unknown	NR	Courtship	grunt	
159	Tavolga	1958	North America	NR	Summer	tank	NR	*Bathygobius soporator*	Demersal	Male	NR	NR	FM	Summer	Courtship	grunt	
160	Rowland	1978	North America	NR	NR	tank	11	*Hemichromis bimaculatus*	Benthopelagic	Both	NR	NR	SSM	NR	Territorial Aggression	purr	
160	Rowland	1978	North America	NR	NR	tank	11	*Hemichromis bimaculatus*	Benthopelagic	Both	NR	NR	SSM	NR	Territorial Aggression	thump	
161	Nelissen	1978	NR	NR	NR	tank	12	*Tropheus brichardi*	Demersal	NR	NR	NR	Unknown	NR	Territorial Aggression	rattle	
161	Nelissen	1978	NR	NR	NR	tank	18	*Tropheus duboisi*	Demersal	NR	NR	NR	Unknown	NR	Territorial Aggression	rattle	
162	Crawford	1997	Africa	6 hr every 12 hr	Summer	in situ	NR	*Pollimyrus isidori*	Demersal	Male	NR	NR	SSM	Summer	Courtship	moan	
162	Crawford	1997	Africa	5 min	Summer	tank	5	*Pollimyrus isidori*	Demersal	Male	56.2(0.4)	NR	SSM	Summer	Courtship	moan	
163	Lamml	2006	Africa		Summer	tank	4	*Pollimyrus marianne*	Benthopelagic	Male	60(3.8)	NR	SSM	Summer	Courtship	moan	
163	Lamml	2006	Africa		Summer	tank	1	*Pollimyrus marianne*	Benthopelagic	Male	52	NR	SSM	Summer	Courtship	grunt	
163	Lamml	2006	Africa		Summer	tank	4	*Pollimyrus marianne*	Benthopelagic	Male	60(3.8)	NR	SSM	Summer	Courtship	moan	
163	Lamml	2006	Africa		Spring	tank	10	*Pollimyrus castelnaui*	Demersal	Male	59(2.9)	NR	SSM	Summer	Courtship	moan	
163	Lamml	2006	Africa		Spring	tank	9	*Pollimyrus castelnaui*	Demersal	Male	59(2.9)	NR	SSM	Summer	Courtship	grunt	
164	Tellechea	2012	South America	4-6 hr	Winter-Spring	in situ	29	*Cynoscion guatucupa*	Benthopelagic	Male	NR	NR	SSM	Winter-spring	Courtship	drum	
164	Tellechea	2012	South America	2 hr	Winter	tank	31	*Cynoscion guatucupa*	Benthopelagic	Male	23.55(6.67;14-36)	NR	SSM	Winter-spring	Courtship	drum	
164	Tellechea	2012	South America	2 hr	Winter	tank	38	*Cynoscion guatucupa*	Benthopelagic	Male	24.84(6.85;14-36)	NR	SSM	Winter-spring	Disturbance	drum	
165	Ueng	2007	Asia	24 hr	Spring	concrete tank	40	*Argyrosomus japonicus*	Benthopelagic	Female	NR	919	SSM	Spring	Courtship	drum	
165	Ueng	2007	Asia	24 hr	Spring	concrete tank	46	*Argyrosomus japonicus*	Benthopelagic	Male	NR	922	SSM	Spring	Courtship	drum	
166	Mok	1983	North America	3.5 hr	Winter-Summer	in situ	NR	*Bairdiella chrysoura*	Demersal	NR	NR	NR	Unknown	Spring-summer	Spawning	knock	

166	Mok	1983	North America	3.5 hr	Winter-Summer	in situ	NR	*Cynoscion nebulosus*	Demersal	Male	NR	NR	Unknown	Spring-Autumn	Spawning	grunt	
166	Mok	1983	North America	3.5 hr	Winter-Summer	in situ	NR	*Cynoscion nebulosus*	Demersal	Male	NR	NR	Unknown	Spring-Autumn	Spawning	knock	
167	Lobel	1996	Oceana	NR	Spring	in situ	NR	*Ostracion meleagris*	Reef	Male	NR	NR	Unknown	Spring	Agonistic	bump	
168	Lobel	1995	Oceana	NR	Spring	in situ	25	*Dascyllus albisella*	Reef	Male	NR	NR	Unknown	NR	Courtship	pulse	
168	Lobel	1995	Oceana	NR	Spring	in situ	25	*Dascyllus albisella*	Reef	Male	NR	NR	Unknown	NR	Spawning	pulse	
169	Salmon	1968	Oceana	NR	Autumn-Winter	concrete tank	NR	*Balistes vetula*	Reef	NR	NR	NR	PGM	NR	Disturbance	pulse	1
169	Salmon	1968	Oceana	NR	Autumn-Winter	concrete tank	NR	*Balistes vetula*	Reef	NR	NR	NR	PGM	NR	Disturbance	pulse	2
169	Salmon	1968	Oceana	NR	Autumn-Winter	concrete tank	NR	*Melichthys piceus*	Reef	NR	NR	NR	PGM	NR	Disturbance	pulse	1
169	Salmon	1968	Oceana	NR	Autumn-Winter	concrete tank	NR	*Melichthys piceus*	Reef	NR	NR	NR	PGM	NR	Disturbance	pulse	2
169	Salmon	1968	Oceana	NR	Autumn-Winter	tank	NR	*Rhinecanthus rectangulus*	Reef	NR	NR	NR	PGM	NR	Disturbance	pulse	1
169	Salmon	1968	Oceana	NR	Autumn-Winter	tank	NR	*Rhinecanthus rectangulus*	Reef	NR	NR	NR	PGM	NR	Disturbance	pulse	2
170	Torricelli	1986	Europe	NR	Summer	tank	5	*Padogobius martensii*	Demersal	Male	NR	NR	PGM	Spring-summer	Agonistic	pulse	
170	Torricelli	1986	Europe	NR	Summer	tank	5	*Padogobius martensii*	Demersal	Male	NR	NR	PGM	Spring-summer	Courtship	pulse	
171	Torricelli	1990	Europe	NR	Spring	tank	20	*Padogobius martensii*	Demersal	Male	NR	74.5(12.5;55-93)	PGM	Spring-summer	Courtship	pulse	
171	Torricelli	1990	Europe	NR	Autumn-Spring	tank	30	*Padogobius martensii*	Demersal	Male	NR	72.9(6.6;55-86)	PGM	Spring-summer	Territorial Aggression	pulse	
172	Stout	1975	North America	10 sounds per individual	Spring	tank	8	*Notropis analostanus*	Benthopelagic	Male	NR	NR	Unknown	Spring-summer	Courtship	knock	
172	Stout	1975	North America	10 sounds per individual	Spring	tank	8	*Notropis analostanus*	Benthopelagic	Male	NR	NR	Unknown	Spring-summer	Courtship	purr	
172	Stout	1975	North America	10 sounds per individual	Spring	tank	3	*Notropis analostanus*	Benthopelagic	NR	NR	NR	Unknown	Spring-summer	Territorial Aggression	knock	1
172	Stout	1975	North America	10 sounds per individual	Spring	tank	3	*Notropis analostanus*	Benthopelagic	Male	NR	NR	Unknown	Spring-summer	Territorial Aggression	knock	2
172	Stout	1975	North America	10 sounds per individual	Spring	tank	4	*Notropis analostanus*	Benthopelagic	Male	NR	NR	Unknown	Spring-summer	Territorial Aggression	knock	
173	Hawkins	1978	Europe	NR	NR	tank	NR	*Gadus morhua*	Benthopelagic	Both	NR	NR	SSM	Spring	Agonistic	grunt	
173	Hawkins	1978	Europe	NR	NR	in situ	1	*Melanogrammus aeglefinus*	Demersal	Male	NR	NR	SSM	Winter-spring	Agonistic	grunt	
174	Hazlett	1962	North America	NR	Summer	concrete tank	43	*Epinephelus striatus*	Reef	NR	NR	(330-580)	SSM	Winter-Spring	Disturbance	grunt	
175	Ladich	1989	Europe	30 min every 2 hr	Spring-Summer	tank	12	*Cottus gobio*	Demersal	Both	(90-135)	NR	CBS	NR	Agonistic	knock	
176	Lagardere	2005	Oceana	NR	Summer	tank	15	*Carapus boraborensis*	Demersal	Both	(160-300)	NR	SSM	NR	Agonistic	knock	1
176	Lagardere	2005	Oceana	NR	Summer	tank	15	*Carapus boraborensis*	Demersal	Both	(160-300)	NR	SSM	NR	Agonistic	knock	2
176	Lagardere	2005	Oceana	20 seconds	Summer	tank	12	*Carapus homei*	Reef	Both	(90-160)	NR	SSM	NR	Agonistic	knock	1
176	Lagardere	2005	Oceana	20 seconds	Summer	tank	12	*Carapus homei*	Reef	Both	(90-160)	NR	SSM	NR	Agonistic	knock	2

177	Brown	1978	North America	15 min	NR	tank	NR	*Herotilapia multispinosa*	Benthopelagic	Male	NR	(75-95)	SSM	NR	Courtship	growl	
177	Brown	1978	North America	15 min	NR	tank	NR	*Herotilapia multispinosa*	Benthopelagic	Both	NR	(75-95)	SSM	NR	Territorial Aggression	volley	
178	Myrberg	1972	North America	NR	NR	in situ	9	*Eupomacentrus partitus*	Reef	Both	NR	(40-80)	SSM	Spring-summer	Agonistic	pop	
178	Myrberg	1972	North America	NR	Spring-summer	in situ	3	*Eupomacentrus partitus*	Reef	Male	NR	(65-80)	SSM	Spring-summer	Courtship	grunt	
178	Myrberg	1972	North America	NR	NR	in situ	9	*Eupomacentrus partitus*	Reef	Both	NR	(40-80)	JTS	Spring-summer	Feeding	stridulation	
178	Myrberg	1972	North America	NR	NR	in situ	3	*Eupomacentrus partitus*	Reef	Male	NR	(65-80)	SSM	Spring-summer	Territorial Aggression	Chirp	
178	Myrberg	1972	North America	NR	NR	tank	8	*Eupomacentrus partitus*	Reef	Both	NR	(40-80)	SSM	Spring-summer	Agonistic	pop	
178	Myrberg	1972	North America	NR	Spring-summer	tank	3	*Eupomacentrus partitus*	Reef	Male	NR	(70-80)	SSM	Spring-summer	Courtship	grunt	
178	Myrberg	1972	North America	NR	NR	tank	8	*Eupomacentrus partitus*	Reef	Both	NR	(40-80)	JTS	Spring-summer	Feeding	stridulation	
178	Myrberg	1972	North America	NR	NR	tank	3	*Eupomacentrus partitus*	Reef	Male	NR	(70-80)	SSM	Spring-summer	Territorial Aggression	Chirp	
179	Luczkovich	1999	North America	every 15-60 min	Spring	in situ		*Bairdiella chrysoura*	Demersal	Male	NR	NR	Unknown	Spring	Spawning	cluck	
179	Luczkovich	1999	North America	every 15-60 min	Spring	in situ		*Cynoscion regalis*	Demersal	Male	NR	NR	SSM	Spring	Spawning	purr	
180	Mann	1998	Oceana	NR	Spring	in situ	NR	*Dascyllus albisella*	Reef	Both	NR	NR	Unknown	Spring	Agonistic	pop	
180	Mann	1998	Oceana	NR	Spring	in situ	NR	*Dascyllus albisella*	Reef	Both	NR	NR	Unknown	Spring	Agonistic	Chirp	
180	Mann	1998	Oceana	NR	Spring	in situ	NR	*Dascyllus albisella*	Reef	Male	NR	NR	Unknown	Spring	Courtship	pulse	1
180	Mann	1998	Oceana	NR	Spring	in situ	NR	*Dascyllus albisella*	Reef	Male	NR	NR	Unknown	Spring	Courtship	pulse	2
181	Parmentier	2006	Africa	NR	Summer	tank	32	*Carapus mourlani*	Reef	NR	NR	(60-100)	SSM	NR	Territorial Aggression	pulse	1
181	Parmentier	2006	Africa	NR	Summer	tank	32	*Carapus mourlani*	Reef	NR	NR	(60-100)	SSM	NR	Territorial Aggression	pulse	2

Appendix E Meta-analysis Data

Data used for the meta-analysis of fish sounds to inform acoustic deterrence considering: lead author; year of publication; paper number; Latin name (species); zone of habitation (retrieved from fishbase); sonic mechanism (CBS – cranial bone stridulation; FM – fin movement; JTS – jaw/teeth stridulation; PGM – pectoral girdle muscle; PSS – pectoral spine stridulation; SSM – Sonic swimbladder mechanism); behavioural context; N (number of replicates); pulse period standard deviation (PP SD); PP with the sample size standard deviation correction (PP sdnew); pulse duration standard deviation (PD SD); PD with the sample size standard deviation correction (PD sdnew); pulses per sound standard deviation (PPS SD); PPS with the sample size standard deviation correction (PPS sdnew); sound duration standard deviation (SD SD); sound duration with the sample size standard deviation correction (SD sdnew). NA – Not applicable.

Lead Author	Year	Paper Number	Latin name	Zone of habitation	Sonic mechanism	Behaviour	N	PP SD	PP sdnew	PD	PD SD	PD sdnew	PPS	PPS SD	PPS sdnew	SD	SD SD	SD sdnew
Fish	1972	1	*Cynoscion xanthulu*	Benthopelagic	SSM	Courtship	1	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Stout	1975	2	*Notropis analostanus*	Benthopelagic	Unknown	Courtship	8	NA	NA	NA	NA	NA	NA	NA	NA	19.30	3.30	1636.69
Stout	1975	2	*Notropis analostanus*	Benthopelagic	Unknown	Courtship	8	NA	NA	NA	NA	NA	NA	NA	NA	49.10	17.80	1636.69
Stout	1975	2	*Notropis analostanus*	Benthopelagic	Unknown	Territorial Aggression	3	NA	NA	NA	NA	NA	NA	NA	NA	47.80	16.20	1636.69
Stout	1975	2	*Notropis analostanus*	Benthopelagic	Unknown	Territorial Aggression	4	NA	NA	NA	NA	NA	NA	NA	NA	47.00	10.30	1636.69
Stout	1975	2	*Notropis analostanus*	Benthopelagic	Unknown	Territorial Aggression	3	NA	NA	NA	NA	NA	NA	NA	NA	48.70	14.30	1636.69
Hawkins	1978	3	*Melanogrammus aeglefinus*	Demersal	SSM	Agonistic	1	NA	NA	NA	NA	NA	4.00	2.11	4.15	54.40	29.42	1636.69
Rowland	1978	4	*Hemichromis bimaculatus*	Benthopelagic	SSM	Territorial Aggression	11	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Rowland	1978	4	*Hemichromis bimaculatus*	Benthopelagic	SSM	Territorial Aggression	11	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Crawford	1986	5	*Pollimyrus isidori*	Demersal	SSM	Courtship	1	NA	NA	NA	NA	NA	NA	NA	NA	280.00	57.00	1636.69
Crawford	1986	5	*Pollimyrus isidori*	Demersal	SSM	Courtship	1	NA	NA	NA	NA	NA	NA	NA	NA	310.00	58.00	1636.69
Crawford	1986	5	*Pollimyrus isidori*	Demersal	SSM	Courtship	1	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Crawford	1986	5	*Pollimyrus isidori*	Demersal	SSM	Courtship	1	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Torricelli	1986	6	*Padogobius martensii*	Demersal	PGM	Agonistic	5	NA	NA	NA	NA	NA	NA	NA	NA	780.00	190.00	1636.69
Torricelli	1986	6	*Padogobius martensii*	Demersal	PGM	Courtship	5	NA	NA	NA	NA	NA	NA	NA	NA	460.00	60.00	1636.69
Ladich	1989	7	*Cottus gobio*	Demersal	CBS	Agonistic	12	NA	NA	NA	NA	NA	4.80	0.68	4.15	48.30	8.80	1636.69
Torricelli	1990	8	*Padogobius martensii*	Demersal	PGM	Courtship	20	NA	NA	NA	NA	NA	NA	NA	NA	479.00	119.00	1636.69
Torricelli	1990	8	*Padogobius martensii*	Demersal	PGM	Territorial Aggression	30	NA	NA	NA	NA	NA	NA	NA	NA	1315.00	642.00	1636.69
Lobel	1995	9	*Dascyllus albisella*	Reef	Unknown	Courtship	25	5.00	71.66	NA	NA	NA	6.00	4.00	4.15	262.00	57.00	1636.69
Lobel	1995	9	*Dascyllus albisella*	Reef	Unknown	Courtship	6	5.00	71.66	NA	NA	NA	6.00	4.00	4.15	262.00	57.00	1636.69

Lobel	1995	9	*Dascyllus albisella*	Reef	Unknown	Spawning	25	11.00	71.66	NA	NA	NA	3.00	1.00	4.15	127.00	45.00	1636.69
Lobel	1995	9	*Dascyllus albisella*	Reef	Unknown	Spawning	6	11.00	71.66	NA	NA	NA	3.00	1.00	4.15	127.00	45.00	1636.69
Almada	1996	10	*Gaidropsarus mediterraneus*	Demersal	Unknown	Territorial Aggression	2	NA	NA	6.90	1.69	32.00	NA	NA	NA	81.00	30.52	1636.69
Amorim	1996	11	*Chromis viridis*	Reef	Unknown	Territorial Aggression	5	1.64	71.66	7.90	NA	NA	2.10	1.19	4.15	15.70	7.35	1636.69
Bischof	1996	12	*Macropodus opercularis*	Pelagic	FM	Agonistic	34	10.90	71.66	NA	NA	NA	NA	NA	NA	NA	NA	NA
Mann	1997	13	*Dascyllus albisella*	Reef	Unknown	Courtship	4	NA	NA	16.40	3.00	32.00	NA	NA	NA	NA	NA	NA
Lobel	1998	14	*Copadichromis conophorus*	Benthopelagic	Unknown	Courtship	5	6.58	71.66	6.70	1.54	32.00	10.00	2.80	4.15	181.00	59.20	1636.69
Lobel	1998	14	*Tramitichromis intermedius*	Demersal	Unknown	Courtship	2	4.85	71.66	6.20	1.18	32.00	9.30	1.60	4.15	199.20	43.80	1636.69
Pruzsinsky	1998	15	*Corydoras paleatus*	Demersal	PSS	Agonistic	21	2.53	71.66	NA	NA	NA	11.30	2.85	4.15	11.30	2.85	1636.69
Pruzsinsky	1998	15	*Corydoras paleatus*	Demersal	PSS	Courtship	21	0.17	71.66	NA	NA	NA	14.40	2.32	4.15	17.30	2.65	1636.69
Dos Santos	2000	16	*Halobatrachus didactylus*	Demersal	SSM	Courtship	21	NA	NA	NA	NA	NA	44.70	6.87	4.15	674.60	114.11	1636.69
Dos Santos	2000	16	*Halobatrachus didactylus*	Demersal	SSM	Disturbance	19	NA	NA	NA	NA	NA	1.00	0.00	4.15	72.80	37.05	1636.69
Hawkins	2000	17	*Melanogrammus aeglefinus*	Demersal	SSM	Agonistic	6	1.50	71.66	NA	NA	NA	2.00	0.00	4.15	24.90	2.00	1636.69
Hawkins	2000	17	*Melanogrammus aeglefinus*	Demersal	SSM	Spawning	6	0.50	71.66	NA	NA	NA	2.00	0.00	4.15	24.30	1.40	1636.69
Hawkins	2000	17	*Melanogrammus aeglefinus*	Demersal	SSM	Spawning	6	2.40	71.66	NA	NA	NA	2.00	0.00	4.15	25.20	2.90	1636.69
Hawkins	2000	17	*Melanogrammus aeglefinus*	Demersal	SSM	Spawning	6	0.20	71.66	NA	NA	NA	2.00	0.00	4.15	25.50	1.40	1636.69
Hawkins	2000	17	*Melanogrammus aeglefinus*	Demersal	SSM	Spawning	6	0.90	71.66	NA	NA	NA	2.00	0.00	4.15	26.30	1.30	1636.69
Johnson	2000	18	*Cyprinodon bifasciatus*	Benthopelagic	Unknown	Courtship	5	NA	NA	NA	NA	NA	1.00	0.00	4.15	57.00	28.00	1636.69
Johnson	2000	18	*Cyprinodon bifasciatus*	Benthopelagic	Unknown	Territorial Aggression	15	NA	NA	53.00	NA	NA	1.00	0.00	4.15	53.00	28.00	1636.69
Johnston	2000	19	*Etheostoma crossopterum*	Benthopelagic	Unknown	Courtship	11	NA	NA	NA	NA	NA	NA	NA	NA	600.00	150.00	1636.69
Johnston	2000	19	*Etheostoma crossopterum*	Benthopelagic	Unknown	Courtship	11	NA	NA	NA	NA	NA	NA	NA	NA	960.00	310.00	1636.69
Johnston	2000	19	*Etheostoma crossopterum*	Benthopelagic	Unknown	Territorial Aggression	11	NA	NA	NA	NA	NA	NA	NA	NA	460.00	160.00	1636.69
Johnston	2000	19	*Etheostoma crossopterum*	Benthopelagic	Unknown	Territorial Aggression	11	NA	NA	NA	NA	NA	NA	NA	NA	660.00	310.00	1636.69
Johnston	2000	19	*Etheostoma nigripinne*	Benthopelagic	Unknown	Courtship	11	NA	NA	NA	NA	NA	NA	NA	NA	740.00	420.00	1636.69
Johnston	2000	19	*Etheostoma nigripinne*	Benthopelagic	Unknown	Territorial Aggression	11	NA	NA	NA	NA	NA	NA	NA	NA	580.00	260.00	1636.69
Johnston	2000	20	*Pimephales notatus*	Demersal	Unknown	Territorial Aggression	8	NA	NA	NA	NA	NA	NA	NA	NA	220.00	100.00	1636.69
Johnston	2000	20	*Pimephales notatus*	Demersal	Unknown	Territorial Aggression	8	NA	NA	NA	NA	NA	NA	NA	NA	530.00	2400.00	1636.69
Lindstrom	2000	21	*Pomatoschistus minutus*	Demersal	PGM	Courtship	8	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Bremner	2002	22	*Melanogrammus aeglefinus*	Demersal	SSM	Courtship	1	NA	NA	NA	NA	NA	NA	NA	NA	3350.00	1810.00	1636.69
Bremner	2002	22	*Melanogrammus aeglefinus*	Demersal	SSM	Courtship	1	NA	NA	NA	NA	NA	NA	NA	NA	4380.00	1980.00	1636.69

Edds-Walton	2002	23	*Opsanus tau*	Reef	SSM	Courtship	1	NA	NA	NA	NA	NA	NA	NA	NA	238.30	15.50	1636.69
Edds-Walton	2002	23	*Opsanus tau*	Reef	SSM	Courtship	1	NA	NA	NA	NA	NA	NA	NA	NA	291.30	26.20	1636.69
Edds-Walton	2002	23	*Opsanus tau*	Reef	SSM	Courtship	1	NA	NA	NA	NA	NA	NA	NA	NA	302.80	14.80	1636.69
Edds-Walton	2002	23	*Opsanus tau*	Reef	SSM	Courtship	1	NA	NA	NA	NA	NA	NA	NA	NA	350.40	26.90	1636.69
Edds-Walton	2002	23	*Opsanus tau*	Reef	SSM	Courtship	1	NA	NA	NA	NA	NA	NA	NA	NA	359.40	19.50	1636.69
Edds-Walton	2002	23	*Opsanus tau*	Reef	SSM	Courtship	1	NA	NA	NA	NA	NA	NA	NA	NA	372.30	16.30	1636.69
Edds-Walton	2002	23	*Opsanus tau*	Reef	SSM	Courtship	1	NA	NA	NA	NA	NA	NA	NA	NA	398.40	23.40	1636.69
Edds-Walton	2002	23	*Opsanus tau*	Reef	SSM	Courtship	1	NA	NA	NA	NA	NA	NA	NA	NA	400.00	12.90	1636.69
Edds-Walton	2002	23	*Opsanus tau*	Reef	SSM	Courtship	1	NA	NA	NA	NA	NA	NA	NA	NA	432.70	16.40	1636.69
Edds-Walton	2002	23	*Opsanus tau*	Reef	SSM	Courtship	1	NA	NA	NA	NA	NA	NA	NA	NA	446.70	32.40	1636.69
Edds-Walton	2002	23	*Opsanus tau*	Reef	SSM	Courtship	1	NA	NA	NA	NA	NA	NA	NA	NA	471.40	21.10	1636.69
Edds-Walton	2002	23	*Opsanus tau*	Reef	SSM	Courtship	1	NA	NA	NA	NA	NA	NA	NA	NA	557.40	41.50	1636.69
Thorson	2002	24	*Opsanus beta*	Demersal	SSM	Courtship	5	NA	NA	NA	NA	NA	NA	NA	NA	499.00	81.90	1636.69
Amorim	2003	25	*Oreochromis mossambicus*	Benthopelagic	JTS	Courtship	19	14.00	71.66	11.70	1.20	32.00	16.80	8.70	4.15	712.30	457.70	1636.69
Lugli	2003	26	*Padogobius martensii*	Demersal	PGM	Courtship	6	NA	NA	NA	NA	NA	NA	NA	NA	200.00	94.00	1636.69
Lugli	2003	26	*Padogobius martensii*	Demersal	PGM	Courtship	6	NA	NA	NA	NA	NA	NA	NA	NA	164.00	22.00	1636.69
Fine	2004	27	*Micropogonias undulatus*	Demersal	SSM	Disturbance	5	NA	NA	5.70	0.89	32.00	4.00	1.12	4.15	142.10	25.40	1636.69
Finstad	2004	28	*Gadus morhua*	Benthopelagic	SSM	Courtship	29	NA	NA	NA	NA	NA	NA	NA	NA	215.00	825.00	1636.69
Lagardere	2005	29	*Carapus boraborensis*	Demersal	SSM	Agonistic	15	NA	NA	NA	NA	NA	NA	NA	NA	105.00	4.80	1636.69
Lagardere	2005	29	*Carapus boraborensis*	Demersal	SSM	Agonistic	15	NA	NA	NA	NA	NA	NA	NA	NA	264.00	9.00	1636.69
Lagardere	2005	29	*Carapus homei*	Reef	SSM	Agonistic	12	NA	NA	NA	NA	NA	NA	NA	NA	190.00	4.40	1636.69
Lagardere	2005	29	*Carapus homei*	Reef	SSM	Agonistic	12	NA	NA	NA	NA	NA	NA	NA	NA	217.00	20.00	1636.69
Lamml	2005	30	*Pollimyrus marianne*	Benthopelagic	SSM	Courtship	1	1.38	71.66	3.30	0.12	32.00	20.00	3.80	4.15	618.20	126.90	1636.69
Lamml	2005	30	*Pollimyrus marianne*	Benthopelagic	SSM	Courtship	1	1.58	71.66	3.70	0.11	32.00	17.00	5.50	4.15	563.40	144.00	1636.69
Lamml	2005	30	*Pollimyrus marianne*	Benthopelagic	SSM	Courtship	1	2.40	71.66	3.30	0.11	32.00	17.50	4.60	4.15	608.00	159.90	1636.69
Lamml	2005	30	*Pollimyrus marianne*	Benthopelagic	SSM	Courtship	1	NA	NA	NA	NA	NA	NA	NA	NA	573.40	195.70	1636.69
Lamml	2005	30	*Pollimyrus marianne*	Benthopelagic	SSM	Courtship	1	NA	NA	NA	NA	NA	NA	NA	NA	1600.00	650.00	1636.69
Lamml	2005	30	*Pollimyrus marianne*	Benthopelagic	SSM	Courtship	1	NA	NA	NA	NA	NA	NA	NA	NA	2380.00	970.00	1636.69
Lamml	2005	30	*Pollimyrus marianne*	Benthopelagic	SSM	Courtship	1	NA	NA	NA	NA	NA	NA	NA	NA	2580.00	1390.00	1636.69
Lamml	2005	30	*Pollimyrus marianne*	Benthopelagic	SSM	Courtship	1	NA	NA	NA	NA	NA	NA	NA	NA	2800.00	1030.00	1636.69
Lamml	2005	30	*Pollimyrus marianne*	Benthopelagic	SSM	Territorial Aggression	1	NA	NA	NA	NA	NA	NA	NA	NA	570.00	490.00	1636.69
Lamml	2005	30	*Pollimyrus marianne*	Benthopelagic	SSM	Territorial Aggression	1	NA	NA	NA	NA	NA	NA	NA	NA	630.00	680.00	1636.69

Parmentier	2005	31	*Amphiprion akallopisos*	Reef	JTS	Territorial Aggression	10	2.08	71.66	3.00	0.76	32.00	8.70	2.37	4.15	89.00	0.69	1636.69
Parmentier	2005	31	*Amphiprion akallopisos*	Reef	JTS	Territorial Aggression	10	NA	NA	12.80	2.42	32.00	1.00	0.00	4.15	12.80	2.42	1636.69
Parmentier	2005	31	*Amphiprion akallopisos*	Reef	JTS	Territorial Aggression	10	NA	NA	12.80	2.42	32.00	1.00	0.00	4.15	12.80	2.42	1636.69
Parmentier	2005	31	*Amphiprion akallopisos*	Reef	JTS	Territorial Aggression	12	NA	NA	7.40	0.61	32.00	1.00	0.00	4.15	7.40	0.61	1636.69
Parmentier	2005	31	*Amphiprion akallopisos*	Reef	JTS	Territorial Aggression	12	NA	NA	12.10	3.12	32.00	1.00	0.00	4.15	12.10	3.12	1636.69
Ladich	2006	32	*Trichopsis vittata*	Demersal	FM	Courtship	15	NA	NA	NA	NA	NA	NA	NA	NA	42.10	3.26	1636.69
Ladich	2006	32	*Trichopsis vittata*	Demersal	FM	Territorial Aggression	10	NA	NA	NA	NA	NA	NA	NA	NA	44.20	4.36	1636.69
Ladich	2006	32	*Trichopsis vittata*	Demersal	FM	Territorial Aggression	15	NA	NA	NA	NA	NA	NA	NA	NA	46.90	4.36	1636.69
Lamml	2006	33	*Pollimyrus castelnaui*	Demersal	SSM	Courtship	10	6.09	71.66	NA	NA	NA	NA	NA	NA	3000.00	1180.00	1636.69
Lamml	2006	33	*Pollimyrus castelnaui*	Demersal	SSM	Courtship	9	3.75	71.66	3.40	0.19	32.00	21.50	5.93	4.15	674.10	184.40	1636.69
Lamml	2006	33	*Pollimyrus marianne*	Benthopelagic	SSM	Courtship	4	4.10	71.66	NA	NA	NA	NA	NA	NA	2000.00	790.00	1636.69
Lamml	2006	33	*Pollimyrus marianne*	Benthopelagic	SSM	Courtship	1	2.11	71.66	NA	NA	NA	NA	NA	NA	1900.00	1190.00	1636.69
Lamml	2006	33	*Pollimyrus marianne*	Benthopelagic	SSM	Courtship	4	2.90	71.66	3.60	0.35	32.00	16.20	1.95	4.15	546.20	49.40	1636.69
Parmentier	2006	34	*Carapus mourlani*	Reef	SSM	Territorial Aggression	32	NA	NA	15.50	5.00	32.00	1.00	0.00	4.15	15.50	5.00	1636.69
Parmentier	2006	34	*Carapus mourlani*	Reef	SSM	Territorial Aggression	32	NA	NA	22.00	4.20	32.00	2.00	0.00	4.15	54.40	2.10	1636.69
Amorim	2007	35	*Pomatoschistus pictus*	Demersal	PGM	Courtship	20	NA	NA	NA	NA	NA	NA	NA	NA	81.40	3.97	1636.69
de Jong	2007	36	*Parablennius parvicornis*	Demersal	Unknown	Courtship	15	NA	NA	NA	NA	NA	NA	NA	NA	225.00	148.00	1636.69
de Jong	2007	36	*Parablennius parvicornis*	Demersal	Unknown	Courtship	10	NA	NA	NA	NA	NA	NA	NA	NA	191.00	175.00	1636.69
de Jong	2007	36	*Parablennius parvicornis*	Demersal	Unknown	Courtship	16	NA	NA	NA	NA	NA	NA	NA	NA	405.00	167.00	1636.69
Johnston	2007	37	*Codoma ornata*	Benthopelagic	Unknown	Agonistic	5	NA	NA	NA	NA	NA	NA	NA	NA	547.00	295.00	1636.69
Johnston	2007	37	*Codoma ornata*	Benthopelagic	Unknown	Agonistic	5	NA	NA	NA	NA	NA	NA	NA	NA	7770.00	3890.00	1636.69
Johnston	2007	37	*Codoma ornata*	Benthopelagic	Unknown	Courtship	5	NA	NA	NA	NA	NA	NA	NA	NA	660.00	2510.00	1636.69
Lamml	2007	38	*Marcusenius macrolepidotus*	Demersal	Unknown	Territorial Aggression	6	0.16	71.66	2.40	0.13	32.00	NA	NA	NA	1306.00	191.00	1636.69
Lamml	2007	38	*Marcusenius macrolepidotus*	Demersal	Unknown	Territorial Aggression	6	0.50	71.66	2.60	0.11	32.00	NA	NA	NA	1284.00	331.50	1636.69
Lamml	2007	38	*Marcusenius macrolepidotus*	Demersal	Unknown	Territorial Aggression	1	0.81	71.66	2.20	NA	NA	NA	NA	NA	2367.00	553.00	1636.69
Lamml	2007	38	*Marcusenius macrolepidotus*	Demersal	Unknown	Territorial Aggression	1	0.36	71.66	NA	NA	NA	NA	NA	NA	2022.00	378.00	1636.69
Lamml	2007	38	*Marcusenius macrolepidotus*	Demersal	Unknown	Territorial Aggression	3	NA	NA	NA	NA	NA	NA	NA	NA	172.00	35.90	1636.69
Lamml	2007	38	*Marcusenius macrolepidotus*	Demersal	Unknown	Territorial Aggression	1	NA	NA	NA	NA	NA	NA	NA	NA	103.00	9.08	1636.69
Lamml	2007	38	*Marcusenius macrolepidotus*	Demersal	Unknown	Territorial Aggression	1	NA	NA	NA	NA	NA	NA	NA	NA	145.00	9.80	1636.69
Lamml	2007	38	*Marcusenius macrolepidotus*	Demersal	Unknown	Territorial Aggression	5	NA	NA	NA	NA	NA	NA	NA	NA	161.00	33.70	1636.69

Malavasi	2007	39	*Gobius cobitis*	Demersal	Unknown	Territorial Aggression	6	NA	NA	NA	NA	NA	16.00	8.00	4.15	330.00	97.00	1636.69
Malavasi	2007	39	*Gobius niger*	Demersal	Unknown	Courtship	3	NA	NA	NA	NA	NA	15.00	1.00	4.15	347.00	14.00	1636.69
Malavasi	2007	39	*Gobius niger*	Demersal	Unknown	Territorial Aggression	5	NA	NA	NA	NA	NA	19.00	4.00	4.15	435.00	55.00	1636.69
Malavasi	2007	39	*Gobius paganellus*	Demersal	PGM	Courtship	11	NA	NA	NA	NA	NA	31.00	2.00	4.15	351.00	68.00	1636.69
Malavasi	2007	39	*Gobius paganellus*	Demersal	PGM	Territorial Aggression	6	NA	NA	NA	NA	NA	31.00	5.00	4.15	352.00	82.00	1636.69
Malavasi	2007	39	*Pomatoschistus canestrinii*	Demersal	Unknown	Courtship	5	NA	NA	NA	NA	NA	25.00	3.00	4.15	752.00	140.00	1636.69
Malavasi	2007	39	*Pomatoschistus canestrinii*	Demersal	Unknown	Territorial Aggression	4	NA	NA	NA	NA	NA	22.00	4.00	4.15	541.00	133.00	1636.69
Maruska	2007	40	*Abudefduf abdominalis*	Reef	JTS	Courtship	30	258.00	71.66	32.00	7.00	32.00	11.00	6.00	4.15	1793.00	955.00	1636.69
Maruska	2007	40	*Abudefduf abdominalis*	Reef	JTS	Courtship	30	258.70	71.66	91.00	19.00	32.00	11.00	6.00	4.15	1793.00	955.00	1636.69
Maruska	2007	40	*Abudefduf abdominalis*	Reef	JTS	Territorial Aggression	30	93.30	71.66	52.00	28.00	32.00	5.00	2.00	4.15	161.00	122.00	1636.69
Maruska	2007	40	*Abudefduf abdominalis*	Reef	JTS	Territorial Aggression	30	246.00	71.66	30.00	22.00	32.00	1.60	0.50	4.15	1013.00	1067.00	1636.69
Ueng	2007	41	*Argyrosomus japonicus*	Benthopelagic	SSM	Courtship	40	3.00	71.66	10.00	1.00	32.00	15.00	3.20	4.15	316.00	62.00	1636.69
Ueng	2007	41	*Argyrosomus japonicus*	Benthopelagic	SSM	Courtship	46	3.00	71.66	13.00	2.00	32.00	10.50	3.00	4.15	231.00	65.00	1636.69
Vasconcelos	2007	42	*Halobatrachus didactylus*	Demersal	SSM	Territorial Aggression	22	0.80	71.66	NA	NA	NA	7.60	2.25	4.15	NA	NA	NA
Vasconcelos	2007	42	*Halobatrachus didactylus*	Demersal	SSM	Territorial Aggression	22	1.23	71.66	NA	NA	NA	4.40	2.48	4.15	NA	NA	NA
Amorim	2008	43	*Pomatoschistus pictus*	Demersal	PGM	Territorial Aggression	20	0.80	71.66	NA	NA	NA	22.90	9.10	4.15	700.30	326.60	1636.69
Fine	2008	44	*Opsanus tau*	Reef	SSM	Courtship	1	NA	NA	NA	NA	NA	NA	NA	NA	281.00	65.00	1636.69
Fine	2008	44	*Opsanus tau*	Reef	SSM	Courtship	1	NA	NA	NA	NA	NA	NA	NA	NA	376.00	23.00	1636.69
Johnston	2008	45	*Micropterus coosae*	Demersal	Unknown	Territorial Aggression	8	NA	NA	NA	NA	NA	3.50	7.29	4.15	1250.00	77.00	1636.69
Lamml	2008	46	*Petrocephalus catostoma*	Demersal	SSM	Territorial Aggression	3	0.13	71.66	NA	NA	NA	NA	NA	NA	45.30	16.90	1636.69
Lamml	2008	46	*Petrocephalus catostoma*	Demersal	SSM	Territorial Aggression	2	0.14	71.66	NA	NA	NA	NA	NA	NA	41.70	6.50	1636.69
Lamml	2008	46	*Petrocephalus catostoma*	Demersal	SSM	Territorial Aggression	2	0.35	71.66	NA	NA	NA	NA	NA	NA	44.50	8.06	1636.69
Longrie	2008	47	*Oreochromis niloticus*	Benthopelagic	PGM	Territorial Aggression	8	24.00	71.66	NA	NA	NA	2.10	0.40	4.15	314.00	79.00	1636.69
Philips	2008	48	*Cyprinella galactura*	Benthopelagic	SSM	Agonistic	33	NA	NA	27.00	14.00	32.00	NA	NA	NA	321.00	270.00	1636.69
Philips	2008	48	*Cyprinella galactura*	Benthopelagic	SSM	Agonistic	33	NA	NA	NA	NA	NA	NA	NA	NA	166.00	62.00	1636.69
Philips	2008	48	*Cyprinella galactura*	Benthopelagic	SSM	Agonistic	28	NA	NA	NA	NA	NA	NA	NA	NA	69.00	14.00	1636.69
Philips	2008	48	*Cyprinella galactura*	Benthopelagic	SSM	Courtship	15	NA	NA	35.00	14.00	32.00	NA	NA	NA	508.00	443.00	1636.69
Philips	2008	48	*Cyprinella galactura*	Benthopelagic	SSM	Courtship	15	NA	NA	NA	NA	NA	NA	NA	NA	155.00	52.00	1636.69
Philips	2008	48	*Cyprinella galactura*	Benthopelagic	SSM	Courtship	13	NA	NA	NA	NA	NA	NA	NA	NA	72.00	12.00	1636.69
Sebastianutto	2008	49	*Gobius cruentatus*	Demersal	Unknown	Territorial Aggression	9	NA	NA	NA	NA	NA	NA	NA	NA	700.00	180.00	1636.69
Sebastianutto	2008	49	*Gobius cruentatus*	Demersal	Unknown	Territorial Aggression	7	NA	NA	NA	NA	NA	NA	NA	NA	273.30	116.70	1636.69

Sebastianutto	2008	49	*Gobius cruentatus*	Demersal	Unknown	Territorial Aggression	7	NA	NA	NA	NA	NA	NA	NA	NA	333.30	116.70	1636.69
Sebastianutto	2008	49	*Gobius cruentatus*	Demersal	Unknown	Territorial Aggression	7	NA	NA	NA	NA	NA	NA	NA	NA	503.30	156.70	1636.69
Sebastianutto	2008	49	*Gobius cruentatus*	Demersal	Unknown	Territorial Aggression	8	NA	NA	NA	NA	NA	NA	NA	NA	633.30	140.00	1636.69
Simoes	2008	50	*Maylandia zebra*	Demersal	JTS	Agonistic	5	27.06	71.66	NA	NA	NA	4.90	0.99	4.15	524.20	152.95	1636.69
Simoes	2008	50	*Maylandia zebra*	Demersal	JTS	Agonistic	12	23.91	71.66	NA	NA	NA	8.70	3.48	4.15	960.50	295.29	1636.69
Simoes	2008	50	*Maylandia zebra*	Demersal	JTS	Courtship	12	14.37	71.66	NA	NA	NA	8.60	1.67	4.15	671.70	135.95	1636.69
Boyle	2009	51	*Gomphosus varius*	Reef	JTS	Courtship	16	NA	NA	6.00		32.00	3.70		4.15	500.00		1636.69
Boyle	2009	51	*Gomphosus varius*	Reef	JTS	Courtship	16	NA	NA	13.00		32.00	15.80		4.15	1000.00		1636.69
Boyle	2009	51	*Gomphosus varius*	Reef	JTS	Spawning	4	NA	NA	13.00		32.00	15.80		4.15	1000.00		1636.69
Boyle	2009	51	*Thalassoma duperrey*	Reef	JTS	Courtship	7	NA	NA	12.00		32.00	14.80		4.15	400.00		1636.69
Boyle	2009	51	*Thalassoma duperrey*	Reef	JTS	Spawning	2	NA	NA	12.00		32.00	14.80		4.15	400.00		1636.69
Colleye	2009	52	*Amphiprion akallopisos*	Reef	JTS	Territorial Aggression	6	NA	NA	NA	NA	NA	NA	NA	NA	11.30	2.00	1636.69
Colleye	2009	52	*Amphiprion akallopisos*	Reef	JTS	Territorial Aggression	6	NA	NA	NA	NA	NA	NA	NA	NA	16.20	2.80	1636.69
Longrie	2009	53	*Oreochromis niloticus*	Benthopelagic	PGM	Territorial Aggression	5	NA	NA	39.00	2.00	32.00	NA	NA	NA	NA	NA	NA
Longrie	2009	53	*Oreochromis niloticus*	Benthopelagic	PGM	Territorial Aggression	5	NA	NA	75.00	7.00	32.00	NA	NA	NA	NA	NA	NA
Parmentier	2009	54	*Dascyllus albisella*	Reef	Unknown	Courtship	6	6.42	71.66	30.00	4.47	32.00	NA	NA	NA	NA	NA	NA
Parmentier	2009	54	*Dascyllus aruanus*	Reef	Unknown	Courtship	3	2.80	71.66	13.00	3.68	32.00	NA	NA	NA	NA	NA	NA
Parmentier	2009	54	*Dascyllus aruanus*	Reef	Unknown	Courtship	4	9.33	71.66	14.00	3.19	32.00	NA	NA	NA	NA	NA	NA
Parmentier	2009	54	*Dascyllus trimaculatus*	Reef	Unknown	Courtship	6	5.26	71.66	15.20	5.08	32.00	NA	NA	NA	NA	NA	NA
Parmentier	2009	54	*Dascyllus trimaculatus*	Reef	Unknown	Courtship	5	12.53	71.66	15.90	4.63	32.00	NA	NA	NA	NA	NA	NA
Parmentier	2009	54	*Dascyllus flavicaudus*	Reef	Unknown	Courtship	4	8.32	71.66	28.40	6.12	32.00	NA	NA	NA	NA	NA	NA
Parmentier	2009	54	*Dascyllus flavicaudus*	Reef	Unknown	Courtship	5	8.86	71.66	25.60	5.88	32.00	NA	NA	NA	NA	NA	NA
Rubow	2009	55	*Porichthys notatus*	Demersal	SSM	Agonistic	5	NA	NA	NA	NA	NA	NA	NA	NA	46.60	7.00	1636.69
Boyle	2010	56	*Hemitaurichthys polylepis*	Reef	SSM	Agonistic	2	NA	NA	34.00	1.41	32.00	NA	NA	NA	113.00	118.79	1636.69
Boyle	2010	56	*Hemitaurichthys polylepis*	Reef	SSM	Disturbance	4	NA	NA	35.00	4.00	32.00	NA	NA	NA	106.00	38.00	1636.69
Kierl	2010	57	*Cottus paulus*	Demersal	PGM	Agonistic	9	117.90	71.66	34.60	29.40	32.00	3.10	1.60	4.15	310.90	388.80	1636.69
Kierl	2010	57	*Cottus paulus*	Demersal	PGM	Agonistic	9	NA	NA	37.30	27.10	32.00	1.00	0.00	4.15	37.30	27.10	1636.69
Kierl	2010	57	*Cottus paulus*	Demersal	PGM	Courtship	9	142.40	71.66	40.90	23.60	32.00	3.00	1.40	4.15	539.10	529.60	1636.69
Kierl	2010	57	*Cottus paulus*	Demersal	PGM	Courtship	9	NA	NA	35.50	20.80	32.00	1.00	0.00	4.15	35.50	20.80	1636.69
Lechner	2010	58	*Synodontis schoutedeni*	Benthopelagic	SSM	Disturbance	6	1.76	71.66	NA	NA	NA	NA	NA	NA	NA	NA	NA
Lechner	2010	58	*Synodontis schoutedeni*	Benthopelagic	SSM	Disturbance	6	0.86	71.66	NA	NA	NA	NA	NA	NA	NA	NA	NA
Lechner	2010	58	*Synodontis schoutedeni*	Benthopelagic	SSM	Disturbance	4	1.36	71.66	NA	NA	NA	NA	NA	NA	NA	NA	NA
Lechner	2010	58	*Synodontis schoutedeni*	Benthopelagic	SSM	Disturbance	5	1.30	71.66	NA	NA	NA	NA	NA	NA	NA	NA	NA
Lechner	2010	58	*Synodontis schoutedeni*	Benthopelagic	SSM	Disturbance	6	2.38	71.66	NA	NA	NA	NA	NA	NA	NA	NA	NA
Parmentier	2010	59	*Synodontis decorus*	Benthopelagic	PSS	Disturbance	1	0.40	71.66	1.00	0.20	32.00	17.00	0.00	4.15	NA	NA	NA
Parmentier	2010	59	*Synodontis decorus*	Benthopelagic	PSS	Disturbance	1	1.00	71.66	1.00	0.10	32.00	11.00	1.41	4.15	NA	NA	NA

Tellechea	2010	60	*Micropogonias furnieri*	Demersal	SSM	Courtship	1	536.00	71.66	19.70	0.68	32.00	NA	NA	NA	NA	NA	NA
Tellechea	2010	60	*Micropogonias furnieri*	Demersal	SSM	Courtship	1	793.00	71.66	17.80	0.45	32.00	NA	NA	NA	NA	NA	NA
Tellechea	2010	60	*Micropogonias furnieri*	Demersal	SSM	Disturbance	112	10.06	71.66	19.80	8.22	32.00	NA	NA	NA	NA	NA	NA
Amorim	2011	61	*Halobatrachus didactylus*	Demersal	SSM	Courtship	13	1.70	71.66	NA	NA	NA	NA	NA	NA	686.80	190.20	1636.69
Amorim	2011	61	*Halobatrachus didactylus*	Demersal	SSM	Courtship	13	1.40	71.66	NA	NA	NA	NA	NA	NA	723.10	161.90	1636.69
Barimo	2011	62	*Opsanus tau*	Reef	SSM	Agonistic	1	NA	NA	NA	NA	NA	NA	NA	NA	71.00	11.20	1636.69
Barimo	2011	62	*Opsanus tau*	Reef	SSM	Agonistic	1	NA	NA	NA	NA	NA	NA	NA	NA	80.00	30.30	1636.69
Barimo	2011	62	*Opsanus tau*	Reef	SSM	Courtship	1	NA	NA	NA	NA	NA	NA	NA	NA	227.00	22.40	1636.69
Barimo	2011	62	*Opsanus tau*	Reef	SSM	Courtship	1	NA	NA	NA	NA	NA	NA	NA	NA	266.00	23.40	1636.69
Barimo	2011	62	*Opsanus tau*	Reef	SSM	Courtship	1	NA	NA	NA	NA	NA	NA	NA	NA	278.00	25.70	1636.69
Barimo	2011	62	*Opsanus tau*	Reef	SSM	Courtship	1	NA	NA	NA	NA	NA	NA	NA	NA	291.00	25.30	1636.69
Barimo	2011	62	*Opsanus tau*	Reef	SSM	Courtship	1	NA	NA	NA	NA	NA	NA	NA	NA	366.00	15.80	1636.69
Boyle	2011	63	*Forcipiger flavissimus*	Reef	PGM	Territorial Aggression	4	NA	NA	74.00	14.00	32.00	1.00	0.00	4.15	74.00	14.00	1636.69
Boyle	2011	63	*Forcipiger longirostris*	Reef	PGM	Territorial Aggression	14	NA	NA	98.00	37.42	32.00	1.00	0.00	4.15	98.00	37.42	1636.69
Colleye	2011	64	*Amphiprion akallopisos*	Reef	JTS	Territorial Aggression	11	12.40	71.66	12.50	3.40	32.00	73.80	12.40	4.15	NA	NA	NA
Colleye	2011	64	*Amphiprion akindynos*	Reef	JTS	Territorial Aggression	2	15.90	71.66	13.30	1.90	32.00	106.10	15.90	4.15	NA	NA	NA
Colleye	2011	64	*Amphiprion chrysogaster*	Reef	JTS	Territorial Aggression	1	11.10	71.66	17.70	1.30	32.00	114.00	11.10	4.15	NA	NA	NA
Colleye	2011	64	*Amphiprion chrysopterus*	Reef	JTS	Territorial Aggression	1	24.90	71.66	18.90	1.10	32.00	160.90	24.90	4.15	NA	NA	NA
Colleye	2011	64	*Amphiprion clarkii*	Reef	JTS	Territorial Aggression	6	30.70	71.66	15.40	2.90	32.00	109.10	30.70	4.15	NA	NA	NA
Colleye	2011	64	*Amphiprion frenatus*	Reef	JTS	Territorial Aggression	6	24.70	71.66	14.30	2.50	32.00	106.90	24.70	4.15	NA	NA	NA
Colleye	2011	64	*Amphiprion latifasciatus*	Reef	JTS	Territorial Aggression	1	18.20	71.66	10.30	0.80	32.00	123.50	18.20	4.15	NA	NA	NA
Colleye	2011	64	*Amphiprion melanopus*	Reef	JTS	Territorial Aggression	2	22.00	71.66	11.60	2.20	32.00	90.20	22.00	4.15	NA	NA	NA
Colleye	2011	64	*Amphiprion nigripes*	Reef	JTS	Territorial Aggression	2	18.10	71.66	9.40	1.40	32.00	124.70	18.10	4.15	NA	NA	NA
Colleye	2011	64	*Amphiprion ocellaris*	Reef	JTS	Territorial Aggression	4	21.70	71.66	9.70	1.50	32.00	106.90	21.70	4.15	NA	NA	NA
Colleye	2011	64	*Amphiprion percula*	Reef	JTS	Territorial Aggression	2	18.30	71.66	8.20	1.90	32.00	88.80	18.30	4.15	NA	NA	NA
Colleye	2011	64	*Amphiprion perideraion*	Reef	JTS	Territorial Aggression	2	18.40	71.66	11.00	1.90	32.00	67.80	18.40	4.15	NA	NA	NA
Colleye	2011	64	*Amphiprion polymnus*	Reef	JTS	Territorial Aggression	2	27.40	71.66	13.30	1.90	32.00	97.60	27.40	4.15	NA	NA	NA
Colleye	2011	64	*Premnas biaculeatus*	Reef	JTS	Territorial Aggression	1	16.00	71.66	30.50	1.60	32.00	123.10	16.00	4.15	NA	NA	NA
Millot	2011	65	*Pygocentrus nattereri*	Pelagic	SSM	Agonistic	30	5.48	71.66	4.00	5.48	32.00	NA	NA	NA	140.00	93.11	1636.69
Millot	2011	65	*Pygocentrus nattereri*	Pelagic	SSM	Agonistic	30	NA	NA	3.00	5.48	32.00	1.00	0.00	4.15	3.00	5.48	1636.69
Nelson	2011	66	*Epinephelus morio*	Reef	SSM	Courtship	10	NA	NA	NA	NA	NA	33.00	16.00	4.15	113.00	42.00	1636.69

Nelson	2011	66	*Epinephelus morio*	Reef	SSM	Courtship	10	NA	NA	NA	NA	NA	4.00	1.00	4.15	161.00	33.00	1636.69
Nelson	2011	66	*Epinephelus morio*	Reef	SSM	Courtship	10	NA	NA	NA	NA	NA	NA	NA	NA	700.00	200.00	1636.69
Nelson	2011	66	*Epinephelus morio*	Reef	SSM	Courtship	10	NA	NA	NA	NA	NA	NA	NA	NA	1800.00	200.00	1636.69
Nelson	2011	66	*Epinephelus morio*	Reef	SSM	Courtship	10	NA	NA	NA	NA	NA	NA	NA	NA	153.00	43.00	1636.69
Papes	2011	67	*Platydoras armatulus*	Demersal	PSS	Disturbance	8	2.26	71.66	NA	NA	NA	27.90	13.29	4.15	277.20	115.97	1636.69
Papes	2011	67	*Platydoras armatulus*	Demersal	PSS	Disturbance	8	1.34	71.66	NA	NA	NA	25.20	11.40	4.15	326.60	146.24	1636.69
Papes	2011	67	*Platydoras armatulus*	Demersal	PSS	Disturbance	8	0.89	71.66	NA	NA	NA	16.70	12.75	4.15	277.50	225.17	1636.69
Papes	2011	67	*Platydoras armatulus*	Demersal	PSS	Disturbance	8	NA	NA	NA	NA	NA	6.00	1.70	4.15	71.50	16.69	1636.69
Papes	2011	67	*Platydoras armatulus*	Demersal	PSS	Disturbance	8	NA	NA	NA	NA	NA	7.90	2.83	4.15	94.80	28.28	1636.69
Papes	2011	67	*Platydoras armatulus*	Demersal	PSS	Disturbance	8	NA	NA	NA	NA	NA	7.70	3.39	4.15	122.70	30.55	1636.69
Papes	2011	67	*Platydoras armatulus*	Demersal	PSS	Disturbance	8	NA	NA	NA	NA	NA	7.80	3.11	4.15	67.10	10.18	1636.69
Papes	2011	67	*Platydoras armatulus*	Demersal	PSS	Disturbance	8	NA	NA	NA	NA	NA	7.60	0.85	4.15	88.40	12.45	1636.69
Papes	2011	67	*Platydoras armatulus*	Demersal	PSS	Disturbance	8	NA	NA	NA	NA	NA	6.20	2.55	4.15	91.00	24.89	1636.69
Parmentier	2011	68	*Heniochus chrysostomus*	Reef	SSM	Disturbance	5	0.06	71.66	NA	NA	NA	NA	NA	NA	56.60	1.00	1636.69
Parmentier	2011	68	*Heniochus chrysostomus*	Reef	SSM	Disturbance	5	NA	NA	5.50	0.03	32.00	2.00	0.00	4.15	11.60	0.10	1636.69
Parmentier	2011	69	*Holocentrus rufus*	Reef	SSM	Disturbance	2	0.30	71.66	4.10	0.20	32.00	NA	NA	NA	NA	NA	NA
Parmentier	2011	69	*Myripristis kuntee*	Reef	SSM	Disturbance	5	0.10	71.66	4.20	0.10	32.00	NA	NA	NA	NA	NA	NA
Parmentier	2011	69	*Myripristis violacea*	Reef	SSM	Disturbance	11	0.10	71.66	6.80	0.20	32.00	7.60	0.11	4.15	NA	NA	NA
Parmentier	2011	69	*Neoniphon sammara*	Reef	SSM	Disturbance	11	0.10	71.66	5.90	0.10	32.00	NA	NA	NA	NA	NA	NA
Parmentier	2011	69	*Neoniphon sammara*	Reef	SSM	Disturbance	5	2.40	71.66	6.90	0.10	32.00	NA	NA	NA	NA	NA	NA
Parmentier	2011	69	*Sargocentron diadema*	Reef	SSM	Disturbance	5	0.10	71.66	6.80	2.00	32.00	NA	NA	NA	NA	NA	NA
Speares	2011	70	*Etheostoma oophylax*	Benthopelagic	Unknown	Courtship	12	32.65	71.66	42.00	25.00	32.00	6.10	3.33	4.15	377.00	244.00	1636.69
Speares	2011	70	*Etheostoma oophylax*	Benthopelagic	Unknown	Courtship	12	NA	NA	62.00	81.00	32.00	1.00	0.00	4.15	62.00	81.00	1636.69
Speares	2011	70	*Etheostoma oophylax*	Benthopelagic	Unknown	Courtship	12	NA	NA	NA	NA	NA	NA	NA	NA	457.00	326.00	1636.69
Speares	2011	70	*Etheostoma oophylax*	Benthopelagic	Unknown	Territorial Aggression	12	21.38	71.66	23.00	4.00	32.00	6.60	2.67	4.15	312.00	171.00	1636.69
Speares	2011	70	*Etheostoma oophylax*	Benthopelagic	Unknown	Territorial Aggression	12	NA	NA	35.00	21.00	32.00	1.00	0.00	4.15	35.00	21.00	1636.69
Speares	2011	70	*Etheostoma oophylax*	Benthopelagic	Unknown	Territorial Aggression	12	NA	NA	NA	NA	NA	NA	NA	NA	392.00	277.00	1636.69
Tellechea	2011	71	*Iheringichthys labrosus*	Demersal	PSS	Disturbance	30	0.21	71.66	0.10	0.05	32.00	NA	NA	NA	17.10	0.47	1636.69
Tellechea	2011	71	*Iheringichthys labrosus*	Demersal	SSM	Disturbance	30	1.21	71.66	1.30	1.20	32.00	NA	NA	NA	120.00	2.32	1636.69
Tellechea	2011	72	*Pogonias cromis*	Demersal	SSM	Courtship	6	NA	NA	NA	NA	NA	NA	NA	NA	184.00	6.15	1636.69
Tellechea	2011	72	*Pogonias cromis*	Demersal	SSM	Disturbance	6	2.39	71.66	24.00	1.75	32.00	NA	NA	NA	440.00	220.00	1636.69
Tellechea	2011	72	*Pogonias cromis*	Demersal	SSM	Disturbance	12	4.54	71.66	23.00	2.10	32.00	NA	NA	NA	520.00	250.00	1636.69
Bertucci	2012	73	*Metriaclima zebra*	Demersal	SSM	Territorial Aggression	17	11.09	71.66	7.50	0.50	32.00	8.10	1.30	4.15	654.20	113.19	1636.69
Bertucci	2012	73	*Metriaclima zebra*	Demersal	SSM	Territorial Aggression	20	15.06	71.66	9.40	1.04	32.00	6.80	0.92	4.15	571.20	103.38	1636.69
Colleye	2012	74	*Amphiprion frenatus*	Reef	JTS	Territorial Aggression	9	2.40	71.66	10.30	NA	NA	3.20	0.26	4.15	35.90	9.59	1636.69
Colleye	2012	75	*Amphiprion clarkii*	Reef	JTS	Territorial Aggression	18	13.30	71.66	14.80	0.60	32.00	4.30	1.60	4.15	NA	NA	NA

Colleye	2012	75	*Amphiprion clarkii*	Reef	JTS	Territorial Aggression	18	15.20	71.66	13.70	0.80	32.00	5.50	2.00	4.15	NA	NA	NA
Colleye	2012	75	*Amphiprion clarkii*	Reef	JTS	Territorial Aggression	18	12.40	71.66	14.90	0.70	32.00	6.40	2.60	4.15	NA	NA	NA
Colleye	2012	75	*Amphiprion clarkii*	Reef	JTS	Territorial Aggression	18	20.40	71.66	14.80	0.90	32.00	5.00	1.90	4.15	NA	NA	NA
Colleye	2012	75	*Amphiprion clarkii*	Reef	JTS	Territorial Aggression	18	16.40	71.66	14.90	0.80	32.00	3.90	2.10	4.15	NA	NA	NA
Colleye	2012	75	*Amphiprion clarkii*	Reef	JTS	Territorial Aggression	18	19.30	71.66	13.00	0.70	32.00	4.40	3.30	4.15	NA	NA	NA
Colleye	2012	75	*Amphiprion clarkii*	Reef	JTS	Territorial Aggression	18	11.90	71.66	15.80	0.70	32.00	3.40	1.80	4.15	NA	NA	NA
Colleye	2012	75	*Amphiprion clarkii*	Reef	JTS	Territorial Aggression	18	12.90	71.66	15.20	0.80	32.00	4.80	1.70	4.15	NA	NA	NA
Colleye	2012	75	*Amphiprion clarkii*	Reef	JTS	Territorial Aggression	18	14.50	71.66	13.60	0.90	32.00	4.20	2.40	4.15	NA	NA	NA
Colleye	2012	75	*Amphiprion clarkii*	Reef	JTS	Territorial Aggression	18	10.10	71.66	10.80	1.30	32.00	3.70	1.60	4.15	NA	NA	NA
Colleye	2012	75	*Amphiprion clarkii*	Reef	JTS	Territorial Aggression	18	20.20	71.66	15.90	0.70	32.00	4.40	2.50	4.15	NA	NA	NA
Colleye	2012	75	*Amphiprion clarkii*	Reef	JTS	Territorial Aggression	18	15.40	71.66	14.90	0.80	32.00	4.90	2.10	4.15	NA	NA	NA
Colleye	2012	75	*Amphiprion clarkii*	Reef	JTS	Territorial Aggression	18	16.30	71.66	19.70	0.90	32.00	5.00	2.10	4.15	NA	NA	NA
Colleye	2012	75	*Amphiprion clarkii*	Reef	JTS	Territorial Aggression	18	14.30	71.66	15.90	0.90	32.00	4.10	2.10	4.15	NA	NA	NA
Colleye	2012	75	*Amphiprion clarkii*	Reef	JTS	Territorial Aggression	18	23.50	71.66	13.50	0.90	32.00	3.30	1.60	4.15	NA	NA	NA
Colleye	2012	75	*Amphiprion clarkii*	Reef	JTS	Territorial Aggression	18	15.50	71.66	15.10	0.60	32.00	2.90	1.10	4.15	NA	NA	NA
Colleye	2012	75	*Amphiprion clarkii*	Reef	JTS	Territorial Aggression	18	20.30	71.66	15.30	0.90	32.00	4.60	1.90	4.15	NA	NA	NA
Colleye	2012	75	*Amphiprion clarkii*	Reef	JTS	Territorial Aggression	18	13.50	71.66	15.50	0.90	32.00	5.50	2.60	4.15	NA	NA	NA
Danley	2012	76	*Cynotilapia afra*	Benthopelagic	Unknown	Courtship	1	6.61	71.66	9.30	1.19	32.00	13.10	5.86	4.15	446.20	189.87	1636.69
Danley	2012	76	*Labeotropheus fuelleborni*	Benthopelagic	Unknown	Courtship	1	5.68	71.66	9.20	0.76	32.00	11.50	3.87	4.15	363.80	148.29	1636.69
Danley	2012	76	*Maylandia aurora*	Demersal	Unknown	Courtship	1	8.57	71.66	12.40	2.33	32.00	11.80	3.52	4.15	375.80	125.35	1636.69
Danley	2012	76	*Maylandia callainos*	Demersal	Unknown	Courtship	1	4.25	71.66	5.30	0.99	32.00	10.90	2.88	4.15	204.70	107.67	1636.69
Danley	2012	76	*Maylandia zebra*	Demersal	JTS	Courtship	1	13.48	71.66	16.10	4.60	32.00	17.20	11.59	4.15	763.30	407.11	1636.69
Danley	2012	76	*Petrotilapia nigra*	Demersal	Unknown	Courtship	1	4.61	71.66	10.00	3.00	32.00	18.30	8.51	4.15	422.30	217.36	1636.69
Knight	2012	77	*Agamyxis pectinifrons*	Demersal	PSS	Disturbance	7	NA	NA	NA	NA	NA	NA	NA	NA	121.70	10.05	1636.69
Knight	2012	77	*Agamyxis pectinifrons*	Demersal	PSS	Disturbance	7	NA	NA	NA	NA	NA	NA	NA	NA	131.40	2.91	1636.69
Knight	2012	77	*Agamyxis pectinifrons*	Demersal	SSM	Disturbance	7	NA	NA	NA	NA	NA	NA	NA	NA	276.30	42.07	1636.69
Knight	2012	77	*Amblydoras affinis*	Demersal	PSS	Disturbance	5	NA	NA	NA	NA	NA	NA	NA	NA	78.90	2.00	1636.69
Knight	2012	77	*Amblydoras affinis*	Demersal	PSS	Disturbance	5	NA	NA	NA	NA	NA	NA	NA	NA	95.60	2.68	1636.69
Knight	2012	77	*Amblydoras affinis*	Demersal	SSM	Disturbance	5	NA	NA	NA	NA	NA	NA	NA	NA	88.00	42.26	1636.69
Knight	2012	77	*Hemidoras morrisi*	Demersal	PSS	Disturbance	12	NA	NA	NA	NA	NA	NA	NA	NA	57.70	1.73	1636.69

Knight	2012	77	*Hemidoras morrisi*	Demersal	PSS	Disturbance	12	NA	NA	NA	NA	NA	NA	NA	NA	67.40	2.42	1636.69
Knight	2012	77	*Hemidoras morrisi*	Demersal	PSS	Disturbance	12	NA	NA	NA	NA	NA	NA	NA	NA	74.70	22.86	1636.69
Knight	2012	77	*Megalodoras uranoscopus*	Demersal	PSS	Disturbance	10	NA	NA	NA	NA	NA	NA	NA	NA	126.20	6.01	1636.69
Knight	2012	77	*Megalodoras uranoscpous*	Demersal	PSS	Disturbance	10	NA	NA	NA	NA	NA	NA	NA	NA	98.40	3.79	1636.69
Knight	2012	77	*Megalodoras uranoscpous*	Demersal	PSS	Disturbance	10	NA	NA	NA	NA	NA	NA	NA	NA	70.60	12.97	1636.69
Knight	2012	77	*Oxydoras niger*	Demersal	PSS	Disturbance	3	NA	NA	NA	NA	NA	NA	NA	NA	83.40	2.77	1636.69
Knight	2012	77	*Oxydoras niger*	Demersal	PSS	Disturbance	3	NA	NA	NA	NA	NA	NA	NA	NA	93.00	5.02	1636.69
Knight	2012	77	*Oxydoras niger*	Demersal	SSM	Disturbance	3	NA	NA	NA	NA	NA	NA	NA	NA	138.70	21.48	1636.69
Maruska	2012	78	*Astatotilapia burtoni*	Benthopelagic	JTS	Courtship	22	13.39	71.66	NA	NA	NA	8.50	4.10	4.15	239.50	136.80	1636.69
Mosharo	2012	79	*Batrachoides gilberti*	Demersal	SSM	Courtship	1	NA	NA	NA	NA	NA	NA	NA	NA	298.00	34.00	1636.69
Mosharo	2012	79	*Batrachoides gilberti*	Demersal	SSM	Courtship	1	NA	NA	NA	NA	NA	NA	NA	NA	305.00	35.00	1636.69
Mosharo	2012	79	*Batrachoides gilberti*	Demersal	SSM	Courtship	1	NA	NA	NA	NA	NA	NA	NA	NA	308.00	34.00	1636.69
Mosharo	2012	79	*Batrachoides gilberti*	Demersal	SSM	Courtship	1	NA	NA	NA	NA	NA	NA	NA	NA	334.00	43.00	1636.69
Mosharo	2012	79	*Batrachoides gilberti*	Demersal	SSM	Courtship	1	NA	NA	NA	NA	NA	NA	NA	NA	343.00	37.00	1636.69
Mosharo	2012	79	*Batrachoides gilberti*	Demersal	SSM	Courtship	1	NA	NA	NA	NA	NA	NA	NA	NA	435.00	11.00	1636.69
Mosharo	2012	79	*Sanopus astrifer*	Reef	SSM	Courtship	1	NA	NA	NA	NA	NA	NA	NA	NA	232.00	36.00	1636.69
Mosharo	2012	79	*Sanopus astrifer*	Reef	SSM	Courtship	1	NA	NA	NA	NA	NA	NA	NA	NA	234.00	37.00	1636.69
Mosharo	2012	79	*Sanopus astrifer*	Reef	SSM	Courtship	1	NA	NA	NA	NA	NA	NA	NA	NA	249.00	25.00	1636.69
Scharer	2012	80	*Epinephelus striatus*	Reef	SSM	Courtship	12	NA	NA	NA	NA	NA	NA	NA	NA	1600.00	300.00	1636.69
Tellechea	2012	81	*Cynoscion guatucupa*	Benthopelagic	SSM	Courtship	31	84.00	71.66	28.80	7.04	32.00	4.40	1.66	4.15	219.00	83.70	1636.69
Tellechea	2012	81	*Cynoscion guatucupa*	Benthopelagic	SSM	Courtship	29	NA	NA	28.60	4.72	32.00	NA	NA	NA	NA	NA	NA
Tellechea	2012	81	*Cynoscion guatucupa*	Benthopelagic	SSM	Disturbance	38	2.39	71.66	7.40	1.63	32.00	27.20	8.60	4.15	NA	NA	NA
Amorim	2013	82	*Pomatoschistus pictus*	Demersal	PGM	Courtship	19	3.39	71.66	NA	NA	NA	27.20	11.90	4.15	692.90	343.83	1636.69
Bolgan	2013	83	*Pomatoschistus pictus*	Demersal	PGM	Courtship	5	2.60	71.66	NA	NA	NA	22.00	9.60	4.15	575.20	242.90	1636.69
Bolgan	2013	83	*Pomatoschistus pictus*	Demersal	PGM	Territorial Aggression	6	2.60	71.66	NA	NA	NA	32.70	10.20	4.15	1062.00	347.00	1636.69
Colleye	2013	84	*Cottus perifretum*	Benthopelagic	PGM	Territorial Aggression	9	9.04	71.66	38.50	7.60	32.00	4.00	0.90	4.15	229.80	41.50	1636.69
Colleye	2013	84	*Cottus rhenanus*	Benthopelagic	PGM	Territorial Aggression	9	5.04	71.66	30.30	3.90	32.00	3.20	0.50	4.15	128.10	21.30	1636.69
Longrie	2013	85	*Oreochromis niloticus*	Benthopelagic	PGM	Territorial Aggression	5	60.85	71.66	NA	NA	NA	3.10	2.65	4.15	620.70	267.22	1636.69
Parmentier	2013	86	*Gobius paganellus*	Demersal	PGM	Territorial Aggression	18	NA	NA	NA	NA	NA	11.00	5.00	4.15	192.00	52.50	1636.69
Parmentier	2013	86	*Gobius paganellus*	Demersal	PGM	Territorial Aggression	15	NA	NA	NA	NA	NA	31.00	7.00	4.15	344.00	109.00	1636.69
Parsons	2013	87	*Glaucosoma hebraicum*	Reef	SSM	Disturbance	1	NA	NA	NA	NA	NA	3.40	2.36	4.15	380.00	390.00	1636.69
Parsons	2013	87	*Glaucosoma hebraicum*	Reef	SSM	Disturbance	1	NA	NA	NA	NA	NA	3.60	1.50	4.15	390.00	290.00	1636.69
Pedroso	2013	88	*Pomatoschistus minutus*	Demersal	PGM	Courtship	21	NA	NA	NA	NA	NA	24.80	12.20	4.15	797.20	395.40	1636.69
Pedroso	2013	88	*Pomatoschistus pictus*	Demersal	PGM	Courtship	16	NA	NA	NA	NA	NA	23.30	6.50	4.15	628.80	171.80	1636.69
Bertucci	2014	89	*Haemulon flavolineatum*	Reef	JTS	Disturbance	9	NA	NA	NA	NA	NA	6.00	2.00	4.15	47.00	11.00	1636.69

Boyle	2014	90	*Synodontis angelica*	Benthopelagic	PSS	Disturbance	3	NA	NA	39.00	24.25	32.00	6.40	5.20	4.15	1060.00	1195.12	1636.69
Boyle	2014	90	*Synodontis angelica*	Benthopelagic	PSS	Disturbance	3	NA	NA	NA	NA	NA	NA	NA	NA	185.00	18.38	1636.69
Boyle	2014	90	*Synodontis euptera*	Benthopelagic	PSS	Disturbance	4	NA	NA	16.00	4.00	32.00	4.20	2.20	4.15	1020.00	700.00	1636.69
Boyle	2014	90	*Synodontis euptera*	Benthopelagic	PSS	Disturbance	4	NA	NA	NA	NA	NA	NA	NA	NA	242.00	103.92	1636.69
Boyle	2014	90	*Synodontis grandiops*	Demersal	PSS	Disturbance	6	NA	NA	29.00	17.15	32.00	19.60	12.74	4.15	3900.00	2253.53	1636.69
Boyle	2014	90	*Synodontis grandiops*	Demersal	PSS	Disturbance	6	NA	NA	NA	NA	NA	NA	NA	NA	193.00	78.26	1636.69
Boyle	2014	90	*Synodontis marmorata*	Benthopelagic	PSS	Disturbance	7	NA	NA	17.00	2.65	32.00	4.60	1.85	4.15	890.00	423.32	1636.69
Boyle	2014	90	*Synodontis marmorata*	Benthopelagic	PSS	Disturbance	7	NA	NA	NA	NA	NA	NA	NA	NA	183.00	247.52	1636.69
Ghahramani	2014	91	*Ictalurus furcatus*	Demersal	PSS	Disturbance	10	NA	NA	4.00	0.90	32.00	11.70	2.70	4.15	93.80	44.80	1636.69
Holt	2014	92	*Cyprinella venusta*	Benthopelagic	Unknown	Courtship	18	1.37	71.66	7.10	0.99	32.00	22.20	10.51	4.15	133.40	62.57	1636.69
Holt	2014	92	*Cyprinella venusta*	Benthopelagic	Unknown	Courtship	18	3.27	71.66	7.30	0.85	32.00	32.20	13.57	4.15	79.10	31.03	1636.69
Holt	2014	92	*Cyprinella venusta*	Benthopelagic	Unknown	Territorial Aggression	14	NA	NA	13.50	3.69	32.00	1.00	0.00	4.15	13.50	3.69	1636.69
Holt	2014	92	*Cyprinella venusta*	Benthopelagic	Unknown	Territorial Aggression	14	NA	NA	15.20	3.65	32.00	1.00	0.00	4.15	15.20	3.65	1636.69
Kever	2014	93	*Ophidion rochei*	Demersal	SSM	Courtship	1	2.80	71.66	7.50	2.80	32.00	34.50	4.60	4.15	NA	NA	NA
Kever	2014	93	*Ophidion rochei*	Demersal	SSM	Courtship	1	1.60	71.66	15.30	1.70	32.00	32.30	3.40	4.15	NA	NA	NA
Kever	2014	93	*Ophidion rochei*	Demersal	SSM	Courtship	1	0.70	71.66	10.40	1.40	32.00	31.70	1.30	4.15	NA	NA	NA
Kever	2014	93	*Ophidion rochei*	Demersal	SSM	Courtship	1	2.30	71.66	12.90	2.90	32.00	36.60	4.70	4.15	NA	NA	NA
Kever	2014	93	*Ophidion rochei*	Demersal	SSM	Courtship	1	0.90	71.66	10.90	2.60	32.00	28.30	4.00	4.15	NA	NA	NA
McIver	2014	94	*Porichthys notatus*	Demersal	SSM	Agonistic	3	NA	NA	NA	NA	NA	NA	NA	NA	73.80	24.00	1636.69
McIver	2014	94	*Porichthys notatus*	Demersal	SSM	Courtship	9	NA	NA	NA	NA	NA	NA	NA	NA	70000.00	88780.00	1636.69
Mensinger	2014	95	*Opsanus tau*	Reef	SSM	Courtship	1	NA	NA	NA	NA	NA	NA	NA	NA	331.60	13.30	1636.69
Mensinger	2014	95	*Opsanus tau*	Reef	SSM	Courtship	1	NA	NA	NA	NA	NA	NA	NA	NA	385.30	6.80	1636.69
Mensinger	2014	95	*Opsanus tau*	Reef	SSM	Courtship	1	NA	NA	NA	NA	NA	NA	NA	NA	398.20	21.10	1636.69
Mensinger	2014	95	*Opsanus tau*	Reef	SSM	Courtship	1	NA	NA	NA	NA	NA	NA	NA	NA	403.00	7.20	1636.69
Mensinger	2014	95	*Opsanus tau*	Reef	SSM	Courtship	1	NA	NA	NA	NA	NA	NA	NA	NA	467.00	6.70	1636.69
Oliviera	2014	96	*Hippocampus reidi*	Reef	CBS	Courtship	5	NA	NA	30.00	15.21	32.00	1.00	0.00	4.15	20.00	15.21	1636.69
Oliviera	2014	96	*Hippocampus reidi*	Reef	CBS	Courtship	5	NA	NA	18.80	9.62	32.00	1.00	0.00	4.15	18.80	9.62	1636.69
Oliviera	2014	96	*Hippocampus reidi*	Reef	CBS	Disturbance	8	31.11	71.66	34.90	2.83	32.00	NA	NA	NA	NA	NA	NA
Oliviera	2014	96	*Hippocampus reidi*	Reef	CBS	Disturbance	8	22.63	71.66	36.30	3.68	32.00	NA	NA	NA	NA	NA	NA
Bertucci	2015	97	*Epinephelus marginatus*	Reef	SSM	Courtship	1	40.00	71.66	52.00	11.00	32.00	3.00	1.00	4.15	712.00	360.00	1636.69
Bertucci	2015	97	*Epinephelus marginatus*	Reef	SSM	Courtship	2	NA	NA	NA	NA	NA	1.00	0.00	4.15	NA	NA	NA
Ladich	2015	98	*Trichopsis vittata*	Demersal	FM	Territorial Aggression	11	0.99	71.66	NA	NA	NA	6.20	0.33	4.15	NA	NA	NA
Ladich	2015	98	*Trichopsis vittata*	Demersal	FM	Territorial Aggression	11	1.89	71.66	NA	NA	NA	7.50	1.33	4.15	NA	NA	NA
Ladich	2015	98	*Trichopsis vittata*	Demersal	FM	Territorial Aggression	11	2.42	71.66	NA	NA	NA	7.00	1.33	4.15	NA	NA	NA
Lim	2015	99	*Hippocampus comes*	Reef	PGM	Disturbance	5	NA	NA	NA	NA	NA	NA	NA	NA	46.30	16.60	1636.69
Tricas	2015	100	*Chaetodon auriga*	Reef	JTS	Territorial Aggression	5	0.00	71.66	93.00	43.00	32.00	2.00	0.00	4.15	677.00	0.00	1636.69

Tricas	2015	100	*Chaetodon kleinii*	Reef	JTS	Territorial Aggression	3	NA	NA	17.00	13.00	32.00	1.00	0.00	4.15	17.00	13.00	1636.69
Tricas	2015	100	*Chaetodon multicinctus*	Reef	FM	Territorial Aggression	7	121.00	71.66	418.00	381.00	32.00	2.80	0.96	4.15	1030.00	656.00	1636.69
Tricas	2015	100	*Chaetodon multicinctus*	Reef	Unknown	Territorial Aggression	9	107.00	71.66	25.00	25.00	32.00	3.60	0.59	4.15	680.00	630.00	1636.69
Tricas	2015	100	*Chaetodon ornatissimus*	Reef	FM	Territorial Aggression	1	161.00	71.66	366.00	390.00	32.00	2.00	0.00	4.15	1085.00	243.00	1636.69
Tricas	2015	100	*Chaetodon ornatissimus*	Reef	FM	Territorial Aggression	1	NA	NA	134.00	47.00	32.00	1.00	0.00	4.15	134.00	47.00	1636.69
Tricas	2015	100	*Chaetodon unimaculatus*	Reef	PGM	Territorial Aggression	3	NA	NA	52.00	38.00	32.00	1.00	0.00	4.15	52.00	38.00	1636.69
Tricas	2015	100	*Forcipiger flavissimus*	Reef	FM	Territorial Aggression	2	15.00	71.66	54.00	19.00	32.00	5.30	1.89	4.15	852.00	286.00	1636.69
Tricas	2015	100	*Forcipiger flavissimus*	Reef	Unknown	Territorial Aggression	3	291.00	71.66	29.00	14.00	32.00	2.00	0.00	4.15	590.00	290.00	1636.69
Vicente	2015	101	*Pomatoschistus pictus*	Demersal	PGM	Courtship	3	1.04	71.66	7.50	0.52	32.00	33.70	7.27	4.15	658.40	164.89	1636.69
Vicente	2015	101	*Pomatoschistus pictus*	Demersal	PGM	Courtship	6	1.96	71.66	8.10	0.98	32.00	40.10	5.14	4.15	795.90	60.99	1636.69
Vicente	2015	101	*Pomatoschistus pictus*	Demersal	PGM	Courtship	6	1.22	71.66	7.80	1.71	32.00	32.50	10.29	4.15	691.40	210.66	1636.69
Vicente	2015	101	*Pomatoschistus pictus*	Demersal	PGM	Courtship	7	1.59	71.66	8.70	0.79	32.00	39.60	10.85	4.15	923.80	273.31	1636.69
Vicente	2015	101	*Pomatoschistus pictus*	Demersal	PGM	Courtship	6	1.22	71.66	8.30	0.49	32.00	39.70	5.63	4.15	931.80	130.31	1636.69
Vicente	2015	101	*Pomatoschistus pictus*	Demersal	PGM	Courtship	8	0.57	71.66	9.20	1.41	32.00	41.10	6.22	4.15	1034.60	140.86	1636.69
Vicente	2015	101	*Pomatoschistus pictus*	Demersal	PGM	Courtship	8	1.70	71.66	9.70	0.85	32.00	39.20	6.51	4.15	1139.30	191.48	1636.69
Vicente	2015	101	*Pomatoschistus pictus*	Demersal	PGM	Courtship	8	1.98	71.66	9.80	0.57	32.00	41.50	8.77	4.15	1310.70	269.83	1636.69
Vicente	2015	101	*Pomatoschistus pictus*	Demersal	PGM	Courtship	6	4.16	71.66	10.00	0.49	32.00	33.60	7.10	4.15	1128.00	256.71	1636.69
Zhang	2015	102	*Sebastiscus marmoratus*	Demersal	SSM	Disturbance	20	103.00	71.66	28.00	2.80	32.00	7.00	1.60	4.15	NA	NA	NA
Zhang	2015	102	*Sebastiscus marmoratus*	Demersal	SSM	Disturbance	20	261.00	71.66	37.00	4.30	32.00	2.60	1.60	4.15	NA	NA	NA
Horvatic	2016	103	*Neogobius ?uviatilis*	Benthopelagic	PGM	Courtship	8	NA	NA	NA	NA	NA	12.00	2.90	4.15	161.00	38.50	1636.69
Horvatic	2016	103	*Neogobius ?uviatilis*	Benthopelagic	PGM	Territorial Aggression	8	NA	NA	NA	NA	NA	12.70	1.30	4.15	179.00	29.50	1636.69
Horvatic	2016	103	*Neogobius ?uviatilis*	Benthopelagic	PGM	Territorial Aggression	5	NA	NA	NA	NA	NA	12.20	1.30	4.15	163.60	20.50	1636.69
Melotte	2016	104	*Pygocentrus nattereri*	Pelagic	SSM	Disturbance	12	0.60	71.66	NA	NA	NA	11.70	3.00	4.15	86.40	27.60	1636.69
Melotte	2016	104	*Serrasalmus compressus*	Benthopelagic	SSM	Disturbance	7	0.40	71.66	NA	NA	NA	10.00	1.50	4.15	71.80	12.00	1636.69
Melotte	2016	104	*Serrasalmus eigenmanni*	Benthopelagic	SSM	Disturbance	10	0.60	71.66	NA	NA	NA	8.40	1.40	4.15	74.90	13.70	1636.69
Melotte	2016	104	*Serrasalmus elongatus*	Benthopelagic	SSM	Disturbance	9	0.50	71.66	NA	NA	NA	18.60	5.10	4.15	123.70	29.70	1636.69
Melotte	2016	104	*Serrasalmus manueli*	Benthopelagic	SSM	Disturbance	4	0.60	71.66	NA	NA	NA	8.30	1.30	4.15	89.80	14.80	1636.69
Melotte	2016	104	*Serrasalmus marginatus*	Benthopelagic	SSM	Disturbance	6	0.40	71.66	NA	NA	NA	10.10	2.00	4.15	70.50	13.90	1636.69
Melotte	2016	104	*Serrasalmus rhombeus*	Benthopelagic	SSM	Disturbance	8	0.60	71.66	NA	NA	NA	7.20	1.10	4.15	62.60	8.80	1636.69
Melotte	2016	104	*Serrasalmus spilopleura*	Benthopelagic	SSM	Disturbance	7	0.40	71.66	NA	NA	NA	10.10	2.30	4.15	73.10	17.80	1636.69
Montie	2016	105	*Sciaenops ocellatus*	Demersal	SSM	Courtship	2	NA	NA	NA	NA	NA	6.20	2.39	4.15	700.00	140.00	1636.69
Montie	2016	105	*Sciaenops ocellatus*	Demersal	SSM	Courtship	2	NA	NA	NA	NA	NA	5.90	2.41	4.15	730.00	170.00	1636.69
Montie	2016	105	*Sciaenops ocellatus*	Demersal	SSM	Courtship	1	NA	NA	NA	NA	NA	2.30	0.65	4.15	410.00	110.00	1636.69
Montie	2016	105	*Sciaenops ocellatus*	Demersal	SSM	Courtship	1	NA	NA	NA	NA	NA	3.60	2.59	4.15	560.00	240.00	1636.69
Parmentier	2016	106	*Pelates quadrilineatus*	Reef	SSM	Disturbance	6	0.30	71.66	NA	NA	NA	NA	NA	NA	84.00	15.00	1636.69

Parmentier	2016	106	*Pempheris oualensis*	Reef	SSM	Disturbance	3	1.00	71.66	3.70	0.50	32.00	NA	NA	NA	49.00	23.00	1636.69
Parmentier	2016	106	*Terapon jarbua*	Demersal	SSM	Disturbance	3	0.60	71.66	NA	NA	NA	NA	NA	NA	81.00	15.00	1636.69
Picciulin	2016	107	*Umbrina cirrosa*	Demersal	SSM	Courtship	30	16.80	71.66	38.00	10.30	32.00	2.40	1.10	4.15	186.50	16.80	1636.69
Parmentier	2017	108	*Rhinecanthus aculeatus*	Reef	FM	Disturbance	11	NA	NA	NA	NA	NA	10.50	6.00	4.15	93.00	63.00	1636.69
Parmentier	2017	109	*Pomatoschistus pictus*	Demersal	PGM	Courtship	17	4.00	71.66	NA	NA	NA	21.00	9.00	4.15	NA	NA	NA
Spinks	2017	110	*Neolamprologus pulcher*	Benthopelagic	JTS	Agonistic	4	NA	NA	11.50	3.50	32.00	2.00	0.70	4.15	896.00	804.40	1636.69
Spinks	2017	110	*Neolamprologus pulcher*	Benthopelagic	JTS	Agonistic	7	NA	NA	1.50	0.50	32.00	NA	NA	NA	NA	NA	NA
Tellechea	2017	111	*Umbrina canosai*	Demersal	SSM	Disturbance	34	23.16	71.66	27.30	22.62	32.00	NA	NA	NA	NA	NA	NA
Parmentier	2018	112	*Genypterus chilensis*	Bathydemersal	SSM	Courtship	9	4.00	71.66	6.00	5.00	32.00	12.00	3.00	4.15	221.00	31.00	1636.69
Parmentier	2018	112	*Genypterus maculatus*	Demersal	SSM	Courtship	11	2.00	71.66	NA	NA	NA	NA	NA	NA	332.00	87.00	1636.69
Parmentier	2018	112	*Genypterus maculatus*	Demersal	SSM	Courtship	11	171.00	71.66	52.00	13.00	32.00	NA	NA	NA	NA	NA	NA
Radford	2018	113	*Zeus faber*	Benthopelagic	SSM	Disturbance	10	1.00	71.66	18.00	1.00	32.00	8.00	0.00	4.15	139.00	4.00	1636.69
Rountree	2018	114	*Pygocentrus nattereri*	Pelagic	SSM	Disturbance	39	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Rountree	2018	114	*Serrasalmus maculatus*	Pelagic	Unknown	Disturbance	12	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Rountree	2018	114	*Serrasalmus sanchezi*	Benthopelagic	Unknown	Disturbance	3	1.73	71.66	NA	NA	NA	8.30	1.04	4.15	83.00	24.25	1636.69
Rountree	2018	114	*Serrasalmus spp.*	NA	Unknown	Disturbance	27	NA	NA	138.00	15.59	32.00	8.40	1.56	4.15	62.00	15.59	1636.69
Smith	2018	115	*Prochilodus argenteus*	Benthopelagic	SSM	Courtship	3	2.42	71.66	13.50	1.91	32.00	NA	NA	NA	5100.00	866.03	1636.69
Smith	2018	115	*Prochilodus argenteus*	Benthopelagic	SSM	Courtship	3	NA	NA	15.70	6.41	32.00	1.00	0.00	4.15	15.70	6.41	1636.69
Smith	2018	115	*Prochilodus costatus*	Benthopelagic	SSM	Courtship	3	0.35	71.66	9.70	2.60	32.00	NA	NA	NA	4700.00	1558.85	1636.69
Smith	2018	115	*Prochilodus costatus*	Benthopelagic	SSM	Courtship	3	NA	NA	14.50	6.06	32.00	1.00	0.00	4.15	14.50	6.06	1636.69
Smith	2018	115	*Prochilodus lineatus*	Benthopelagic	SSM	Courtship	3	5.54	71.66	11.30	2.42	32.00	NA	NA	NA	5200.00	692.82	1636.69
Smith	2018	115	*Prochilodus lineatus*	Benthopelagic	SSM	Courtship	3	NA	NA	10.00	1.04	32.00	1.00	0.00	4.15	10.00	1.04	1636.69
Horvatic	2019	116	*Perccottus glenii*	Demersal	PGM	Courtship	3	NA	NA	NA	NA	NA	9.70	1.40	4.15	89.70	16.80	1636.69
Horvatic	2019	116	*Perccottus glenii*	Demersal	PGM	Courtship	6	NA	NA	NA	NA	NA	8.70	0.90	4.15	95.50	7.30	1636.69
Horvatic	2019	116	*Perccottus glenii*	Demersal	PGM	Courtship	6	NA	NA	NA	NA	NA	7.60	1.10	4.15	99.90	32.80	1636.69
Tellechea	2019	117	*Macrodon atricauda*	Demersal	SSM	Courtship	5	92.61	71.66	25.80	6.18	32.00	13.00	2.38	4.15	230.00	92.40	1636.69
Tellechea	2019	117	*Macrodon atricauda*	Demersal	SSM	Disturbance	5	3.31	71.66	19.00	2.95	32.00	NA	NA	NA	NA	NA	NA
Bolgan	2020	118	*Argyrosomus regius*	Benthopelagic	SSM	Courtship	17	1.90	71.66	NA	NA	NA	12.40	5.50	4.15	220.50	86.10	1636.69
Bolgan	2020	118	*Argyrosomus regius*	Benthopelagic	SSM	Spawning	17	2.00	71.66	NA	NA	NA	34.30	15.20	4.15	594.90	305.50	1636.69
Bolgan	2020	118	*Sciaenops ocellatus*	Demersal	SSM	Spawning	8	16.00	71.66	NA	NA	NA	10.10	2.60	4.15	656.60	153.20	1636.69
Bolgan	2020	118	*Umbrina cirrosa*	Demersal	SSM	Courtship	5	45.30	71.66	NA	NA	NA	2.10	0.30	4.15	360.40	41.30	1636.69
Bolgan	2020	118	*Umbrina cirrosa*	Demersal	SSM	Spawning	5	10.50	71.66	NA	NA	NA	2.50	0.50	4.15	513.90	125.40	1636.69
Holt	2020	119	*Cottus carolinae*	Demersal	PGM	Territorial Aggression	12	446.90	71.66	6.20	1.60	32.00	5.00	3.70	4.15	4100.00	1300.00	1636.69
Holt	2020	119	*Cottus carolinae*	Demersal	PGM	Territorial Aggression	5	NA	NA	NA	NA	NA	NA	NA	NA	390.30	250.40	1636.69
Liesch	2020	120	*Trichopsis pumila*	Benthopelagic	FM	Territorial Aggression	13	1.19	71.66	NA	NA	NA	2.10	0.69	4.15	NA	NA	NA
Liesch	2020	120	*Trichopsis pumila*	Benthopelagic	FM	Territorial Aggression	12	5.92	71.66	NA	NA	NA	1.10	0.21	4.15	NA	NA	NA
Pereira	2020	121	*Argyrosomus regius*	Benthopelagic	SSM	Courtship	10	3.00	71.66	NA	NA	NA	28.00	14.00	4.15	574.00	304.00	1636.69
Pereira	2020	121	*Argyrosomus regius*	Benthopelagic	SSM	Disturbance	6	1.00	71.66	NA	NA	NA	16.00	3.00	4.15	133.00	29.00	1636.69

Pereira	2020	121	*Argyrosomus regius*	Benthopelagic	SSM	Disturbance	4	2.00	71.66	NA	NA	NA	15.00	6.00	4.15	220.00	85.00	1636.69
Boyle	2015	122	*Acanthodoras cataphractus*	Demersal	SSM	Disturbance	3	NA	NA	NA	NA	NA	NA	NA	NA	252.00	176.00	1636.69
Boyle	2015	122	*Acanthodoras cataphractus*	Demersal	SSM	Disturbance	3	NA	NA	NA	NA	NA	NA	NA	NA	589.00	514.00	1636.69
Boyle	2015	122	*Agamyxis pectinifrons*	Demersal	SSM	Disturbance	3	NA	NA	NA	NA	NA	NA	NA	NA	246.00	2.00	1636.69
Boyle	2015	122	*Agamyxis pectinifrons*	Demersal	SSM	Disturbance	3	NA	NA	NA	NA	NA	NA	NA	NA	613.00	271.00	1636.69
Boyle	2015	122	*Platydoras hancockii*	Demersal	SSM	Disturbance	7	NA	NA	NA	NA	NA	NA	NA	NA	76.00	74.00	1636.69
Boyle	2015	122	*Platydoras hancockii*	Demersal	SSM	Disturbance	7	NA	NA	NA	NA	NA	NA	NA	NA	265.00	147.00	1636.69
Ladich	2020	123	*Trichopsis schalleri*	Benthopelagic	FM	Territorial Aggression	1	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA

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