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FACULTY OF ENGINEERING & PHYSICAL SCIENCES

Civil, Maritime and Environmental Engineering

Group behavioural responses of cyprinid fishes to artificial acoustic stimuli: Implications for fisheries management

by

Helen Ann Laura Currie

BSc (Hons), MSc, MRSB, AFHEA

ORCID ID [0000-0001-5792-3488](https://orcid.org/0000-0001-5792-3488)

Thesis for the degree of Doctor of Philosophy

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The only thing that overcomes hard luck is hard work.

- Harry Golden.

University of Southampton

ABSTRACT

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Rising levels of anthropogenic underwater sound may have negative consequences on freshwater ecosystems. Additionally, the biological relevance of sound to fish and observed responses to human-generated noise promote the use of acoustics in behavioural guidance technologies that are deployed to control the movement of fish. For instance, acoustic stimuli may be used to prevent the spread of invasive fishes or facilitate the passage of vulnerable native species at man-made obstructions. However, a strong understanding of fish response to acoustics is needed for it to be effectively deployed as a fisheries management tool, but such information is lacking. Therefore, this thesis investigated the group behavioural responses of cyprinids to acoustic stimuli. A quantitative meta-analysis and experimental studies conducted in a small-tank or large open-channel flume were used to address key knowledge gaps that are necessary to improve the sustainability of acoustic deterrent technologies, and assist in conservation efforts to reduce the negative impacts of anthropogenic noise.

Current understanding on the impact of anthropogenic noise on fishes (marine, freshwater and euryhaline species) was quantified. The impact of man-made sound is greatest for fish experiencing anatomical damage, for adult and juveniles compared to earlier life-stages, and for fish occupying freshwater environments. These findings suggest a review of the current legislation covering aquatic noise mitigation which commonly focus on marine-centric strategies, thereby undervaluing the susceptibility of freshwater fish to the rising levels of anthropogenic sound. Limitations and knowledge gaps within the literature were also identified, including: 1) group behavioural responses to sound, 2) the response of fish to different fundamental acoustic properties of sound, 3) system longevity (*e.g.* habituation to a repeated sound exposure), and 4) site-specific constraints.

Fish movement and space use were quantified using fine-scale behavioural metrics (*e.g.* swimming speed, shoal distribution, cohesion, orientation, rate of tolerance and signal detection theory) and their collective response to acoustics assessed using two approaches. First, a still-water small tank set-up allowed for the careful control of confounding factors while investigating cyprinid group response to fundamental acoustic properties of sound (*e.g.* complexity, pulse repetition rate, signal-to-noise ratio). Second, a large open-channel flume enabled the ability of a shoal to detect and respond to acoustic signals to be quantified under different water velocities.

Shoals of European minnow (*Phoxinus phoxinus*), common carp (*Cyprinus carpio*) and roach (*Rutilus rutilus*) altered their swimming behaviour (*e.g.* increased group cohesion) in response to a simple low frequency tonal stimulus. The pulse repetition rate of a signal was observed to influence the long-term behavioural recovery of minnow to an acoustic stimulus. Furthermore, signal detection theory was deployed to quantify the impact of background masking noise on the group behavioural response of carp to a tonal stimulus, and investigate how higher water velocities commonly experienced by fish in the wild may influence the response of roach to an acoustic stimulus. Fine-scale behavioural responses were observed the higher the signal-to-noise ratio, and discriminability of an acoustic signal and the efficacy at which fish were deterred from an insonified channel was greatest under higher water velocities.

The information presented in this thesis significantly enhances our understanding of fish group responses to man-made underwater sound, and has direct applications in freshwater conservation, fish passage and invasive species management.

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
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List of Accompanying Materials

Currie, Helen, Ann Laura (2020). Dataset for: Collective behaviour of the European minnow (*Phoxinus phoxinus*) is influenced by signals of differing acoustic complexity. University of Southampton. doi: 10.5258/SOTON/D1182 [Dataset].

Currie, Helen, Ann Laura (2020) Dataset for: Group behavior and tolerance of Eurasian minnow (*Phoxinus phoxinus*) to tones of differing pulse repetition rate. University of Southampton. doi:10.5258/SOTON/D1231 [Dataset].

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List of Accompanying Materials

Research Thesis: Declaration of Authorship

Print name:	Helen Ann Laura Currie
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Title of thesis:	Group behavioural responses of cyprinids to artificial acoustic stimuli: Implications for fisheries management
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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:

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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;
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 - **Currie, H.A.L.**, White, P.R., Leighton, T.G., and Kemp, P.S. (2021). Collective behaviour of the European minnow (*Phoxinus phoxinus*) in response to signals of differing acoustic complexity. *Behav. Process.* **189**, 104416. doi:10.1016/j.beproc.2021.104416.
 - **Currie, H.A.L.**, White, P.R., Leighton, T.G., and Kemp, P.S. (2020). Group behavior and tolerance of European minnow (*Phoxinus phoxinus*) in response to tones of differing pulse repetition rate. *J. Acoust. Soc. Am.* **147(3)**, 1709-1718. doi: 10.1121/10.0000910.
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- **Currie, H.A.L.**, White, P.R., Leighton, T.G., and Kemp, P.S. (2019). Group behavioural response of juvenile common carp (*Cyprinus carpio*) to simultaneously masked tonal stimuli. *Proc. Mtgs. Acoust.* **37(1)**, 010008. doi: 10.1121/2.0001180.
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Definitions and Abbreviations

A. Referenced nomenclature

A.1 Fish order

Clupeiformes the order of ray-finned fish, including herring (Clupeidae) and anchovy (Engraulidae) families, including many important forage and food fishes. These fishes are physostomes, whereby a pneumatic duct connects the gas-filled swimbladder to the gut.

Ostariophysi the second largest superorder of fish, including 68% of all freshwater species. This superorder shares two common features: the possession of Weberian apparatus and the production of alarm substance.

Pleuronectiformes the ray-finned demersal fish order of flatfishes including important food fish such as flounders, soles, turbot, plaice and halibut.

A.2 Fish family and subfamily

Achiridae flatfish known as American soles

Acipenseridae known commonly as sturgeon

Amphiprioninae subfamily of the Pomacentridae family

Anguillidae catadromous ray finned, elongated/ snake-like fish including freshwater eels

Atherinidae Old World silversides

Apogonidae ray-finned fishes known as cardinalfishes

Batrachoididae only family in the order Batrachoidiformes. Commonly known as toadfish. Males commonly known to vocalise

Carangidae ray-finned fishes including jacks, pompanos, jack mackerels, runners and scads

Catostomidae suckers of the order Cypriniformes; almost exclusive to North America

Centrarchidae known commonly as sunfishes

Cichlidae common name cichlids; found in tropical America, mainland Africa, Madagascar and southern Asia

Clinidae temperate blennies of the order Blennioformes

Clupeidae ray-finned fish including herrings, shads, sardines, hilsa and menhadens; important food sources

Cyprinidae family of freshwater fish known as cyprinids, including carps, true minnows and relatives such as barbs and barbels; carp known to be highly invasive in at least 32 countries outside its native range

Cypinodontidae small killifish known as pupfish

Doradidae family of catfishes known as thorny catfishes, raphael catfishes or talking catfishes native to South America

Engraulidae small common forage fishes known as anchovies; important commercial fisheries species

Esocidae singular genus family, *Esox* spp., known commonly as pike and pickerel

Fundulidae family of topminnows and North American killifishes

Gadidae family of several important commercial marine species including cod, haddock, whiting and pollock

Gasterosteidae family of fishes including sticklebacks

Gobiidae bony fishes comprising more than 2000 species in more than 200 genera, commonly known as the true gobies

Hemiramphidae halfbeaks, spipe fish or spipefish

Holocentridae ray-finned fish split into two subfamilies: Holocentrinae, known as squirrelfish; and Myripristinae known as soldierfish

Ictaluridae group of catfish native to North America; sometimes known as ictalurids; important food source and sporting fish

Lutjanidae snappers, including the red snapper, an important food fish; inhabit tropical and subtropical ocean regions

Mormyridae elephantfish, native to Africa. Largest family in the order Osteoglossiformes; popular aquarium fishes

Moronidae the temperate basses, popular food source fishes

Mugilidae the mullets or grey mullets, found worldwide in coastal temperate and tropical waters; important food source in Mediterranean Europe since Roman times

Myliobatidae eagle rays, large cartilaginous fishes living in the open ocean

Percidae family of ray finned fishes found throughout brackish and freshwater of the Northern Hemisphere, containing more than 200 species

Pimelodidae long-whiskered catfishes

Polyodontidae basal Chondrosteian ray-finned fishes known as paddlefish; referred to as “primitive fish”, evolving with few morphological changes according to fossil records dating back to the Early Cretaceous

Pomacentridae ray-finned fishes, including damselfishes and clownfishes

Pseudochromidae consisting of around 152 species commonly known as dottybacks

Salmonidae the only living family in the order Salmoniformes; ray-finned fishes including salmon, trout, chars, freshwater whitefishes and grayling; contains highly important commercial fisheries species

Sciaenidae known as drums or croakers in reference to their sound production abilities; consisting of nearly 300 species

Scombridae including some of the most important and familiar fish foods; the mackerel, tuna, and bonito family

Sebastidae commonly known as rockfishes, scorpionfishes, sea ruffes and rockcods

Siganidae the rabbitfish or spinefoots; commercially important food fish

Sparidae sea breams and porgies; found in shallow temperate and tropical waters

Syngnathidae seahorses, pipefishes and seadragons; display a common fused jaw trait

A.3 Fish species

Common name (*Latin name*)

Alewife (*Alosa pseudoharengus*)

Allis shad (*Alosa alosa*)

Ambon damselfish (*Pomacentrus amboinensis*)

Atlantic bluefin tuna (*Thunnus thynnus*)

Atlantic cod (*Gadus morhua*)

Atlantic herring (*Clupea harengus*)

Atlantic mackerel (*Scomber scombrus*)

Atlantic pollack (*Pollachius pollachius*)

Atlantic salmon (*Salmo salar*)

Australian anchovy (*Engraulis australis*)

Australian clownfish (*Amphiprion rubrocinctus*)

Ayu (*Plecoglossus altivelis*)

Banded killifish (*Fundulus diaphanous*)

Bighead carp (*Hypophthalmichthys nobilis*)

Black rockfish (*Sebastes melanops*)

Blacktail shiner (*Cyprinella venusta*)

Blueback herring (*Alosa aestivalis*)

Bluegill sunfish (*Lepomis macrochirus*)

Blue rockfish (*Sebastes mystinus*)

Bluestripe seaperch (*Lutjanus kasmira*)

Blunt-headed wrasse (<i>Thalassoma amblycephalum</i>)	Golden grey mullet (<i>Liza aurata</i>)
Bocon toadfish (<i>Amphichthys cryptocentrus</i>)	Golden shiner (<i>Notemigonus crysoleucas</i>)
Broad whitefish (<i>Coregonus nasus</i>)	Goldfish (<i>Carassius auratus</i>)
Brown dottedback (<i>Pseudochromis fuscus</i>)	Green chromis (<i>Chromis veridis</i>)
Brown meagre (<i>Sciaena umbra</i>)	Grey snapper (<i>Lutjanus griseus</i>)
Brown trout (<i>Salmo trutta</i>)	Gudgeon (<i>Gobio gobio</i>)
Cape silverside (<i>Atherina breviceps</i>)	Gulf menhaden (<i>Brevoortia patronus</i>)
Channel catfish (<i>Ictalurus punctatus</i>)	Guppy (<i>Poecilia reticulata</i>)
Charcoal damsel (<i>Pomacentrus brachialis</i>)	Haplochromine cichlid (<i>Nyassachromis microcephalus</i>)
Chinese sucker (<i>Myxocyprinus asiaticus</i>)	Hogchoker (<i>Trinectes maculatus</i>)
Chinook salmon (<i>Oncorhynchus tshawytscha</i>)	Horse mackerel (<i>Trachurus trachurus</i>)
Common carp (<i>Cyprinus carpio</i>)	Iberian barbel (<i>Luciobarbus bocagei</i>)
Common chub (<i>Squalius cephalus</i>)	Lake chub (<i>Couesius plumbeus</i>)
Common dace (<i>Leuciscus leuciscus</i>)	Lake sturgeon (<i>Acipenser fulvescens</i>)
Common goby (<i>Pomatoschistus microps</i>)	Lake Victoria cichlid (<i>Haplochromis piceatus</i>)
Common roach (<i>Rutilus rutilus</i>)	Large African mouthbreeder (<i>Tilapia macrocephala</i>)
Convict cichlid (<i>Amatitlania nigrofasciata</i>)	Largemouth bass (<i>Micropterus salmoides</i>)
Daffodil cichlid (<i>Neolamprologus pulcher</i>)	Lemon damsel (<i>Pomacentrus moluccensis</i>)
Damselfish (<i>Pomacentrus wardi</i>)	Lined Raphael catfish (<i>Platydoras costatus</i>)
Eastern mosquitofish (<i>Gambusia holbrooki</i>)	Lined seahorse (<i>Hippocampus erectus</i>)
Elephantfish (<i>Pollimyrus adspersus</i>)	Longnose killifish (<i>Fundulus similis</i>)
Estuarine round-herring (<i>Gilchristella aestuaria</i>)	Longspine cardinalfish (<i>Apogon doryssa</i>)
Eurasian perch (<i>Perca fluviatilis</i>)	Longspine squirrelfish (<i>Holocentrus rufus</i>)
European eel (<i>Anguilla anguilla</i>)	Lusitanian toadfish (<i>Halobatrachus didactylus</i>)
European minnow (<i>Phoxinus phoxinus</i>)	Mediterranean damselfish (<i>Chromis chromis</i>)
European pilchard (<i>Sardinia pilchardus</i>)	Mediterranean killifish (<i>Aphanius fasciatus</i>)
European sea bass (<i>Dicentrarchus labrax</i>)	Mississippi silvery minnow (<i>Hybognathus nuchalis</i>)
European sprat (<i>Sprattus sprattus</i>)	Nagasaki damsel (<i>Pomacentrus nagasakiensis</i>)
Fathead minnow (<i>Pimephales promelas</i>)	Nassau grouper (<i>Epinephalus striatus</i>)
Fifteenspine stickleback (<i>Spinachia spinachia</i>)	New Zealand bigeye (<i>Pempheris adspersa</i>)
Giant danio (<i>Devario aequipinnatus</i>)	Nile tilapia (<i>Oreochromis niloticus</i>)
Giant kelpfish (<i>Heterostichus rostratus</i>)	Northern pike (<i>Esox lucius</i>)
Gilthead sea bream (<i>Sparus aurata</i>)	Olive rockfish (<i>Sebastes serranoides</i>)
Glowlight tetra (<i>Hemigrammus erythrozonus</i>)	Orange chromide (<i>Etroplus maculatus</i>)

Oscar (<i>Astronotus ocellatus</i>)	Slender lionhead cichlid (<i>Steatocranus tinanti</i>)
Pacific herring (<i>Clupea pallasii</i>)	Spiny chromis (<i>Acanthochromis polyacanthus</i>)
Paddlefish (<i>Polyodon spathula</i>)	Spotted sea trout (<i>Cynoscion nebulosus</i>)
Painted goby (<i>Pomatoschistus pictus</i>)	Striped bass (<i>Morone saxatilis</i>)
Pallid sturgeon (<i>Scaphirhynchus albus</i>)	Thicklip grey mullet (<i>Chelon labrosus</i>)
Pencil-streaked rabbitfish (<i>Siganus doliatus</i>)	Three-by-two garfish (<i>Hemiramphus robustus</i>)
Pictus catfish (<i>Pimelodus pictus</i>)	Three-spined stickleback (<i>Gasterosteus aculeatus</i>)
Pinecone soldierfish (<i>Myripristis murdjan</i>)	Threespot dascyllus (<i>Dascyllus trimaculatus</i>)
Pinfish (<i>Lagodon rhomboides</i>)	Topmouth gudgeon (<i>Pseudorasbora parva</i>)
Pink snapper (<i>Pagrus auratus</i>)	Tropical damselfish (<i>Chromis viridis</i>)
Plainfin midshipman (<i>Porichthys notatus</i>)	Two-spotted goby (<i>Gobiusculus flavescens</i>)
Pumpkinseed sunfish (<i>Lepomis gibbosus</i>)	Vermilion rockfish (<i>Sebastes miniatus</i>)
Rainbow trout (<i>Oncorhynchus mykiss</i>)	White bass (<i>Morone chrysops</i>)
Red drum (<i>Sciaenops ocellatus</i>)	White-spotted eagle ray (<i>Aetobatus ocellatus</i>)
Red-mouthed goby (<i>Gobius cruentatus</i>)	White trevally (<i>Pseudocaranx dentex</i>)
Red saddleback anemonefish (<i>Amphiprion ephippium</i>)	Whiting-pout (<i>Trisopterus luscus</i>)
Round goby (<i>Neogobius melanostomus</i>)	Yellow perch (<i>Perca flavescens</i>)
Sabre squirrelfish (<i>Sargocentron spiniferum</i>)	Yellow saddle goatfish (<i>Parupeneus cyclostomus</i>)
Sailfish (<i>Istiophorus platypterus</i>)	Zebrafish (<i>Danio rerio</i>)
Saithe (<i>Pollachius virens</i>)	
Sheepshead minnow (<i>Cyprinodon variegatus</i>)	
Silver carp (<i>Hypophthalmichthys molitrix</i>)	

A.4 Non-fish species

Capulidae the cap snails or shells, a family of marine gastropod molluscs in the clade Littorinimorpha

Chaoboridae commonly known as phantom midges or glassworms is a family of common midges

Lepidoptera order of insects including moths and butterflies

Myrmeleontidae family of around 2000 species of insects known as the antlions

Common name (*Latin name*)

American tree sparrow (<i>Spizella arborea</i>)	Barbary ground squirrel (<i>Atlantoxerus getulus</i>)
	Barnacle goose (<i>Branta leucopsis</i>)

Bighorn sheep (<i>Ovis canadensis</i>)	Harris' hawk (<i>Parabuteo unicinctus</i>)
Black footed albatross (<i>Diomedea nigripes</i>)	Hermit crab (<i>Pagurus acadianus</i>)
Bottlenose dolphin (<i>Tursiops truncatus</i>)	Honeybee (<i>Apis mellifera</i>)
Brandt's vole (<i>Lasiopodomys brandtii</i>)	House sparrow (<i>Passer domesticus</i>)
Burrowing mayfly (<i>Dolania americana</i>)	Lesser wax moth (<i>Achroia grisella</i>)
Canada goose (<i>Branta canadensis</i>)	Lion (<i>Panthera leo</i>)
Caribbean hermit crab (<i>Coenobita clypeatus</i>)	Mealworm beetle (<i>Tenebrio molitor</i>)
Carrion crow (<i>Corvus corone corone</i>)	Mexican colonial web-building spider (<i>Metepeira incrassata</i>)
Cape gannet (<i>Morus capensis</i>)	Musk-oxen (<i>Ovibos moschatus</i>)
Common redshank (<i>Tringa totanus</i>)	Natterer's bat (<i>Myotis nattereri</i>)
Cooper's hawk (<i>Accipiter cooperii</i>)	Northern lapwing (<i>Vanellus vanellus</i>)
Dark-eyed junco (<i>Junco hyemalis</i>)	Norway rat (<i>Rattus norvegicus</i>)
Desert locust (<i>Schistocerca gregaria</i>)	Pine engraver beetle (<i>Ips pini</i>)
Emperor penguin (<i>Aptenodytes forsteri</i>)	Red wood ant (<i>Formica rufa</i>)
Eurasian lynx (<i>Lynx lynx</i>)	Rocky mountain elk (<i>Cervus elaphus nelsoni</i>)
Eurasian oystercatcher (<i>Haematopus ostralegus</i>)	Rook (<i>Corvus frugilegus</i>)
European bee-eater (<i>Merops apiaster</i>)	Sand fiddler crab (<i>Uca pugilator</i>)
European robin (<i>Erithacus rubecula</i>)	Snowshoe hare (<i>Lepus americanus</i>)
Evening bat (<i>Nycticeius humeralis</i>)	Spider mite (<i>Phytoseiulus persimilis</i>)
Greater mouse-eared bat (<i>Myotis myotis</i>)	Spotted hyenas (<i>Crocuta crocuta</i>)
Greater sage-grouse (<i>Centrocercus urophasianus</i>)	Water flea (<i>Daphnia magna</i>)
Green turtle (<i>Chelonia mydas</i>)	Water skater (<i>Halobates robustus</i>)
Grey wolf (<i>Canis lupus</i>)	White-tailed deer (<i>Odocoileus virginianus</i>)
Hallowell's toad (<i>Bufo maculatus</i>)	Wild boar (<i>Sus scrofa</i>)
Harbour seal (<i>Phoca vitulina</i>)	Yellow-bellied marmot (<i>Marmota flaviventris</i>)

B. Acronyms

ABR	Auditory Brainstem Response
ACI	Acoustic Complexity Index
ADV	Acoustic Doppler Velocimeter
AEP	Auditory Evoked Potential
ANOVA	Analysis of Variance

BCa	Bias Corrected and accelerated
CI	Confidence Interval
DAQ	Data Acquisition Device
FAR	False Alarm Rate
ICER	International Centre for Ecohydraulics Research
IUCN	International Union for Conservation of Nature
OBN	Octave Band Noise
PRI	Pulse Repetition Interval
PRR	Pulse Repetition Rate
ROC	Receiver Operating Characteristic
RMS	Root-mean-square
SDT	Signal Detection Theory
SL	Standard Length
SMD	Standardised Mean Difference
SNR	Signal-to-Noise Ratio
SEL_{SS}	Single-strike sound exposure level, measured in dB re 1 $\mu\text{Pa}^2 \text{ s}$
SPL	Sound Pressure Level, measured in dB re 1 μPa (in water)
TTS	Temporary Threshold Shift

C. Notation

Notation	Unit	Description
n	Count	Sample size (or number of fish)
$d.f.$		Degrees of freedom: <i>i.e.</i> the number of values in the final calculation of a

statistic that are free to vary, commonly expressed as:

$$d.f. = N - 1$$

s.e.

Standard error of the mean ($\sigma_{\bar{x}}$): the standard deviation (σ) of the sampling distribution (N), defined as:

$$\sigma_{\bar{x}} = \frac{\sigma}{\sqrt{N}}$$

MAD

Median Absolute Deviation: A robust measure of dispersion, defined as the median of the absolute deviations from the data's median (\tilde{X}), where:

$$MAD = (|X_i - \tilde{X}|)$$

p

p -value, probability value or asymptotic significance

ρ

kg/m³

Ambient density

P

Pa

Pressure

λ

m

Wavelength

f

Hz

Sound frequency

c

m s⁻¹

Speed of sound

ε

m

Particle motion, expressed as displacement

u

m s⁻¹

Particle motion, expressed as velocity

a

m s⁻²

Particle motion, expressed as acceleration

d'

Z score

Discriminability (in standard deviation units, Z score)

C

Z score

Response criterion (in standard deviation units, Z score)

\bar{u}

m s⁻¹

Time-averaged mean of the longitudinal velocity component

\bar{v}	m s^{-1}	Time-averaged mean of the lateral velocity component
\bar{w}	m s^{-1}	Time-averaged mean of the vertical velocity component
U	m s^{-1}	Mean water velocity – calculated as three dimensional velocity magnitude
σ		Standard deviation – in reference to the standard deviation of velocity (<i>e.g.</i> σ_u , the standard deviation of the longitudinal velocity, in m s^{-1})

D. General terminology

Abiotic component Non-living physical and chemical elements in the environment, which affect individual organisms and ecosystems

Acclimation Process by which an organism physiologically adjusts to a change in its environment

Acoustic Complexity The complexity of an acoustic signal. Signals may be simple (*e.g.* pure tone), or more complex, where they can always be represented as the combination of tonal signals (*i.e.* “Fourier synthesis”)

Acoustic Complexity Index An algorithm used to directly quantify complex sounds by computing the variability of the intensities registered in audio recordings

Acoustic pressure The local pressure deviation from the ambient pressure, caused by a sound wave

Acoustic masking Process where the threshold of hearing for a sound is raised owing to the presence of another (masking) sound, and the amount by which it is raised, expressed in dB

Active Space The area or volume around an individual where communication with conspecifics can occur

Ambient noise Background level of sound in the environment, not including the signal(s) of interest

Anthropocentrism Interpreting or regarding the world primarily in terms of human values or experience

Anthropogenic Human-made or impact of human activity

Audiogram A graph of hearing threshold level, displayed as a function of frequency

Auditory Evoked Potential The electrical potential of the auditory nervous system upon presentation of an acoustic stimulus; can be obtained from electrodes placed on the head

Biotic component Any living component that affects another organism, or shapes the ecosystem

Comodulation masking release A decrease in the expected amount of masking (*i.e.* release), occurring for coherently modulated sound (*i.e.* with amplitude fluctuations consistent across a range of frequencies)

Conservation Principles and practice of science to protect species from extinction, maintain/restore habitats, enhance ecosystem services, and protect biological diversity

Conspecific Individuals belonging to the same species

Critical Bandwidth Bandwidth of white noise where the detection threshold of a tone at the centre of the band of white noise no longer increases with increasing width of the noise band. Commonly used as an estimate of the bandwidth of the auditory filter with the same centre frequency

Critical Ratio Difference between sound pressure level (SPL) of a pure tone that is just audible in the presence of a continuous noise of constant spectral density, and its SPL, expressed in dB

Diadromous Fish migrations that occur between freshwater and marine environments

Ecosystem services Ecological characteristics, functions or processes that contribute to human wellbeing (directly, or indirectly)

Fish pass A structure (*e.g.* a series of stepped pools) over which water flows, located on or adjacent to anthropogenic barriers (*e.g.* dam or weir) and designed to enable the passage of upstream moving fish

Fitness The ability of an organism to survive and reproduce (contribution to the gene pool of next generation) in a given environment, relative to the contribution made by others within a population

Freshwater fishes Fish that live all, or a critical part of their life in brackish or inland freshwater environments, such as lakes and rivers

Habitat The home or environment of an organism that contains necessary resources and optimal physical and biotic factors allowing for the survival and reproduction of a particular species, or life-stage

Habitat connectivity The degree of connectivity between separate patches of habitat and the ease at which individuals of a species can traverse the space between patches, enabling gene and other crucial exchanges

Habitat fragmentation The subdivision of habitat into smaller unconnected fragments. May occur as a result of natural or anthropogenic activity, leading to the creation of a barrier between the subdivided habitats that may reduce overall habitat area, reduce habitat quality, and increase risk of extinction

Habituation The long-term process whereby without adequate recovery time from exposure to a stimulus, or with a series of frequent exposures over time, responses of an individual to the same stimulus cease to be observed

Heterospecific Individual organisms belonging to a different species from one another

Hydrodynamics The study of liquids in motion, used synonymously with hydraulics

Impingement The unintended entrapment of a fish against a structure

Interspecific Occurring among individuals belonging to different species

Intraspecific Occurring among individuals of a single species

Masking (in reference to signals): the change in perception of one signal in the presence of another

Migration Lifecycle essential movements of animals from one area to another. Takes place on a seasonal, or ontogenetic basis to facilitate spawning/ breeding, feeding or refuge

Mitigation An action intended to reduce the adverse impact of an activity

Natural Capital The world's stocks of natural assets (*e.g.* water, forests, clean air) that provide a flow of benefits to people and the economy

Noise Unwanted or disruptive disturbance within a useful frequency band

$1/3$ octave band level The sound level contained within a frequency band that is $1/3$ of an octave wide

Potamodromous Fish migrations that occur solely within freshwater

Power spectral density Sound power divided by bandwidth, used to describe how the power of a sound is distributed with frequency, expressed in dB re $1 \mu\text{Pa}^2 \text{Hz}^{-1}$

Signal-to-noise ratio The difference between the signal and noise levels (dB)

Sinewave A single frequency sinusoidal wave that describes a continuous, smooth periodic oscillation, fluctuating up and down as a function of time

Swimbladder Internal gas-filled organ that contributes to the buoyancy of many bony fish, allowing them to control water depth while conserving energy. Also functions as a resonating air chamber in the production or receipt of sound

Tolerance An instantaneously demonstrable behavioural state (measured at a point in time), whereby a novel stimulus no longer provokes a substantial response after multiple presentations, leading to a short-term decline in the frequency, or magnitude of response

Water velocity The speed at which water flows, typically measured in cm s^{-1} or m s^{-1}

CHAPTER 1 Research Introduction

Freshwater ecosystems account for less than 1.2% of the world's surface area (Shiklomanov, 1993), yet globally, the natural capital of wetlands, rivers and lakes contributes an estimated US\$28.9 trillion in ecosystem services per year (data collation: 2011; US\$ relative value: 2007: Constanza *et al.*, 1997; 2014). Freshwater systems are also among the most modified networks on the planet, with more than two thirds of large rivers no longer free flowing because of habitat fragmentation (more than 99% of rivers in Great Britain contain artificial barriers: Grill *et al.*, 2019; Jones *et al.*, 2019). Humans have modified freshwater river systems for thousands of years to facilitate agricultural irrigation, flood control, fisheries management, provisioning of drinking water, sanitation, recreation, transport, and electricity production (Westing, 1986; WCD, 2000). While such projects boast benefits from an anthropocentric viewpoint (*e.g.* economic revenue), conversely, many lesser known adverse societal and environmental costs exist that are not compatible with sustainable development (Moreira and Poole, 1993; Dudgeon, 2000).

River systems have internationally valued cultural, religious, social, recreational, and economic worth (Westing, 1986; Sadoff and Grey, 2002), and many human populations are dependent on predictable migrations of freshwater fish for their subsistence and livelihoods (Barlow *et al.*, 2008). For instance, the Lower Mekong basin boasts one of the world's most productive fisheries, worth between US\$4.3 and US\$7.8 billion per year (Lamberts and Koponen, 2008; Hortle, 2009). In Cambodia, the Tonle Sap floodplain ecosystem provisions 70% of the 65.5 kg/ person/ year average per capita fish consumption (Van Zalinge *et al.*, 2004; Baran *et al.*, 2014) to around 1.7 million locals (Sok *et al.*, 2019). With a global incentive to meet growing demands for food, water and renewable energy (*e.g.* water-energy-food nexus framework: WEF, 2011; Sarkodie and Owusu, 2020), the recent boom in hydropower development within the Lower Mekong adds to the greater than 2.8 million dams already in existence worldwide (Lehner *et al.*, 2011; Zarfl *et al.*, 2015).

Modifications to aquatic habitats (*e.g.* dams, weirs, barrages, channelisation or water abstraction) impede the movement of freshwater fish migrations that range from short-distanced movements

of < 100 m (*e.g.* resident species: Fausch *et al.*, 2002), to iconic journeys of > 5000 km (*e.g.* European eel, *Anguilla anguilla*: Aarestrup *et al.*, 2009). These lifecycle essential migrations may be extremely important to the survival of a species (Northcote, 1978; Jordan and Wortley, 1985) and take place on a seasonal, or ontogenetic basis to facilitate spawning, feeding, or refuge (Lucas and Baras, 2001). Migratory fish also serve a wide range of important functions within an ecosystem; influencing nutrient cycling and transportation of sediment (Deegan, 1993; Atkinson *et al.*, 2019) or larvae (Černý *et al.*, 2003), acting as ecosystem engineers (Moore, 2006), and forming essential components of complex aquatic and terrestrial food webs (Albouy *et al.*, 2019; Reis *et al.*, 2020). The extent to which fish movements are impacted by infrastructure varies substantially and can depend on species-specific factors (*e.g.* behaviour; swimming ability; timing of migration: Northcote, 1998), river hydrology, and obstruction type or size. Regardless, no matter their size, barriers to fish migratory routes can be potentially detrimental to entire populations (Birnie-Gauvin *et al.*, 2017); reducing the availability of potential habitat (Birnie-Gauvin *et al.*, 2017; Wu *et al.*, 2019) and affecting genetic fitness (Liao *et al.*, 2006; Junker *et al.*, 2012), reducing community diversity (Turgeon *et al.*, 2019), and preventing the completion of successful migrations across life-stages including sexually mature adults, juveniles and drifting fertilised eggs (Esguícero and Arcifa, 2010; Suzuki *et al.*, 2011; Pelicice *et al.*, 2015; Wu *et al.*, 2019). Downstream passage through hazardous routes at hydropower facilities (*e.g.* turbines or overflows) note mortality rates of fish by the tonnage. For example, in a single dewatering event at the Três Marias Dam (São Francisco River, Minas Gerais, Brazil), up to 2.5 tonnes of fishes were removed from the draft tube (de Andrade *et al.*, 2012). Injury or death can occur as a direct result of shear force (from abrupt changes in velocity: Boys *et al.*, 2018; Colotelo *et al.*, 2018) or mechanical blade strike (Boys *et al.*, 2018), or, via the indirect physiological effects of rapid pressure fluctuations, including supersaturation (elevated total dissolved gas: Arntzen *et al.*, 2009), or barotrauma (Brown *et al.*, 2014; Beirão *et al.*, 2018).

Many best-practice technologies and mitigation techniques have been deployed to reduce the issues of delayed fish migration, direct injuries, and mortalities (Deng *et al.*, 2007; Richmond and Romero-Gomez, 2014; Beirão *et al.*, 2018). One strategy considered a necessity is the implementation of physical screening systems which block access to hazardous areas (*e.g.* turbine intakes or extraction points) and guide fish to safer preferred routes, such as fish passes. This precautionary approach is utilised extensively as a fisheries management technique in, for example, the USA, where such apparatus has been installed at over 3000 water diversion points along California's Central Valley (Moyle and Israel, 2005). While such screens are believed to achieve their purpose, evaluation to quantify their effectiveness on a site-by-site basis does not exist due to associated expenses. Furthermore, maintenance and installation accumulate high

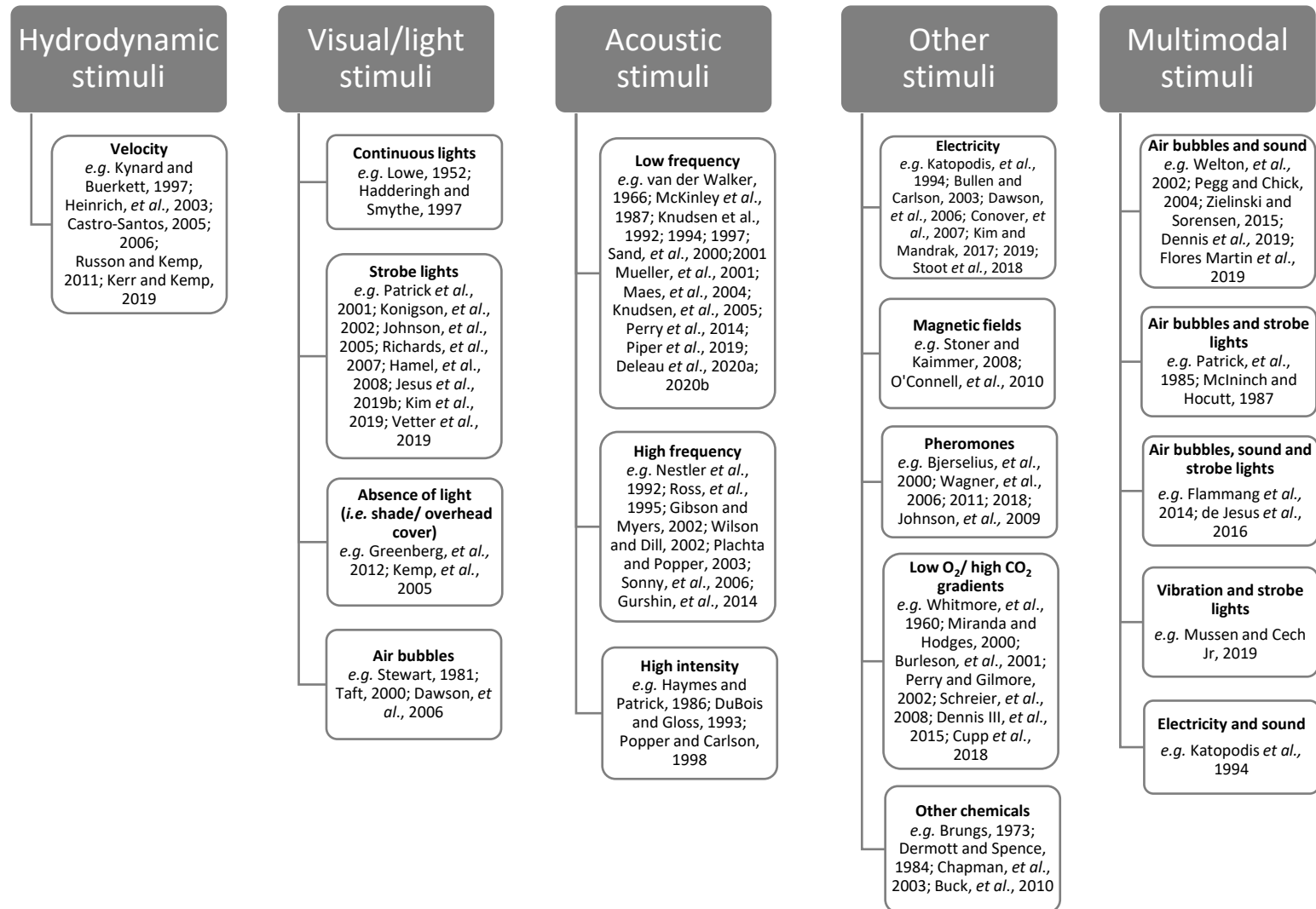


Figure 1.1: Many studies have hypothesised, tested and implemented differing stimuli for use in behavioural deterrence, attractant and guidance systems, and have observed varying degrees of efficacy.

costs and engineering challenges (*e.g.* self-cleaning technologies), and fish interactions at such interfaces have been observed to cause stress, injury, and mortalities where high sweeping approach velocities exist (Kennish, 1992; Young *et al.*, 2010). An alternative or collaborative system could include behavioural deterrents, attractants, or guidance systems when the effectiveness of a physical screen alone is limited (*e.g.* repelling small sized juvenile stages).

Animal repellent or attraction systems are necessary non-lethal mitigation approaches where human-wildlife conflicts arise (Noatch and Suski, 2012; Blackwell *et al.*, 2016). Singular and multimodal behavioural systems have been trialled in fisheries management, deploying a range of stimuli, including strobe lighting, hydrodynamic cues, air bubbles, and sound (see Figure 1.1 for an extensive list: *e.g.* Lowe, 1952; Welton *et al.*, 2002; Dawson *et al.*, 2006; Richards *et al.*, 2007; Deleau *et al.*, 2020a). Yet, perhaps owing to limitations in technological design processes, the efficacies of these systems vary greatly (Turnpenny *et al.*, 1998; Chapter 2.6; 2.7). More efficient guidance technologies are required to reduce large-scale fish mortality at anthropogenic hazards (*e.g.* hydropower dams, water abstraction sites: Buysse *et al.*, 2014; Beirão *et al.*, 2018), increase river connectivity for native migratory species (Lange *et al.*, 2018; Wilkes *et al.*, 2018), and control invasive species spread (*e.g.* silver carp, *Hypophthalmichthys molitri*: Vetter *et al.*, 2015).

Habitat degradation, alteration and loss may be the largest threat to all migratory fish and has led to an approximate 76% decline in freshwater fish, with migratory populations in Europe, the most urbanised region in the world, plummeting by 93% (WWF, 2020). Anthropogenic activity has, however, brought other emerging or intensified threats that disproportionately impact the biodiversity of freshwater ecosystems including climate change (Darwall and Freyhof, 2015), invasive species (Rahel and Olden, 2008), contaminants (Hughes *et al.*, 2013) and infectious disease (Okamura and Feist, 2011), microplastics (Horton *et al.*, 2018), light (Jechow and Hölker, 2019) and sound pollution (Cox *et al.*, 2018). Human populations often contribute to substantial levels of environmental noise on account of their reliance on electricity and engines (Reid *et al.*, 2019). This has been well documented in terrestrial systems, however, most aquatic noise research, mitigation efforts, and policies are marine-centric, despite the proximity of road networks, industrial infrastructure and urban development to freshwater ecosystems (Bevelhimer *et al.*, 2016; He *et al.*, 2019; Reid *et al.*, 2019). Man-made sound can negatively impact the anatomy (Halvorsen *et al.*, 2013), physiology (Bruintjes and Radford, 2014) or behaviour (Shafiei Sabet *et al.*, 2015) of freshwater fishes (Chapter 2.2).

Sound is important to the ecology of fishes as it provisions individual animals with a sense of their extended environment, and facilitates predator-prey interactions and information transfer, *i.e.* communication (*e.g.* mating: Amorim *et al.*, 2013; territorial defence: Millot *et al.*, 2011; or social

grouping: van Oosterom *et al.*, 2016). Combined with the biological relevance of sound to fish, the range of responses to anthropogenic noise pollution support the use of sound in behavioural guidance systems (Carlson and Popper, 1997). An understanding of freshwater fish response to sound is two-fold. First, to better understand the impact of noise pollution on the most diverse and dynamic range of species on Earth; and second, to facilitate the development of more effective acoustic behavioural technologies for the control or protection of fish.

1.1 General aims and objectives

The general aim of this research thesis is to:

Better quantify group behavioural responses of cyprinid fishes to acoustic stimuli to aid conservation efforts, and the development of acoustic deterrent or guidance systems.

To meet this aim, the following objectives were addressed:

1. Review current literature and highlight research trends and bias and identify knowledge gaps that may assist in understanding how fish respond to sound.
2. Assess how the complexity of acoustic stimuli influences the group behavioural responses of fish in a highly controlled and well measured experimental environment.
3. Assess how temporal characteristics of an acoustic stimuli influence the rate of behavioural tolerance in fish groups.
4. Utilise Signal Detection Theory to assess the influence of background masking noise on group behavioural responses to acoustic stimuli.
5. Assess the manipulation of upstream migrating cyprinid group behaviour using acoustic stimuli under different experimentally controlled water velocities.

1.2 Thesis overview

Objective 1 is met with a general literature review and quantitative meta-analysis presented in Chapter 2. Objectives 2, 3, and 4 were met by undertaking tightly controlled experiments within an acoustically isolated room, in a still-water acrylic flume, the results of which are presented in Chapters 4, 5, and 6, respectively. The final objective, 5, was met by performing an experiment in a large indoor open-channel flume, and results of this work are presented in Chapter 7.

Chapter 3 provides an overview and rationale of the general methodologies used throughout the experimental research and provides a background on the subject species. Results chapters are presented as independent sections of research, and each incorporates a stand-alone introduction, methods, results, and discussion section to meet the objectives.

Finally, Chapter 8 discusses all the thesis findings in relation to its general aim. This highlights how knowledge gained may be applied to improving current designs and use of acoustic guidance technologies. Areas for future research and conclusions are provided alongside an overview regarding the impact of the thesis results and its novel contribution to the scientific field, the environment, economy, and society.

CHAPTER 2 Literature review

2.1 The ecology of fishes and sound

Aquatic animals gain vital information from the acoustic signals present within their environment (Hawkins and Myrberg, 1983), with auditory responsiveness in fishes observed from just two days post hatching (Tanimoto *et al.*, 2009). Acoustic signals perform a crucial role in the life-history strategies of fishes and are used to facilitate a variety of survival functions, including navigation (Simpson *et al.*, 2005a), sexual selection (Bass and McKibben, 2003; Amorim *et al.*, 2004; Parmentier *et al.*, 2010), conspecific interactions (Amorim *et al.*, 2004; Salas *et al.*, 2018), and predator avoidance (Myrberg, 1981). Owing to the nature of underwater sound, auditory signals can travel large distances in all directions (propagating hundreds of metres to kilometres), providing rapid, three-dimensional information that is less limited than other available sensory information (*e.g.* visual signals under dark or turbid conditions, or chemical signals downstream of a targeted receiver: Mickle and Higgs, 2017; Popper and Hawkins, 2019). The contextual influences of a sound are many (Bass and McKibben, 2003; Simpson *et al.*, 2005a; Ward *et al.*, 2011), including: whether or not an animal is a group-living species (Kastelein *et al.*, 2008), the current behavioural state of an individual (Bruintjes and Radford, 2013; Jolles *et al.*, 2020), the sound source (Cox *et al.*, 2018) or temporal properties of a noise (Neo *et al.*, 2015b), and the ambient background noise within the surrounding acoustic environment (Lugli and Fine, 2003; Holt and Johnston, 2015).

Acoustic energy is characterised by two different components, these being the directional particle motion and scalar pressure waves. All teleost fish are sensitive to the displacement components of sound, particularly at lower frequencies. These are detected through the use of two independent, yet highly related sensory systems, known as the mechanosensory lateral line system (neuromast hair cells), and the more dominant auditory system (Webb *et al.*, 2008b). The latter uses the inner ear otolith organs, a dense mass that moves in response to the inertia of a sound wave over the receptive sensory hair cells of the epithelia (Popper and Fay, 2011). The inner ear is typically comprised of an anterior, a posterior and a horizontal semi-circular canal and three otolith end organs, the lagena, utricle and saccule, with the latter acting as the primary

auditory organ in many species. The calcified otolith sits atop the macula, a sensory epithelium that contains numerous hair cells (Figure 2.1A: Myrberg, 2001; Montgomery *et al.*, 2006).

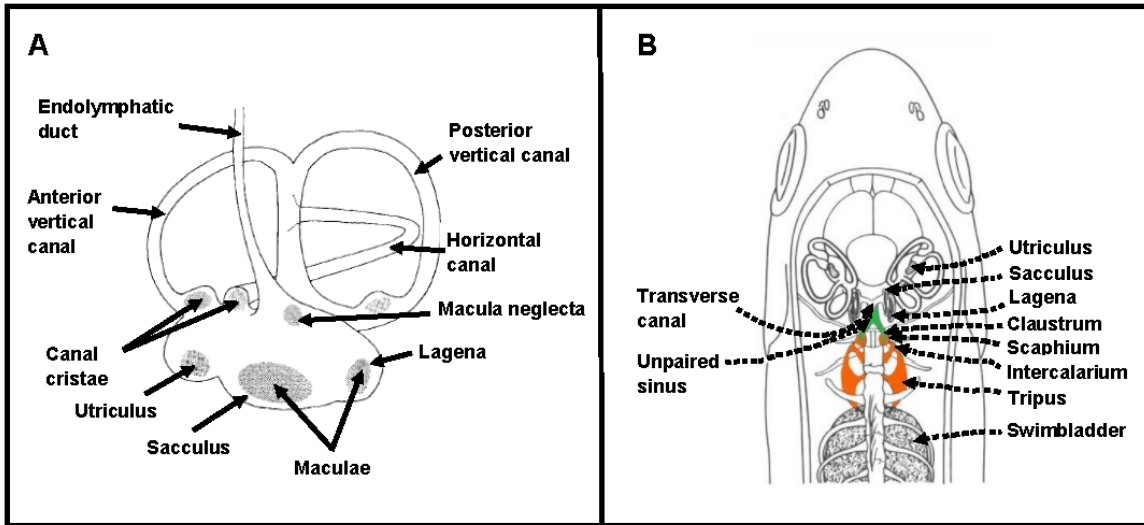


Figure 2.1: (A) General inner ear labyrinth of bony fishes (adapted from Myrberg, 2001. Reproduced with the permission of Springer Nature); and (B) the anterior end of the swimbladder in otophysan fishes connects to a series of bones (Weberian ossicles) that move and stimulate the inner ear when the wall of the swimbladder moves in response to sound pressure (source: adapted from <https://www.ahukini.net/fishhear>).

While the hearing mechanisms of fishes are dominated by particle motion sensors, the pressure component of sound is also detectable by a select few families of fish. A graded spectrum of responses exist that are most likely reliant on the relative contribution of sound pressure detection to the typical overall hearing ability of a species (Popper and Fay, 2011; Putland *et al.*, 2019). For example, the most extensive use of sound pressure is observed in otophysan fishes (*e.g.* cypriniforms). This large group of freshwater fishes possess accessory hearing structures (Weberian ossicles) which transmit oscillations from the gas-filled swimbladder (or other air bubble) to the inner ear (Figure 2.1B). These specialisations allow for an enhanced auditory sensitivity to the sound pressure component, across a wider range of frequencies (Popper and Fay, 2011). This evolutionary adaptation is likely driven by the nature of sound propagation within extremely shallow water (*e.g.* riverine environments), allowing for an otherwise limited range of detection beyond the low frequency cut-off (Amoser and Ladich, 2005).

The hearing capabilities of fish are generally represented using audiograms, depicting the lowest detectable level for a tone as a function of frequency (Popper *et al.*, 2003; Ladich and Fay, 2013). Data for audiograms are typically acquired using psychophysical or electrophysiological experimentation (*e.g.* Kojima *et al.*, 2005). The latter uses methodologies known as auditory evoked potentials (AEP: Paulraj *et al.*, 2015) or auditory brainstem responses (ABR: Skoe and

Kraus, 2010) to record brain or nerve activity associated with the detection of an acoustic stimulus. Audiograms exist for over 111 different fish species, from 51 families (Ladich and Fay, 2013), providing important information on the frequency range of hearing. Nevertheless, there are several interpretative constraints with this data. Firstly, there are currently no international standards for measuring procedures, and therefore direct comparisons between species cannot be made accurately (Leighton *et al.*, 2019). For example, psychophysical studies use a variety of behavioural conditioning types (*e.g.* avoidance conditioning: Tavalga, 1974; cardiac or respiratory suppression: Buerkle, 1968; Hawkins and Johnstone, 1978; Fay, 1983), and AEP experiments use a range of acoustic stimuli types (*e.g.* tone burst of 10 ms duration with a 2 ms rise-fall time gated through a Hanning window: Radford *et al.*, 2012; in comparison to a 50 ms tone burst gated through a Hanning window: Mann *et al.* 2007), and experimental set-ups (*e.g.* in-air vs in-water speakers: Ladich and Wysocki, 2009; or fish partially vs totally submerged in water: Mann *et al.*, 2007; Lechner *et al.*, 2008). Differences in methodologies may have led to a large variation in the measured hearing thresholds. For instance, a 60 dB range (at some frequencies) for behavioural and ~30 dB range for AEP has been suggested for goldfish (*Carassius auratus*: Ladich and Fay, 2013; Leighton *et al.*, 2019). Secondly, challenges occur when attempting to characterise the sensitivity of fish hearing within the particle motion domain (*e.g.* issues in small tanks: Akamatsu *et al.*, 2002; Gray *et al.*, 2016; Chapter 3.2) and therefore most audiograms are produced for the pressure component of sound, despite the sensitivity of all fish to the former component. Putland *et al.* (2019) postulated that all fish may have similar particle motion hearing and any differences in overall sensitivity are likely due to the presence of differing ancillary hearing structures that would allow for a species-specific continuum in detection of the pressure component. Although a plausible hypothesis, studies characterising particle motion values are still required to better understand the absolute hearing capabilities of a wider range of fish (Montgomery and Radford, 2017). Finally, it is also worth noting that most audiometry experiments focus on the hearing of adult fishes (Ladich and Fay, 2013), thereby neglecting to consider the importance of sound and the auditory system across the varying stages of the fish life cycle.

Sound plays an important role in the ecology of fishes from an early larval life-stage. Many coral species use reef sound in combination with other cues to orient to suitable settlements, and larvae can discriminate between differing habitat sounds (*e.g.* fringing reefs, lagoons, or silent reefs: Radford *et al.*, 2011), or sounds that differ in frequency (*e.g.* high vs low: Simpson *et al.*, 2005a). Juvenile and adult reef fishes have also been observed to use sound as an orientation cue during nocturnal foraging movements (Simpson *et al.*, 2008), and playback of “healthy” coral reef sound has even been used as a successful conservation management tool to enhance fish community development on degraded habitats (Gordon *et al.*, 2019). Even so, while it has been

theorised that fish use a local acoustic soundscape to orient or migrate ('auditory scene analysis': Bregman, 1994; Fay, 2009), relatively little data exists on the use of environmental sound for orientation or navigation at later life-stages (van Opzeeland and Slabbekoorn, 2012). Similarly, little is known about the navigation abilities of the early developmental stages of freshwater fish in rivers, or how they may use environmental cues, such as sound, to reach suitable habitats (Lechner *et al.*, 2016).

The ability to detect sound is universal across all tested fish species, however, not all fish can produce sound. Of the greater than 34,000 species of fish (Froese and Pauly, 2019), at least 800, from over 100 families are known to produce sounds via a range of mechanisms (Bass and Ladich, 2008; Kasumyan, 2008; Popper and Hawkins, 2019). The two main mechanisms of sound production are the intrinsic or extrinsic (direct and indirect) sonic muscle vibration of the swimbladder (Bass and Ladich, 2008); and the stridulation of modified pectoral fins and girdles (Fine and Parmentier, 2015; Ladich and Schulz-Mirbach, 2016). Most sounds are typically of short duration, with swimbladder derived sounds generally tonal or narrowband in nature (Fine *et al.*, 2001), compared to stridulatory sounds that are more typically broadband pulses, and thereby cover a wider range of frequencies (Hawkins, 1986; Putland *et al.*, 2019). Further evidence exists of other sound producing mechanisms, however, these have yet to be well categorised (*e.g.* use of substrate vibration: Whang and Janssen, 1994; Colleye *et al.*, 2013).

'Grunts,' 'growls,' 'moans,' 'thumps,' 'whistles,' 'clicks,' 'drums' and 'hums,' all facilitate a variety of functions, including sexual selection, predator avoidance, and feeding (Amorim *et al.*, 2004; Millot *et al.*, 2011; Salas *et al.*, 2018). Many adult fishes produce sounds in diurnal patterns (*e.g.* at dawn), and seasonally in choruses that last from weeks to months (Parsons *et al.*, 2017). While sonic muscles exist in the individuals of both sexes for many species, in others, sexual dimorphism occurs where they are only prevalent in the males (*e.g.* species of the family Sciaenidae: Kasumyan, 2008). Regardless, it is typically males that vocalise to attract a mate and signify their fitness. For example, higher drumming activity in male painted gobies (*Pomatoschistus pictus*) is a good predictor of size, condition factor (Fulton's *K*) and fat reserves (Amorim *et al.*, 2013), and calling rate and effort are good indicators of gonad size in the Lusitanian toadfish (*Halobatrachus didactylus*: Amorim *et al.*, 2010). Males also produce sounds when defending territory (Myrberg, 1997; Bass and McKibben, 2003; Parmentier *et al.*, 2010) and during competitive or aggressive interactions with hetero- or conspecifics (*e.g.* feeding events: Amorim *et al.*, 2004; Millot *et al.*, 2011). Contexts other than sexual selection or competition may also elicit sound production in fish. For example, in the presence of a predator, Nassau groupers (*Epinephalus striatus*) have been observed to produce sudden loud startling sounds to distract and assist an escape (Myrberg,

1981), and longspine squirrelfish (*Holocentrus rufus*) respond to conspecific alarm calls by seeking refuge, or engaging in predator mobbing behaviour (Winn *et al.*, 1964).

Sound is of clear ecological importance for fishes, and anthropogenic noise (*e.g.* shipping, pile driving, *etc.* see Chapter 2.2) is increasingly being reported to have negative impacts on fish behaviour, which include the masking of communicative signals (Vasconcelos *et al.*, 2007; de Jong *et al.*, 2018), and alterations to group coordinated movement (Kastelein *et al.*, 2008), orientation and cohesion behaviour (Herbert-Read *et al.*, 2017a). Anthropogenic noise is globally recognised as a cause for concern, and several international agreements exist with objectives to monitor and mitigate the impacts of underwater sound pollution on aquatic life (*e.g.* the Helsinki Commission, 1988; the OSPAR Convention, 1992; and the Marine Strategy Framework Directive, 2008). When combined with the biological relevance of sound to fish, the range of fish responses to this ubiquitous transboundary pollutant (Slabbekoorn *et al.*, 2010) supports the use of acoustics as a viable mitigation tool in freshwater fisheries management (Popper and Carlson, 1998).

2.2 The impacts of anthropogenic noise on fishes: a meta-analysis

Noise pollution originating from a variety of man-made sources is a pervasive issue of concern for both marine and freshwater ecosystems. Relatively little is known about whether the impact of noise on resident fish, or those migrating through these contrasting aquatic environments, differ. A meta-analysis, using a combination of approaches was conducted to ascertain: 1) whether anthropogenic noise negatively impacts fishes; 2) the nature of these impacts (anatomical, physiological, or behavioural); 3) how impacts vary across developmental life-stages; and 4) whether impacts vary between freshwater and marine environments. The PRISMA protocol was deployed to suitably search, identify and screen eligible peer-reviewed studies obtained from bibliographic search engine databases. Relevant articles were critically appraised and meta- and quantitative-data extracted into a database for analyses (vote counting and calculation of effect size). Anthropogenic noise tended to negatively impact fish and the magnitude of the effect differed with the nature of the impact, life-stage, and habitat type (marine, freshwater, or euryhaline). Impacts were greatest for fish experiencing anatomical damage, for adults and juveniles compared to earlier life-phases, and for those occupying freshwater environments. This review discusses the contextually dependent nature of these results and quantifies the magnitude of impact throughout interconnected aquatic habitats, and across a diverse range of life-history strategies (*e.g.* diadromy). There is a need for researchers and policy makers to consider the wider impacts of noise across, freshwater, estuarine and marine habitats. Such an approach may assist the development of more bespoke noise mitigation or conservation techniques.

2.2.1 Introduction

2.2.1.1 Is there an impact?

Anthropogenic noise increasingly disrupts the acoustic environments in which aquatic organisms live (Slabbekoorn *et al.*, 2010; Radford *et al.*, 2014). Many sources of underwater noise exist including ships and recreational boats, seismic exploration, construction, naval sonar, and marine mammal deterrent devices. Underwater noise can also originate from airborne sound or vibration propagating into the water, *e.g.* via substrate transmission (Hildebrand, 2009; Holt and Johnston, 2015). Noise is defined as any unwanted or disturbing sound, and is detrimentally driving environmental change (WHO, 2011), with impacts witnessed across differing taxa (*e.g.* marine mammals: Madsen *et al.*, 2006, and invertebrates: Day *et al.*, 2016) and ecosystems (Halpern *et al.*, 2008). Noise can cause interference with communicative sounds (Bass and McKibben, 2003; Branstetter *et al.*, 2018), induce uni- or cross-modal irregular behaviour (Hasan *et al.*, 2018; Roberts and Laidre, 2019), or even cause hearing loss, be that temporary or permanent (Kastak *et al.*, 2008; Finneran, 2015). Anthropogenic noise fields can be characterised with different acoustic measures, including frequency, sound pressure level, particle velocity or acceleration, and temporal waveform. The impacts of noise on aquatic fauna are not usually simply related to a single acoustic parameter. Regardless, evidence to date suggest impacts can be extremely far reaching and responsible for multiple mechanisms of damage.

2.2.1.2 What is the impact?

Sound tends to travel greater distances underwater than it does in air, hence the area influenced is wider reaching. The impact of a noise depends on three factors: the physical properties of the sound field, the hearing capabilities of the individual detecting that sound, and the context within which the sound is perceived (Popper and Fay, 2011). Human-generated noise is highly diverse in its characteristics, and can therefore affect the anatomical structure (Smith *et al.*, 2006), behaviour (Wysocki *et al.*, 2006) and/ or the physiological functioning (Crovo *et al.*, 2015) of an individual animal in numerous ways (Dooling *et al.*, 2015; Kunc *et al.*, 2016). Fishes exposed to noise for both chronic (Smith *et al.*, 2006), or acute exposure periods (Casper *et al.*, 2013b; 2017) may experience permanent hearing damage or other non-auditory tissue injuries. Temporary changes in hearing ability through an auditory threshold shift have also been observed, for example, in fathead minnow (*Pimephales promelas*: Scholik and Yan, 2001) and goldfish (*Carassius auratus*: Smith *et al.*, 2004b). Anatomical damage may have a detrimental knock-on effect on fish behaviour. Noise has been observed to interrupt spawning activity (*e.g.* gobies, *Gobiusculus flavescens* and *Pomatoschistus pictus*: de Jong *et al.*, 2018; Sierra-Flores *et al.*, 2015; Vasconcelos *et al.*, 2007), alter territorial behaviour (*e.g.* *Gobius cruentatus*: Sebastianutto *et al.*, 2011), or

cause spatial avoidance reactions (*e.g.* Atlantic cod, *Gadus morhua*: Handegard *et al.*, 2003; and European eel, *Anguilla anguilla*: Deleau *et al.*, 2019; 2020). In addition, intense noise may even change gene expression within the inner ear of a fish (Andrews *et al.*, 2014), and can lead to increased stress responses across a range of life-stages (Simpson *et al.*, 2005b; Wysocki *et al.*, 2006; Crovo *et al.*, 2015; Celi *et al.*, 2016).

2.2.1.3 Does impact vary between life-stage?

The hearing capabilities of an individual are both species specific, and differ dependent on its current life-stage (Blaxter and Hoss, 1981). Auditory responsiveness in fish has been observed from just 40 hours post fertilisation (zebrafish, *Danio rerio*: Tanimoto *et al.*, 2009), and stress responses to noise from 3 days post fertilisation in embryos (coral reef fishes, *Amphiprion* spp.: Simpson *et al.*, 2005b). Stress responses of fish to anthropogenic noise disruption could cause reduced growth rates (Filiciotto *et al.*, 2013), or suppress embryonic and larval stage development (de Soto *et al.*, 2013). Ontogenetic alterations may impact the survival of an individual, with smaller larvae more susceptible to predation (Atlantic cod: Nedelec *et al.*, 2015). Stressors, including noise, induce artificial fluctuations in the environment by an order of magnitude greater than natural conditions, and can impact early life-stage likelihood of survival if individuals are unable to adapt. Owing to reductions in available phenotypic and genetic variability at later life-stages, early life-stage mortality rates can have repercussions on overall population dynamics (Gagliano *et al.*, 2017). Conversely, not all species are affected at their early life-stages, however, may be impacted as juveniles or adults (Wysocki *et al.*, 2007b; Bruintjes and Radford, 2014). These impacts may differ greatly dependent on behavioural or functional processes which are specific to a certain life-stage, and critical to survival and functioning (Slabbekoorn *et al.*, 2010).

2.2.1.4 How does impact vary between environment?

While individual studies to date highlight the negative impacts of anthropogenic noise on both freshwater and marine fish species, policy interest and literature reviews considering these effects tend to have a highly marine-centric focus (*e.g.* Slabbekoorn *et al.*, 2010; de Soto *et al.*, 2016; Hawkins and Popper, 2017). This is despite data indicating that anthropogenic noise is prevalent across both marine and freshwater ecosystems (Cox *et al.*, 2016; Mickle and Higgs, 2017). It is important to consider that many fish species not only inhabit these aquatic environments, but may traverse between habitats which vary significantly in their physical properties. Flow depth and velocity, sediment transport, depth, salinity and temperature all interact with acoustic sound fields in different ways. Subsequently, although marine and freshwater fish share a common ancestry and similar characteristics (Carrete Vega and Wiens, 2012), individuals may be more or less impacted by a noise, dependent on the surrounding

aquatic environment. This may be of particular concern for euryhaline (adaptive to a range of salinities) or migratory fish species which live as residents, or pass through marine, estuarine (transitional), and freshwater environments during varying developmental phases of their lives (*e.g.* IUCN red listed European eel). For these species, there may be greater potential to experience cumulative impacts of differing forms, intensities and durations of noise exposure.

Understanding the broad-scale impacts of anthropogenic noise on fish will aid in improving conservation strategies and assist in the development of more appropriate life-stage and environmental specific policy standards, objectives, and measures. Using two differing methods (vote counting and effect size calculation), a meta-analysis was conducted with the aim of reviewing the current state of knowledge on how anthropogenic noise impacts fish. The investigation looked to answer four key questions: (1) is there an impact of noise on fish?; (2) what is the impact: behavioural, anatomical, physiological, or a combination of all three?; (3) does this vary between life-stage?; and (4) how does it vary between environment: marine, freshwater or euryhaline (both)? Secondary objectives of the literature review were to provide a database to assist with evidence collation and enable gaps in understanding or biases within this research field to be identified. Specifically, this review will summarise: topic publication history; noise sources investigated; article outputs by geographical location; author and research group collaboration/affiliation; top investigated subject species; popular scientific journal resources; and top-cited key research articles.

2.2.2 Research methodology

2.2.2.1 Literature search, inclusion criteria and data extraction

A comprehensive screening process was undertaken utilising the PRISMA (Figure 2.2: Preferred Reporting Items for Systematic Reviews and Meta-Analysis) protocol (Liberati *et al.*, 2009; Moher *et al.*, 2009; Nakagawa *et al.*, 2017). To identify suitable peer-reviewed studies for use in a meta-analysis investigating the effect of anthropogenic noise on fishes, literature searches were conducted using bibliographic search engines “Web of Science” and “SCOPUS”. More than one database was utilised within this search as only moderate overlap (40 – 50%) in article output exists between the two in a number of major fields (Mongeon and Paul-Hus, 2016). Fixed search term operators were expressed within a set of specified subject categories and were selected based on commonly noted terminology in the field of fish bioacoustics (Table 2.1). Document type outputs were limited to articles and peer-reviewed conference papers within the last 50 years and therefore dated from 1970, up to the time the literature search was conducted. Grey literature (*e.g.* technical reports) was not included. However, citations are discussed owing to their validity

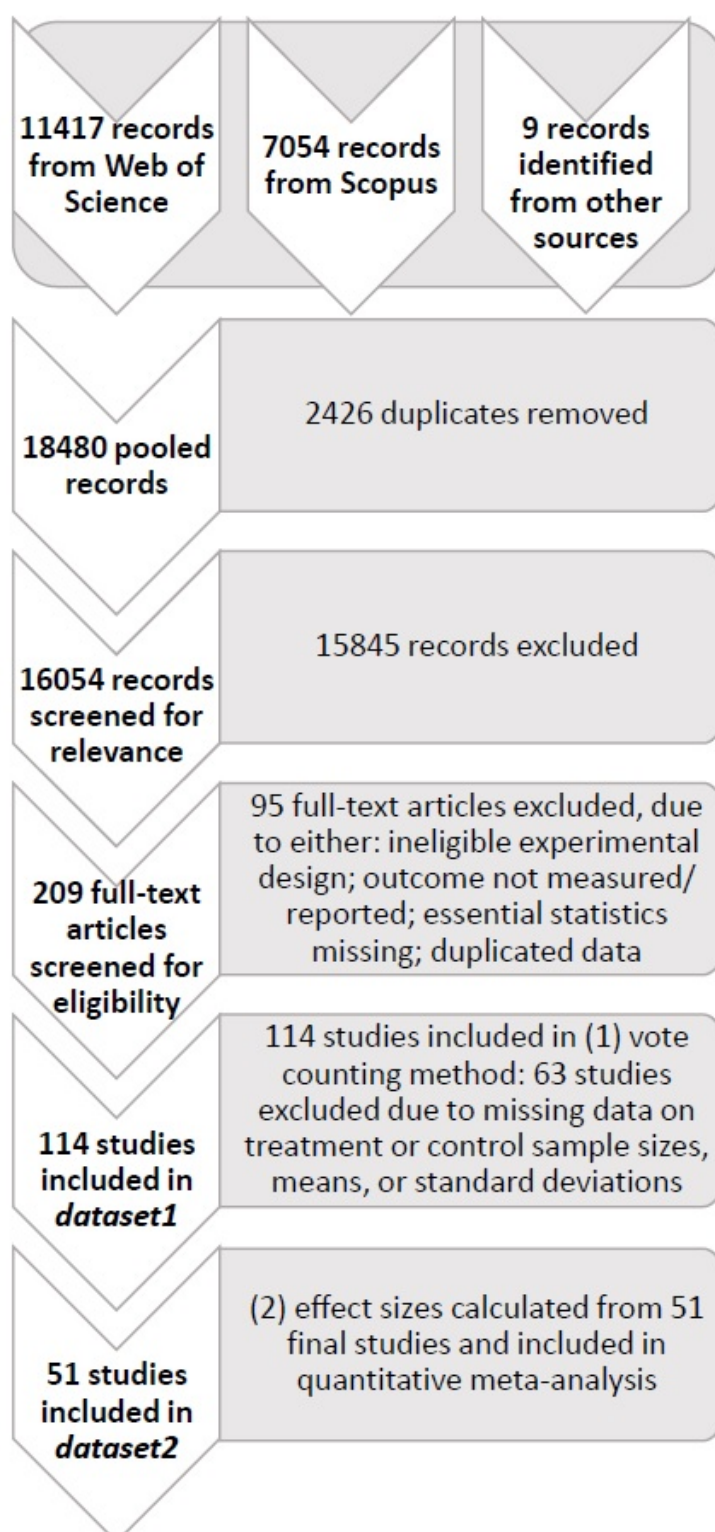


Figure 2.2: Literature refinement for use in meta-analysis with the four key elements of PRISMA: 'identification'; 'screening'; 'eligibility'; and 'included'.

in estimating effects of sound on fishes and their applicability within technical and regulatory decision making (for an descriptive review of the grey literature on the effects of anthropogenic noise on fish, see Popper and Hastings, 2009). Additionally, relevant articles within the bibliographies of identified papers were scrutinised and relevant literature which met the methodological prerequisites was added to the database.

Table 2.1: Search databases fixed search term operators and specified subject categories.

WoS Core Collection	Search Words in Title	"fish*" AND "noise*" OR "sound*" OR "acoustic"
	Specified Subject Categories	"Marine Freshwater Biology"; "Fisheries"; "Environmental Sciences"; "Acoustics"; "Ecology"; "Zoology"; "Behavioural Sciences"; "Engineering Environmental"; "Biology"; "Neurosciences"; "Biodiversity Conservation"; "Evolutionary Biology"; and "Environmental Studies"
	Search date	13 th October 2018
SCOPUS	Search Words in Title	"fish*" AND "noise*" OR "sound*" OR "acoustic"
	Specified Subject Categories	"Environmental Science"; "Engineering"; "Agricultural and Biological Sciences"; and "Neuroscience"
	Search date	13 th October 2018

Papers were manually screened for suitability of inclusion, with each study required to meet certain specifications: studies not properly controlled for prevention of pseudo-replication, observer bias or impacts of confounding variables were excluded (Milinski, 1997). For example, behavioural studies where response could not explicitly be assigned to presence of noise when a visual stimulus also exists (*e.g.* Graham and Cooke, 2008); results of studies were required to have appropriate statistical power and have indicated a statistical test value regarding an impact of noise. Finally, papers were limited to studies specifically investigating response to anthropogenic noise (measured in either domain: sound pressure or particle motion) as opposed to natural ambient noise sources.

To reduce the problem of "multiple testing" when investigating subgroups within multiple studies, a limited number of investigative effect variables were set, with pre-defined group associations to

reduce any uncertainty of resulting statistical analyses (Gates, 2002). Therefore, to answer the key questions and objectives of this study, analysis was further limited to studies reporting a specific set of explanatory variables (or where information was available elsewhere in literature), namely: focal species name; life-stage (or age-class); aquatic ecosystem type (marine, freshwater, or euryhaline). Solitary or group living species, could not be looked at as a variable as a result of testing type sometimes not catering to the species natural life-history strategy (*e.g.* auditory threshold test).

Age-class of focal species were categorised dependent on the sexual maturity of test individuals within a study group, as either 'adult', 'juvenile', 'larvae', or 'eggs'. Studies from which required information was unavailable on all variables were deemed not to meet the inclusion criteria for the meta-analysis. Furthermore, the journal title, year of publication, tested parameter (behaviour, physiology, or anatomy), authors and affiliations, and native region of the subject species were noted and entered into a database.

2.2.2.2 Statistical analyses

Statistical analyses were performed using software programme IBM SPSS Statistics v.22.0 (IBM Corp. IBM SPSS Statistics for Windows, Armonk, NY: IBM Corp) and RStudio (v 3.2.2: The R Foundation for Statistical Computing, Vienna, Austria, <http://www.r-project.org/>).

To provide weighting of evidence to this study, two methods were deployed to investigate if an overall impact of anthropogenic noise on fish existed. First, the simple (1) vote counting method (Bushman, 1994; Cooper *et al.*, 2009) was used to allow for the initial inclusion of a greater range of publications that would otherwise be excluded using more-in-depth quantitative analytical approaches. The larger sample size of cases provides an additional strength and consistency of evidence to the study. In isolation, however, the vote counting method fails to consider the sample size and statistical precision of each included study. It therefore does not provide details regarding the magnitude or direction of the biological effect of interest. Consequently, when data was available from *dataset1* regarding control and treatment group sample sizes, means and standard deviations, (2) a meta-analysis combining the magnitudes of study outcomes (effect sizes) could be calculated (final *dataset2*; $n = 51$). This method was used to address all four research objectives of this study.

2.2.2.2.1 Vote counting (1)

The vote counting method (Bushman, 1994; Cooper *et al.*, 2009) was utilised to compare the number of cases within *dataset1* finding a statistically significant effect of anthropogenic noise on fish behaviour, anatomy, or physiology, versus those that did not ("Yes" or "No" response). A

“case” was defined as the response of an individual species, at a particular life-stage, with respect to one tested response to noise (behavioural, physiological, or anatomical). A single research article could include multiple cases owing to a number of species, life-stages or parameters being investigated. Vote counting assumes that for a null hypothesis to be true, the population correlation, or effect size would be zero. The frequency of significant positive and negative results would therefore be assumed as equal (Hedges and Olkin, 1980). A chi-squared test was used to assess whether this was the case (Hunter and Schmidt, 1990).

2.2.2.2.2 Effect size calculation (2)

The effect sizes and associated variances of individually tested parameters within individual studies were first calculated. Effect sizes characterise the magnitude of a relationship, or the difference between two variables, and the variance is used to calculate confidence intervals which reflect the precision of this estimate. Study weights are typically calculated using the inverse of the variance, with larger studies providing more precise representations of a true population, and subsequently provide heavier weighting in the summary analysis.

The standardised mean difference (Hedge’s g : Hedges and Olkin, 1985) indicates the overall effect and weight of a study, based on its sample sizes (n_1 and n_2), control and treatment group means (\bar{X}_1 and \bar{X}_2 respectively), and standard deviations (s_1 and s_2). Hedge’s g was chosen as an effect size estimator as it corrects well for small sample bias. However, to get g , effect size is first computed as Cohen’s d (1988; Del Re, 2015):

$$d = \frac{\bar{X}_1 - \bar{X}_2}{\sqrt{\frac{(n_1-1)s_1^2 + (n_2-1)s_2^2}{n_1 + n_2 - 2}}} \quad (\text{Equation 2.1})$$

The variance of d (\mathcal{V}_d) is given by:

$$\mathcal{V}_d = \frac{2}{\tilde{n}} + \frac{d^2}{2(n_1 + n_2)} \quad (\text{Equation 2.2})$$

where, \tilde{n} , indicates the harmonic mean. Cohen’s d may then be converted to Hedge’s g through the computation of correction factor \mathcal{J} :

$$\mathcal{J} = 1 - \frac{3}{4 \times df - 1} \quad (\text{Equation 2.3})$$

where, df , are the degrees of freedom. Finally, correction factor \mathcal{J} is used to calculate Hedge’s g :

$$g = J \cdot d \quad (\text{Equation 2.4})$$

and variance of g (\mathcal{V}_g) is given as:

$$\mathcal{V}_g = J^2 \cdot \mathcal{V}_d \quad (\text{Equation 2.5})$$

Many studies produced outputs on two or more measures of a single sample, each providing an estimate of treatment efficacy. Therefore, in advance of analysis, dependent effect sizes were aggregated per study, or “case”, using the univariate BHHR procedure (Borenstein *et al.*, 2009), with a conservative imputation of $r = 0.5$. This accounted for correlation among within-study effect sizes and reduces the chance of biased estimates.

In advance of investigating the summary effect across all case outcomes, the directionality of each case effect size was coded to reflect whether noise positively or negatively affects responses (Cox *et al.*, 2018). An omnibus test was performed using a random-effects model to produce a forest plot. An inverse variance method was used, incorporating the Sidik-Jonkman estimate of τ^2 (amount of between-study variance, or variance of the distribution of true effect sizes) and Hartung-Knapp adjustment for random-effects. This allowed for a more robust estimate of variance, and was used in conjunction with Hedge’s g . Heterogeneity of the data was also inspected using I^2 (*i.e.* the percentage of variability not caused by sampling error: Higgins and Thompson, 2002) given its standardised interpretation of boundary cut-off values (25% = low; 50% = moderate; 75% = substantial heterogeneity: Higgins *et al.*, 2003):

$$I^2 = \max\left\{0, \frac{Q - (K-1)}{Q}\right\} \quad (\text{Equation 2.6})$$

where, Q , or Cochran’s Q -statistic, is the difference between observed effect sizes and the fixed-effect model estimate of the effect size, which is subsequently squared, weighted and summed, and K , denotes all studies within the meta-analysis.

To ensure residual concerns were accounted for, a sensitivity analysis was performed. Outliers and influential study cases in the data were identified where, for extremely small effects the upper bound 95% confidence interval (CI) was lower than the lower bound of the weighted pooled effect, and for large effects, the lower bound CI was higher than the weighted pooled effects higher bound (Viechtbauer and Cheung, 2010). The pooled literature was scrutinised using

Dffits value, Cook's distance, covariance ratios, and Baujat plot analysis (Baujat *et al.*, 2002; Harrer *et al.*, 2019). Any study exerting extreme influences on the weighted pooled result was removed from *dataset2* prior to the omnibus test. The final *dataset2* consisted of 82 case effect sizes from 51 studies.

Subgroup analyses was also performed on a case-by-case basis to investigate the effect of noise dependent on impact (anatomy, physiology, behaviour), life-stage (adult, juvenile, larvae, eggs), and environment (euryhaline, freshwater, marine). Weighted pooled effects were calculated and analysed per subgroup using a mixed-effects-model. Differences between the effects observed within subgroups were compared per investigative variable through calculation of the standard error of differences (SE_{Diff}), which allows for the calculation of confidence intervals, and subsequently, significance tests:

$$SE_{Diff} = V_A + V_B + V_C + \dots + \frac{\hat{T}_G^2}{m} \quad (\text{Equation 2.7})$$

in which SE_{Diff} depends on the variance (V_A , V_B , and V_C) within the Subgroups *A*, *B*, and *C*; \hat{T}_G^2 is the estimated variance between the subgroups; and m , the number of subgroups. Subgroup analyses is reliant on entire number of studies in the meta-analysis to be greater than 10 to allow for sufficient power (Higgins and Thompson, 2004).

2.2.2.2.3 Literature identification

The top 10 most important papers from *dataset1* were identified by uploading the bibliometric information into NAILS (Network Analysis Interface for Literature Studies), an open source Social Network Analysis project (Knutas *et al.*, 2015). Analytical tools were accessed from a GitHub repository and data processed in RStudio. Once initiated, NAILS used citation data of the records to calculate new metrics including "PageRank" (counts of the number and quality of links to a paper allowing for rough estimation of importance); and "In-Degree" (number of citations coming into a paper in a directed graph). An automated report based on data input was produced, providing an overview of productive authors/journals and top publications based on calculated metrics.

To provide an even further weighting of evidence, included journal articles from *dataset1* were scrutinised for statements citing the impacts of anthropogenic noise on fish in either a positive/

no impact or negative context, and totals tallied per journal. This allowed for the quantitative inclusion of publications that failed to meet the criteria of the primary investigative methods.

2.2.2.2.4 Bibliometric mapping

Bibliometric distance-based maps of *dataset1* were constructed using freeware programme VOSviewer (van Eck and Waltman, 2010). The software builds maps via the visualisation of similarities technique. Input is obtained from a normalised co-occurrence matrix that corrects for differences in total numbers of occurrences or co-occurrences of items via a similarity measure known as “association strength” or “proximity index”. Items are then mapped based on the similarity matrix, with distance between any pair representing their similarity. The map was finally translated, rotated and reflected to ensure consistent results (van Eck and Waltman, 2010).

2.2.3 Results

2.2.3.1 Meta-analysis

2.2.3.1.1 Impact

The (1) vote counting method found anthropogenic noise to have a significantly negative impact (150 of 202 cases: $\chi_1^2 = 47.55$; $p < 0.001$). The negative effect was reflected by (2) an overall standardised mean difference (SMD: Hedge’s *g*) of -0.82 (*CI* = -0.60, -1.04), indicating a large treatment effect at post-testing ($t = -7.53$; $p < 0.01$; Figure 2.3).

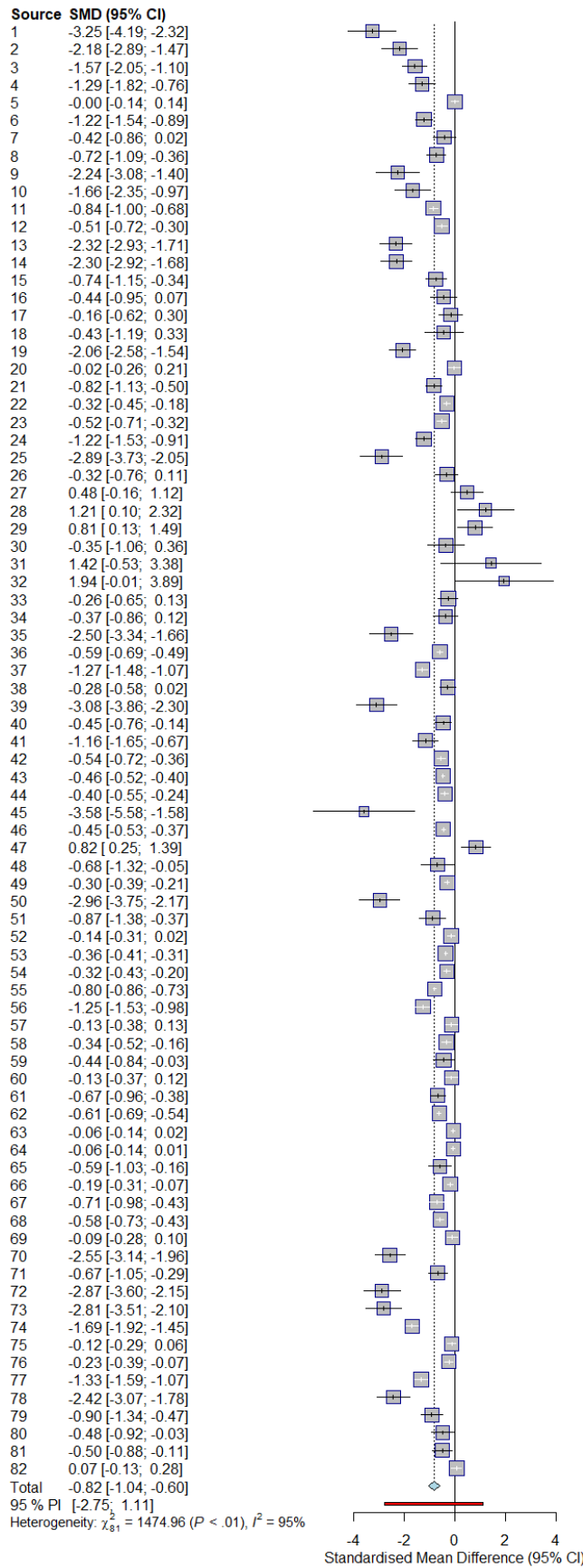


Figure 2.3: Forest plot of 82 cases from dataset2 illustrating an overall negative effect of noise on fishes (SMD: -0.82; CI = -0.60, -1.04). Note: Light-blue diamond indicates overall SMD, and red bar, 95% Prediction Interval (PI).

2.2.3.1.2 Anatomy, physiology, and behaviour

A negative impact was observed across all investigated parameters with 26 cases addressing anatomical responses (SMD = -1.53; CI = -1.13, -1.94), 25 investigating behaviour (SMD = -0.62; CI = -0.37, -0.87), and 31 regarding physiological responses (SMD = -0.38; CI = -0.11, -0.66). A random effects model indicated the difference in magnitude of negative effect between subgroup impacts to be significant ($\chi^2_2 = 21.7$; $p < 0.01$; Figure 2.4A). The magnitude of effect was greater for anatomical impacts than behavioural or physiological. Among the 114 studies included in *dataset1*, only 15 investigated more than one type of impact.

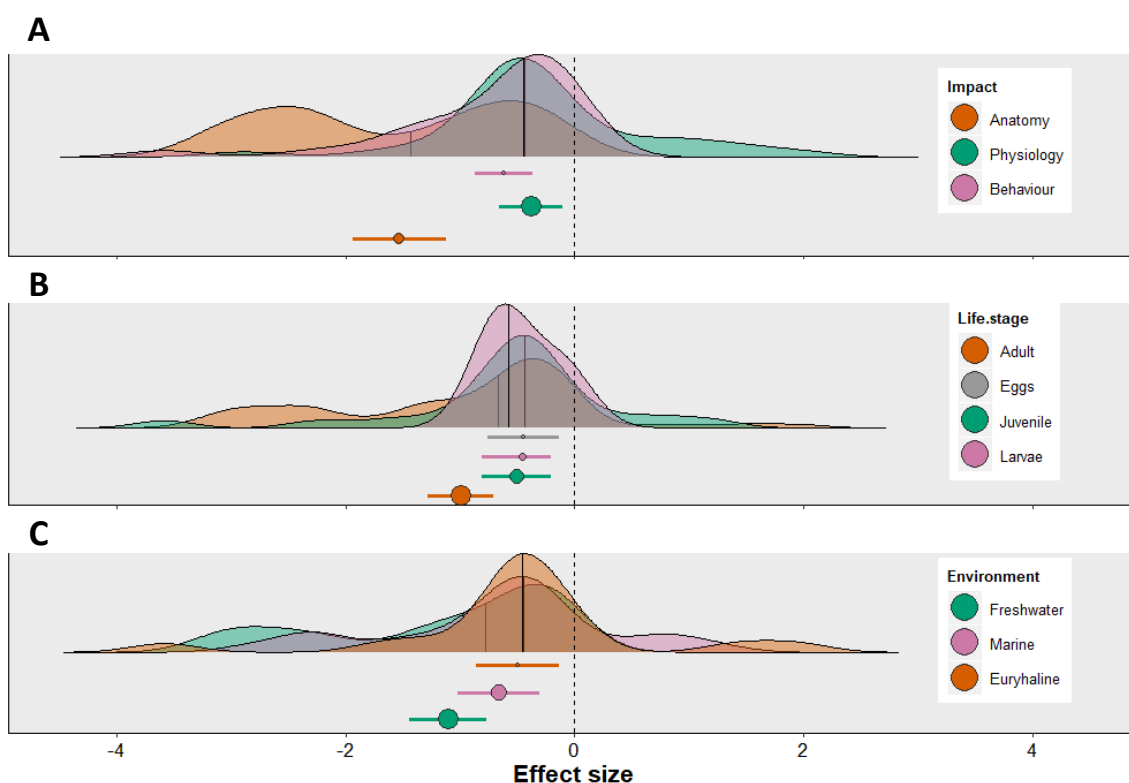


Figure 2.4: Posterior probability distribution of subgroup effect sizes calculated from dataset2 illustrating the negative impact of anthropogenic noise on: **(A)** impact (anatomy, physiology, behaviour); **(B)** life-stage (adult, juvenile, larvae, eggs); and **(C)** environment (freshwater, marine, euryhaline). *Note:* Dotted vertical line indicates zero effect, with data to the left highlighting a negative effect. Points and associated error bars show standardised mean differences (SMD) of subgroup analysis mixed effect models with upper and lower 95% confidence intervals (CI) indicated as error bars. Point size is proportional to the number of effect sizes within a group.

2.2.3.1.3 Life-stage

The negative effect of noise differed between life-stages ($\chi^2_2 = 9.07$; $p < 0.05$; Figure 2.4B). Adults ($n = 53$; $SMD = -1$; $CI = -0.71, -1.28$) were most impacted, compared to juveniles ($n = 25$; $SMD = -0.51$; $CI = -0.21, -0.81$), larvae ($n = 3$; $SMD = -0.45$; $CI = -0.09, -0.82$) and eggs ($n = 1$; $SMD = -0.45$; $CI = -0.14, -0.76$).

2.2.3.1.4 Aquatic environment

Differences in the magnitude of effect were also observed between environment ($\chi^2_2 = 6.4$; $p < 0.05$; Figure 2.4C). Species from freshwater systems experienced the greatest negative effect ($SMD = -1.11$; $CI = -0.17, -1.44$), followed by marine ($SMD = -0.66$; $CI = -0.31, -1.02$), and finally euryhaline species ($SMD = -0.5$, $CI = -0.13, -0.86$).

2.2.3.2 Literature database

2.2.3.2.1 PRISMA summary

Searches returned 11 417 and 7054 articles from Web of Science and SCOPUS respectively, of which there was a 34.3% overlap in output. A further 9 records were identified through other sources, thereby totalling 18 480 articles which met the key search term parameters of the literature search (“fish*” AND “noise*” OR “sound*” OR “acoustic*”). The search term parameter “noise*” resulted in a weighted return of non-topical engineering and physics journal articles. Subsequently, after screening abstracts for relevance, 209 articles published since 1970 were discerned to be directly related to the investigative topic of “impacts of anthropogenic noise on fish”, with the majority (69.4%) published after 2010 (Figure 2.5). Further manual screening indicated that 114 papers met the final criteria for inclusion in the vote counting analysis, with other studies lacking the necessary explanatory variables or failing to meet the set prerequisites of the study. From the vote counting method, the 114 articles yielded a total of 202 “cases”, and effect sizes of 82 “cases” from 51 studies were included in omnibus analysis (Appendix A: Supplementary Table A.1).

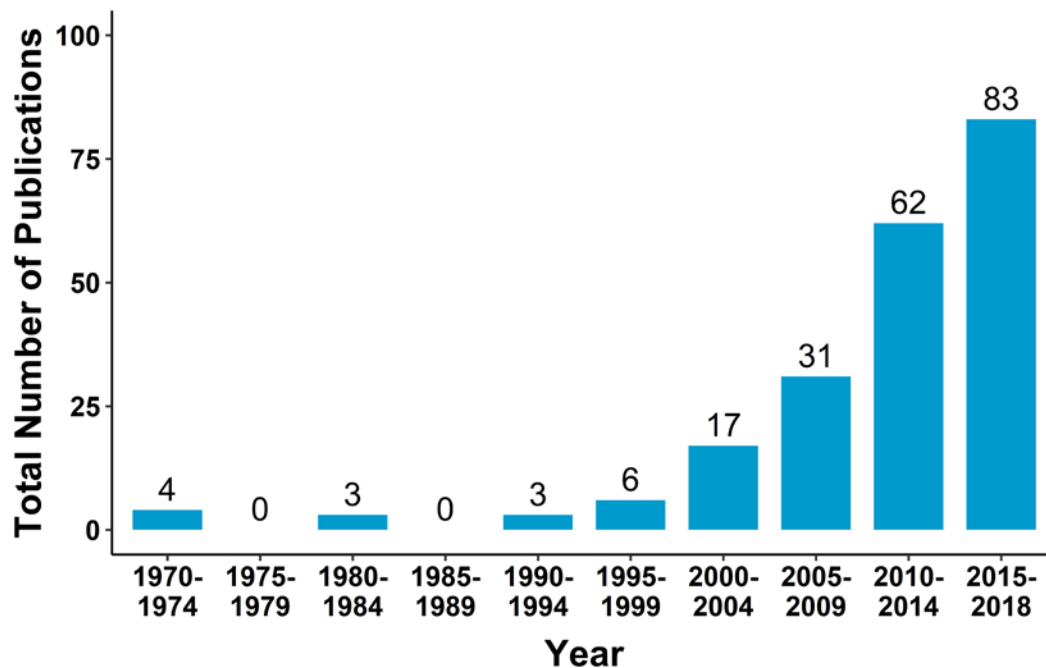


Figure 2.5: Number of relevant studies identified from the literature since 1970, investigating impacts of noise on fish (total = 209).

From *dataset1*, within the 114 articles, 938 citations were referenced negatively, and 131 positively in direct reference to the impacts of anthropogenic noise on fish (Figure 2.6). These references were noted to be from a total of 249 studies published within 94 different academic journals from the year 1967 onwards. The most citations originated from ‘The Journal of the Acoustical Society of America’ (JASA). This is in line with JASA being among the top 2 most popular journals to publish in for this topic, based on articles included in the meta-analysis. Articles from JASA were also the most referenced and cited within the dataset (Figure 2.7; Table 2.2). A total of 54 articles cited only negative impacts, compared to 4 describing only positive (or no impact) effects.

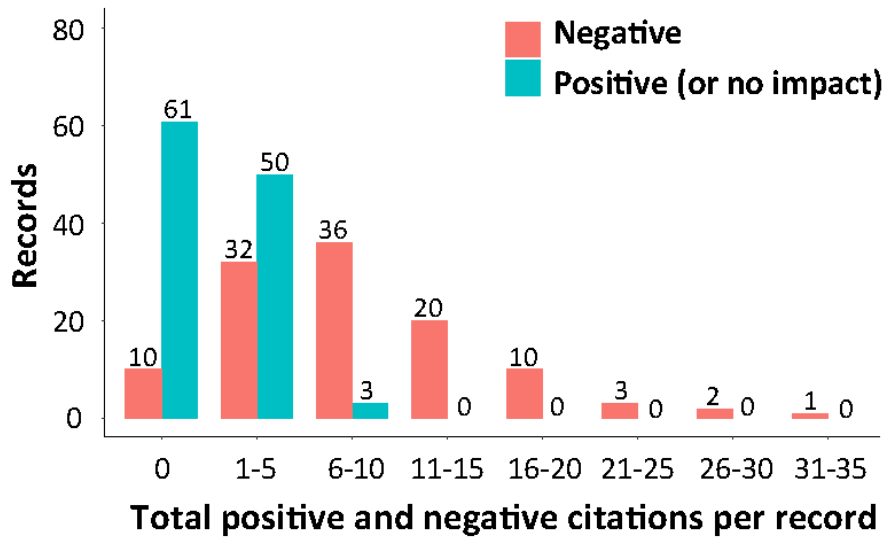


Figure 2.6: Total number of positive (or no impact) and negative citations regarding impacts of anthropogenic noise on fishes.

Table 2.2: Top 10 important papers within meta-analysis data network with Web of Science citation count and page rank score among the citation network.

Rank	Author and Year	Journal	Species Category	In-Degree	WoS TimesCited	PageRank
1	Smith <i>et al.</i> , 2004a	<i>J. Exp. Biol.</i> 207, 427-435.	Freshwater	32	151	0.0007161
2	Wysocki <i>et al.</i> , 2006	<i>Biol. Conserv.</i> 128, 501-508.	Freshwater	31	119	0.0006816
3	Scholik and Yan, 2001	<i>Hear. Res.</i> 152, 17-24.	Freshwater	28	83	0.0006250
4	Hastings <i>et al.</i> , 1996	<i>J. Acoust. Soc. Am.</i> 99, 1759-1766.	Freshwater	25	63	0.0006487
5	Popper <i>et al.</i> , 2005	<i>J. Acoust. Soc. Am.</i> 117, 3958-3971.	Freshwater	23	98	0.0006227
6	McCauley <i>et al.</i> , 2003	<i>J. Acoust. Soc. Am.</i> 113, 638-642.	Marine	21	147	0.0006503
7	Amoser and Ladich, 2003	<i>J. Acoust. Soc. Am.</i> 113, 2170-2179.	Freshwater	20	59	0.0005276
8	Picciulin <i>et al.</i> , 2010	<i>J. Exp. Mar. Biol. Ecol.</i> 386, 125-132.	Marine	20	59	0.0005013
9	Wysocki <i>et al.</i> , 2007	<i>Aquaculture</i> 272, 687-697.	Euryhaline	19	54	0.0005374
10	Codarin <i>et al.</i> , 2009	<i>Mar. Pollut. Bull.</i> 58, 1880-1887.	Marine	16	110	0.0004713

Note: Articles sorted by in-degree citation network of dataset, with ties broken by citation count, followed by page rank.

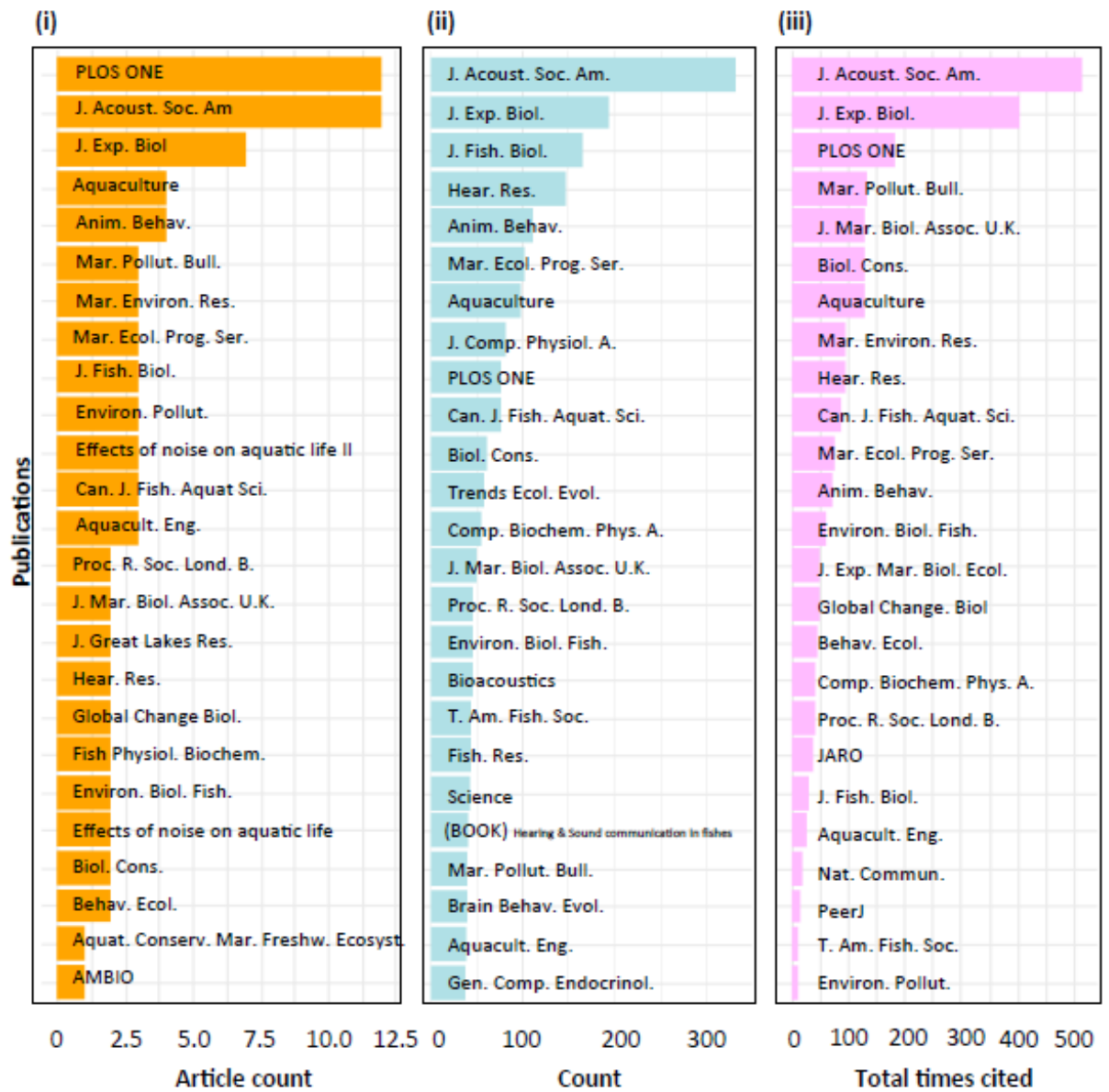


Figure 2.7: (i) Most popular publication journals; (ii) most referenced publication journals; and (iii) most cited publication journals within *dataset1* investigating impacts of anthropogenic noise on fish.

2.2.3.2.2 Geographical and research group affiliations

Publications were regionally biased. Sixty-nine publications (60.5%) included researchers from Europe (Figure 2.8) with the majority based in the U.K. (total: 28; 24.5%). Fifty-three (46.5%) had input from authors associated with North American institutions which were highly weighted to the U.S.A. (total: 43; 38%). Researchers from Oceania contributed to 15 articles (13%), and 4 from Asian groups (3.5%). There were no regional research affiliations from either South America or Africa. Research group and geographical affiliations are further apparent through cluster analyses visualisation networks of co-authorship and co-citations among the literature (Figure 2.9).

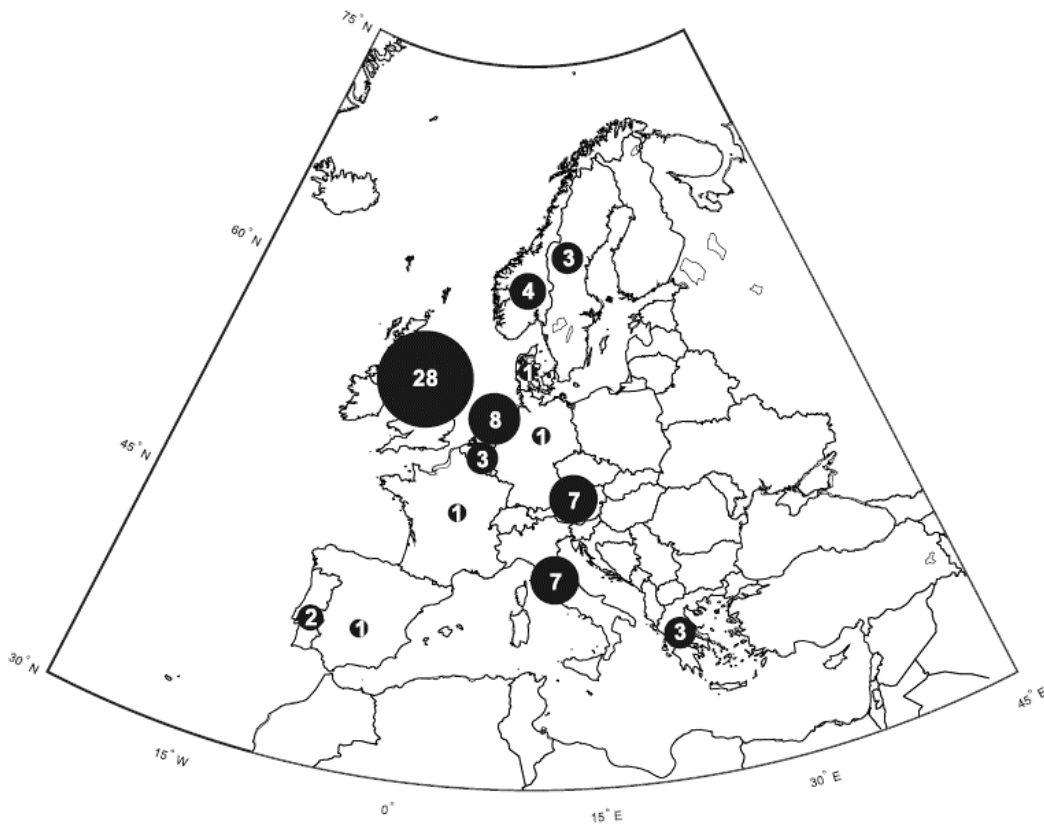


Figure 2.8: Geographical affiliations of authors in Europe within *dataset1* publications.

Note: Circle size represents weighting influence of region.

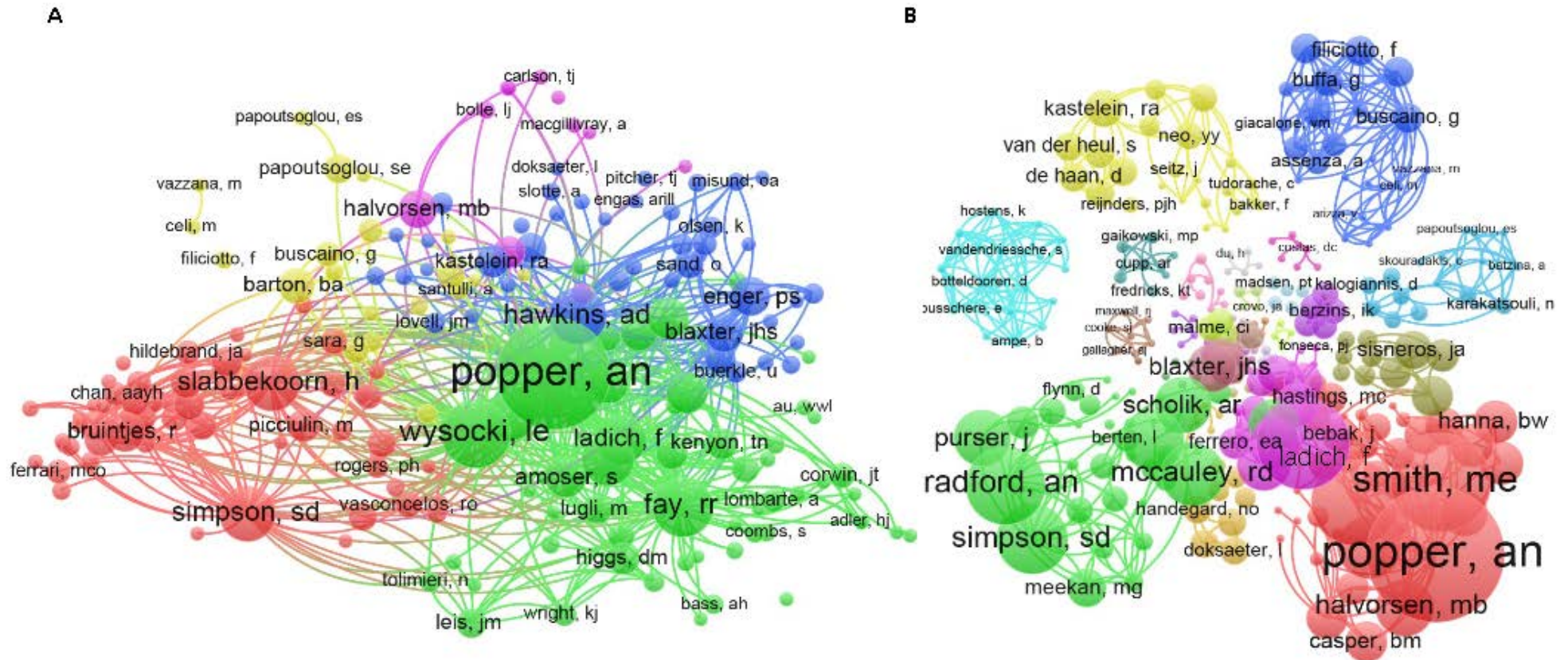


Figure 2.9: (A) Citation network among *dataset1* literature; and (B) co-authorship network and clusters among researchers.

2.2.3.2.3 Focal species and research context

Within the 114 articles, 90 different species and subspecies were investigated: 37 freshwater and 42 different marine species were studied respectively, alongside 11 euryhaline fish species (Figure 2.10). Most papers focused solely on freshwater species (41), followed by marine (39), then euryhaline (26). A further 8 papers looked at a combination of the differing species category types. Most cases involved laboratory testing (35 freshwater; 28 euryhaline; 26 marine), however enclosure field tests were also conducted (16 marine; and 10 freshwater and euryhaline respectively). Only 4 free-field open water experiments were included in the analysis, with only 1 of these investigating a freshwater species. A limited number of studies (5 total: 2 marine and 3 euryhaline) combined laboratory and complimentary field studies within their analysis.

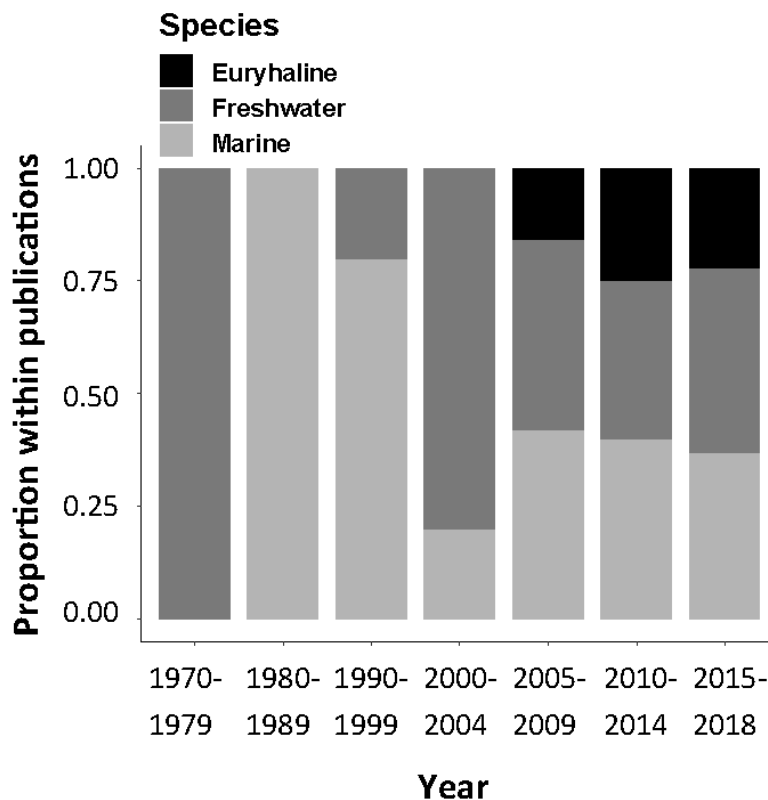


Figure 2.10: Proportion of studies investigating the impact of anthropogenic noise on freshwater, marine or euryhaline focal species over time within *dataset1*.

The top 10 most frequently used subject species were; European sea bass (*Dicentrarchus labrax*); Atlantic herring (*Clupea haerengus*); goldfish; zebrafish (*Danio rerio*); gilthead sea bream (*Sparus aurata*); rainbow trout (*Oncorhynchus mykiss*); European eel; northern pike (*Esox Lucius*); three-spined stickleback (*Gasterosteus aculeatus*); and Atlantic cod. Among these top 10 species of

investigation, only 2 (*G. morhua* and *A. anguilla*) are listed as “vulnerable” or worse according to the IUCN red list on conservation status, with the European eel currently classified as “critically endangered”. The majority of these species are of commercial relevance from across the fisheries, ornamental aquatic and sporting industries. In line with an increased awareness of the anthropogenic noise problem, studies were conducted across a range of investigative reasoning (Table 2.3). This included, but was not limited to: ecological, commercial, or conservational concern; data to inform industrial mitigation efforts; maximising growth performance in aquaculture; and fundamental phylogenetic or ontogenetic understanding.

Table 2.3: Range of noise types investigated and examples of study objectives.

Noise types in <i>dataset1</i> (N studies)	Examples of study objectives
AQUACULTURE	
Aquaculture ambient noise (8)	Investigating the impact of noise on rate of growth, egg development, body condition, disease resistance, and survival in fisheries and aquaculture facilities ^{a, b} ; music to reduce impacts of stress in aquaculture fish ^c ; impact of marine mammal deterrents on fish ^d ; and animal health and stress induced from noise in public aquariums ^e .
Acoustic pinger (2)	
Classical music (3)	
INDUSTRIAL/ RECREATIONAL	
Airgun/ watergun noise (11)	Understanding effects on hearing, communication and spawning success ^f ; changes in individual or group swimming ^g , orientation ^h , anti-predator ⁱ , or escape behaviour ^l in proximity to noise sources; gene identification to assess effects of loud sounds ^k ; behavioural, physiological or anatomical (e.g. barotrauma) ^l effects and recovery from impacts of industrial or shipping activity ^m ; chronic effects of noise on hatching success, larval growth and survival ⁿ ; context or condition-dependent impacts of noise ^{o, p} ; stress induced changes in physiology ^q ; cross-modal effects or attention shifts (e.g. distraction from chemical cues) ^r ; habituation or tolerance to noise ^s ; alterations to foraging, sheltering, and parental care ^t ; and covariable interaction effects on predator-prey dynamics ^u
Motor boat engine noise (22)	
Pile driving noise (11)	
Road traffic noise (1)	
Ship engine noise (12)	
Simulated ship engine noise (1)	
Sonar (5)	
Wind power noise (1)	
GENERAL	
Broadband noise (7)	Understanding hearing sensitivity, noise induced threshold shifts or hearing loss ^v ; ontogenetic development of acoustically evoked behavioural responses ^w ; impacts of noise on behaviour (e.g. swimming speed, startle responses, group responses) ^{x, y} ; the Lombard effect ^z ; noise to direct fish away from an undesirable location (i.e. developing acoustic deterrent or guidance systems) ^{aa, bb} ; and responses to differences in acoustic stimuli timing or structure (e.g. continuous shipping noise compared to impulsive pile-driving) ^{cc} .
Brown noise (3)	
Tonal frequencies (12)	
White noise (18)	

Example references: ^a Wysocki *et al.*, 2007; ^b Davidson *et al.*, 2009; ^c Papoutsoglou *et al.*, 2013; ^d Goetz *et al.*, 2015; ^e Anderson *et al.*, 2011; ^f Codarin *et al.*, 2009; ^g Herbert-Read *et al.*, 2017; ^h Holles, *et al.*, 2013; ⁱ Simpson *et al.*, 2015; ^j Berthe and Lecchini, 2016; ^k Andrews *et al.*, 2014; ^l Casper *et al.*, 2013b; ^m Brintjes *et al.*, 2016; ⁿ Brintjes and Radford, 2014; ^o Brintjes and Radford, 2013; ^p Purser *et al.*, 2016; ^q Celi *et al.*, 2016; ^r Hasan *et al.*, 2018; ^s Nedelec *et al.*, 2016; ^t McLaughlin and Kunc, 2015; ^u McCormick *et al.*, 2018; ^v Amoser and Ladich, 2003; ^w Alderks and Sisneros, 2013; ^x Blaxter and Hoss, 1981; ^y Neo *et al.*, 2015; ^z Holt and Johnston, 2014; ^{aa} Vetter *et al.*, 2017; ^{bb} Zielinski and Sorensen, 2017; ^{cc} Neo *et al.*, 2014. *Note:* some studies investigated more than one noise type.

2.2.4 Discussion

This review used global datasets from comparable studies to quantify: 1) whether an impact of anthropogenic noise on fish exists; 2) what these impacts are; 3) if they vary across life-stages; and 4) how they differ between aquatic environments. Clear evidence was found to support that unwanted noise from sources including pile driving activity, motor boat and ship engines, airguns and sonar, negatively impacts fish. Anthropogenic noise had a significantly negative effect on fish anatomy, physiology, and behaviour across differing life-stages and a range of aquatic environments. Crucially, the degree of these negative impacts differed extensively, with the greatest magnitude of effect observed in studies investigating anatomical damage. The impact of noise was also greater among adult and juvenile life-stages, and for freshwater fish species.

A large proportion of the studies included in this meta-analysis (87.7% of *dataset1*; 90.2% of *dataset2*) found anthropogenic noise to have a negative impact on fish. For instance, noise has been observed to reduce fish foraging effort and efficiency (*e.g.* convict cichlids, *Amatitlania nigrofasciata*: McLaughlin and Kunc, 2015; zebrafish: Shafiei Sabet *et al.*, 2015; three-spined stickleback, and European minnow, *Phoxinus phoxinus*: Voellmy *et al.*, 2014a), modify coordinated movements within groups (*e.g.* sea bass: Herbert-Read *et al.*, 2017a), impair conspecific or mating communication (*e.g.* brown meagre, *Sciaena umbra*, Mediterranean damselfish, *Chromis chromis*, and red-mouthed goby, *Gobius cruentatus*: Codarin *et al.*, 2009), alter parental care and offspring survival (*e.g.* largemouth bass, *Micropterus salmoides*: Maxwell *et al.*, 2018; spiny chromis, *Acanthochromis polyacanthus*: Nedelec *et al.*, 2017), impact navigation or orientation behaviour (*e.g.* Apogonidae *sp.*, reef settlement: Holles *et al.*, 2013; Simpson *et al.*, 2005b; 2010), and increase stress levels (*e.g.* blacktail shiner, *Cyprinella venusta*: Crovo *et al.*, 2015; giant kelpfish, *Heterostichus rostratus*: Nichols *et al.*, 2015). The range of impacts observed may be highly context dependent (Bruitjes and Radford, 2013; Maxwell *et al.*, 2018), however, they clearly indicate the overwhelmingly negative implications of anthropogenic noise on fish.

The negative effects of noise were shown to impact fish anatomy (*e.g.* hearing loss: Smith *et al.*, 2006; swimbladder damage: Casper *et al.*, 2017), behaviour (*e.g.* communication: Sebastianutto *et al.*, 2011; foraging: Shafiei Sabet *et al.*, 2015; and predator avoidance: Simpson *et al.*, 2015) and physiology (*e.g.* ontogeny: Nedelec *et al.*, 2015; homeostasis: Nichols *et al.*, 2015). The magnitude of effect was greatest for cases investigating anatomical impacts of noise exposure. Temporary hearing loss may result in short-term behavioural adjustments including, for example, reductions in conspecific communication (Sebastianutto *et al.*, 2011), or alterations in schooling behaviour (Herbert-Read *et al.*, 2017a). Studies investigating the longer-term behavioural consequences of

hearing loss in response to chronic and impulsive noise exposures are however less common, yet are necessary to understand whether impacts are temporary, or permanent, and whether they have wider reaching implications (*e.g.* population or community-level impacts). For instance, although noise exposure can lead to significant loss of hair cell bundles within several saccule regions, there is the potential for recovery (Smith *et al.*, 2006). Nevertheless, this does depend on the stimuli frequency and exposure time; or the auditory sensitivity of an affected individual and its proximity to a noise source. A select few studies (15 in *dataset1*) investigated more than one impact under the same set of acoustic conditions. For example, two complimentary studies investigated the impact of seismic airgun noise on three species of freshwater fish (*Couesius plumbeus*, *E. Lucius* and *Coregonus nasus*) and found temporary hearing threshold shifts (Popper *et al.*, 2005), but no damage to the inner ear tissues (Song *et al.*, 2008). These results emphasise the importance of a point expressed by Mickle and Higgs (2017), that there is a need to assess across more than one parameter when testing species response to noise, thus ensuring interpretations of results are better informed. Furthermore, while analyses indicated noise to have the greatest impact on anatomy, it is important to consider the specific study conditions, with only a select few combining laboratory and field findings (*e.g.* Simpson *et al.*, 2016; Ferrari *et al.*, 2018). Such comparisons are important to allow for ecological validation of experiments performed in situ. This is of importance as it is highly likely, for example, that the proximity of an individual to a noise source under real-world conditions will drive behavioural changes or induce a physiological response (*e.g.* chronically induced stress) rather than cause anatomical damage or mortalities more commonly observed at close range. Behavioural responses of fish to isolated noise exposure events have been well described, and these can be induced through a range of mechanistic channels. For example, noise can act as a uni- or crossmodal distraction (*e.g.* impairment of alarm cue detection: Hasan *et al.*, 2018), overlap with a species hearing range, or mask important acoustic information (*e.g.* communication calls: Codarin *et al.*, 2009). Further research is required to better understand the effects of, and habituation or sensitisation to repeated exposures of intense noise over time (Chapter 5). Recent work on European sea bass (Neo *et al.*, 2018) suggests that responses to regular interactions may be context or even diel dependent, however, data on free-ranging fish is required to validate findings and appropriately mitigate. Additionally, all but two studies included in this meta-analysis solely focused on noise pollution in isolation. However, it is becoming increasingly apparent that the interaction and potentially synergistic effects between varying drivers of anthropogenic change (*e.g.* rising temperatures or carbon dioxide levels: Poulton *et al.*, 2017; McCormick *et al.*, 2018) on fish anatomy, physiology and behaviour, also require investigation.

Anthropogenic noise was quantitatively confirmed to have a significant negative effect across all life-stages. However, the magnitude of this effect differed, with adults and juveniles being more impacted than larvae and eggs. Individuals within the early developmental stages adapt well to natural environmental fluctuations (Hamdoun and Epel, 2007), for instance, in response to ambient noise. However, it is unlikely that they are more robust to anthropogenic disturbances than adults, as such interference drives conditions beyond normal environmental variability (Bruitjes and Radford, 2014). To better quantify the magnitude of this effect, more data on egg, larvae and embryo stage response variables are required, as studies on these life-stages were limited. Studies assessing the hearing capabilities of coral reef fish have indicated similar sensitivities in both larvae and juveniles (Wright *et al.*, 2005), however other studies report both ontogenetic and interspecific differences with large detection variances (Wright *et al.*, 2011; Alderks and Sisneros, 2013). Even if an impact of anthropogenic noise does not result in immediate or delayed mortalities of early life-stage individuals, they could still have implications at a later phase of life (Gagliano *et al.*, 2017). For instance, there may be impacts on development or growth and function of varying organ systems (de Soto *et al.*, 2013), or effects on behaviour having repercussions on longer-term survival (Popper and Hastings, 2009b), communities and populations (Slabbekoorn *et al.*, 2019). Understanding responses to noise across developmental stages is important as hearing capabilities will vary, as may any elicited behavioural response.

Noise had a detrimental effect on fish species from across the full range of aquatic habitats. Anthropogenic noise is an internationally transboundary pollutant of concern with cumulative and synergistic effects across a range of ecosystems (*i.e.* marine, estuarine and freshwater), (Hatch and Fristrup, 2009; Mickle and Higgs, 2017; Rouillard *et al.*, 2018). Be that as it may, differences were observed in the degree of impact between habitat type. While proposed legislation surrounding noise mitigation tends to exhibit a largely marine-centric focus (*e.g.* Marine Strategy Framework Directive), intriguingly, the magnitude of this negative effect was greatest for freshwater fish species. Two-thirds of all freshwater fishes possess morphological hearing specialisations that allow for the enhancement of auditory sensitivity and frequency range detection (Amoser and Ladich, 2005). In addition to particle velocity, fish with otophysic connections can detect pressure components over a much broader frequency range, at much lower sound intensities. Potentially, this may increase their susceptibility to high intensity anthropogenic disturbances within an already acoustically “messy” environment (*i.e.* shallow-water river bottom topographies), (Popper and Hastings, 2009b; Tonolla *et al.*, 2010). While the effect of noise was least for euryhaline species, similar to freshwater migratory fish, many must traverse large areas of geographical space to complete complex life cycles. These migratory species may therefore be more susceptible to the impacts of cumulative, or multiple noise

exposure events. Many diadromous fishes rely on cortisol as a critical endocrine factor to mediate growth and other physiological changes in advance of entering differing aquatic salinities (*e.g.* gill ionocyte structure and function: Zydlewski and Wilkie, 2012). The implications are that the internal condition of an organism (*e.g.* metabolic status) may alter its behaviour (*e.g.* IUCN red listed “critically endangered” European eel: Edeline, 2007; Simpson *et al.*, 2015; Bruintjes *et al.*, 2016), or potentially even delay migration. Despite some studies identifying impacts to fish cortisol levels, it remains unknown whether there are any associated energetic costs of noise induced stress or implications for survival.

It is important to note common caveats to interpretation of any quantitative literature review. First, a lack of negative results may be biased through an absence of publications associated with such outcomes (Thornton and Lee, 2000). In this review (*dataset2*), only seven cases reported a positive impact of “noise” on fish, and six of these were in response to classical music. These cases found music to reduce captive aquaculture induced stress (cortisol levels), (Pickering, 1990), subsequently promoting muscle growth and an improved body condition (*e.g.* common carp, *Cyprinus carpio*; rainbow trout, gilthead sea bream: Papoutsoglou *et al.*, 2007; 2013; 2015). Second, when investigating the impacts of noise on fish, the complexity of fish biology (*e.g.* hearing capabilities, age, life-history strategy) and temporal and structural differences of noise stimuli tested among studies (*e.g.* acoustic complexity, frequency range, impulsive vs chronic, signal intensity) may influence the heterogeneity of a statistical model when assessing an overall impact of noise on fish. That said, recent work by Kunc and Schmidt (2019) investigating impacts of noise across taxon, suggest such attributes (*e.g.* phylogeny and species) to minimally influence model heterogeneity. Furthermore, results reflect those of Cox *et al.* (2018) who found that while the specific type of noise (*e.g.* broadband, music, natural: Chapter 4) may differentially impact fish responses, multiple species exposed to noise under a range of experimental conditions, as opposed to a select few highly sensitive species, were similarly negatively impacted.

A number of biases in the field of anthropogenic noise and its impacts on fish were identified. These included authorship, geographical affiliation, and species studied. Cluster analysis provided visual representations of co-authorship and co-citation networks, demonstrating existing bias, with the majority of the top 10 most important papers within the meta-analysis network (*dataset1*) originating from the same clusters (Table 2.2). Understanding these biases are important to ensure progression within the field of fish bioacoustics. Researchers should consider both complementary and contrasting perspectives, approaches and avenues of inquiry to address a broader spectra of collaborative ideas, and to prevent partisan idealism. Widening the collaborative clusters identified within this meta-analysis could be beneficial, and should be inclusive of early career researchers who

can provide novel viewpoints which either build-, improve-upon, or question commonly accepted stances within the field. It should however be noted that outputs of bibliographic search engines were also limited to those written in English, which may have influenced the assessment of geographical bias. Worldwide, research groups tend to focus on a limited number of species, typically concentrating on those of interest to local surrounding ecosystems, or for utilisation as ideal “model” subject specimens when investigating fundamental research questions (*e.g.* goldfish). Despite the identification of over 34 thousand fish species worldwide (Froese and Pauly, 2019), the impact of noise has only been investigated on a very small fraction ($\frac{69}{25\,000}$: *dataset1*). Given the number of extant fish species and problematic sound sources, note should be taken of recent commentary by Popper *et al.* (2020) that future work investigating fundamental research questions should take a more standardised approach to aid in cross-study data comparisons. However, it is also important to note that spatial or taxonomic bias in understanding may prove problematic (Kemp *et al.*, 2012b). Regionally obtained, or species-specific knowledge may favour relatively conspicuous species and might not be applicable to contextually differing scenarios. Additionally, while many fish species are similar, the ecological impacts of anthropogenic noise will vary due to differences in life-history and species-specific, or inter-individual behaviour (*e.g.* anti-predator behaviour in European minnow and three-spined stickleback: Voellmy *et al.*, 2014b; Mittelbach *et al.*, 2014). It is paramount that we understand where any bias lies, as this will aid in the development of future collaborations between principal stakeholders to better identify and address critical research questions from both global and more localised perspectives.

This meta-analysis is the first to quantitatively assess the interconnectivity of aquatic ecosystems, thereby considering differing migratory or resident life-history strategies, when examining the impacts of anthropogenic noise on fish. It highlights how aquatic noise negatively impacts fish anatomy, physiology and behaviour, and how the magnitude of this impact differs dependent on life-stage and habitat. While a breadth of studies have investigated a range of differing species types, habitats, and life-stages through an array of laboratory and field studies, there is a real need to understand the complexity and variability of reported responses in a broader ecological context. It is recommended that the underwater noise problem moves away from the current marine-centric focus and instead should be internationally recognised across the diversity of aquatic ecosystems inhabited by fish. A number of policies written as part of protected area legislation do not currently encompass anthropogenic noise, and those that do still struggle to mitigate against its pervasive impacts (Buxton *et al.*, 2017). There is a real need to not only introduce noise mitigation into environmental protection policies, but to also ensure that these are highly integrated (Borja *et al.*, 2010). Such a tactic should prevent overlapping policy standards, objectives, and measures which

may deter from successful implementation of conservation protections for our increasingly impacted aquatic ecosystems (Rouillard *et al.*, 2018).

2.3 Collective behaviour of fishes

Displays of collective group behaviour are common across differing animal taxa including: birds (*e.g.* starling murmurations: Netjinda *et al.*, 2015), mammals (*e.g.* herding buffalo: Tambling *et al.*, 2012; sheep flocks: Ginelli *et al.*, 2015; and human social vortices: Silverberg *et al.*, 2013; Bottinelli *et al.*, 2016), insects (*e.g.* ant vortices: Schneirla, 1944; Cheng *et al.*, 2009; or caterpillar milling: Fabre, 1899), crustaceans (*e.g.* crab migration: Green, 1997), amphibians (*e.g.* tadpole formation: Pizzatto *et al.*, 2016), and fishes (*e.g.* schooling or shoaling behaviour: Pitcher, 1983). Anthropogenic sound is known to detrimentally affect the behaviour and physiology of individual animals (see Chapter 2.2 for a detailed overview). Its disruption to collective behaviour, such as shoaling in fish, however, remains poorly understood. This is despite the importance of collective behaviour to many fish species that adopt a group living strategy, benefitting from social information exchange and anti-predator defence (Handegard *et al.*, 2012). Collective navigation may even facilitate fish passage through human-made barriers among mass migratory species (*e.g.* Chinook salmon, *Oncorhynchus tshawytscha*: Okasaki *et al.*, 2020). It is therefore important to understand these group compositions and how they may be impacted by human generated noise.

Decision trade-offs exist surrounding the costs and benefits to individual animals living in groups, and fitness gains and hazards involved must be compared to the alternative of living alone (Table 2.4). Although group association improves overall foraging success (Day *et al.*, 2001; Dutta, 2014), reduces energetic costs of locomotion (Marras *et al.*, 2015; Li *et al.*, 2020), and normally provides enhanced protection from predators (Landeau and Terborgh, 1986; Handegard *et al.*, 2012), it may also result in increased competition (Alexander, 1974; Chicoli *et al.*, 2014). For example, strong species and size assortment occur in fish shoals (Hoare *et al.*, 2000; Svensson *et al.*, 2000; Killen *et al.*, 2017), thus contributing to the 'oddity effect' (Table 2.4). In other words, conspicuousness provides an advantage by reducing the chance of predation (Landeau and Terborgh, 1986; Theodorakis, 1989). Conversely, smaller individuals within groups made up of larger individuals will most likely be outcompeted for food (Peuhkuri, 1997; Seppä *et al.*, 1999). While the costs are generally outweighed by many benefits, the trade-off experienced by each individual within a group may be highly context dependent (Killen *et al.*, 2017).

In social species, segregative selection among groups is common, with subgroup formation commonly attained according to varying phenotypical traits (*e.g.* size, sex, age, relatedness: Krause and Ruxton, 2002). This strategy exploits the ‘confusion effect’ (Table 2.4), making it more difficult for predators to target a single individual among several visually similar individuals (Cattelan and Griggio, 2018). Subsequently, within any given group, a homogeneous distribution of characteristics may be observed relative to an overall population (Killen *et al.*, 2017). While a “swarm”, for instance, may appear to act as a single entity, it is in fact made up of a group of individuals working within that collective, constituted by a complex feedback matrix through interactions with other individuals and the surrounding environment (Riley, 2014). Common transitions between dynamically stable collective states (*e.g.* swarming, milling or parallel groups: Couzin *et al.*, 2002; Tunstrøm *et al.*, 2013) are, however, most likely driven by phenotypic differences (*i.e.* physical, cognitive and behavioural expression) among grouping individuals (Couzin *et al.*, 2002; Jolles *et al.*, 2020). Group size is important to consider, as the stability of a group is influenced by the number of members, with the distance between fish going down as the number of individuals goes up (Partridge, 1980; Pulliam and Caraco, 1984). Larger groups are often better equipped to solve cognitive tasks in comparison to smaller groups, or lone individuals (Ioannou, 2017). For example, the collective response of European minnow (*Phoxinus phoxinus*) to a broadband acoustic stimulus was found to be universal in comparison to those of solitary individuals, which were more diverse (Short *et al.*, 2020). Transitions between dynamically-stable collective states of fish are influenced by both internal (*i.e.* changing behaviour of group members) and external (*i.e.* boundary-dependent) factors, and are commonly observed through an increase in speed (Tunstrøm *et al.*, 2013).

In collective groups of fish, two further distinctions exist for the mechanism behind the formation of groups: “shoaling,” and “schooling” (Pitcher, 1983). Functionally, the two have similarities (Ruxton *et al.*, 2007), both acting advantageously as an anti-predator strategy. Shoaling behaviour achieves such a function through a dilution effect (Pitcher and Parrish, 1993; Bumann *et al.*, 1997), while schooling creates a confusion effect using the synchronisation of moving individuals (Milinski, 1977a; Milinski, 1977b; Tosh *et al.*, 2006) and can accelerate transmission of an alert signal across a group before the predator is even seen by some individuals (‘Trafalgar effect’: Table 2.4; Treherne and Foster, 1981). Concisely, a shoal is defined as a group of fish remaining together for social reasons, while a school is defined as a group of fish swimming in a synchronised or polarised manner (Pitcher, 1983; Delcourt and Poncin, 2012).

Models of collective motion assume interaction rules that determine how individuals respond to the movements and positioning of a neighbour (Couzin *et al.*, 2002). These rules allow us to better understand how fish exhibit collective behavioural patterns, make decisions, and transmit

information throughout a group (Herbert-Read *et al.*, 2011). Three key principles have been identified for the social interactions of fish and are listed in order of priority. Firstly, individuals continually attempt to maintain a “zone of repulsion”, or a minimum distance between themselves and others to maintain personal space or avoid collision (Couzin *et al.*, 2002). This is mainly mediated by changes in acceleration (Herbert-Read *et al.*, 2011). Secondly, when not performing an avoidance manoeuvre to satisfy the first principle, individuals maintain a degree of group cohesion (local attraction), aligning themselves with their neighbours (directionality), and avoiding isolation (Couzin *et al.*, 2002). Varying mechanisms have been proposed to explain attraction and alignment: (1) ternary (or higher level) interactions, where a fish would turn toward an average of all neighbours; or (2) simple pairwise stochastic interactions, where instead, individuals actively regulate the distance to a paired neighbour (pairwise copying interaction) and mediate this through more randomised independent movements (stochastic turning). While time series data simulations of these interaction rules appear similar, their derived corresponding mesoscopic models show two very different quantitative interactions within the deterministic (or drift) term. The former model deterministic term is cubic, while the latter is linear, from which the underlying mathematical function of the behaviour has been derived and applied to actual experimental data (Jhawar and Guttal, 2020; Jhawar *et al.*, 2020). In contrast to classical models of collective motion, independent studies have inferred from analysis that at the fine-level scale, fish follow very simple pairwise stochastic interactions (Herbert-Read *et al.*, 2011; Jhawar and Guttal, 2020; Jhawar *et al.*, 2020). Therefore, despite the highly correlated positions and directions of all shoal members, the third rule is that individuals only respond to a single nearest neighbour. Speed, group cohesion and alignment are therefore fundamental to the collective behaviour of fish and important metrics to quantify in experimental studies investigating fish response to environmental stimuli, such as acoustics.

The social aggregations of fish may be aided by sounds (Moulton, 1960). Distinct pressure pulses produced by the motions of swimming fish within a group may be important for maintaining group cohesion under poor visual conditions, and fish can detect these and their directionality several lengths away from the initial source (Gray and Denton, 1991). Fish are capable of swimming blindfolded (*e.g.* Saithe, *Pollachius virens*: Pitcher *et al.*, 1976) and schooling is severely disrupted when the posterior lateral line nerve is severed, indicating the importance of this system to collective behaviour. Some fish may also emit contact calls to maintain loose shoaling structures (McCauley and Cato, 2000). Vocalisations (*e.g.* ‘knocks’ and ‘growls’) are even produced by some larval species (*e.g.* grey snapper, *Lutjanus griseus*) at very early pre-settlement life-history stages (Staaterman *et al.*, 2014). The exact function and physiological mechanisms are unknown, however, it is hypothesised that these sounds may be used to maintain group cohesion at night when visual cues

Table 2.4: Costs and benefits of group living¹

	Function	Strategy	Definition	Species examples	References	
	Anti-predator	Confusion effect	More difficult for predators to single out and capture prey as the number of prey items in a group increase	Water flea (<i>Daphnia magna</i>); desert locust (<i>Schistocerca gregaria</i>);*Mississippi silvery minnow (<i>Hypognathus nuchalis</i>); mealworm (<i>Tenebrio molitor</i>);*Mediterranean killifish (<i>Aphanius fasciatus</i>)	Neill and Cullen, 1974; Milinski, 1977a; 1977b; Gillet <i>et al.</i> , 1979; Landeau and Terborgh, 1986; Schradin, 2000; Cattelan and Griggio, 2018	
		Information transfer ('Trafalgar effect')	Individuals responding to alarmed behaviour of other conspecifics	Mexican colonial web-building spider (<i>Metepeira incassata</i>);*banded killifish (<i>Fundulus diaphanous</i>);*Gulf menhaden (<i>Brevoortia patronus</i>);*herring (<i>Clupea harengus</i>)	Treherne and Foster, 1981; Godin and Morgan, 1985; Uetz <i>et al.</i> , 2002; Handegard <i>et al.</i> , 2012; Rieucan <i>et al.</i> , 2016	
		Many-eyes theory	Larger groups allow for better detection of predators and reduction of individual vigilance	Dark-eyed junco (<i>Junco hyemalis</i>); American tree sparrow (<i>Spizella arborea</i>); bighorn sheep (<i>Ovis canadensis</i>); Barbary ground squirrel (<i>Atlantoxerus getulus</i>)	Lima, 1995; Rieucan and Martin, 2008; van der Marel <i>et al.</i> , 2019	
		Dilution effect	Individual group members have a reduced probability of being the one attacked when encountering a predator (by-product of social interaction)	Water skater (<i>Halobates robustus</i>); Rocky mountain elk (<i>Cervus elaphus nelsoni</i>); spider mites (<i>Phytoseiulus persimilis</i>)	Treherne and Foster, 1982; Delm, 1990; Pitcher and Parrish, 1992; Bumann <i>et al.</i> , 1997; Hebblewhite and Pletscher, 2002; Lehtonen and Jaatinen, 2016; Dittmann and Schausberger, 2017	
		Predator swamping	Inundating predators through synchronous presentation of multiple individuals above the upper catch rate level	Snowshoe hare (<i>Lepus americanus</i>); pine engraver beetle (<i>Ips pini</i>); burrowing mayfly (<i>Dolania americana</i>); green turtle (<i>Chelonia mydas</i>)	Sweeney and Vannote, 1982; Ims, 1990; Aukema and Raffa, 2004; Santos <i>et al.</i> , 2016	
		Selfish herd	Actively putting other conspecifics between oneself and a predator via aggregation	Sand fiddler crab (<i>Uca pugilator</i>); musk-oxen (<i>Ovibos moschatus</i>); Hallowell's toad (<i>Bufo maculatus</i>); redshank (<i>Tringa totanus</i>)	Hamilton, 1971; Heard, 1992; Morton <i>et al.</i> , 1994; Spieler and Linsenmair, 1999; Viscido and Wetthey, 2002; Quinn and Cresswell, 2006; Algar <i>et al.</i> , 2019	
		Parasite/ disease defence	<i>Per capita</i> risk of infection may be reduced if lower between-group transmission compensates for more than the higher within-group transmission	Butterfly larvae (<i>Lepidoptera sp.</i>);*bluegill sunfish (<i>Lepomis macrochirus</i>); carrion crow (<i>Corvus corone corone</i>)	Mooring and Hart, 1992; Côté and Gross, 1993; Côté and Poulin, 1995; Wilson <i>et al.</i> , 2003; Canestrari <i>et al.</i> , 2009	
	Benefits	Foraging	Group hunting	Prey otherwise too large, dangerous, or agile to detain solely may be captured	Lion (<i>Panthera leo</i>); grey wolf (<i>Canis lupus</i>); bottlenose dolphin (<i>Tursiops truncatus</i>); Harris' hawk (<i>Parabuteo unicinctus</i>);*sailfish (<i>Istiophorus platypterus</i>);*yellow saddle goatfish (<i>Parupeneus cyclostomus</i>)	Bednarz, 1988; Packer and Ruttan, 1988; Gazda <i>et al.</i> , 2005; Dutta, 2014; Herbert-Read <i>et al.</i> , 2016; Steinegger <i>et al.</i> , 2020
			Information transfer	Individuals which source food return to colony or roost prior to a return trip to the source	Evening bat (<i>Nycticeius humeralis</i>);*guppy (<i>Poecilia reticulata</i>); cape gannet (<i>Morus capensis</i>); honeybee (<i>Apis mellifera</i>); red wood ant (<i>Formica rufa</i>)	Ward and Zahavi, 1973; Barta and Giraldeau, 2001; Day <i>et al.</i> , 2001; Thiebault <i>et al.</i> , 2014; Łopuch and Tofilski, 2017; Reznikova, 2020
			Coarse/fine-level enhancement	Behaviour of others acting as an indicator to a source of food	*Golden shiner (<i>Notemigonus crysoleucas</i>); barnacle goose (<i>Branta leucopsis</i>); rook (<i>Corvus frugilegus</i>)	Drent and Swierstra, 1977; Reebbs and Gallant, 1997; Galef Jr. and Giraldeau, 2001

¹ *Note*: Many strategies may be limited by or dependent on a minimal/ maximal group size. * indicates exemplar fish species.

	Reduction of energetic costs	Spatial position within group (e.g. hydrodynamic advantage)	Specific shaped formations (e.g. diamond lattice or V-shape) designed to limit energy expenditure during experiencing impacts from drag or vortices	Canada goose (<i>Branta canadensis</i>);*golden grey mullet (<i>Liza aurata</i>);*goldfish (<i>Carassius auratus</i>)	Hainsworth, 1987; Krause, 1994; Killen <i>et al.</i> , 2012; Hemelrijk <i>et al.</i> , 2015; Marras <i>et al.</i> , 2015; Li <i>et al.</i> , 2020
		Huddling	Reduction of surface area to colder or warmer surroundings prevents heat and/or water loss	Emperor penguin (<i>Aptenodytes forsteri</i>); Natterer's bat (<i>Myotis nattereri</i>); Brandt's vole (<i>Lasiopodomys brandtii</i>)	Ancel <i>et al.</i> , 1997; Boratyński <i>et al.</i> , 2015; Zhang <i>et al.</i> , 2018
		Navigation (e.g. mass migration)	Social interactions between individuals may facilitate obstruction passage (e.g. at dams)	*Chinook salmon (<i>Oncorhynchus tshawytscha</i>)	Okasaki <i>et al.</i> , 2020
	Mate acquirement	Lekking	Attendance of a 'lek', or common breeding ground with the sole purpose of gaining sperm as a resource. Better pool of genes and chance of reproduction in larger groups	Norway rat (<i>Rattus norvegicus</i>); greater sage-grouse (<i>Centrocercus urophasianus</i>); lesser wax moth (<i>Achroia grisella</i>);*haplochromine cichlid (<i>Nyassachromis microcephalus</i>)	McClintock <i>et al.</i> , 1982; Gibson and Bradbury, 1985; Cordes <i>et al.</i> , 2014; Magalhaes <i>et al.</i> , 2017
Costs	Increased attack rate by predators	Oddity effect	Larger groups (density rather than number <i>per se</i>) are more visually intense or detectable and therefore more prone to attack by predators	Water flea (<i>Daphnia magna</i>);*Mississippi silvery minnow (<i>Hybognathus nuchalis</i>); redshank (<i>Tringa totanus</i>);*wrasse (<i>Thalassoma amblycephalum</i>)	Ohguchi, 1978; Landeau and Terborgh, 1986; Cresswell, 1994; Stier <i>et al.</i> , 2013; Duffield and Ioannou, 2017; Dobbins <i>et al.</i> , 2019
	Competition for food resources	Kleptoparasitism	Potential for a conspecific to steal a food item off another	Eurasian oystercatcher (<i>Haematopus ostralegus</i>); spotted hyenas (<i>Crocuta crocuta</i>); gastropods (<i>Capulidae sp.</i>); Eurasian lynx (<i>Lynx lynx</i>)	Stillman <i>et al.</i> , 1996; Carbone <i>et al.</i> , 1997; Sirot, 2000; Fassio <i>et al.</i> , 2015; Krofel <i>et al.</i> , 2019
		Aggression amongst conspecifics	Aggression may be exhibited for reasons unrelated to foraging, e.g. social dominance; potentially interfering with foraging processes	House sparrow (<i>Passer domesticus</i>)	Ruxton <i>et al.</i> , 1992; Holmgren, 1995; Rands <i>et al.</i> , 2006; Tuliozi <i>et al.</i> , 2018
		Pseudo-interference	With limited food resources, the size of a group of foragers can adversely impact individuals even when no aggressive displays take place	Redshank (<i>Tringa tetanus</i>); wild boar (<i>Sus scrofa</i>); white-tailed deer (<i>Odocoileus virginianus</i>)	Selman and Goss-Custard, 1988; Cherry <i>et al.</i> , 2015; Podgórski <i>et al.</i> , 2016
		Interference from lie and wait predators	Shadowing of group individuals by con- or heterospecifics causing direct competition for food resources or potentially interfering via accidentally alerting prey to danger	Ant lion (Neuroptera: Myrmeleonidae);*sea trout (<i>Salmo trutta</i>)	Wilson, 1974; Elliott, 2002
		Overlapping with conspecifics	General interference amongst one another, including an exhaustion of resources		Ruxton, 1995
		Behavioural modification to conspecifics	Individuals responding to other conspecific false startle or alert behaviour - <i>i.e.</i> where no danger actually exists – and increasing energetic costs	*Glowlight tetra (<i>Hemigrammus erythrozonus</i>);*giant danio (<i>Devario aequipinnatus</i>)	Godin <i>et al.</i> , 1988; Chicoli <i>et al.</i> , 2014
	Increased parasite load	Higher levels of contact parasites	Positive relationships between group size, brood proximity, parasite burden and subsequent risk-taking behaviour	European bee-eater (<i>Merops apiaster</i>); yellow-bellied marmot (<i>Marmota flaviventris</i>); greater mouse-eared bat (<i>Myotis myotis</i>);*three-spined stickleback (<i>Gasterosteus aculeatus</i>)	Van Vuren, 1996; Hoi <i>et al.</i> , 1998; Postawa and Szubert-Kruszyńska, 2014; Demandt <i>et al.</i> , 2018
	Reduced parental care	Brood parasitism	Large number of nests simultaneously available to coloniality of parasite	Black footed albatross (<i>Diomedea nigripes</i>); redshank (<i>Tringa tetanus</i>); northern lapwing (<i>Vanellus vanellus</i>)	Yom-Tov, 2001; Niemczynowica <i>et al.</i> , 2015; Median and Langmore, 2019
		Cuckoldry	Potential for extra-pair copulation	Cooper's hawks (<i>Accipiter cooperii</i>);*bluegill sunfish (<i>Lepomis macrochirus</i>);*fifteenspine stickleback (<i>Spinachia spinachia</i>)	Moller and Birkhead, 1993; Westneat and Sherman, 1997; Rosenfield <i>et al.</i> , 2015; DeWoody and Avise, 2001

are reduced (Staaterman *et al.*, 2014). Nocturnal planktivorous fish (*e.g.* New Zealand bigeye, *Pempheris adspersa*) have been observed to increase group cohesion and calling rates in response to conspecific vocalisations, suggesting the use of contact calls to maintain group cohesion (van Oosterom *et al.*, 2016). The few previous studies investigating the group responses of fish to sound (*e.g.* tuna, *Thunnus thynnus*: Sarà *et al.*, 2007; and sea bass, *Dicentrarchus labrax*: Herbert-Read *et al.*, 2017a) suggest that anthropogenic noise may also alter the collective behaviour of fish (*e.g.* reduced group cohesion). Data surrounding the collective responses of freshwater fishes to acoustic stimuli is however lacking, and are required to assist in conservation efforts mitigating the negative impacts of anthropogenic noise within freshwater habitats. It will also aid in the development of more effective behavioural guidance systems as many migratory species employ group-living social structures.

2.4 Underwater acoustics and the physical properties of sound

An appreciation of the physics of sound is critical to understanding how animals receive and utilise underwater sound, or how they respond to anthropogenically driven changes in their acoustic environment. Sound is a form of mechanical energy that travels through an elastic medium as a waveform (Urlick, 1983). As a sound wave propagates underwater, the amplitude (A) of the wave relates to the amount of acoustic energy it carries, or the acoustic intensity (I). Intensity of a sound wave refers to the average amount of energy as a function of time in a specified direction through a unit area, and is expressed as:

$$I = \left(\frac{p^2}{\rho c} \right) \quad \text{(Equation 2.8)}$$

where p , is the RMS (root-mean-square) pressure (measured in pascals; Figure 2.11) obtained from measurements, ρ is the density of the medium (kg/m^3), and c represents the speed of sound (m s^{-1}), (Dahl *et al.*, 2007). For a pure sinewave, the RMS pressure level relates to the intensity, or amplitude as:

$$p_{rms} = \frac{A}{\sqrt{2}} \quad \text{(Equation 2.9)}$$

Sound travels faster and farther underwater, where the speed of sound is approximately 1480 m s^{-1} (around 5 times faster than in air). However, the speed of sound and the paths along which it propagates vary dependant on the temperature, pressure, and salinity of water (Urlick, 1983).

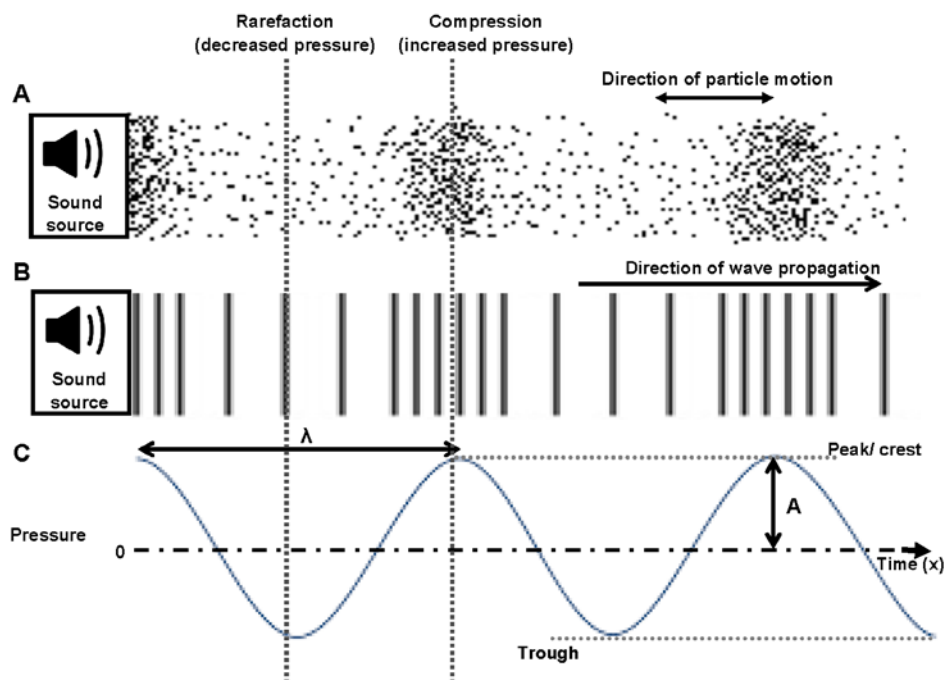


Figure 2.11: Representation of a propagating sound wave showing: **(A)** oscillating particles about their mean positions; **(B)** compressions and rarefactions; and **(C)** a transverse representation of the wave, showing wavelength (λ) and amplitude (A).

The frequency (f) of a sound wave is expressed in hertz (Hz) and corresponds to the number of cycles of the wave per second. The wavelength (λ), is the distance in meters between one crest (or trough) to the next. The relationship between frequency, wavelength and speed of sound is defined as:

$$\lambda = \frac{c}{f} \quad (\text{Equation 2.10})$$

The sound pressure is commonly expressed on a logarithmic scale known as dB (decibels), relative to a reference pressure (in water the common convention is to select, $p_{ref} = \text{dB re } 1 \mu\text{Pa}$), where sound pressure level (SPL) in dB is defined as:

$$SPL = 20 \log_{10} \left(\frac{p}{p_{ref}} \right) \quad (\text{Equation 2.11})$$

Driven by the pressure gradient, particles next to a vibrating sound source follow an ellipsoidal motion around their resting position, and do not travel with the wave (Figure 2.11). The back and

forth motions are transmitted to adjacent particles within the medium. This component is known as particle motion, which may be expressed as displacement (m), velocity (m s^{-1}), or acceleration (m s^{-2}), and for a sinusoidal acoustic wave, can be linked by the following equations (Nedelec *et al.*, 2016a):

Velocity and acceleration:

$$|a| = \omega|u| \quad (\text{Equation 2.12})$$

where, a is acceleration, u is particle velocity, and $\omega = 2\pi f = \text{angular frequency}$.

Velocity and displacement:

$$|\varepsilon| = \frac{|u|}{\omega} \quad (\text{Equation 2.13})$$

where, ε is displacement.

A relationship exists between sound pressure and particle motion, and so the particle acceleration component may be calculated from the same dataset using a gradient based approximation (Kinsler *et al.*, 1982):

$$a = -\frac{1}{\rho} \nabla P \quad (\text{Equation 2.14})$$

Under acoustically far and free-field conditions, sound pressure amplitude varies inversely with distance (Nedelec *et al.*, 2016a). This Fraunhofer zone, typically assumes a range, R , at which $R > a^2 / \lambda$ and $R > a$, where a is the radius of the source. Here, it is both far from the source, and far from any boundaries that may cause reflections to influence the shape of the wave front. Under such conditions, particle motion is in phase with the pressure, and may be approximated using:

$$p = Z \cdot u \quad (\text{Equation 2.15})$$

where, Z is the characteristic impedance of the medium (or the 'resistance' against motion), and is defined as:

$$Z = \rho c \quad (\text{Equation 2.16})$$

The relationship does not hold within the acoustic near-field, which is comprised of 2 regions. These are the reactive near-field, where energy mainly circulates with relatively little propagation (typically assumes $R < \lambda$), and the Fresnel zone ($R < a^2 / \lambda$). Here, complex constructive and destructive interference occurs between the wave fronts, and consequently, sound pressure is no longer in

phase with the particle motion component (Nedelec *et al.*, 2016a). Boundaries between near- and far-field zones are not well-defined, with gradual transitions differing between low (condition: $R > \lambda$) and high (condition: $R > a^2 / \lambda$) frequencies.

2.5 Shallow riverine soundscapes

Owing to a military defence imperative, expertise in shallow water acoustics grew dramatically over the last century, facilitating the understanding of, and capability to measure and model the marine environment (Leighton *et al.*, 2019). An increase in human generated underwater acoustic signals (*e.g.* resulting from shipping, construction, or sonar activities: Sarà *et al.*, 2007; Greene Jr. and Moore, 1995; see Chapter 2.2) has led to a growing appreciation regarding the need to protect marine fauna from the adverse effects of anthropogenic noise. Man-made sound is pervasive across marine and freshwater ecosystems, yet, compared to marine shallow water seas and oceans, freshwater riverine environments are much less studied in the field of underwater acoustics (Vračar and Mijić, 2011). Rivers were traditionally deemed not to have much significance in the field of hydroacoustics (Vračar and Mijić, 2011), with habitat assessments more typically focussed on geomorphic properties and flow characteristics (Leopold and Maddock, 1953; Wohl and Merritt, 2008; Tonolla *et al.*, 2010). As such, there is little data regarding ambient noise levels in rivers, or specific physical features that can impact the sound field. Environmental scientists and bioacousticians are however beginning to recognise the potential for anthropogenic sound sources to impact the composition and distribution of fish within ecosystems extraneous to, or interconnected with the marine environment. Such assessments provide a more comprehensive understanding as to the soundscapes freshwater fish may be inhabiting, and with gradually increasing noise sources, to which they are having to adapt (*e.g.* Wysocki *et al.*, 2007a; Amoser and Ladich, 2010; Tonolla *et al.*, 2010; Marley *et al.*, 2016; Putland and Mensinger, 2020).

Sound fields within rivers have high reverberation, and are more complex, and less predictable than those of deeper marine or estuarine systems (with shallow water defined up to ~ 500 m^[2]) (Katsnelson *et al.*, 2012). Acoustic conditions are influenced by fluctuating depths and narrow channels, differing topographies, air entrapment, hydraulic conditions, and temperature and salinity clines (Tonolla *et al.*, 2010). In general, frequencies below 100 Hz within rivers tend to be dominated by high energy ambient noise that is generally produced by hydrodynamic and turbulent processes. This can be followed by a ‘noise window,’ encompassing relatively low noise levels within the

² In marine systems, shallow water tends to be the region from the end of the surf zone, out to the continental shelf break. In more general acoustic terms, it may be defined as any environment where acoustic applications are impacted by surface and bottom boundaries (Katsnelson *et al.*, 2012)

frequency range of 100-300 Hz, and may finally be trailed by a lessening steep rise of energy at around 1-2 kHz (Lugli and Fine, 2003). Above 100 Hz, anthropogenic factors originating from ships, boats, traffic on riverbanks, and other human activities in the local vicinity, are the main dominating influence on ambient riverine noise (Vračar and Mijić, 2011; Holt and Johnston, 2015). One contributor to ambient noise at frequencies higher than 1000 Hz is wind, and its influence within rivers is much more complex than in seas, oceans, or large lakes. For instance, the terrain relief provided by riverbanks necessitates the distribution of wind velocities over a smaller surface area, and annual river flow fluctuations impact the conversion of wind to underwater noise energy (McConnell *et al.*, 1992). Riverine habitats are exceptionally diverse, and highly engineered banks and channels in combination with other abiotic factors create multiple boundary environments that can also influence sound propagation and the pressure/ particle velocity relationship. The differences between the acoustic properties of deeper marine environments with fewer boundary limitations or propagation interference, and those of highly engineered freshwater habitats, are commonly overlooked in the study of fish bioacoustics (Chapter 3.2).

Freshwater ecosystems encompass many distinct habitat types, both ecologically and acoustically (Amoser and Ladich, 2005; Wysocki *et al.*, 2007a; Tonolla *et al.*, 2010). Wysocki *et al.* (2007a) and Tonolla *et al.* (2010) investigated the acoustic signatures of European river habitats within Austria and Switzerland, respectively. Wysocki *et al.* (2007a) classified habitats as: 'stagnant lakes,' 'slow-flowing backwaters,' 'faster-flowing streamlets,' and 'large fast flowing rivers,' while Tonolla *et al.* (2010) arguably deployed a more applicable habitat description and classification system for use in fish biology and fisheries management. Tonolla *et al.* (2010) included five commonly defined hydrogeomorphological habitat types: 'pools,' 'riffles,' 'runs with streambed sediment transport,' 'runs without streambed transport,' and 'step pools.' For each habitat, they acoustically mapped the sound pressure levels (dB re 1 μ Pa: broadband frequency range 0.03 – 16 kHz) across a temporal and spatial scale, finding clear differences between habitat types, with each exhibiting a distinguishable acoustic signature. Unsurprisingly, habitats encompassing higher turbulence showed the highest energies, with step-pools exhibiting the highest broadband mean value (SPL \leq 150 dB re 1 μ Pa). Average relative roughness of habitat substrata was responsible for water breaking the surface and entraining air (Tonolla *et al.*, 2010). Rapid entrainment of air, followed by a collapse of air bubbles as a result of turbulence (*i.e.* cavitation) may occur from secondary splashes and bubbles (Urlick, 1983). Pressure changes can cause dissolved air bubbles to dilate and collapse after reaching a critical size (Leighton, 1994), subsequently producing a short pulse of sound (*e.g.* between 0.1-1 kHz within SPL peaks in riffles and step-pools: Tonolla *et al.*, 2010). Streambed sediment transport was responsible for differences in acoustic signatures between habitat types at higher frequencies (*e.g.* 2-16 kHz), but

had a lesser effect than turbulence (Tonolla *et al.*, 2010). Significant year-round variability of ambient noise has also been noted to occur and is particularly the case for stagnant water and stream habitat types (Amoser and Ladich, 2010). Ambient noise can change with season (Amoser and Ladich, 2010), lunar (Radford *et al.*, 2015) and tidal rhythms (Coers *et al.*, 2008), or across even shorter time frames (*e.g.* minutes: Amorim *et al.*, 2018). These studies indicate that abiotic sources of ambient underwater sound are highly dependent on the hydraulic conditions (*e.g.* flow depth and velocity, sediment transport), while biotic sources might only contribute to the acoustic signature in stagnant or slow flowing water conditions (Wysocki *et al.*, 2007a). Noise sources are likely to differ in intensities and spectral composition dependent on abiotic, biotic, or any anthropogenic factors within differing aquatic ecosystems.

The acoustic signatures at weir or micro-hydropower turbine sites are not well studied and may be dominated by high levels of lower frequency noise. Plane edges and larger amounts of water at natural riverine barriers (*e.g.* waterfalls) produce more bubbles, while man-made weirs create differing amounts of bubbles with a variety of hydraulic jump sizes (for in depth description of bubble acoustics see Leighton, 1994). Additionally, the material at the point of impact can cause an increase in higher frequencies. Johnson *et al.* (2014) investigated the acoustics of broad crest, flat v, and crump type weirs, and found that all three were mid (> 160 Hz) to high frequency (> 2 kHz) dominant, with large SPLs observed for higher frequencies (unweighted SPL measurements: dBz).

Comparatively, a more dynamic range was observed at lower frequencies (Johnson *et al.*, 2014). Water depth and substrate composition can cause sounds below a certain frequency to attenuate extremely rapidly (Rogers and Cox, 1988; Forrest *et al.*, 1993), and rises in background ambient noise levels at sites of interest could overpower acoustic deterrent signals designed to deter target fish species from hazardous areas (such as turbine intakes), potentially masking information transfer, and the subsequent detection and response by fish (Wiley, 1994; Brumm and Slabbekoorn, 2005; Langemann and Klump, 2005).

Installation of micro-hydro power stations (*e.g.* hydrodynamic screws: Figure 2.12) could have detrimental impacts on migratory fish species, however, such projects are considered to have massive untapped potential throughout Europe, as decentralised sources could better satisfy local electricity demands (Manzano-Agugliaro *et al.*, 2017). The UK currently houses around 120 small hydro plants (Manzano-Agugliaro *et al.*, 2017) and approximately 20,000-30,000 weirs (Driscoll, 2008; Johnson *et al.*, 2014). Of these, 1677 ^[3] are recorded as decommissioned historical micro-hydro

³ Note that this value most likely understates the real potential due to insufficient data within The Restor Hydro project database (Punys *et al.*, 2019)

sites, with the majority only requiring moderate restoration efforts to facilitate a potential capacity of up to 40 kW (Punys *et al.*, 2019). It is vital that the underwater acoustic signatures of any sites proposing the installation of an acoustic deterrent system (*e.g.* weirs, turbines, water abstraction points) to facilitate fish passage are well understood, thereby optimising the effectiveness of such technologies.

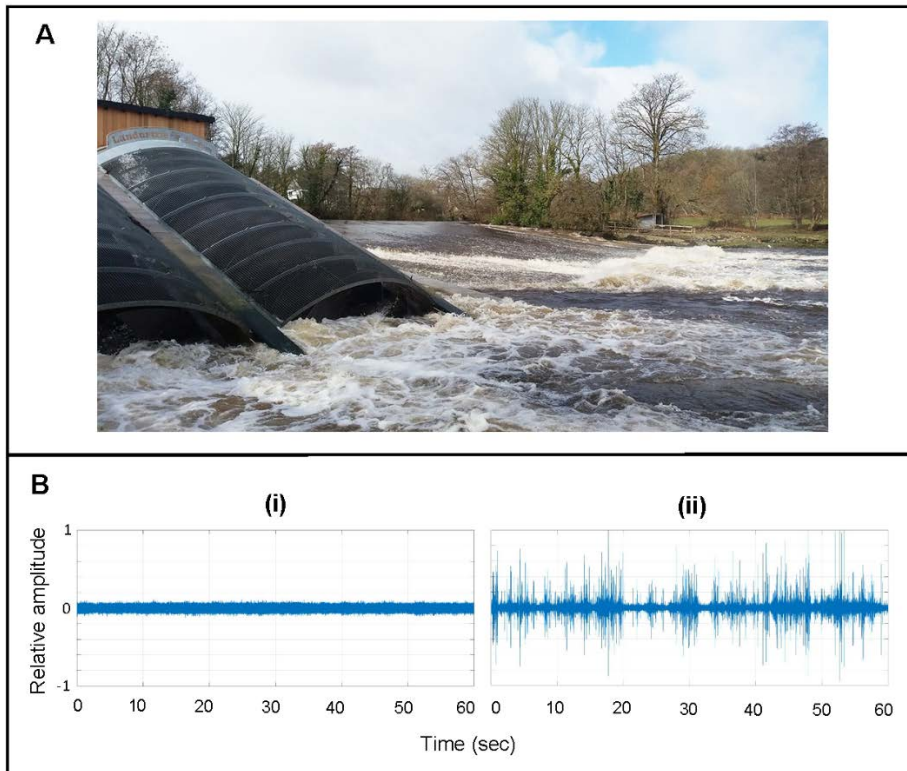


Figure 2.12: (A) Example micro-hydro power site at Totnes Weir hydro power plant ($50^{\circ} 26'20.1''\text{N}$, $3^{\circ} 41'24.5''\text{W}$) encompassing two “fish friendly” hydrodynamic Archimedes screw turbines, generating approximately 1, 250 MWh of electricity a year (source: <https://tresoc.co.uk/project/totneshydro/> ©Tresoc 2017); and (B) time domain waveforms of acoustic recordings taken (i) directly upstream, where when in operation, the turbine powerhouse produces a low frequency hum (0-3 kHz; SPL RMS: 118.5 dB re 1 μPa) into the surrounding environment; and (ii) downstream of the weir, where the dominating noise source is due to increasing water velocities and surrounding biotic factors such as bubbles (SPL RMS: 125.1 dB re 1 μPa).

2.6 Acoustic masking and signal detection theory

Anthropogenic noise (*e.g.* at weirs, dams) is capable of masking encoded signals, where the ability of a receiver to detect and respond to a sound of interest is degraded by the presence of another (the masker), (Wiley, 1994; Brumm and Slabbekoorn, 2005; Langemann and Klump, 2005; Erbe *et al.*, 2016). By raising a signal, or auditory detection threshold, masking noise can reduce the “active

space” of a signal, potentially having unknown consequences for reproductive processes (Hansen *et al.*, 2005), or predator avoidance (Simpson *et al.*, 2015). Studies of mammals (marine and terrestrial: Richardson *et al.*, 1995; Siemers and Schaub, 2010), birds (Reijnen *et al.*, 1995; Proppe *et al.*, 2013), anurans (Bee and Swanson, 2007; Lengagne, 2008) and fish (Vasconcelos *et al.*, 2007), all point to the conclusion that anthropogenic noise disturbance is capable of masking signals (Fletcher, 1940), and can create a negative domino effect, impacting taxa across different individual, population and ecosystem levels (Krause, 1993; Kunc *et al.*, 2016). Subsequently, the potential for acoustic masking should be considered when performing experiments investigating the behavioural responses of fish to sound, either within the context of better understanding the impact of anthropogenic noise or the efficacy of acoustic deterrent devices.

A range of habitat, receiver, and acoustic source factors are relevant to the effective receipt and response of an individual to an acoustic stimulus. When emitted from a sound source (*e.g.* underwater speaker or animal sender), a signal is comprised of specific spectral characteristics at a set source level, and travels through the surrounding habitat where it experiences propagation losses (*e.g.* scattering and absorption). The acoustic characteristics of the received signal depend on this propagation environment, alongside the position of the receiver relative to the source (Erbe *et al.*, 2016). Different environments have different ambient noise patterns, as habitat-dependent sound transmission properties are related to microclimate and vegetation structure (Wiley and Richards, 1982; Urick, 1983). Man-made noise is highly pervasive, and aquatic environments are subject to substantial and largely uncontrolled degradation of opportunities to perceive natural sounds (Klump, 1996). Degradation impairs extraction of information encoded in a signal, however, it also allows receivers to assess the distance, or range of a signaller (Naguib and Wiley, 2001). Background noise acts as a crucial constraint on signal transmission (Ryan and Brenowitz, 1985) as detection and recognition of signals is dependent on the signal-to-noise ratio (SNR), (Klump, 1996). SNR is the difference in dB (RMS: root mean square) between a received signal (V_s) in microvolts (μV), and the background noise floor (V_n) where:

$$SNR = 10 \log_{10} \left(\frac{V_s}{V_n} \right) \quad (\text{Equation 2.17})$$

Ideally, $V_s > V_n$, thereby allowing for a high SNR and the possibility of a detection. When $SNR \leq 0$, the signal ranges from unreadable, to undetectable, owing to competition with the background noise level.

Acoustic masking of a signal is not only determined by the spectral characteristics or intensity of a signal relative to the noise at the location of the receiver, but is also dependent on features of the

receiving auditory system. These features include the hearing sensitivity of an individual (summarised by basic metrics including: the audiogram, critical ratios, and directivity index), masking release mechanisms, temporal integration of acoustic energy, and frequency selectivity (Erbe *et al.*, 2016). Cyprinid fishes (Chapter 3.1.1), for example, have frequency-selective auditory filters meaning they are capable of distinguishing between tones that differ in frequency (Dijkgraaf, 1952; Fay and Popper, 1980). The similarity of cyprinids to many other investigated vertebrate taxa suggests auditory filters to be a primitive feature of all auditory systems (Popper and Fay, 1993). This discriminable ability does however vary as a function of frequency, whereby, for any given frequency, the critical band is the smallest band of frequencies around it which activate the same part of the calciferous otolith structures (*i.e.* the natural auditory filters). This is deemed to be the band of audio frequencies within which an additional tone would obscure, or “mask” the first due to perception interference. These bandwidths generally fall within $\frac{1}{3}$ octave bands, thereby increasing with increasing frequency (Figure 2.13). It is not a fixed function, as animals do not passively accept how signals and noise enter from the surrounding soundscape, and can therefore be altered by the auditory mechanism itself (Zwicker, 1961; Brumm and Slabbekoorn, 2005). Not all frequency components of the noise floor are equally effective at promoting this effect. For the case of a pure tone in combination with a masking noise, only a narrowband of frequencies around the sinewave appropriately mask the tone, which activates cell clusters responsible for tone sensitive triggering of neurons (Scharf, 1970). The power (intensity) of the masking band must also be at least equal to that of the tone (*i.e.* the critical band: Fletcher, 1940).

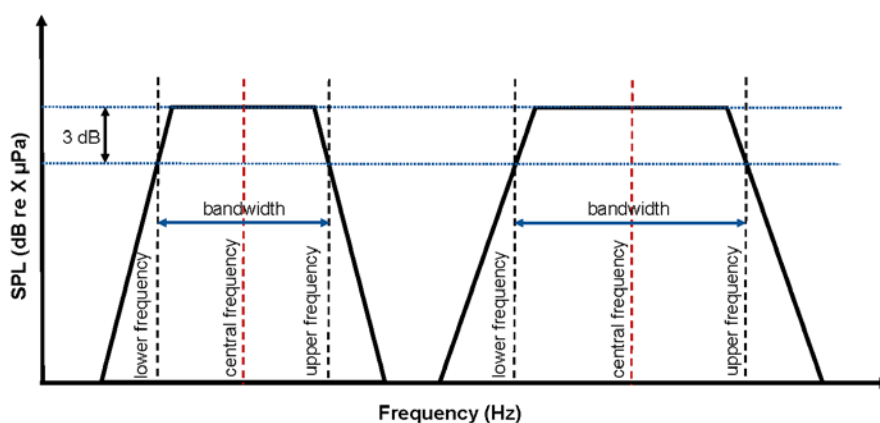


Figure 2.13: The bandwidth of the critical band increases with frequency.

The critical band can be difficult to obtain via direct measurements as it involves procuring numerous thresholds under varying bandwidths of noise. As such, an indirect determination may instead be calculated through the use of the “critical ratio equal power” method (Hawkins and Stevens, 1950;

Cahn *et al.*, 1969; Hawkins and Chapman, 1975; Richardson *et al.*, 1995). This is the SNR with reference to the spectrum level of a broad, flat band of noise (dB Hz⁻¹). Such estimates are, however, consistently smaller than their directly measured counterparts (*e.g.* in humans, by a factor of 2.5), and therefore requires a correction factor to convert to the critical band, in Hz (Scharf, 1970):

$$\text{Critical band} = \log_{10}^{-1} \left(\frac{\text{critical ratio in dB} + 4}{10} \right) \quad (\text{Equation 2.18})$$

Despite being purely empirically derived, the critical band is relevant regarding the theory of frequency analysis, whereby the trend for increasing bandwidth with increasing frequency holds (Tavolga, 1974; Wysocki and Ladich, 2005b).

While masking functions obtained through critical band experiments (*e.g.* Hawkins and Chapman, 1975) generally produce a v-shaped plot when measuring the relative masking effect of noise at differing frequencies, evidence from earlier studies suggests species with more acute, and wider hearing ranges, have narrower critical bands (*e.g.* goldfish, *Carrassius auratus*: Tavolga, 1974). Furthermore, psychophysical studies also using goldfish have found that masking functions are more frequency selective than can be described by a simple filter of bandwidth, whereby there may in fact be multiple observed peaks (Fay *et al.*, 1978). As such, even when details surrounding ambient noise conditions are available, it is difficult to irrefutably ascertain the discriminability of a tonal signal from physiological data alone.

The development of acoustic deterrent systems are commonly based on our understanding of the aforementioned hearing thresholds, acoustic masking, signal-to-noise ratios and critical bands; parameters that are mostly obtained through experiments investigating auditory sensitivity (*e.g.* electrophysiological methods: ABR: Kojima *et al.*, 2005; and AEP: Amoser and Ladich, 2005; or classical behavioural: Fay, 1988; and operant conditioning methods: Yan and Popper, 1992). This may be problematic given that the physiological capabilities of an individual to detect an acoustic signal, do not directly translate to the elicitation of a desirable behavioural response from a fisheries management perspective (Kemp *et al.*, 2012a).

Species diversity and differences in interspecific behaviours are responsible for variation in behavioural guidance system success (Schilt, 2007), including: complexities in life cycle strategy, individual boldness or general activity (Budaev and Zworykin, 2002; Jolles *et al.*, 2020), variation dependent on geographical region, or changes in behaviour over time (*e.g.* developmental stage: Huntingford, 1993; motivational status: Colgan, 1993; physiological condition: Giorgi *et al.*, 1988; prior experience or associated learning: Kieffer and Colgan, 1992; and tolerance or habituation: Mueller *et al.*, 1998). Understanding the relationship between stimulus and fish response is key to

designing effective behavioural deterrent technologies, however, present-day guidance systems vary in efficacy and are commonly assessed using relatively simplistic metrics (*e.g.* percentage of deflection or attraction: Kynard and O’Leary, 1993; Kynard and Horgan, 2001). There is a need to better quantify wild fish behaviour, based on the ability of a fish to discriminate and appropriately respond to stimuli from a fisheries management perspective. Kemp *et al.* (2012a) advised the use of Signal Detection Theory (SDT: Swets, 1996; Stanislaw and Todorov, 1992; Wicken, 2002) as one facilitative conceptual framework to understand, quantify, or even manipulate the behaviour of actively migrating fish (Kemp *et al.*, 2012a; Kerr and Kemp, 2019).

SDT examines the relationship between magnitude and perceived intensity of a signal (or stimulus) and the ability of a receiver to discriminate between signal and noise (Swets, 1996; Stanislaw and Todorov, 1999; Wickens, 2002; Kemp *et al.*, 2012a). SDT is comprised of two independent components (Green and Swets, 1966). Firstly, information-processing: whereby, owing to the effect of signal masking, discriminability decreases with increasing levels of internal or external background noise. The behavioural performance also depends on a second decision-making, or response generating component, known as individual bias; a factor that considers the probability of eliciting a response upon detecting a signal (see also Chapter 6.2.5). At any given stage, a signal is either present, or it is not. Subsequently, a fish will either detect the signal and respond appropriately (*e.g.* repelled or attracted), or it will not. As such, four possible signal-response outcomes exist in the presence or absence of a specific environmental stimulus: ‘hit,’ ‘miss,’ ‘false alarm,’ or ‘correct non-response’ (Figure 2.14: Kemp *et al.*, 2012a), indicating the basic principles of SDT to be a good place to start when quantifying fish response to an acoustic stimulus in the presence of a masking noise.

		RESPONSE	
		YES	NO
SIGNAL	PRESENT	HIT: <i>Correct response</i>	MISS: <i>Incorrect response</i>
	ABSENT	FALSE ALARM: <i>Incorrect response</i>	CORRECT NON-RESPONSE: <i>Correct response</i>

Figure 2.14: Signal detection theory: the four potential signal-response outcomes (from Kemp *et al.*, 2012a. Reproduced with the permission of Elsevier Ltd.).

2.7 The use of sound to guide fish

Interest in the use of sound to control the movement of fish has been investigated since the late 1940s (Burner and Moore, 1962), (and for an extensive review on acoustic deterrents to manage fish populations, see Putland and Mensinger, 2019) and the earliest patents for acoustic guidance systems date back to the 1980s (*e.g.* Kowalewski *et al.*, 1987: U.S. patent document number: 4, 646, 276; Class 367/139). Acoustic deterrents generally use custom built sound sources (Knudsen *et al.*, 1992; Sand *et al.*, 2001; Knudsen *et al.*, 2005; Sonny *et al.*, 2006), bubble curtains (Zielinski and Sorensen, 2015) and/ or underwater speakers (Maes *et al.*, 2004) to produce an amplified and omni-directional sound field. Devices range in expense, size, and accessibility, with the latter available via a select few specialist companies with proprietary rights to their products, thereby making it difficult for third parties to test equipment efficacies (Popper and Carlson, 1998; Putland and Mensinger, 2019). Maes *et al.* (2004), however, tested and published the efficacy of their product (Fish Guidance Systems, Southampton, UK) in reducing impingement and mortality rates of a range of fish species at a power plant cooling-water abstraction site. They installed a sound projector array of 20 large Acoustic Fish Deterrent (AFDs) devices and projected a randomised selection of frequencies in the range of 20-600 Hz, pulsed every 0.2 s at an output intensity of 174 dB (re 1 μ Pa). The setup reduced impingement by 59.6%, however, signal detection was highly variable between species, and the overall reduction in fish impingement was driven by the decline in gobies, representing 78% of the entire catch. Pleuronectiformes (*i.e.* flatfishes) were observed as non-responsive in comparison to a > 87.9% decrease in entrainment of individuals with accessory hearing structures, such as Clupeiformes (*e.g.* Atlantic herring, *Clupea harengus*; European sprat, *Sprattus sprattus*; Maes *et al.*, 2004).

Extensive literature focuses on the use of sound to deter Clupeiformes (*e.g.* herring and shad: Nestler *et al.*, 1992; Ross *et al.*, 1995; Gibson and Myers, 2002; Maes *et al.*, 2004), as they are often impinged against physical screens at power plants (Lough *et al.*, 1985). Little to some success has been reported for varying frequencies (*e.g.* low frequency vs ultrasound) or even time of day. For example, Nestler *et al.* (1992) observed ultrasonic pure tones (> 24.6 kHz at 190 dB re 1 μ Pa) to repel blueback herring (*Alosa aestivalis*) from a dam at night, but not during the day. Acoustic deterrents have also been tested on a range of migratory species belonging to fish families that are commonly impinged or experience high mortalities at freshwater anthropogenic hazards (*e.g.* hydropower turbines). For example, the response of Salmoniformes (*e.g.* rainbow trout, *Oncorhynchus mykiss*: van der Walker, 1966; Atlantic salmon, *Salmo salar*: Knudsen *et al.*, 1994) and critically endangered Anguilliformes (*e.g.* European eel, *Anguilla anguilla*: Sand *et al.*, 2000; Piper *et al.*, 2019; Deleau *et al.*, 2020b) have been tested in response to infrasound deterrents; and Cypriniformes (*e.g.* common roach, *Rutilus*

rutilus; common dace, *Leuciscus leuciscus*; common chub, *Squalius cephalus*: Wood *et al.*, 1994; and Iberian barbel, *Luciobarbus bocagei*: Jesus *et al.*, 2019a) have shown deterrence rates of > 80% to acoustic deterrents. Again, the proprietary nature of the technology used by Wood *et al.* (1994) restricts information available on source level or frequency selection, while Jesus *et al.* (2019a) reported strong responses to an approximate 140 dB re 1 μ Pa sine sweep of up to 2000 Hz.

Behavioural guidance technologies are appealing in theory, as they may be applied to direct native species away from anthropogenic hazards (*e.g.* weirs, turbines, water abstraction and pumping stations), towards safer routes (*e.g.* fish passes), or limit the spread of invasive species (*e.g.* common carp, *Cyprinus carpio*: Putland and Mensinger, 2019). Use of non-physical barriers has risen globally (Carlson and Popper, 1997; Piper *et al.*, 2019), and the avoidance response of many invasive species to sound has driven an interest in the use of acoustic stimuli as a tool in fisheries management, despite mixed results in laboratory and field testing (Taylor *et al.*, 2005; Ruebush, 2012; Murchy *et al.*, 2017; Vetter *et al.*, 2017). Such systems may enhance, or even replace more costly physical screens (Coutant, 2001). In practice, however, systems are commonly developed based on audiograms of target species hearing frequency and sensitivity, which may explain the variation in technology efficacies (Chapter 2.6) that are rarely higher than 50% (Putland and Mensinger, 2019). Implementation via this approach commonly neglects to consider behavioural strategies (*e.g.* group-living species: Chapter 4; 5; 6; and 7), system longevity (*e.g.* owing to the effects of behavioural tolerance or habituation after repeated stimulus exposure Chapter 5), or site specific constraints (*e.g.* background masking noise: Chapter 6; multimodal effects of varying velocities: Chapter 7). Investigation of these topics forms the basis of the research conducted in this thesis. Improving our understanding in these areas is essential if we are to reduce or mitigate impacts of anthropogenic noise on freshwater fish, or more effectively use sound to protect fish at river infrastructure and/ or limit the spread of more invasive species.

CHAPTER 3 **Research methodology**

The following chapter provides an overview on the fish species studied (ecology, distribution, and conservation status), and details on facilities, equipment, and software used during the research in this thesis. The rationale as to why specific techniques were employed are also included. More detailed methodologies are provided in each experimental research section (Chapters 4-7).

3.1 Subject species

3.1.1 Cyprinids

Coarse fish species such as cyprinids often dominate fish community abundance in middle and lower reaches of temperate regions. Owing to their wide geographical distribution relative to human activities, this freshwater fish family may be particularly vulnerable to the impacts of anthropogenic noise. Cyprinids play an important role in energy and nutrient cycling regimes (Lucas *et al.*, 1998), and are often invaluable within recreational fisheries. Many species of cyprinid are recognised as migratory, yet their movements are increasingly impeded by barriers such as weirs, or other impounding infrastructure, that fragments riverine habitat. Additionally, the artificial introduction of some species (*e.g.* carp) to non-native regions (*e.g.* U.S.A., Australia) costs countries billions of dollars annually in aquatic invasive species management (Pimental *et al.*, 2000). Understanding the responses of freshwater cyprinid fishes to underwater sound is necessary to mitigate for the negative impacts of anthropogenic noise, and to develop effective fisheries management technologies (*e.g.* behavioural guidance systems) that will assist in the conservation of native species and control of invasives.

Cyprinids belong to a group of fish with hearing specialisations, known as 'otophysines' (Rosen *et al.*, 1970; Chapter 2.1). The presence of accessory hearing structures (Weberian ossicles) connects the swimbladder to the inner ear. These connections provide these fish with an enhanced auditory sensitivity, across a wide frequency range, and at a low hearing threshold (Frisch, 1938; Hawkins and Myrberg, 1983; Ladich and Popper, 2004). A frequency-selective auditory filter further allows cypriniforms to distinguish between tones differing in frequency by as little as 3-5% (*e.g.* *Carassius auratus*: Dijkgraaf, 1952; Fay and Popper, 1980). These hearing features, combined with the biological importance of cyprinids and their interest to fisheries management, identify

cypriniformes to be an ideal model family group for investigating fish group response to acoustic stimuli.

Model species used during experiments were selected in accordance with the specific research question being investigated. See individual research chapters (Chapter 4, 5, 6, and 7) for further details on model species selection.

3.1.1.1 European minnow (*Phoxinus phoxinus*)

European (Eurasian, or common) minnow (Figure 3.1) are found across a wide geographical and habitat range within Europe and northern Asia. Minnow migrate within freshwater systems where individuals can easily disperse downstream, covering a spread of three to seven kilometres per year (Lasach Intíre Éireann, 2016). Spawning takes place several times between April and August on stone and gravel substrates, with eggs hatching after between five to ten days, dependent on temperature (Farnham Angling Society, 2010). Preference for stony substratum acts as shelter from predators, particularly for fry which develop quickly into sexually mature fish within their first year (Jacobsen, 1979). While records indicate individuals may live up to 13 years (alpine lake: Øcre Heimdalsvatn), (Museth, 2002), reports from some UK sites suggest a maximum of three years (River Frome), (Mills, 1987), with variation in life-history traits observed dependent on age, growth rate, and size at sexual maturity.



Figure 3.1: European minnows (*Phoxinus phoxinus*) exhibiting shoaling behaviour within an aquarium tank.

While listed as of 'least concern' on the IUCN red list, the conservational status of the European minnow varies greatly dependent on location (Frier, 1994; Hesthagen and Sanlund, 2006; IUCN, 2016). For example, in Germany, minnows are listed as an endangered native species (Museth *et al.*, 2007), while in Britain, they are highly abundant and inhabit clean, well-oxygenated shallow water within lake bottoms, most upland rivers and lakes, and some lowland rivers (Copp, 1992; Museth, 2002). In some regions of Europe (*e.g.* Norway) minnow are considered non-native and have been observed to cause major changes in benthic communities (Brittain *et al.*, 1988; Brittain *et al.*, 1995), potentially having an impact on salmonids or other fish species. For example, reductions of up to 50% in salmonid recruitment have been observed after minnow introduction, and minnows may prey on salmonid larvae (Borgstrøm *et al.*, 1996; Huusko and Sutela, 1997; Museth *et al.*, 2007).

Minnows are facultative schoolers, and therefore stay in shoals most of the time, however, the structure and form of these groups are highly variable (Breder, 1967). Individuals behave relatively independently within a group in the absence of a predator. Conversely, high polarisation behaviour may be observed upon detection of a threat (Partridge, 1980). For example, individuals within a shoal may become more aligned in relation to one another (Parr, 1927). Minnows actively select which shoal to join based on the relative size of conspecifics within a group. The greater the variation in shoal member size, the greater the competition (Ward and Krause, 2001), although, in the presence of predators, individuals will actively avoid small shoal groups, instead selectively joining larger schools (Hager and Helfman, 1991).

Given the high variability of minnow group behaviour, the designation of shoal size during experimentation is important because the number of group members can influence overall structure and cohesion, an effect known as the "loose cruising association" (Nursall, 1973). The information transfer-response time of one individual reacting to the startle response of a conspecific is highly dependent on shoal size. For example, groups of four to six minnows integrate well and respond much faster than shoals of two to three fish (Partridge, 1980). This may be observed through lower response latencies and greater group cohesion (*i.e.* decreased inter-individual distance), (Partridge, 1980).

No known audiogram exists for European minnows, however it has been speculated that they may hear up to 5 kHz in frequency (Dijkgraaf and Verheijen, 1950). In the absence of a subject specific audiogram, the auditory thresholds of closely related species must be relied upon to

determine feasible acoustic stimuli selection (e.g. *Pimephales promelas*: Scholik and Yan, 2001: Figure 3.2).

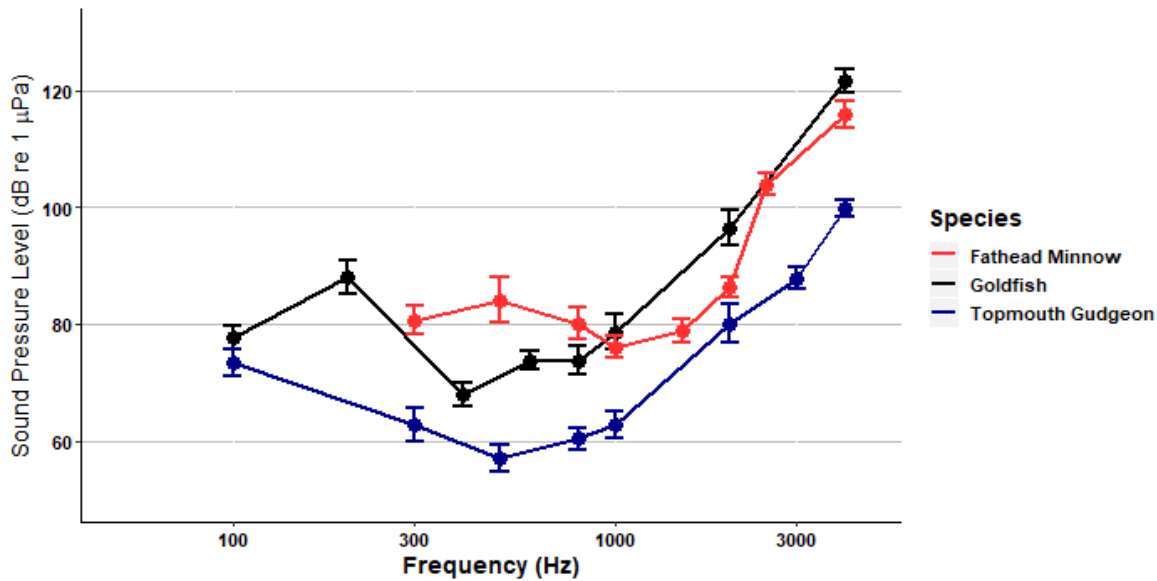


Figure 3.2: Audiograms of small cyprinid species: goldfish (*Carassius auratus*: via ABR technique: Smith *et al.*, 2004); fathead minnow (*Pimephales promelas*: via ABR technique: Scholik and Yan, 2001); and topmouth gudgeon (*Pseudorasbora parva*: via AEP technique: Scholz and Ladich, 2006), indicating assumed hearing thresholds for subject species *Phoxinus phoxinus*).

3.1.1.2 Common carp (*Cyprinus carpio*)

Common (or Eurasian) carp (Figure 3.3) are found across a wide geographical range as a result of worldwide introduction, stocked for human consumption and sport fishing. Carp inhabit warm, deep, minimal flow waters, including lowland rivers and vegetated lakes (Freyhof and Kottelat, 2008a). Spawning occurs every year between May and June, during which fish migrate to and from breeding grounds, sometimes travelling hundreds of kilometres (NSW, 2010). Males are sexually mature after three to five years, and females from four to six, dependent on latitude. While a 6 kg female can produce up to 1.5 million eggs, reproductive success is highly dependent on water flooding regimes in combination with optimum temperatures ($> 18^{\circ} \text{C}$). Carp live up to 50 years of age, with adults ranging in size from 30 – 60 cm in length, however, it is not uncommon for these fish to reach up to 20 kg (McCrimmon, 1968; Tomelleri and Eberle, 1990; Freyhof and Kottelat, 2008a).



Figure 3.3: Common carp (*Cyprinus carpio*) exhibiting social shoaling behaviour.

In Europe and Asia, wild carp are listed as ‘vulnerable’ on the IUCN red list (Freyhof and Kottelat, 2008a) as native populations are declining. Numerous factors including overfishing and water pollution have led to their decline, alongside many other commercially important species of carp (e.g. Silver: *Hypophthalmichthys molitrix*; Bighead: *Aristichthys nobilis*: Ban *et al.*, 2017). Human-made barriers (e.g. Three Gorges Dam, Yangtze River, China) which block the natural connectivity of many waterways have also affected fish numbers. Dams impact population densities across life stages (Xie *et al.*, 2007; Li *et al.*, 2013; Ban *et al.*, 2017) by changing natural hydrological conditions (Cheng *et al.*, 2018), and restricting migratory movements (Duan *et al.*, 2009; Ban *et al.*, 2017) and gene flow (e.g. via genetic bottlenecks or introduced domesticated stocks causing hybridised strains: Liao *et al.*, 2006). There is therefore a requirement to conserve native populations from human disturbance.

Conversely, common carp are arguably the most dangerous aquatic invasive species (AIS) in the world. They have detrimentally impacted water quality, native fish communities and aquatic macrophytes (Taylor *et al.*, 1984; Weber and Brown, 2009) across the majority of continents (Vilizzi *et al.*, 2014; Crichingo *et al.*, 2016; Stuart and Conallin, 2018). The migratory nature (Dauphinais *et al.*, 2018) and high fecundity (Marshall *et al.*, 2018) of this freshwater species allows for rapid establishment (Koehn, 2004) which often reaches extreme abundance levels (e.g. > 1.800 kg/ha: Farrier *et al.*, 2018). Consequently, the economic costs of AIS fish management are sizeable (e.g. US\$1 billion – US\$5.7 billion annually: Pimental *et al.*, 2000), and are likely greater if

considering ecosystem damage (Lovell *et al.*, 2006). In Australia, for example, carp management alone costs in excess of an estimated AUD\$200 million annually (Koehn *et al.*, 2000). Restoration and management efforts are necessary to mitigate the impacts of AIS such as carp.

Large adult carp are generally considered solitary, however, as juveniles, they are a strongly shoaling species. For example, *H. molitrix* and *H. nobilis* are both strong aggregators, and fish density does not appear to influence group behaviour (Ghosal *et al.*, 2016). Species-specific grouping techniques do however differ, and Ghosal *et al.* (2016) observed one species to form a single large shoal, while the other species subdivided into smaller groups of two to three individuals. In mixed-species groups, individuals readily shoal with one another, but, this is not observed when integrating common carp, which belong to a differing feeding guild (Ghosal *et al.*, 2016). Such strategies indicate that aggregations may in part facilitate predator avoidance and foraging efforts. Additionally, isolated carp under experimental conditions display behavioural indicators of extreme stress, and therefore testing individuals as opposed to groups may confound results. As such, it is recommended that carp are tested and housed in small groups (Huntingford *et al.*, 2010).

Auditory sensitivity and acoustically derived behavioural responses in common carp have been well studied using a number of differing methods (*e.g.* ABR, cardiac conditioning: Popper, 1972; Kojima *et al.*, 2005). As mentioned earlier (Chapter 2.1), different techniques have seen variation in reported hearing sensitivities by as much as 60 dB (in goldfish, *Carassius auratus*), however, Kojima *et al.* (2005) compared outputs obtained through ABR, electrocardiogram (ECG) and other behavioural conditioning techniques using common carp and found that results did not significantly differ. All three methods indicate an optimum frequency of around 1000 Hz and responses may be obtained between 100 – 3000 Hz (Figure 3.4).

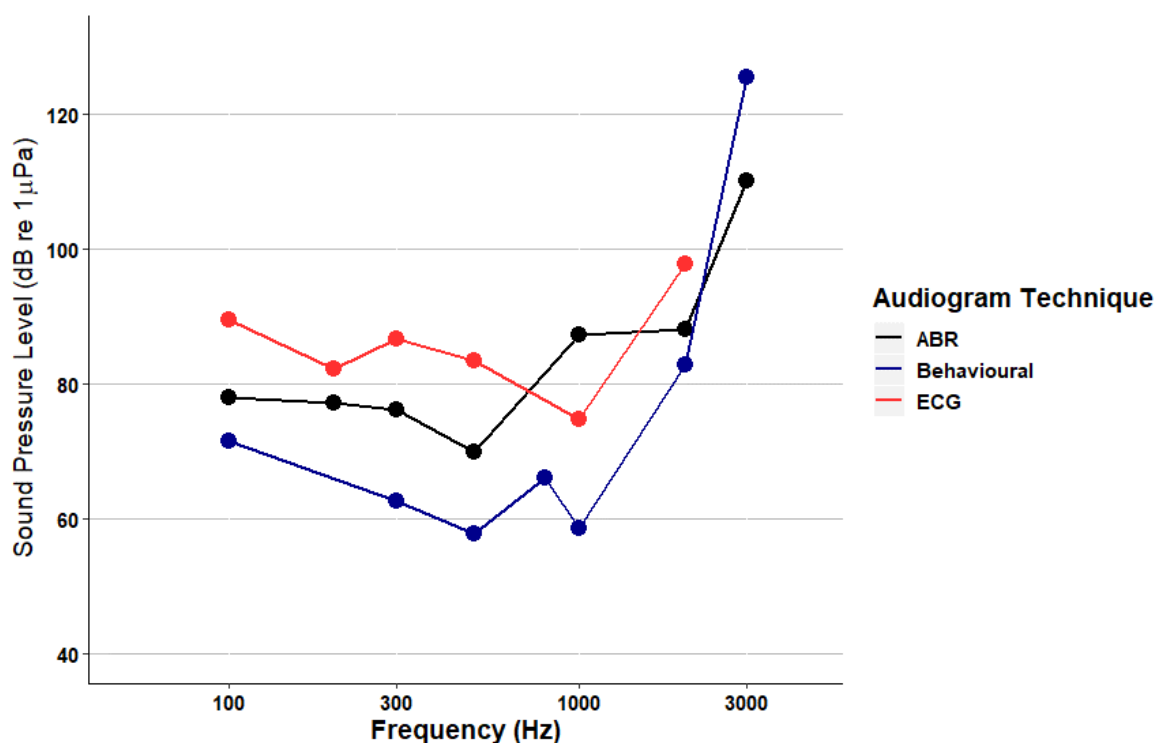


Figure 3.4: Audiograms of common carp (*Cyprinus carpio*) via three different techniques (ABR; ECG: cardiac conditioning; and behavioural) indicating hearing thresholds of subject species (c.f. Kojima *et al.*, 2005).

3.1.1.3 Common roach (*Rutilus rutilus*)

Common roach (Figure 3.5) are native to most of Europe and western Asia and are categorised of “least concern” on the IUCN red list (Freyhof and Kottelat, 2008b). They are however considered invasive in north eastern Italy (Kottelat and Freyhof, 2007) and Ireland (Stokes *et al.*, 2006) where they have been implicated in the reduction of several fish species (e.g. brown trout, *Salmo trutta*: Kennedy and Strange, 1978; rudd, *Scardinius erythrophthalmus*: Cragg-Hine, 1973; and perch, *Perca fluviatilis*: Johannson and Persson, 1986) due to competitive superiority (Johannson and Persson, 1986), food web disruption (Rosell, 1994), hybridisation (Rocabayera and Veiga, 2019), and degradation of habitat (Ferguson, 2008). In the Murray-Darling basin, Australia, roach were introduced as a sporting fish in the late 1800s and are now considered a nuisance species, but of non-native status (Rocabayera and Veiga, 2019).



Figure 3.5: Shoal of three common roach (*Rutilus rutilus*) in aquarium tank.

Roach can generally be found in lowland river systems and lakes, and brackish coastal lagoons (Kottelat and Freyhof, 2007). Males mature after two to three years, and prior to spawning season they develop breeding tubercles, an ornament of both inter- and intrasexual selection that consists of small horns (Kortet *et al.*, 2004). Their role and function are still unknown, but they may convey tactile or hydrodynamic cues that signify the quality of an individual (*e.g.* parasite load, resistance, or offspring survival: Kortet and Taskinen, 2004; Wedekind *et al.*, 2001) during the pre-spawning behaviour of fish (Kortet *et al.*, 2004). The seasonal spawning migration can be divided into two periods, a pre-spawning period (early February – late March) where individuals begin moving to backwaters; and the main spawning migration (April – May), when females reach the final stages of sexual maturation and water temperatures have risen above 12°C. At this time large groups of roach migrate to backwaters or further upstream to spawn (Kestemont *et al.*, 1999; Prchalová *et al.*, 2006), where they do so in shoals (Kottelat and Freyhof, 2007). Females lay between 5,000 to 200,000 sticky eggs of < 1.5 mm diameter onto dense vegetation or moss within shallow water (Pinder and Freshwater Biological Association, 2001; Total Fishing UK, 2017), and mating involves non-resource based lekking (see Table 2.4: Wedekind, 1996). Fry hatch within four to ten days, and as adults will range in length from 20 cm to 40 cm, living up to 25 years of age (Total Fishing UK, 2017).

Common roach are known for their shoaling behaviour (Christensen and Persson, 1993; Eklöv and Persson, 1995) as an antipredator strategy, and mass feeding (L'Abée-Lund and Vøllestad, 1987) and spawning migrations (Kestemont *et al.*, 1999; Prchalová *et al.*, 2006). Roach at the front of

shoals tend to steer a group (Bumann and Krause, 1993), with nutritionally deficient individuals more often leading than satiated shoal members (Krause *et al.*, 1992; Krause *et al.*, 1998). This allows hungry individuals primary access to food, but also may expose them to more predators (Bumann *et al.*, 1997). Motivation to move at a specific time to find food, based on previous experience, may also determine roach shoal leadership, and leadership may act as a form of social facilitation by increasing the tendency of less bold individuals to reciprocate conspecific behaviour (Reebs, 2000). Although the foraging or capture rate of prey (*e.g.* *Chaoborus* sp.) appears to be unaffected by group size, conversely, swimming activity may increase within larger shoals (Linløkken *et al.*, 2010).

The auditory sensitivity of common roach using ABR techniques (Amoser *et al.*, 2004) indicate that physiological responses may be obtained between 100 – 4000 Hz, with best sensitivities recorded for 500 Hz at 60 dB re 1 μ Pa. Additionally, behavioural changes have been noted in response to frequencies outside this range (Karlsen *et al.*, 2004; Andersson *et al.*, 2007). For example, roach displayed c- and s-type escape responses (Chapter 3.6) to a low frequency infrasound (6.7 Hz) stimulus (Karlsen *et al.*, 2004).

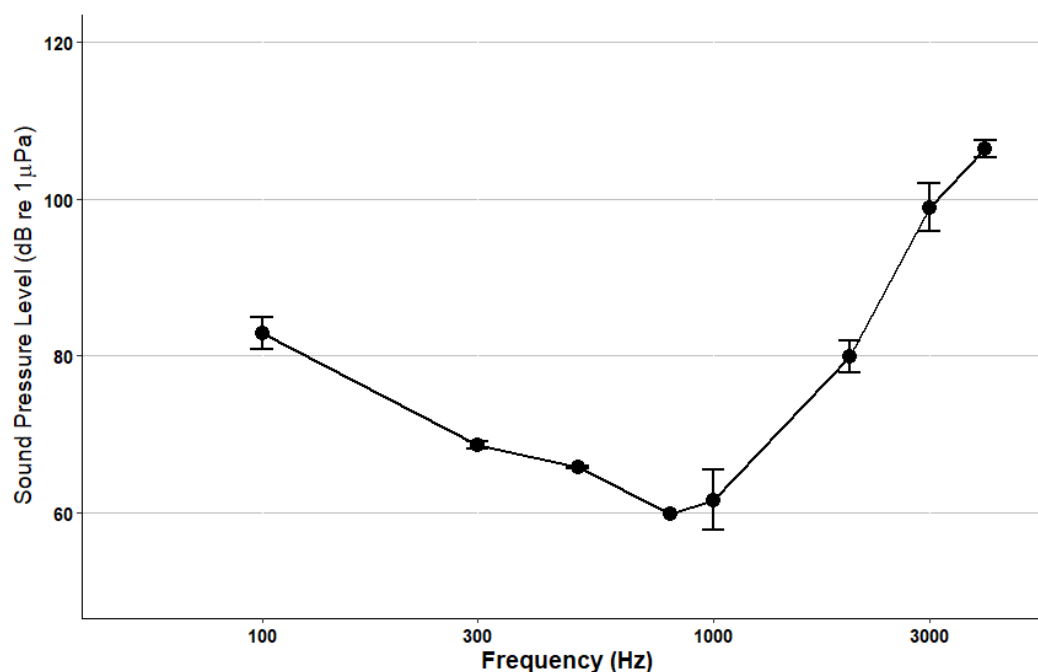


Figure 3.6: Audiogram of common roach (*Rutilus rutilus*: via AEP technique) indicating hearing thresholds of subject species (*c.f.* Amoser *et al.*, 2004).

3.2 Experimental facility: still-water conditions

To meet objectives 2 (how acoustic complexity influences group responses) 3 (how temporal characteristics influence rate of behavioural tolerance), and 4 (assess the influence of background masking noise on group responses to acoustic stimuli), assessment of fish behaviour in response to sound stimuli that differed in acoustic characteristics (*e.g.* frequency, complexity, pulse repetition rate, SNR) was required. In this case, a still-water “tank” (municipal tap water: pH: 7.8, Ammonia: 0 ppm, Nitrite: 0 ppm, Nitrate: *ca.* 20 ppm), provided the best option, as a homogenous and fully replicable acoustic field could be deployed, and confounding variables could be tightly controlled.

Practical experimentation took place in the University of Southampton’s International Centre for Ecohydraulics Research (ICER) facility at Chilworth Science Park, SO16 7NP. Experiments under still-water conditions were performed within a subdivided section (86 cm x 30.8 cm x 30.2 cm) of an acrylic flume (300 cm x 30.8 cm x 30.2 cm: 1.2 cm thickness), within an acoustically isolated chamber (470 cm x 320 cm x 240 cm), (Figure 3.7). See individual research chapters (4.2.2; 5.2.2; 6.2.2) for further details on the experimental arena setup.



Figure 3.7: Section view schematic of still-water flume set-up within acoustically isolated chamber.

A reductionist approach using a stable, reproducible acoustic field within a tank, provides valuable reference data for modelling and field studies, and allows for the careful control of confounding factors (*e.g.* influence of sensory stimuli [*e.g.* olfactory, mechanical, visual cues] other than acoustic treatment of interest; influence of third party on fish behaviour [*e.g.* predator, experimenter]), (Rice *et al.*, 2010; Slabbekoorn, 2016). Nevertheless, no approach is without its limitations. It is commonly argued that tank-based studies do not fully replicate more “real world”

environments owing to the nature of near-field conditions within a small tank, relative to acoustic wavelength (Akamatsu *et al.*, 2002; Gray *et al.*, 2016). For example, for frequencies between 50 – 1000 Hz, the wavelength ranges from approximately 1.5 – 30 m, equating to heights much greater than standard tank dimensions. Sound stimuli generated within small tank laboratory setups promote highly complex acoustic conditions, in that a tank's small size, large impedance, wall material properties (which influence resonance frequencies), and sound speed differences between the water and surrounding air, produce high levels of particle motion within the sound field (Akamatsu *et al.*, 2002). This is understood to differ from large-scale “natural” aquatic environments, which are under free-field, open boundary conditions (*e.g.* oceans or deep lakes: Chapter 2.4). Such conditions are far removed from the natural aquatic habitats of many marine species, but as previously mentioned, freshwater systems are extremely variable, shallow-watered environments (sometimes < 1 m in depth), and are subject to significant man-made infrastructure (*e.g.* fish passes, dams and weirs: Chapter 2.5). Under such circumstances, boundary conditions within channels of similar dimensions to laboratory tanks (or flumes) would correspondingly produce strong wall reflections. Fish would be near to the pressure-release water/air interface, which would dampen sound propagation along channels of less than a quarter wavelength in depth (Leighton *et al.*, 2019). Testing acoustic stimuli within tanks may in fact produce an acoustic environment more akin to these riverine field conditions, than would a deeper, more “natural” open-water setup.

3.3 Experimental facility: flow conditions

To meet objective 5, assessment of fish behaviour to acoustic stimuli under differing velocities was required. In this case, an open-channel flume experiment provided the best option, as allowance for uniformity of hydrodynamic and acoustic conditions within sub-divided experimental channels could be tightly controlled.

Practical experimentation under flow-conditions was therefore undertaken in a physically separated section of a re-circulatory indoor open channel flume (model HM 161: GUNT, Hamburg: working length: 16 m, width: 0.6 m, depth: 0.8 m: Figure 3.8), located at the ICER facility, Boldrewood Innovation Campus, University of Southampton, SO16 7QF, UK. The sidewalls are made of tempered glass, and the floor of corrosion resistant stainless steel. The flume is fed by a series of five closed-circuit water-tanks (1 x 3600 L and 4 x 4300 L) filled with municipal tap water (pH: 7.8, Ammonia: 0 ppm, Nitrite: 0 ppm, Nitrate: *ca.* 20 ppm), and driven by two main centrifugal pumps with a maximum flow discharge capacity of $0.06 \text{ m}^3 \text{ s}^{-1}$. Water depth is

controlled using an overshoot weir at the downstream end of the channel. A double section of roller track (Item Industrietechnik, Germany) runs along the top of each longitudinal flume wall. This allowed for precision grid referencing when using measuring equipment for velocity and acoustic mapping. Recording equipment was attached to an inbuilt depth gauge and advanced along pre-allocated positions using a moveable section of Item rail. Further structures associated with the experiment were attached to the railing using cable ties, or alternatively secured into the otherwise uniform rectangular channel by fastening into available screw holes, positioned at set increments along the top edge of the flume channel wall. Consistent lighting was monitored and maintained throughout trials, with white sheeting used to provide better contrast of fish within video recordings when compared to the background. All webcams used for video recording of trials were non-intrusively positioned overhead. Flume water temperature and in-air background noise levels were also recorded and monitored in advance of running each trial. See Chapter 7.2 for further methodological details.

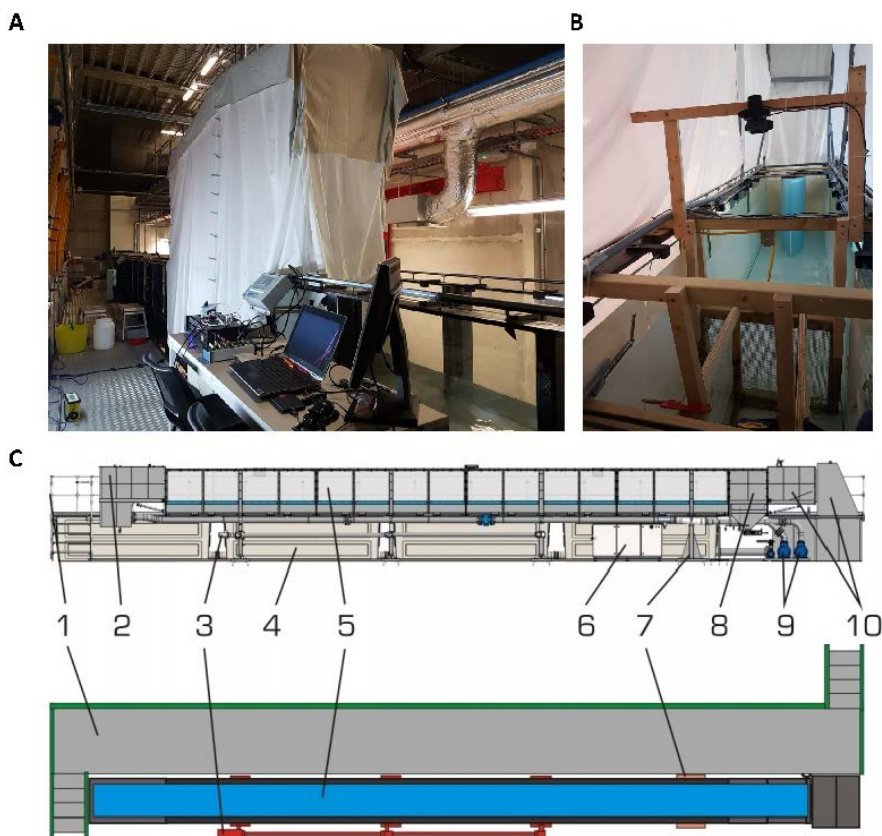


Figure 3.8: (A) Visually and physically isolated section of experimental flume; (B) interior of physically isolated experimental arena and set-up; and (C) schematic of re-circulating flume (where: 1 = gallery; 2 = inlet element; 3 = jacking support with motorised inclination adjustment; 4 = water tank; 5 = experimental section; 6 = switch cabinet; 7 = fixed support; 8 = sediment trap; 9 = pump; and 10 = outlet element). *Note:* Image source: Gunt Hamburg products: <https://bit.ly/2kdYbnu>

3.4 Sound production and measurements

Sound stimuli for all experiments were produced using a basic setup (Figure 3.9). MATLAB was used to generate stimuli of pre-programmed parameters (*e.g.* frequency, intensity, periodicity) through two fully immersed underwater speakers (Electro-Voice UW-30: maximal output 153 dB re 1 μ Pa at 1 m for 150 Hz, frequency response 0.1-10 kHz; Lubell Labs, Columbus, OH). A laptop computer (HP-G62; Windows 7) was connected via USB to a National Instruments data acquisition box, which in turn transmitted the signal via an amplifier to the two speakers, either using one, or two channels, dependent on the experiment. Stimuli were calibrated and the hydrophone checked using a pistonphone (Brüel & Kjær; Type 4229; serial no° 1617564). The sound field was mapped in advance of all experimentation using a hydrophone mounted to a customised rig and connected to either a hydrophone amplifier or charge amplifier. The signal was then relayed back to the laptop computer via the data acquisition box. Pressure amplitude and phase were measured along a regular grid of points, from which the sound field could be intricately described in the sound pressure and particle acceleration domains. For further details see research chapter sections 4.2.3; 5.2.3; 6.2.3; and 7.2.4.

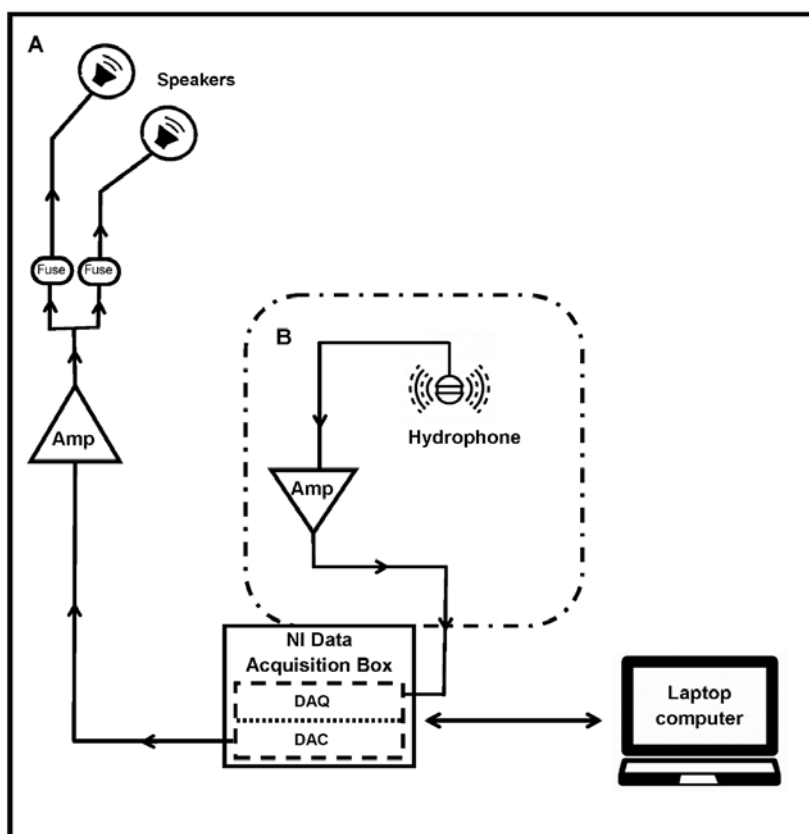


Figure 3.9: Acoustic set-up for (A) generating and (A and B) recording sound during calibration, mapping and experimentation. *Note:* DAQ (data acquisition device) and DAC (digital to analog converter) were housed within a National Instruments (NI) data acquisition box; Amp: Amplifier.

3.5 Hydrodynamic measurements

In line with objective 5, accurate hydraulic data was required to map hydrodynamic conditions within the flume (Chapter 7.2.3). Flow measurements were therefore conducted using an Acoustic Doppler Velocimeter (ADV), (*e.g.* Guiny *et al.*, 2003; Vowles *et al.*, 2014; Kerr *et al.*, 2019). ADVs measure a small sample of the flow at discrete points by emitting short pairs of acoustic pulses and measuring the change in received signal frequency. This shift in frequency can be calculated as:

$$F_{doppler} = -F_{source} \frac{v}{c} \quad (\text{Equation 3.1})$$

where $F_{doppler}$ is the change in received frequency (Doppler shift); F_{source} is the frequency of the transmitted sound; v is the velocity of source relative to receiver; and c is the speed of sound underwater. For a doppler shift to occur, there must be relative motion between the sound and the receiver.

The ADV uses the principle of Doppler shift to collect accurate hydraulic readings across the three planes of water velocity (Voulgaris and Trowbridge, 1998). This data allows for the calculation of varying hydraulic parameters, including mean streamwise velocity (*e.g.* Enders *et al.*, 2009), turbulent kinetic energy (*i.e.* the energy extracted from mean velocities by vortices: *e.g.* Smith *et al.*, 2005), turbulence intensity (*i.e.* the amount of fluctuation about the mean velocity: *e.g.* Russon *et al.*, 2010), or shear stress (*i.e.* where two bodies of water move past one another at differing velocities: *e.g.* Silva *et al.*, 2011).

To ensure the removal of any outliers, a maximum/ minimum threshold filter was applied to all raw ADV data, replacing anomalies with a mean value using a pre-written macro programme in Microsoft Office Excel 2010 (see Cea *et al.*, 2007 for full methodological description). Minimum threshold values were calculated as:

$$u_{\min} = \bar{u} - \sqrt{2 \ln(N)} \sigma_u \quad (\text{Equation 3.2})$$

and maximum as:

$$u_{\max} = \bar{u} + \sqrt{2 \ln(N)} \sigma_u \quad (\text{Equation 3.3})$$

where both velocity thresholds ($u_{\min/\max}$) are described in the longitudinal direction (similar expressions are used for vertical: \bar{w} ; and lateral: \bar{v} components: Cea *et al.*, 2007); \bar{u} is the mean

longitudinal velocity; σ_u is the standard deviation of u ; and N is the total number of velocity readings.

Maintenance of signal-to-noise ratios (*i.e.* measurement of the relative quality of the received signal) and correlation values (*i.e.* the dispersion of the velocity during sampling) within the manufacturer's recommended range (SNR: 20-25; correlation > 70%) ensured that accurate measurements were obtained for hydrodynamic mapping. For further details on ADV sampling, see Chapter 7.2.3.

3.6 Quantification of fish behaviour

Fish behaviour within flumes was predominantly assessed via overhead webcam footage. Experiments were conducted during the day, in line with Cyprinid subject species temporal schedules of activity (Helfman and Pitcher, 1993; Greenwood and Metcalfe, 1998; Prchalová *et al.*, 2006; Jones and Stuart, 2007). Group behaviour was quantified from video recordings using an automated fish tracking programme (Figure 3.10) written in MATLAB (for full details see Short *et al.*, 2020) to provide measurements for group average location, speed, cohesion, and the mean and standard deviation of orientation (Table 3.1).

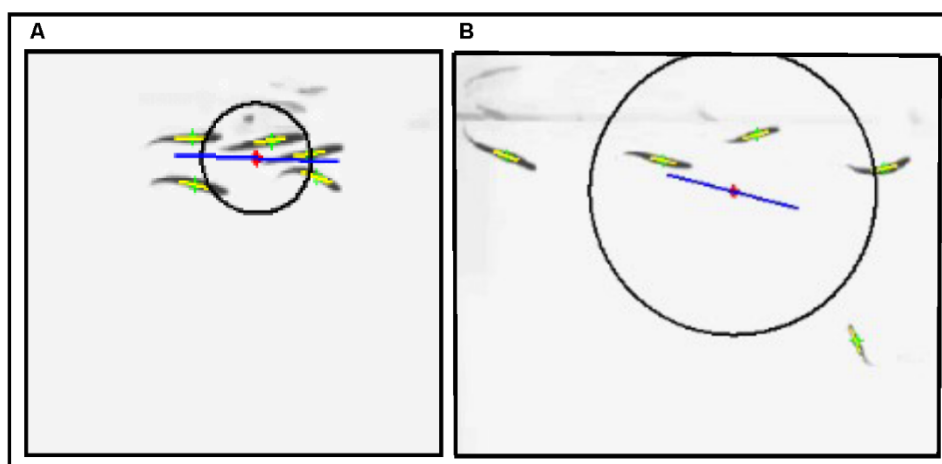


Figure 3.10: Groups of fish were video recorded from overhead using a webcam, and their movements tracked using a programme written in MATLAB. *Note:* **(A)** before onset of acoustic stimuli; and **(B)** fish response to sound in still-water conditions.

Further to automated tracking, behaviour was manually categorised, and discrete events or binary outcomes counted, for example, the presence or absence of a startle response (see Chapters 4.2.5; 5.2.5; 6.2.5; and 7.2.6 for further details).

Table 3.1: Criteria and definitions of group behaviour quantified using video recordings of the response of groups of cyprinids (*e.g.* European minnow) to differing acoustic stimuli.

Group behaviour	Definition	References
Startle response (presence/absence)	Specifically, an ‘escape response’ at the onset of acoustic stimuli. One or more fish within a group were observed to exhibit a clear burst in swimming speed, at an altered angle in comparison to pre-startle swimming speed and direction	Blaxter <i>et al.</i> , 1981 ; Kastelein <i>et al.</i> , 2008 ; Stewart <i>et al.</i> , 2012 ; Bhandiwad <i>et al.</i> , 2013 ; Neo <i>et al.</i> , 2015a ; Nedelec <i>et al.</i> , 2015
Swimming speed (m s ⁻¹)	Mean (\pm s.e.) speed of the mean shoal centre (see ‘shoal distribution’) (strength of response to neighbours decreases greatly as individual speed decreases)	Katz <i>et al.</i> , 2011; Neo <i>et al.</i> , 2015a; 2015b; Short <i>et al.</i> , 2020
Cohesion (m)	Mean distance from the mean shoal centre (measurements taken at centre point of each fish)	Partridge, 1980; Delcourt and Poncin, 2012; Neo <i>et al.</i> , 2015b; Herbert-Read <i>et al.</i> , 2017a; Short <i>et al.</i> , 2020
Orientation (°)	Imaginary horizontal line drawn through fish (head to tail) and the standard deviation of the angle of the fish compared to one another is calculated, <i>i.e.</i> pointing the same direction, or randomly aligned (lower orientation = more aligned)	Partridge, 1980; Couzin <i>et al.</i> , 2002; Herbert-Read <i>et al.</i> , 2017a ; Short <i>et al.</i> , 2020
Shoal Distribution (x,y)	Mean shoal centre ($X_c(n)$) location of fish group in 2D calculated from: Position of the <i>i</i> th fish in the <i>n</i> th video frame, vector $\underline{X}_i(n) = (x_i(n), y_i(n))^t$, where $x_i(n)$ corresponds to distance along length of tank, and $y_i(n)$ to breadth. Therefore: $\underline{X}_c(n) = (x_c(n), y_c(n))^t = (\underline{X}_1(n) + \underline{X}_2(n) + \underline{X}_3(n) + \underline{X}_4(n) + \underline{X}_5(n))/5$	Hassan <i>et al.</i> , 1992, Neo <i>et al.</i> , 2015a

3.7 Statistical analyses

Statistical tests used within research chapters were selected based on the data type and analytical needs of the individual datasets (Table 3.2; for further details see Chapters 4, 5, 6, and 7).

Table 3.2: Assessed parameters, statistical analyses and selective reasoning

	Assessed parameters	Data type and analytical needs	Statistical test(s) selected
Chapter 2.1	Vote-counting	Categorical (binomial) dataset indicating a yes/no response.	<u>Chi-squared test</u> : determines whether an association exists between categorical variables (<i>i.e.</i> independence or relation) by measuring how a model (expected) compares to actual (observed) data.
	Effect sizes	Continuous outcome dataset. Meta-analysis required to investigate the combination or interaction of a group of independent study estimates. For each study an effect size (<i>e.g.</i> standardised mean difference: SMD) is calculated as a summary measure.	^a <u>Fixed and mixed-effects models</u> : ^a allows for pooling of independent effect sizes to provide one overall effect size estimate of the studies. ^b Includes both fixed (between subgroups) and random (within subgroups) effects within the model when considering subgroup analyses.
Chapter 4	Startle response	Binary data (yes/ no response) measured across categorical treatment factors and a control.	<u>Logistic regression model</u> : allows for examining the association of categorical independent variable(s) with one dichotomous (binary) dependent variable through the use of a logit model for binary data that indicates the probability of a certain outcome.
	Group swimming speed; cohesion; and orientation	Normally distributed and equally variable continuous data. Means required assessment across one or more variables that are based on repeated observations of the same subjects (<i>i.e.</i> over time).	<u>Repeated measures ANOVAs</u> : used to detect any overall differences between related means under a study design where changes in the mean scores of the same subjects are measured more than once on the same dependent variable. The acoustic treatment was the between-subjects factor, and time period was the within-subjects factor (<i>i.e.</i> the repeated measures factor).
	Shoal distribution	Continuous nonparametric dataset regarding spatial distribution of individuals over time and proportional environmental (acoustic) space. Require quantification of probability distributions (<i>i.e.</i> use of acoustic space) and assessment of differences between control and treatment groups.	^a <u>Kullback-Leibler Divergence (KLD) with Wilcoxon signed-rank test</u> : ^a (also known as relative entropy) is a measure of how one probability distribution is different from a second, the reference probability distribution (or control). ^b KLDs can then be statistically compared using Wilcoxon signed-rank test which determines whether the ranked control distributions differ from the treatment data.

Chapter 5	Group swimming speed; cohesion; and orientation	Continuous dataset \log_{10} transformed to meet assumptions of normality and homoscedasticity. Means required assessment across one or more variables that are based on repeated observations of the same subjects (<i>i.e.</i> over time).	<u>Repeated measures ANOVA</u> : as explained for Chapter 4
	Time to tolerate	Time series data (\log_{10} transformed dataset) requiring quantification of differences in moving means between control and treatment groups.	<u>Ten second running t-statistic (independent two-sample t-test with assumed equal variance)</u> : t-tests allow for determining whether a significant difference exists between the means of two groups. Use of moving averages allow for the smoothing of time series analysis, with a running t-statistic visually indicating direction of change over time (threshold $p < 0.05$), and the total duration of significant influence.
Chapter 6	Undisturbed continuous startle response; and total number of individuals startling at onset	Discrete nonparametric dataset (count data). Require assessment of differences in medians across control and treatment groups.	<u>Kruskal-Wallis tests</u> : a rank-based nonparametric test which determines whether the medians of two or more groups are different.
	Group swimming speed; cohesion; and orientation	Continuous nonparametric dataset requiring quantification of moving medians across control and treatment groups.	<u>Difference in comparative running p-values (Wilcoxon rank sum tests) calculated via chi-square contingency tables</u> : Wilcoxon rank sum tests determine whether ranked control distributions differ from the treatment data. Differences between proportion of time $p < 0.05$ were calculated per treatment and assessed using chi-squared contingency tables which determine whether observed values statistically differ from expected values.
Chapter 7	Group cohesion; latency time; and passage time	Continuous dataset with minor violations to assumptions of normality and homoscedasticity. Requiring assessment of differences in means across control and treatment groups across two independent factors.	<u>Two-way bootstrapped ANOVA</u> : a bootstrapped statistical test that is robust to violation of assumptions and outliers. Compares the mean differences between groups that have been split on two independent variables (or factors) and determines whether an interaction exists between the two independent factors on the dependent variable.
	Initial response upon entry to route choice decision area	Nominal data (outcome variable) measured across and between categorical treatment factors and a control (predictor variables). Requires assessment surrounding the likelihood of probability of categorical membership.	<u>Multinomial logistic regression model</u> : used to predict the probability of category membership on a dependent variable based on multiple independent variables by modelling the log odds of the nominal outcome variables as a linear combination of the predictor variables.
	Difference in channel selection between treatment and control	Binary data (route choice) measured during the treatment and control conditions.	<u>Goodness-of-fit (χ^2) test</u> : allows for determination of whether treatment data deviates from an expected, or control (50:50) frequency.

CHAPTER 4 **Collective behaviour of the European minnow (*Phoxinus phoxinus*) is influenced by signals of differing acoustic complexity**

Collective behaviour, such as shoaling in fish, benefits individuals through a variety of activities such as social information exchange and anti-predator defence. Human driven disturbance (e.g. anthropogenic noise) is known to affect the behaviour and physiology of individual animals, but the disruption of social aggregations of fish remains poorly understood. Anthropogenic noise originates from a variety of activities and differs in acoustic structure, dominant frequencies, and spectral complexity. The response of groups of fish may differ greatly, depending on the type of noise, and how it is perceived (e.g. threatening or attractive). In a controlled laboratory study, high resolution video tracking in combination with fine scale acoustic mapping was used to investigate the response of groups of European minnows (*Phoxinus phoxinus*), to signals of differing acoustic complexity (sinewave tones vs octave band noise) under low (150 Hz) and high (2200 Hz) frequencies. Fish startled and decreased their mean group swimming speed under all four treatments, with low frequency sinewave tones having the greatest influence on group behaviour. The shoals exhibited spatial avoidance during both low frequency treatments, with more time spent in areas of lower acoustic intensity than expected. This study illustrates how noise can influence the spatial distribution and social dynamics within groups of fish.

4.1 Introduction

The social aggregation of fish is common and has numerous benefits for the individual, including mating (pencil-streaked rabbitfish, *Siganus doliatus*: Fox *et al.*, 2015), foraging (guppy, *Poecilia reticulata*: Day *et al.*, 2001), or reduction of energy expenditure (mullet, *Chelon labrosus*: Hemelrijk *et al.*, 2015). Functionally, collective behaviour is advantageous as an anti-predator strategy (artificial prey computer simulation: Ruxton *et al.*, 2007), whereby schooling can confuse predators (largemouth bass, *Micropterus salmoides*: Landeau and Terborgh, 1986; Larsson, 2009) or accelerate the transmission of an alert signal among conspecifics within a group before a threat is detected first-hand by some individuals (Gulf menhaden, *Brevoortia patronus*: Handegard *et al.*, 2012). However, anthropogenic disturbance can disrupt the collective behaviour of fish, resulting

in the benefits bestowed being lost. For example, modification of group cohesion has been observed in response to exposure to artificial light (Atlantic mackerel, *Scomber scombrus*: Glass *et al.*, 1986; estuarine round-herring, *Gilchristella aestuaria*, and Cape silverside, *Atherina breviceps*: Becker *et al.*, 2013), chemical pollution (golden shiner, *Notemigonus crysoleucas*: Webber and Haines, 2003; Scott and Sloman, 2004), waterway obstruction (*e.g.* silver carp, *Hypophthalmichthys molitrix*, at dams or weirs: Mao, 2018), hypoxia (Atlantic herring, *Clupea harengus*: Domenici *et al.*, 2000; 2017), and noise (sea bass, *Dicentrarchus labrax*: Herbert-Read *et al.*, 2017a). Anthropogenic noise (unwanted, disruptive sound) is a highly pervasive pollutant of international concern (WHO, 2011), and is well known to have detrimental impacts on fish behaviour and ecology (Slabbekoorn *et al.*, 2010; Kunc *et al.*, 2016). The specific causal mechanisms by which acoustic signals influence group behaviour in fish, however, is not fully understood.

Anthropogenic noise may mask communicative calls (Lusitanian toadfish, *Halobatrachus didactylus*: Vasconcelos *et al.*, 2007), impair anti-predator responses (European eel, *Anguilla anguilla*: Simpson *et al.*, 2015), or modify the coordinated movements of fish within a group (*e.g.* sea bass: Herbert-Read *et al.*, 2017a). Previously, the impact of anthropogenic broadband noise (*e.g.* continuous and intermittent Brownian noise: Neo *et al.*, 2014; pile driving noise: Herbert-Read *et al.*, 2017a) on the collective behaviour of fish has been investigated. A gap in understanding, however, exists regarding the influence of “acoustic complexity” on fish aggregations. The acoustic complexity of a signal is not a well-defined concept. For example, complexity is frequently based on the entropy of a signal (Sueur *et al.*, 2014), but also relates to its bandwidth, since this determines the amount of information which can be conveyed (Shannon, 1948). A sinewave represents an example of a simple signal since it has low entropy, and a narrow bandwidth. In this study, complex sound is defined as random-noise like signals which are more informatively complex, having higher entropy and wider bandwidths.

Group behaviour (*e.g.* cohesion and orientation) may be influenced by the structural complexity of the signal (Candolin, 2003), a commonly studied acoustic parameter in animal communication (*e.g.* avian vocalisations: Pieretti *et al.*, 2011), although seldom considered in studies that quantify impacts of anthropogenic noise. Simple tonal (sinewave) signals also appear in the natural environment, albeit relatively infrequently compared to complex signals. For example, tonal bursts are used to maintain a territory (Bocon toadfish, *Amphichthys cryptocentrus*: Salas *et al.*, 2018) or attract a mate (elephantfish, *Pollimyrus adspersus*: Crawford, 1997). Human generated low frequency noise tends to be complex, and is widely spatially distributed (*e.g.* shipping or boating: Sarà *et al.*, 2007; Solan *et al.*, 2016; Amoser *et al.*, 2004; dredging, platform construction

and pile driving: Greene Jr. and Moore, 1995; Solan *et al.*, 2016). However, simple signals are also common, frequently deployed as acoustic deterrents (*e.g.* to limit spread of invasive fishes or direct native species away from anthropogenic hazards: Putland and Mensinger, 2019) and harassment devices (*e.g.* to keep marine mammals away from aquaculture facilities: Götz and Janik, 2013), or as sonar transmissions (Hildebrand, 2009; Kastelein and Hoek, 2010). Both complex and simple signals of anthropogenic origin can be received and processed by fish (Crawford, 1997; Hawkins and Popper, 2014; Stange *et al.*, 2017; Vetter *et al.*, 2017; Putland and Mensinger, 2019).

While complex signals can be represented as the combination of tones, discerning fish behaviour in response to a simple tonal component will not enable the prediction of the response to more complex signals (Hasan *et al.*, 2018). Studies are beginning to address how vast differences in the signal characteristics of anthropogenic sound sources can differentially impact fish swimming behaviour (*e.g.* complexity of 2-stroke vs 4-stroke engine noise: McCormick *et al.*, 2019; temporal structure: Chapter 5), however, a reductionist understanding of how fish groups respond to specific acoustic components of sound stimuli, such as complexity, is still lacking. This study investigated the effect of acoustic complexity on the group behaviour of a shoaling species of fish under experimental conditions by comparing their response to either simple (tonal) or complex (octave band noise) acoustic stimuli. Knowledge surrounding the collective behavioural responsiveness of fish to acoustic signals of differing complexity will aid in conservation efforts to reduce the impact of harmful components of anthropogenic noise, or may be applied to the development of more effective behavioural guidance systems. Using the European minnow (*Phoxinus phoxinus*: Linnæus, 1758) as the model species because of its strong facultative shoaling behaviour (Partridge, 1980; Pitcher *et al.*, 1986; Ward and Krause, 2001) and local abundance, this study tested 250 fish over a total of 50 independent trials in response to four acoustic playback treatments, and one “silent” (ambient noise) control. Quantification of response to two different acoustic frequencies (low: 150 Hz, or high: 2200 Hz) were included as a secondary aim so that a greater understanding of the acoustic range over which minnows respond can be ascertained in light of the fact that no audiogram exists for this species. The study concentrated on five group behaviour metrics commonly used to assess the impacts of environmental stressors on fish behaviour. To quantify the response to the signal, investigation focused on: 1) presence of a startle response at the onset of the signal (*e.g.* Nedelec *et al.*, 2015); 2) group swimming speed (*e.g.* Neo *et al.*, 2015b); 3) cohesion (*e.g.* Herbert-Read *et al.*, 2017a); 4) orientation (*e.g.* Herbert-Read *et al.*, 2017a); and 5) shoal distribution (*e.g.* Neo *et al.*, 2015b) relative to areas of different acoustic intensity. Given the added informative value of more complex acoustic signals, it was

hypothesised that these would elicit a greater deviation in response from the control across the five behaviour metrics in comparison to simple signals. A controlled experimental approach was adopted in which fish response to acoustics was tested in a still-water tank. As opposed to marine species that experience very different acoustic conditions in the wild, this methodology is more appropriate when working with a species that inhabits riverine environments (*e.g.* shallow water, narrow width and anthropogenically modified banks and beds), (Tonolla *et al.*, 2010; Marley *et al.*, 2016; Campbell *et al.*, 2019; Leighton *et al.*, 2019; Chapter 5).

4.2 Materials and methods

4.2.1 Study species and husbandry

In August 2016, 273 adult European minnows (♂ : ♀ unknown) were collected using a seine net from the River Itchen navigation channel, Hampshire, UK (51°02'58.9"N 1°18'42.2"W). The waterway holds environmental designations (*e.g.* Special Area of Conservation) and lacks boating activity. The average width of the slow flowing freshwater channel was 15 m, and depth ranged from 0.34 m in the shallows where fish were mainly acquired, to 0.94 m. Sediment was composed of silt, clay and gravel. Minnows typically inhabit river and lake habitats and are found across a wide geographical within Europe and northern Asia, including the brackish coastal waters of the Baltic Sea (Svirgsden *et al.*, 2018). The species are subjected to a vast range of anthropogenic noise disturbance including boating, shipping, and road traffic noise, sonar, and pile driving (Amoser *et al.*, 2004; Kozaczka and Grelowska, 2011).

Fish were transported to the University of Southampton's International Centre for Ecohydraulics Research facility and gradually introduced over a period of three hours to one of two adjacent holding nets (0.78 m x 0.3 m x 0.62 m; water depth: 0.45 m; stocking density: 3.02 kg/ m³) within a tank (1.5 m x 1.0 m x 0.78 m; water depth: 0.68 m; mean ± s.e. temperature 19.3 ± 0.2°C). All minnows were in good physiological condition (no visible injuries). Fish were allowed to acclimate to captive conditions for five days prior to the start of the experiments. Water quality was maintained using a submersible aerated pump, and monitored to ensure optimum thresholds were not exceeded (NO³⁻ : < 50 mg L⁻¹ ; NO²⁻ : < 1 mg L⁻¹ ; NH₃ : 0 ; and pH: < 8.4). Fish were kept on a 16:8 h light:dark photoperiod cycle, and fed to satiation with commercially available aquarium flaked food. Each fish was subjected to only one treatment. On completion of each trial fish were weighed (wet mass ± s.e.: 2.1 ± 0.1 g) and measured (standard length ± s.e.: 51.6 ± 0.4 mm). Wet mass (One-way ANOVAs: $F_{1,4} = 0.35$; $p = 0.84$) and standard length ($F_{1,4} = 0.43$; $p = 0.79$)

of fish did not differ between the treatments (Appendix B). All experiments were approved by the University of Southampton's Animal Welfare and Ethical Review Board (Ethics ID: 22982).

4.2.2 Experimental arena

Experiments were performed within an acoustically isolated room (Chapter 3.2), with in-air background SPLs monitored using a hand-held recorder (Mini Sound Level Meter N33GJ; measuring level range: 40-130 dB; accuracy: ± 3.5 dB @ 1 kHz, 94 dB under reference conditions; frequency weighting: dB(C); frequency response: 0.315-8 kHz; Maplin, Rotherham, UK). Readings were taken before the commencement of each trial to ensure ambient room conditions were standardised across treatments (averaged SPL of 40 dB re 20 μ Pa). Trials were conducted within a physically (but not acoustically) isolated experimental arena (86 cm x 30.8 cm x 30.2 cm) within a still water acrylic flume (300 cm x 30.8 cm x 30.2 cm), separated by two acoustically transparent dividers made of micro-mesh material (Figure 4.1).

The sound field was generated through two speakers (Electro-Voice UW-30; maximal output 153 dB re 1 μ Pa at 1 m for 150 Hz, frequency response 0.1-10 kHz; Lubell Labs, Columbus, OH, USA), one behind each acoustic baffle, and fully immersed and suspended in place 7 cm from the floor of the flume. The opposing speakers were operating in phase. This set-up allowed for a more homogenous and non-directional acoustic field, ideally preventing left-right bias or orientation towards a source (Buwalda *et al.*, 1983; Schuijff and Hawkins, 1983). Flume water was kept at a constant depth of 27 cm and replaced every ten trials, limiting debris build up within the experimental arena. Experimental flume water changes were used as a precautionary measure to reduce the potential for cumulative effects of chemical alarm substance release ("Schreckstoff", Pfeiffer *et al.*, 1985; Hasan *et al.*, 2018) by fish used in earlier experiments. Water was left to settle overnight, allowing for release of gas bubbles and a return to room temperature (mean \pm s.e.: $18.3 \pm 0.1^\circ\text{C}$).

Fish were visually isolated from the observer using black plastic sheeting attached to a large wooden frame, surrounding the experimental arena. To ensure light levels remained consistent between trials, two external spotlights were used to illuminate the room through two side-windows. Digital video recordings were obtained from a webcam (C920; HD 1080p; 30 frames per second; Logitech Pro, Switzerland) mounted above the tank. To increase contrast of the recordings, white-sheeting was attached outside the experimental arena of the flume and lit from underneath by two PhotoSEL Photography bulbs (pure white full-spectrum flicker free; 85 W, 5000 lumen; SJT Commercial Ltd., UK).

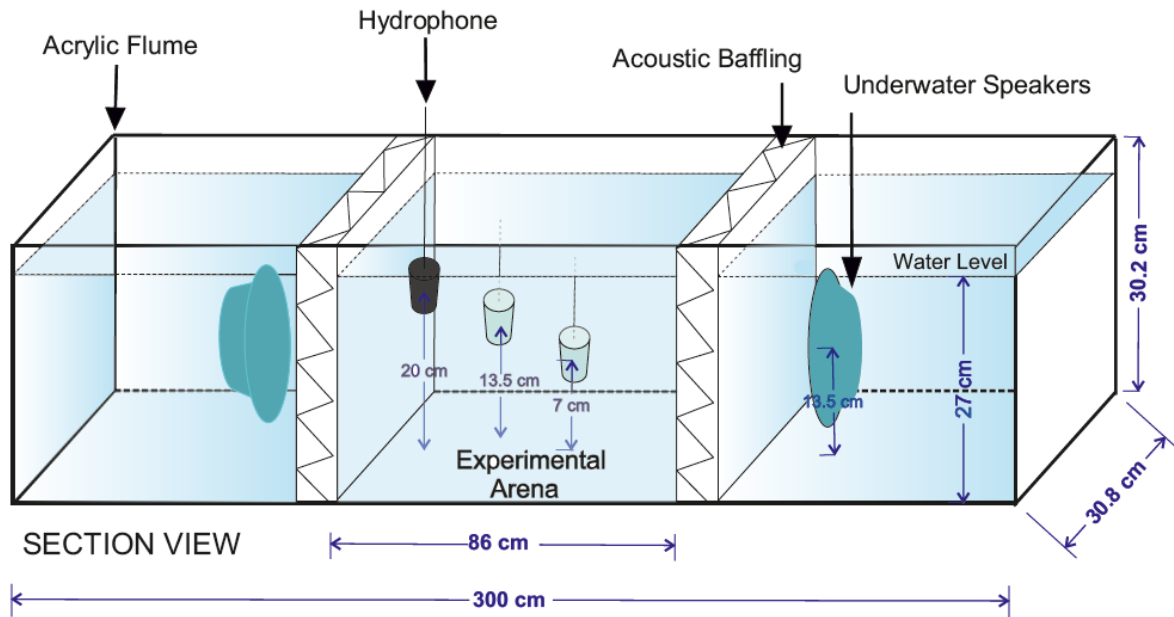


Figure 4.1: Schematic of experimental set-up with hydrophone positions shown for acoustic mapping at three different water depths (7 cm; 13.5 cm; 20 cm).

4.2.3 Acoustic stimuli and mapping protocol

While no audiograms currently exist for the European minnow, a number are available for closely related species (*e.g.* species with hearing specialisations: *Pimephales promelas*: 0.8 – 2 kHz, Scholik and Yan, 2001; and *Pseudorasbora parva*: 0.1 – 4 kHz, Scholz and Ladich, 2006). Combined with anecdotal evidence suggesting European minnows are capable of behaviourally responding to incremental tones up to 5 kHz (Dijkgraaf and Verheijen, 1950; Voellmy *et al.*, 2014a; Hanache *et al.*, 2020), the upper and lower frequency limits of hearing were subsequently estimated. Low (150 Hz) and high (2200 Hz) frequencies deployed in the study were selected to be within the assumed hearing range for European minnow (Short *et al.*, 2020). This range also covers frequency components commonly found in anthropogenically derived sound (*e.g.* boat traffic noise) in shallow water environments (Amoser *et al.*, 2004; Kozaczka and Grelowska, 2011).

Sound samples were produced using custom written MATLAB script (Release 2015b, The Mathworks, Inc., Natick, Massachusetts, USA). A laptop computer connected via USB to a DAQ (NI

USB-6341; National Instruments, UK) in turn transmitted the signal through a MOREL amplifier (MPS 4.400; 70 W, frequency response range approx. 0.01-30 kHz; MorelHifi, Israel), and on to the UW30 underwater speakers. Four acoustic treatments were used in the experiments: 'SINE_150' (150 Hz); 'SINE_2200' (2200 Hz); 'NOISE_150', octave band noise (centred at 150 Hz; frequency range: 106 - 212 Hz); and 'NOISE_2200', octave band noise (centred at 2200 Hz; frequency range: 1556 – 3112 Hz), (Figure 4.2). NOISE_150 and NOISE_2200 were produced by digitally filtering Gaussian white noise (sample rate: 25.6 kHz) using a 4th order elliptic filter with 0.5 dB passband ripple and 20 dB of stopband attenuation, for a signal with centre frequency, f_c , the cut-off frequencies of the filter were $0.7071 f_c$ and $1.414 f_c$. Use of artificial stimuli allowed for tight control over the specific acoustic components being tested. It also ensured easy replicability, and reduced potential for pseudoreplication that may occur when pre-recorded sound samples contain artefacts (Kroodsma *et al.*, 2001). Acoustic stimuli SPLs were standardised in the centre of the experimental arena so the intensities were ~150 dB (re 1 μ Pa) and background ambient noise in the experimental flume was recorded as less than 80 dB (re 1 μ Pa). For SINE_150 and SINE_2200, the SPLs were calculated for the dominant stimulus frequency, whereas for NOISE_150 and NOISE_2200, they were calculated across the whole frequency band.

The 'seewave' package in R was used to further characterise stimuli through calculation of the acoustic complexity index (ACI) for each treatment (Pieretti *et al.*, 2011; McCormick *et al.*, 2019), (sampling rate: 25.6 kHz; FFT 512; hamming window; frequency range: 50-5000 Hz; Figure 4.2). The metric is commonly used to characterise the natural variability of intensities in biotic sounds. Each stimulus involved playback of intermittent sound for one second ON: two seconds OFF, for a total of ten minutes. Stimuli were pulsed to reduce the effects of acclimation and were more likely to evoke a stronger behavioural response (Rankin *et al.*, 2009; Neo *et al.*, 2014; 2018). A control group was tested under the same conditions in the absence of any additional acoustic playback stimuli, and post-experimental trials indicated there to be no confounding influence of an electromagnetic field ($p > 0.5$ for all parameters).

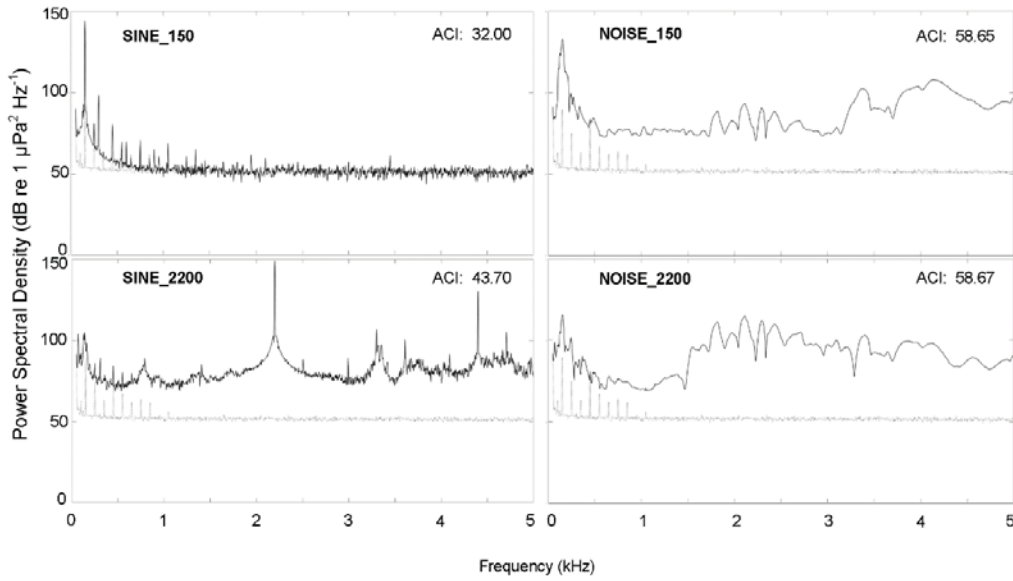


Figure 4.2: Power spectral densities (dB re 1 $\mu\text{Pa}^2 \text{Hz}^{-1}$) and acoustic complexity index (ACI) of acoustic conditions (solid lines) plotted with baseline ambient noise conditions (dotted lines) in the experimental arena (sampling rate: 25.6 kHz; FFT size 8192 (3 Hz bin width); overlap 91.5%; Hanning window; frequency range 50-5000 Hz). *Note:* for ACIs, greater values indicate increasing complexity; a 5 ms ramp-up/ down Hanning taper was used to mitigate for the effects of speaker resonance at lower frequencies; a transient effect was observed for SINE_2200, also explaining the higher ACI for this tonal treatment; broadband levels for tonal stimuli may be slightly raised due to the pulsed nature of the signal; for ambient noise recordings, the peaks at lower frequencies more likely represent electric than acoustic noise.

Prior to exposing fish to signals, the acoustic environment in the arena was quantified for all treatments (Figure 4.2, 4.3, and 4.4). In total, 306 positions within the experimental arena were measured (17 x 6 x 3 grid) using a hydrophone (Type: 8103; manufacturer-calibrated sensitivity - 211 dB re: 1V μPa^{-1} , frequency response 0.1 Hz – 180 kHz; Brüel & Kjær, UK) mounted to a customised rig, and connected to a charge amplifier (Type: 2635; Brüel & Kjær, UK). This was connected to a DAQ where the signal was connected to the laptop computer. A pistonphone (Type: 4229; Brüel & Kjær, UK) was used to confirm hydrophone calibration. The resulting SPLs described the spatial distribution of the sound-field in the tank (Figure 4.3A). The particle acceleration component, a , was calculated as:

$$a = -\frac{1}{\rho} \nabla P \quad (\text{Equation 4.1})$$

where P is the pressure, and ρ is the ambient density.

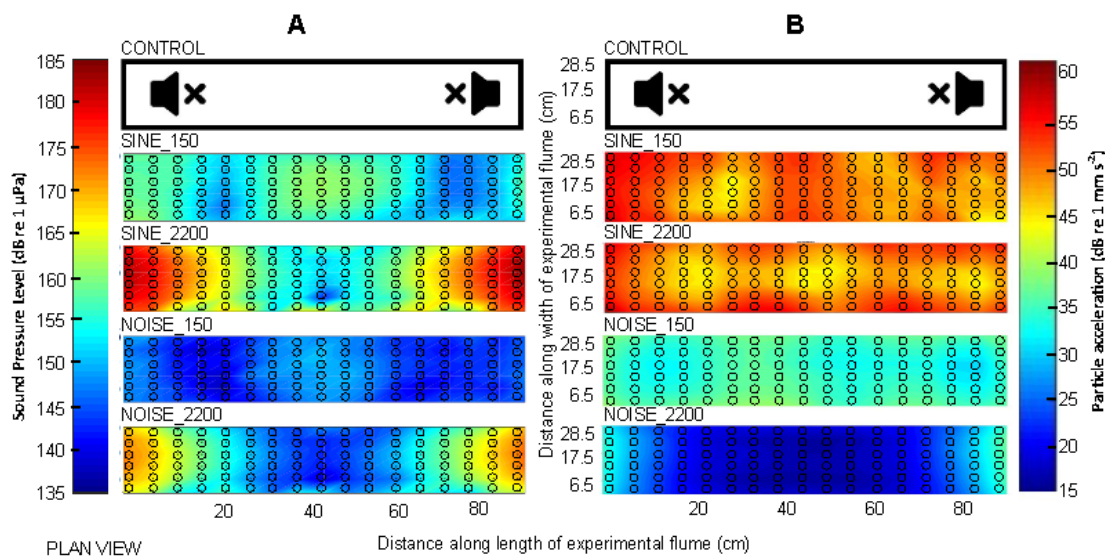


Figure 4.3: Acoustic conditions shown as **(A)** sound pressure level (SPL) (dB re 1 μ Pa) (average of three depths: 7 cm; 13.5 cm; 20 cm – each treatment was standardised at 150 dB re 1 μ Pa in the centre of the tank: Figure 4.4); and **(B)** particle acceleration level (dB re 1 mm s^{-2}), measured at 13.5 cm depth for control (no sound); SINE_150; SINE_2200; NOISE_150; and NOISE_2200 treatments. *Note:* open circles indicate hydrophone matrix positioning.

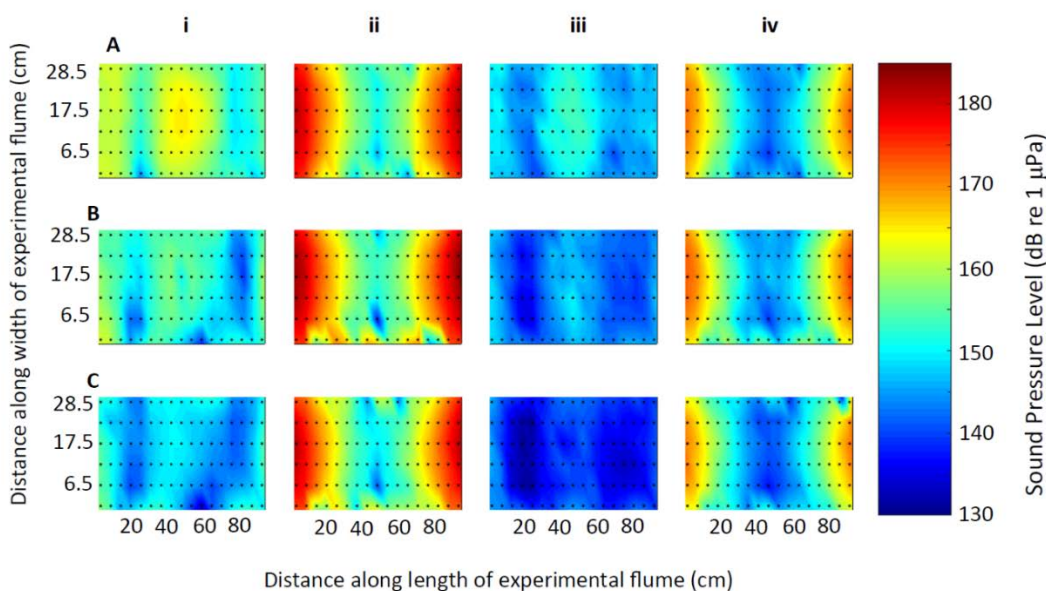


Figure 4.4: Acoustic treatment conditions for **(i)** SINE_150; **(ii)** SINE_2200; **(iii)** NOISE_150; and **(iv)** NOISE_2200, with recordings of SPL taken at three different water depths **(A)** 7 cm; **(B)** 13.5 cm; and **(C)** 20 cm. *Note:* Points indicate hydrophone positioning. Each treatment was standardised at 150 dB re 1 μ Pa in the centre of the tank.

The pressure gradient was computed using a finite difference approach based on the grid measurements of the pressure signal. The root mean square (RMS) of the pressure difference was evaluated independently in each direction (x, y and z), from which the pressure gradient was obtained by dividing the distance between measurements. Based on equation (4.1), the RMS particle acceleration, in one direction, was calculated by dividing by the water density. Total RMS particle acceleration was finally determined through combining values in all three directions, with the results expressed in decibels (dB re 1 mm s⁻²), (Figure 4.3B).

A reductionist and carefully controlled approach using a small tank set-up was used to minimise the influence of confounding factors, and provide a stable, reproducible acoustic field. Owing to the nature of near-field conditions relative to wavelength, highly complex and directionally variable acoustic conditions were recorded (Gray *et al.*, 2016). This was not considered to be problematic as the aim was to investigate how group behaviour varied with acoustic structural complexity, while keeping other acoustic parameters constant.

High levels of particle motion are produced on account of a tank's small size, wall material properties, and the sound speed differences between water and the surrounding air (Akamatsu *et al.*, 2002). In this experiment, with increasing distance from the two speakers, a reduction in particle acceleration was recorded. Although the relationship between the pressure and particle motion components of sound stimuli generated in small tanks is understood to differ from large-scale "natural" aquatic habitats (*e.g.* oceans or deep lakes), the acoustic nature of shallow streams (often < 1 m depth), rivers, or man-made flowing channels, tend to be more complex and remain poorly understood (Campbell *et al.*, 2019). Of course, this is not to suggest that even for these freshwater species that results can be directly extrapolated from tanks to naturally occurring environments without further testing or validation.

4.2.4 Experimental protocol

A total of 50 trials were conducted (ten replicates per treatment and control). For each replicate, five naïve fish of similar size were captured using a micro-mesh (< 1 mm diameter) hand net, and then transported as a group to the experimental arena using a small bucket (1 L capacity) of water (0.35 L). To avoid the confounding influence of order of introduction, fish were introduced as a group directly into the centre of the experimental arena, thus reducing the effects of any left-right or other spatial bias. On introduction the 40 minute video recording period commenced.

Each trial lasted a total of 40 minutes, allowing 20 minutes acclimation (established from pilot study data) prior to presentation of the stimuli that for the treatments involved playback projected simultaneously from the two underwater speakers for ten minutes. Assigning playback to a group was determined using an online random number generator to avoid order effects, and each group of five fish was used once only. Finally, a post-treatment period of ten minutes was included during which exposure to the stimuli ceased.

4.2.5 Behavioural parameters and video tracking

For analyses of startle responses at the onset of the acoustic signal, videos were played-back in a randomly generated order, with the observer blind to treatment. A startle response at the onset of the acoustic stimuli was determined via visual inspection of the videos, and scored at group-level as a binary response based on presence or absence of specific behaviours (Table 3.1).

Fish were tracked using a custom written MATLAB script. Measurements of swimming speed, cohesion, orientation and shoal distribution were taken for each frame, providing an output of 72000 data points for each variable calculated per group ($n = 50$). Individual tracks could become confused and lost when fish paths crossed. However, this did not affect analysis involving group means.

Shoal distribution based on the mean location of the centre of the shoal was calculated every ten seconds per trial exposure, providing 60 x,y shoal distribution reference positions. Co-ordinates were cross referenced with the harmonic averages of SPL measurements taken from the nearest hydrophone position, and frequency counts of time spent in areas of differing acoustic intensity (SPL) recorded. Histograms were produced with counts binned into 5 dB increments.

4.2.6 Statistical analysis

Statistical analyses were performed using a combination of IBM SPSS Statistics v.22.0 (IBM Corp. IBM SPSS Statistics for Windows, Armonk, NY: IBM Corp, USA), freeware programme RStudio (v 3.2.2: <https://rstudio.com/>), and MATLAB.

To assess whether the number of startle responses at the onset of acoustic stimuli differed between treatments, logistic regression analysis was performed across all four treatments and the control. *Post hoc* multiple pairwise comparisons were performed using a Tukey adjustment among group least square means to allow for further investigation between treatments. To

determine if group swimming behaviour changed during the trials, repeated measures Analysis of Variance (ANOVAs) were performed, with treatment as a between-subjects factor, and time period as a within-subjects factor for group swimming speed, cohesion and orientation. Time was divided into four blocks of five-minute bins (Neo *et al.*, 2014): ‘pre-treatment’ (five minutes immediately pre-exposure), ‘start-treatment’ (first five minutes during onset of stimuli), ‘end-treatment’ (second five minutes to the end of the stimuli exposure) and ‘post-treatment’ (five minutes immediately post-exposure). Inclusion of a baseline control within the analyses increased the probability of interaction effects to outperform any main effects. Therefore, when these occurred, repeated measures ANOVAs were conducted for each treatment separately to test for differences over time.

The majority of data met assumptions of normality (Shapiro-Wilks test) and homoscedasticity (Levene’s test), (82% and 93% of data respectively). In cases where it did not the violations were minor and insufficient to challenge assumptions of robustness for the use of ANOVA (Ito, 1980). Mauchly’s test of sphericity was used to assess the univariate approach of repeated measures ANOVAs (Huynh and Mandeville, 1979). When sphericity could not be assumed, Greenhouse-Geisser corrections were utilised for epsilon (ϵ) values less than 0.75; and Huynh-Feldt corrections for values greater than 0.75 (Greenhouse and Geisser, 1959; Huynh and Feldt, 1976). *Post hoc* Bonferroni tests were conducted when differences between factors were highlighted, thereby allowing for further investigation of between factor effects.

The distributions of shoal relative to areas of differing SPL (Figure 4.5) were measured as proportion of total time spent in different areas. To evaluate shoal distribution (Chapter 3, Table 3.1) in relation to acoustic intensity, the Kullback-Leibler Divergence (KLD), (Kullback and Leibler, 1951; Press *et al.*, 2007) was used to calculate the divergence between two probability distributions for each acoustic treatment. These distributions are approximated by two histograms measured across N common bins. These histograms represent the control distribution (P), and the treatment distribution (Q), where:

$$P = \{p_1, \dots, p_N\} \quad (\text{Equation 4.2})$$

$$Q = \{q_1, \dots, q_N\} \quad (\text{Equation 4.3})$$

KLD is defined as:

$$\text{KLD} (P, Q) = \sum_{i=1}^N p_i \log_2 \left(\frac{p_i}{q_i} \right) \quad (\text{Equation 4.4})$$

The constant back-off smoothing technique (absolute discounting) was used to address the infinite KLD value problem (Bigi, 2003; Shahriar *et al.*, 2013), whereby all zero probability values in both P and Q were substituted with a small constant value, 1.67×10^{-4} was used here.

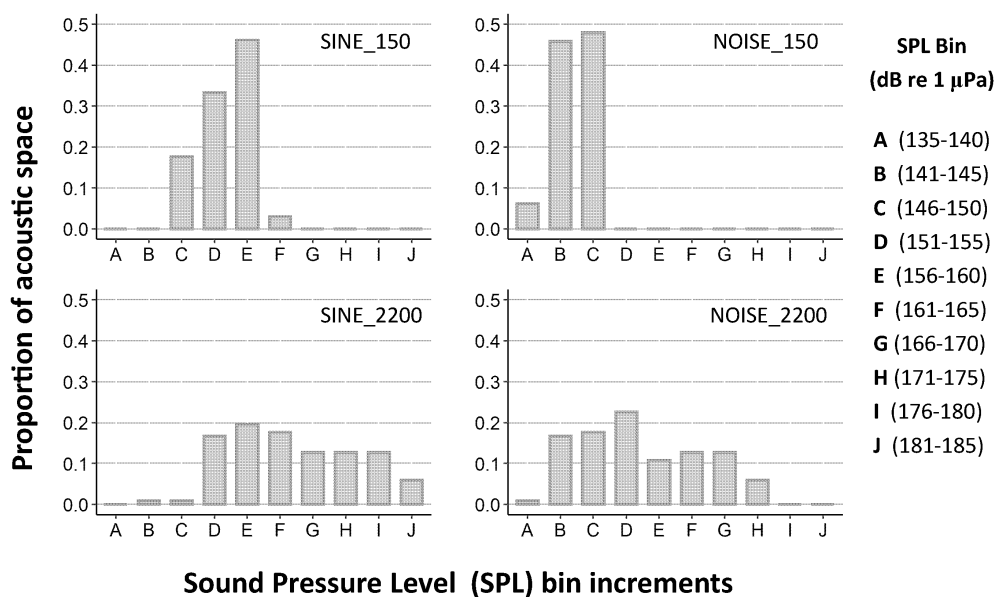


Figure 4.5: Total proportion of acoustic space available to groups of five minnows within the experimental arena, binned into 5 dB (re 1 µPa) increments for the four acoustic treatments: SINE_150; SINE_2200; NOISE_150; NOISE_2200.

To better determine the normal spatial behaviour of groups of fish under control conditions while maintaining data variability, control data was bootstrapped ($n = 10$, $r = 5$) and 25 random samples taken and averaged in relation to the sound-field of each acoustic treatment (Efron, 1982).

Control KLDs per treatment were then computed by comparing the ten minute “exposure” period (P) to the ten minute “post-exposure” period (Q). These KLDs provided an expected divergence in probability distribution per treatment under which acoustic intensity had no influence on the mean location of the shoal centre.

Wilcoxon signed-rank tests were used to compare observed acoustic treatment condition KLDs to the expected control KLDs. As bootstrapping incorporated the means of five control trials (out of

ten), two Wilcoxon signed-rank tests per acoustic treatment were performed, *i.e.* KLDs of five treatment trials were compared to five random control KLDs for that condition. For the spatial distribution of shoals of minnows in response to acoustic intensity to be considered different from the control sample, both *p*-values were independently required to be less than an adjusted α level of 0.22 (thereby limiting the Type I error rate to 0.05).

4.3 Results

4.3.1 Startle response

With the onset of an acoustic stimulus, clear startle responses were observed; but remained absent during the control. Differences were observed between all treatments ($\chi^2 = 21.95$; *d.f.* = 4; $p < 0.001$), accounting for approximately 36% of the model variance (Cox and Snell, Pseudo $R^2 = 0.36$; Figure 4.6). Startle responses were more frequent under SINE_150 (90%) than NOISE_150 (70%), followed by NOISE_2200 (50%) and SINEWAVE_2200 (40%), respectively (Figure 4.6; Table 4.1; Table 4.2).

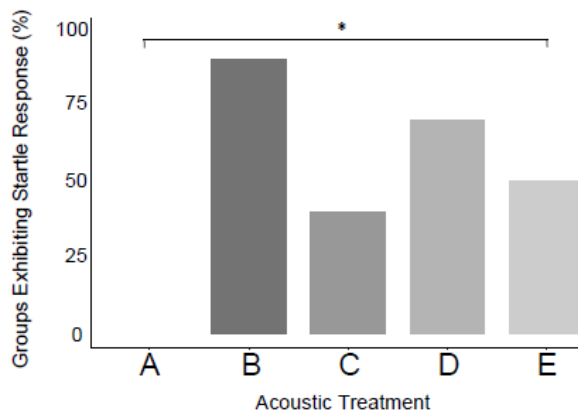


Figure 4.6: Percentage of at least one individual fish within groups ($n = 10$ per condition) of five minnows observed to exhibit a “c-start” at initial onset of acoustic stimuli for (A) control; (B) SINE_150; (C) SINE_2200; (D) NOISE_150; and (E) NOISE_2200. *Note:* * indicates significance of $p < 0.05$.

Table 4.1: Differences in startle response between treatments from *post hoc* multiple pairwise comparisons. *Note:* a single asterisk indicates significance of $p < 0.05$; double asterisk indicates significance of $p < 0.01$.

	CONTROL	SINE_150	SINE_2200	NOISE_150	NOISE_2200
<i>SINE_150</i>	$Z = -5.72; p < 0.01$ **				
<i>SINE_2200</i>	$Z = -4.41; p < 0.01$ **	$Z = 3.10; p < 0.05$ *			
<i>NOISE_150</i>	$Z = -5.41; p < 0.01$ **	$Z = 1.97; p = 0.28$	$Z = -3.03; p < 0.05$ *		
<i>NOISE_2200</i>	$Z = -4.84; p < 0.01$ **	$Z = 3.00; p < 0.05$ *	$Z = -2.18; p = 0.18$	$Z = 2.94; p < 0.05$ *	

4.3.2 Swimming speed

Mean group swimming speed (m s^{-1}) was lower during the acoustic treatment phase (Wilks' Lambda = 0.56; $F_{3,135} = 11.4$; $p < 0.001$; $\eta^2 = 0.44$; Figure 4.7A; Table 4.2) when compared to the pre-treatment control ($p < 0.001$; Figure 4.8) and post-treatment ($p < 0.05$; Figure 4.8). During the acoustic treatment phase, group swimming speed increased gradually for all treatments except for SINE_150, where a rapid increase occurred over the first minute (Figure 4.7A).

Effects of treatment were not significant, although there was an interaction between treatment and time (Wilks' Lambda = 0.44; $F_{12,135} = 3.52$; $p < 0.001$; $\eta^2 = 0.24$). Mean group swimming speed differed over time for SINE_2200 (Wilks' Lambda = 0.13; $F_{3,27} = 15.5$; $p < 0.05$; $\eta^2 = 0.87$), initially decreasing from the pre-treatment control (last minute mean \pm s.e. = $0.09 \pm 0.03 \text{ m s}^{-1}$) during the start-treatment phase (first minute mean \pm s.e. = $0.04 \pm 0.01 \text{ m s}^{-1}$), before rapidly increasing into the end-treatment phase (mean \pm s.e. = $0.12 \pm 0.03 \text{ m s}^{-1}$; $p < 0.05$) to almost double the baseline speed (maximum group speed \pm s.e. = $0.18 \pm 0.03 \text{ m s}^{-1}$; $p < 0.001$). Group swimming speed

decreased for SINE_2200 after the stimuli was turned off during the post-treatment phase (mean \pm s.e. = 0.07 ± 0.01 m s⁻¹; $p < 0.05$). There were similar differences in swimming speed over time for groups exposed to NOISE_2200 (Wilks' Lambda = 0.21; $F_{3,27} = 8.92$; $p < 0.05$; $\eta^2 = 0.79$), but, for this condition post-treatment speed (mean \pm s.e. = 0.13 ± 0.02 m s⁻¹) remained higher than baseline levels (mean \pm s.e. = 0.09 ± 0.02 m s⁻¹) after acoustic stimuli was switched off ($p < 0.05$).

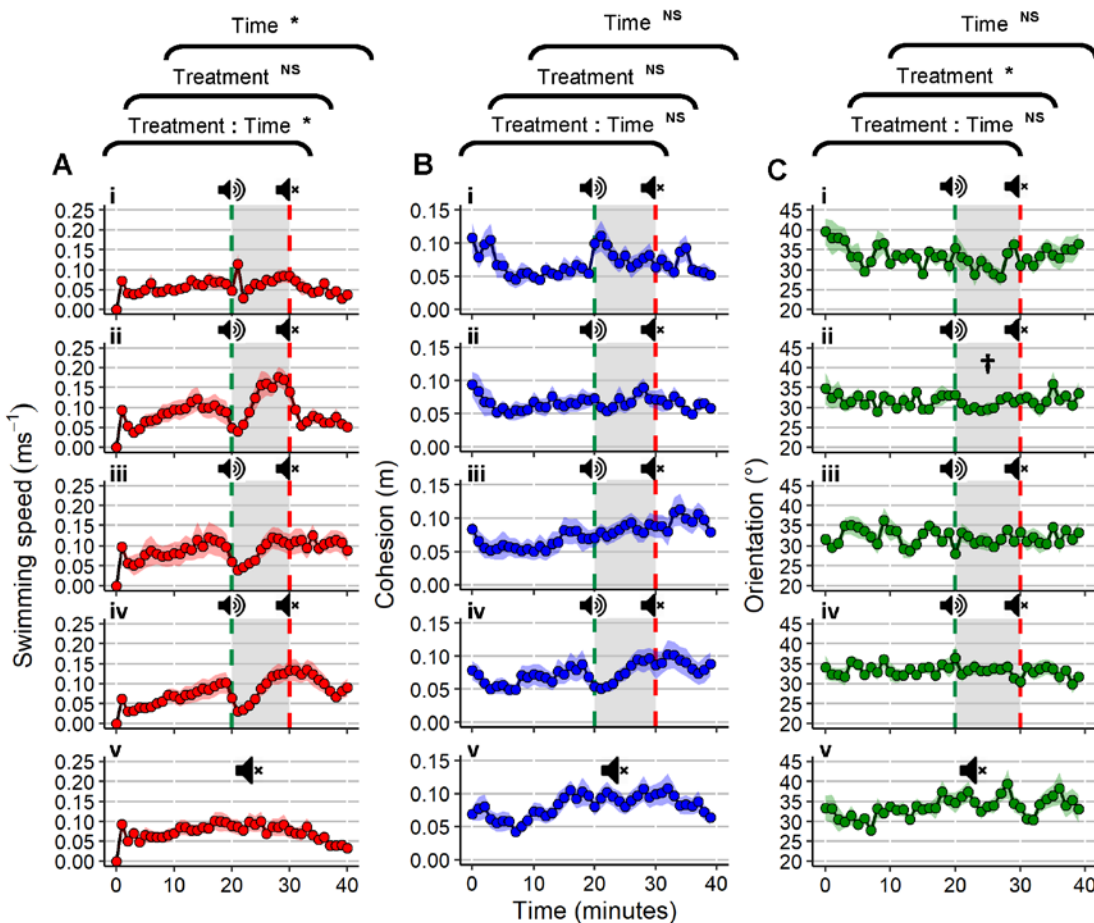




Figure 4.7: (A) Mean swimming speed (m s⁻¹), (red plots); (B) cohesion (m), (blue plots); and (C) orientation (°), (green plots) of groups ($n = 10$ per condition) of five minnows over time (mean \pm s.e.) exposed to SINE_150; SINE_2200; NOISE_150; NOISE_2200; and no playback (control) conditions. *Note:* * indicates significance of $p < 0.05$; and NS symbolises non-significance for repeated measures ANOVA; † indicates a significant difference ($p < 0.05$) of a single treatment from the control using *post hoc* Bonferroni tests. Dashed green lines  portray sound on, and dashed red lines  sound off; areas in grey represent the total acoustic treatment period. Data points are averages per minute across 40 minute trial.

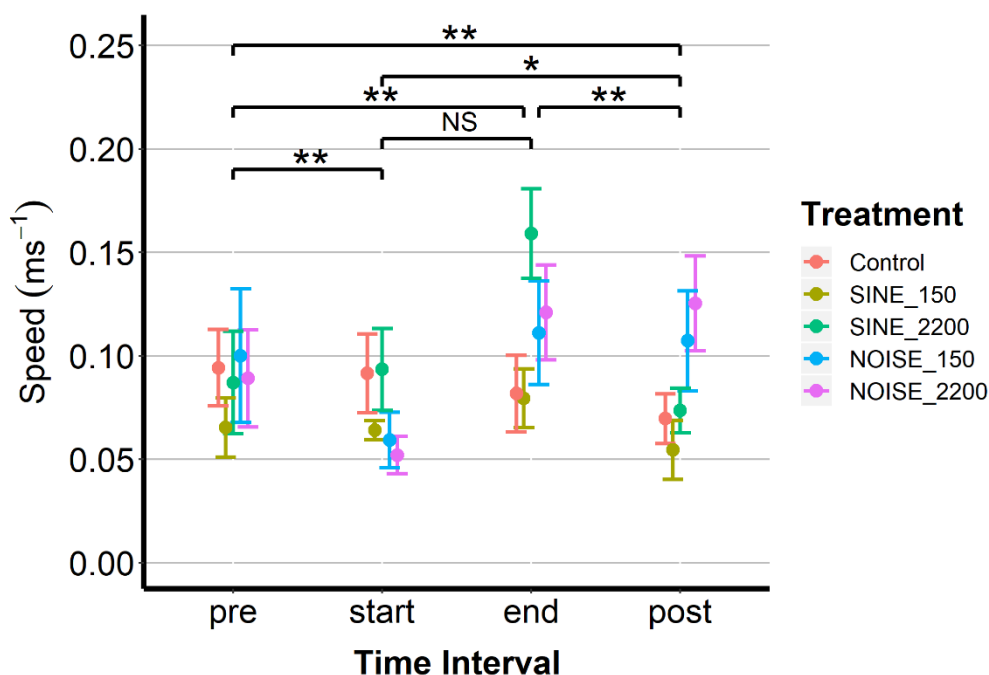


Figure 4.8: Changes in mean (\pm s.e.) swimming speed (m s^{-1}) of groups ($n = 10$ per condition) of five common minnows within 5-minute blocked phases for different acoustic treatments: control; SINE_150; SINE_2200; NOISE_150; and NOISE_2200. *Note:* ** indicates significance of $p < 0.001$; * significance of $p < 0.05$; and **NS** symbolises non-significance for repeated measures ANOVA with *post hoc* Bonferroni tests.

4.3.3 Cohesion

There was no effect of treatment or time on group cohesion (m), and no interaction between treatment and time (Figure 4.7B; Table 4.2). When acclimated within the experimental arena, groups of five minnows typically swam in loose shoals (mean group cohesion \pm s.e.: 0.09 ± 0.02 m), with some individuals swimming on their own, or in close proximity to one or more other fish, utilising the entirety of the tank.

4.3.4 Orientation

Group orientation differed between the control and SINE_2200 treatments ($F_{4,45} = 3.27$; $p < 0.05$; $\eta^2 = 0.23$; *post hoc*: $p < 0.05$; Figure 4.7C; Table 4.2), with an increase observed for fish groups

exposed to SINE_2200. There was no difference over time or an interaction between treatment and time.

4.3.5 Shoal distribution

Shoal distribution of control fish differed from those of treated fish exposed to SINE_150 and NOISE_150, with the latter spending more time than expected in areas of lower acoustic intensity (SPL), ($Z_1 = -1.753$; $p_1 = 0.08$; $Z_2 = -2.023$; $p_2 = 0.04$: and $Z_1 = -2.023$; $p_1 = 0.04$; $Z_2 = -2.023$; $p_2 = 0.04$, respectively; Figure 4.9; Table 4.2). There was no difference for fish exposed to SINE_2200 ($Z_1 = -2.023$; $p_1 = 0.043$; $Z_2 = -0.405$; $p_2 = 0.69$), or NOISE_2200 ($Z_1 = -1.214$; $p_1 = 0.225$; $Z_2 = -2.023$; $p_2 = 0.04$).

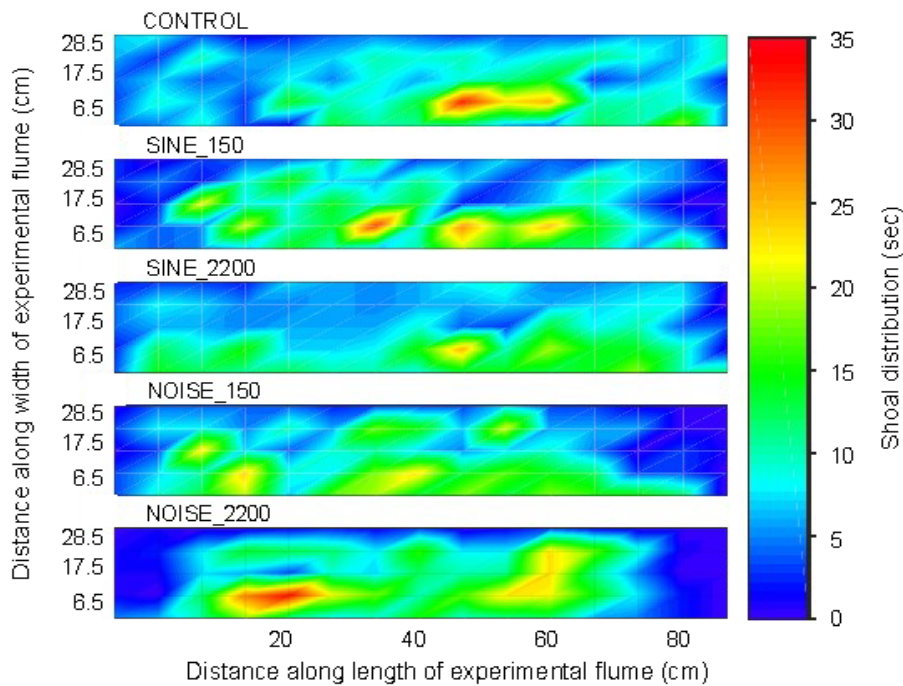


Figure 4.9: Average shoal distribution of groups ($n = 10$ per condition) of five common minnows over the 10 minute treatment exposure period in control (no sound); SINE_150; SINE_2200; NOISE_150; and NOISE_2200 conditions. *Note:* Total availability (Figure 4.5) and cumulative use of acoustic space should be considered when interpreting shoal distributions relative to the acoustic field; data points averaged (mean) per 10 seconds across 10 minute exposure period.

Table 4.2: Overview of behavioural tendencies in response to SINE_150; SINE_2200; NOISE_150; and NOISE_2200. *Note:* an asterisk indicates a statistically significant deviation in behaviour from control data; and a diamond indicates a significant deviation over time.

Treatment	Group behavioural response				
	Startle response (presence/absence)	Swimming speed (m s ⁻¹)	Cohesion (m)	Orientation (°)	Shoal distribution (x,y)
SINE_150	Present: 90% increase *	start-treatment: Rapid increase and decrease; end-treatment: Return to pre- exposure ◊	No effect	No effect	Increase time in areas of lower acoustic intensity *
SINE_2200	Present: 40% increase *	start-treatment: Decrease; end-treatment: Rapid increase ◊	No effect	Increased alignment *	No effect
NOISE_150	Present: 70% increase *	start-treatment: Decrease; end-treatment: Return to pre- exposure ◊	No effect	No effect	Increase time in areas of lower acoustic intensity *
NOISE_2200	Present: 50% increase *	start-treatment: Decrease; end-treatment: Rapid increase ◊	No effect	No effect	No effect

4.4 Discussion

This research chapter investigated the response of European minnow to acoustic stimuli that differed with respect to structural complexity and frequency. SINE_150 consistently elicited the greatest response for all parameters measured. It was hypothesised that the complex acoustic stimuli would elicit a stronger behavioural response, an effect observed in bighead carp (*Hypophthalmichthys nobilis*) exposed to broadband (outboard motor Hp 4-stroke engine: 0.06 – 10 kHz) or pure tone (500, 1000, 1500, and 2000 Hz: Vetter *et al.*, 2017). Contrary to this hypothesis, the simple sinewave tones induced a detectable behavioural response more frequently. While it may be assumed that simple signals may not elicit a reaction by themselves if the specific tonal components have not been shaped by selection for communication purposes (Hebets and Papaj, 2005), they may still have informative value (Candolin, 2003). The results of this study indicate that despite, or perhaps, even owing to their lesser occurrence in nature (*i.e.*

novelty), (Kastelein *et al.*, 2008), simple sinewave tones are still capable of eliciting a measurable response. Minnows may have a high sensitivity to tonal stimuli, an effect observed in humans where tonal signals are perceived as louder than noise of the same intensity (Pinheiro and Ptacek, 1971). Alternatively, stronger reactions to novel disturbances could act as an adaptive survival mechanism (Crawford *et al.*, 2012; Brown *et al.*, 2013), akin to an antipredator response (“risk-disturbance hypothesis”), (Walther, 1969; Frid and Dill, 2002). Equally, the greater response to tonal stimuli may have been induced by the greater levels of particle motion generated by tonal stimuli within the tank set-up, however, such speculation requires further exploration that was not within the scope of this investigation. Perhaps, also owing to an assumed optimum hearing sensitivity within the lower frequency range, the lower frequency tonal treatment had the greatest influence on fish behaviour across all parameters tested in this study. This is an important result to note given the dominance of lower frequency (0.1 – 0.5 kHz) sources of anthropogenic noise (*e.g.* shipping and traffic noise), (Hildebrand, 2009; Holt and Johnston, 2015).

All acoustic treatments elicited a startle response in at least some of the subject fish, a behaviour in which the fish is observed to contract its body and burst swim in an altered direction from a stimulus to initiate escape (Bhandiwad *et al.*, 2013; Nedelec *et al.*, 2015). Startle behaviour among groups of fish has been studied under both field and laboratory conditions using a range of anthropogenic noise, including repeated underwater gun firings (field study: gadoid (bony fish) group behaviour: Wardle *et al.*, 2001), pulsed white noise (laboratory studies: zebrafish, *Danio rerio* group behaviour: Neo *et al.*, 2015a; and European minnow individual and group behaviour: Short *et al.*, 2020), and pure tone sinewaves (tested: 0.1 – 64 kHz; responses: 0.1 – 2kHz), (laboratory study: sea bass, thicklip mullet, *Chelon labrosus*, pout, *Trisopterus luscus*, and horse mackerel, *Trachurus trachurus* group behaviour: Kastelein *et al.*, 2008). As observed in this study, the swimming behaviour exhibited by individual fish tends to return to “baseline” after a few repeated exposures to stimuli in close conjunction with one another. More startle responses were observed at the onset of the lower frequency treatments, with SINE_150 observed to elicit the most. While the startle response is a useful behavioural parameter indicative of an anti-predator reaction (Domenici and Blake, 1997), more in-depth quantifiable analysis will assist understanding of shoal behaviour in response to acoustic stimuli. This information would benefit, for instance, the development of more successful behavioural guidance or deterrence systems used in fisheries management.

The high incidence of startle behaviour observed in response to SINE_150 was associated with a rapid increase in group swimming speed within the first minute of the acoustic treatment. This was followed by a rapid decline in swimming speed to below that observed during the pre-

exposure period. Increases in this behaviour likely indicated hyperactivity, or an anxiety-like behaviour associated with a perceived threat (Stewart *et al.*, 2012; Neo *et al.*, 2014). The initial spike observed when SINE_150 was switched on was not observed under the other treatments, where fish tended to exhibit a decline in swimming speed instead, a behaviour that could enhance information transfer among individuals (Handegard *et al.*, 2012; Miller *et al.*, 2013). Indeed, it has been suggested that this behaviour may reflect an initial increased alertness (juvenile sea bass: Herbert-Read *et al.*, 2017a), potentially enabling more accurate risk assessment and monitoring. Individuals within a group can obtain second-hand information about the surrounding environment through the speed changes of others (Harpaz *et al.*, 2017). While for this experiment it cannot be discerned whether individual fish were gathering such sensory information directly or via behavioural cues exhibited by others, work by Short *et al.* (2020) suggests it to be the latter. Their study investigated responses of both solitary individuals and shoals of five European minnows to anthropogenic noise and found group responses to be universal in comparison to those of individuals which were more variable. Additionally, increases in speed have been noted as highly correlated with other behaviours (*e.g.* polarisation and near neighbour positioning), (Berdahl *et al.*, 2013; Herbert-Read *et al.*, 2017b; Kent *et al.*, 2019).

Previous studies investigating response of marine fish to anthropogenic noise (*e.g.* tuna *Thunnus thynnus* to boat noise: Sarà *et al.*, 2007; and sea bass to pile-driving noise: Herbert-Read *et al.*, 2017a) observed that shoals become less cohesive when exposed. Reduction in group cohesion can be costly if it reduces information sharing, and increases confusion and susceptibility of isolated individuals to predation (Magurran and Pitcher, 1987; Handegard *et al.*, 2012; Ioannou *et al.*, 2012). Further detrimental impacts may accrue if anthropogenic noise masks or distracts from the detection of an additional modal stimulus (*e.g.* visual or chemical cue), (Caribbean hermit crab, *Coenobita clypeatus*: Chan *et al.*, 2010; fathead minnow: Hasan *et al.*, 2018; hermit crab, *Pagurus acadianus*: Roberts and Laidre, 2019). In this research chapter, no effect of treatment on group cohesion was observed, although fish exposed to SINE_150 tended to exhibit a strong startle response and scatter during the first minute, a behaviour referred to as “flash expansion” in which rapid startle and unpredictable movement by group members in multiple directions may have evolved as a beneficial anti-predator evasion tactic (Magurran and Pitcher, 1987). Of interest, however, is the contrasting observations in other recent studies in which group cohesion in shoaling minnows initially increased when exposed to an acoustic stimulus (*e.g.* 150 Hz tonal stimuli: Chapter 5; and 60-2000 Hz random broadband noise: Short *et al.*, 2020). Comparable observations to this study have however been reported in recent work involving another freshwater species, the three-spined stickleback (*Gasterosteus aculeatus*: Ginnaw *et al.*, 2020).

When exposed to multifrequency square tones they observed no change in group cohesion, suggesting this behaviour to be relatively robust to playback of additional noise. The reasons why these differences are observed between studies (*e.g.* acoustic properties), and over time (*e.g.* seasonality), is an interesting avenue for further investigation.

As was the case for group cohesion, the orientation displayed by minnows in this study did not deviate from the baseline levels over time, but was influenced by treatment. When the SINE_2200 stimuli was turned on, fish became more aligned with one another. Increased polarisation within shoals is commonly linked to detection of a predatory threat (Partridge, 1980; Couzin *et al.*, 2002; Herbert-Read *et al.*, 2017a), enabling individuals to gain information and copy movement decisions of others (Harpaz *et al.*, 2017). However, the exhibition of such a response may be context dependent (Herbert-Read *et al.*, 2011), and how this varies with factors such as species, size of the group (Shelton *et al.*, 2015) and setting requires further investigation.

Exposure to noise is assumed to result in the spatial displacement of fish, although empirically derived evidence remains lacking or anecdotal (Hawkins and Popper, 2017). Laboratory studies tend to be limited by the coarse-scale measurement techniques employed. For instance, zebrafish showed no preference between an acoustically “quiet” and “noisy” double-chamber environment (Neo *et al.*, 2015a), and time spent by ayu (*Plecoglossus altivelis*) within 300 cm² blocks, spaced at increments of 10 cm away from a sound source, suggested preference for some frequencies, and avoidance of others (Febrina *et al.*, 2015). This research chapter found that shoals spent more time in areas of lower acoustic intensity during the SINE_150 and NOISE_150 treatments. In this study, high resolution fish tracking was used in combination with fine scale acoustic mapping (*e.g.* Murchy *et al.*, 2017; Zielinski and Sorensen, 2017) to more intricately understand and quantify the spatial distribution of fish in response to the highly complex and variable acoustic intensities (SPL) formed within small tanks (Akamatsu *et al.*, 2002). It is recommended that subsequent work should further refine this approach and consider larger areas of three-dimensional acoustic space, across both the sound pressure and particle motion domains, and attempt to more accurately quantify the positional depth of the model fish used. Furthermore, as tank-based playback studies have previously been ecologically validated through the use of complimentary field experiments (*e.g.* Simpson *et al.*, 2016b; Ferrari *et al.*, 2018), likewise it would be useful to confirm the results of this study in the wild, *e.g.* where fish are confined within large *in situ* outdoor pens or via long-term tracking studies of migratory fish encountering manipulated and well defined acoustic sound fields. This would allow investigation of group responses to acoustic stimuli which differs in complexity under more “natural” settings, and where animals have the option to swim away (Popper and Hastings, 2009a).

Although it is commonly argued that a reductionist approach, such as adopted in tank-based studies, does not fully replicate more “real-world” field conditions, it does allow for careful control of confounding factors, and provides valuable reference data for modelling or field studies (Rice *et al.*, 2010; Slabbekoorn, 2016). Nevertheless, no approach is without its limitations. To better understand the impacts of anthropogenic noise on collective fish behaviour, the complimentary potential of differing methodologies must be drawn on. In this study, stimuli were pulsed at a regular rate to best control for any behavioural tolerance to a constant sound exposure (Neo *et al.*, 2014; Neo *et al.*, 2018; Chapter 5). While tolerance was accounted for within the study design, without more intricately quantifying the magnitude of change for each behavioural metric over time, the effects of tolerance, or motor fatigue, cannot be ruled out. Any reduction in response to a repeated acoustic stimulus over time may alternatively be explained by other forms of sensory adaptation, such as a hearing threshold shift (Rankin *et al.*, 2009). Even so, data regarding temporary threshold shifts (TTS) in closely related species (*e.g. Carassius auratus*: Smith *et al.*, 2004) suggest that both louder and longer durations of acoustic exposure would be required to induce TTS in minnows exposed to the attributes of stimuli used in this study. Species-specific data is of course required to completely rule out this explanation. That said, a continued change in behaviour (*e.g.* increase in group swimming speed) was observed throughout the exposure period for all tested treatments, suggesting a continual response to the acoustic stimuli. Investigation of instantaneously demonstrable behavioural or physiological tolerance to acoustic stimuli is on the rise (*e.g.* Nedelec *et al.*, 2016; Chapter 5), however, the longer-term process of habituation remains somewhat elusive, and requires further attention (Neo *et al.*, 2018; Putland and Mensinger, 2019).

Evidence that fish alter their spatial distributions in response to high acoustic intensities may have important ecological implications. For example, in other taxa, acoustic playback studies have shown that male European robins (*Erithacus rubecula*) move away from a noise source, and do so more frequently at higher acoustic intensities (McLaughlin and Kunc, 2013). Similarly, harbour seals (*Phoca vitulina*) avoid a tidal turbine noise source from a range of 500 m (Hastie *et al.*, 2018). Such behavioural responses to anthropogenic noise may have direct fitness implications or wider impacts on population dynamics (McLaughlin and Kunc, 2013). Underwater, noise can originate from both ground (*e.g.* road traffic; Holt and Johnston, 2015) and water-borne sources, it attenuates less and consequently travels further than in air. Therefore, the spatial impact of noise on fish shoals, as demonstrated in this study, may have extremely far reaching ecological impacts (*e.g.* habitat fragmentation; Barber *et al.*, 2010).

This study found low frequency sinewave tones to have the greatest influence on the behaviour of groups of European minnow. Shoals exhibited spatial avoidance in response to low frequency tones. Knowledge of the spatial distribution and behaviour of fish in response to anthropogenic noise is useful for informing policy makers on the potential impacts of human activities in aquatic environments. It also has application in the development of behavioural guidance systems for use in fisheries management (Popper and Carlson, 1998; Murchy *et al.*, 2017; Piper *et al.*, 2019; Deleau *et al.*, 2020b), or as selective barriers to prevent spread of invasive species (Vetter *et al.*, 2017; Rahel and McLaughlin, 2018). Owing to the large diversity in characteristics of human induced noise (frequency, SPL, particle velocity or acceleration, and temporal waveform), further studies are needed to better understand the context dependent inter- and intra-specific variation in response to a greater range of acoustic stimuli.

CHAPTER 5 **Group behaviour and tolerance of European minnows (*Phoxinus phoxinus*) in response to tones of differing pulse repetition rate**

Behavioural guidance systems are commonly used in freshwater fisheries management. The biological relevance of sound to fish and recorded behavioural responses to human-generated noise supports the viability of acoustics as an effective stimulus in such technologies. Relatively little information exists on the long-term responses and recovery of fish to repeated artificial acoustic exposures. In a controlled laboratory study, the response and tolerance of European minnow (*Phoxinus phoxinus*) shoals to tonal signals (150 Hz of 1s pulse duration) differing only in temporal characteristics ('continuous,' 'slow,' 'intermediate,' or 'fast' pulse repetition rate) were investigated. In comparison to independent control groups, fish increased their mean group swimming speed, and decreased inter-individual distance and orientation in response to the onset of all four acoustic treatments. The magnitude of response, and time taken to develop a tolerance to a treatment differed according to pulse repetition rate. Groups were found to have the greatest and longest lasting response to tone sequences tested in this study when they were pulsed at an intermediate rate of 0.2 s^{-1} . This study illustrates the importance of understanding the response of fish to acoustic signals, and will assist toward the development of longer-term effective acoustic guidance systems.

5.1 Introduction

Aquatic animals gain vital information from the acoustic signals present within their environment (Hawkins and Myrberg, 1983). Natural soundscapes facilitate a variety of survival functions in fish, including: navigation (*e.g.* Apogonidae *sp.* reef settlement: Simpson *et al.*, 2005a), selection of mates (*e.g.* Pomacentridae *sp.* courtship calls: Mann and Lobel, 1997), conspecific interactions (*e.g.* *Amphichthys cryptocentrus* male competition: Salas *et al.*, 2018), and prey seeking and predator avoidance (Ward *et al.*, 2011; Hawkins and Popper, 2018). The response of fish to anthropogenic noise (*e.g.* shipping, naval sonar transmissions, pile driving) are also widely described. Man-made sources of noise mask communicative signals (Vasconcelos *et al.*, 2007; de Jong *et al.*, 2018), and alter coordinated movement (Herbert-Read *et al.*, 2017a), spatial

distribution (Chapter 4), and orientation and cohesion of groups (Herbert-Read *et al.*, 2017a). Evidently, the ubiquitous nature of anthropogenic noise in the environment is cause for concern (Chapter 2.2), with a range of responses to sound having been observed in fish (Slabbekoorn *et al.*, 2010).

The biological relevance of sound to fish and observed responses to human-generated noise support the use of acoustics as a viable mitigation tool in freshwater fisheries management (Popper and Carlson, 1998). Acoustic guidance systems are deployed to reduce fish impingement on screens designed to prevent ingress into water intakes (Maes *et al.*, 2004) and divert individuals to safer routes of passage (*e.g.* *Alosa pseudoharengus*: Dunning *et al.*, 1992; *Salmo salar*: Scruton *et al.*, 2003; *Hypophthalmichthys nobilis*: Taylor *et al.*, 2005; *Anguilla anguilla*: Deleau *et al.*, 2019; Piper *et al.*, 2019), and control range expansion of invasive species (*e.g.* *Hypophthalmichthys molitrix*, Vetter *et al.*, 2015). For effective screening, target fish must be able to detect and localise a sound source above background noise, and subsequently elicit a desirable response. Importantly, the acoustic stimuli also must remain effective with repeated exposure over time (Blumstein, 2016). While interest in the use of sound to control the movement of fish has been investigated since the late 1940s (Burner and Moore, 1962), relatively little information exists on how the behaviour of freshwater fish changes in response to repeated exposure to acoustic signals over time.

Understanding behavioural mechanisms that underpin fish responses to human-generated acoustic stimuli is important in informing sustainable management strategies (Blumstein, 2016). A novel acoustic stimulus may initially provoke a substantial anti-predator response (Voellmy *et al.*, 2016), but, after multiple presentations an instantaneously demonstrable behavioural state (measured at a point in time) known as tolerance may occur, resulting in a short-term decline in the frequency or magnitude of the response (Bejder *et al.*, 2009). Without adequate recovery time, or with a series of frequent exposures over time, the degree of tolerance may change and the longer-term process of habituation could occur, after which responses to the same stimuli cease to be observed (Nisbet, 2000; Bejder *et al.*, 2009; Blumstein, 2016). Rate of recovery may, however, be influenced by the temporal characteristics of the signal (*e.g.* pulse repetition rate, pulse repetition interval, amplitude ramp-up). Studies have investigated these effects on marine fish species (Neo *et al.*, 2014; 2015b) as anthropogenic broadband noise sources are highly variable in their temporal structure. For example, European sea bass (*Dicentrarchus labrax*) were noted to recover more quickly after exposure to continuous than impulsive noise stimuli (Neo *et al.*, 2014). Nevertheless, better understanding of tolerance and habituation-like processes (Geffroy *et al.*, 2015), or recovery of freshwater fish in response to acoustic signals that differ in

temporal characteristics, warrant further investigation. This will aid in the development of more effective behavioural guidance systems and further assist conservation efforts to reduce the negative impacts of anthropogenic noise.

The aim of this laboratory study was to investigate the influence of pulse repetition rate on group behaviour and tolerance of a freshwater shoaling fish. A total of 250 fish were tested across 50 independent trials. Groups of five individuals were independently exposed to one of four acoustic treatments ('continuous,' 'slow,' 'intermediate,' or 'fast' pulse repetition rate) or a "silent" ambient control. The investigation focused on three group behaviours: 1) swimming speed (m s^{-1}); 2) inter-individual distance (m); and 3) orientation ($^{\circ}$). Building on work conducted on marine species (e.g. Neo *et al.*, 2014; 2015b; 2018), it was hypothesised that time taken to develop a tolerance to an acoustic stimulus, or return to baseline behaviour, would be greater for groups exposed to tones with longer intervals between pulses. The European minnow (*Phoxinus phoxinus*), was selected as a model species because of its, facultative shoaling behaviour (Partridge, 1980), local abundance, and observed responses to low frequency acoustic stimuli (Chapter 4).

5.2 Materials and methods

5.2.1 Fish collection and husbandry

In April 2017, 270 adult European minnows were collected with a seine net from the River Itchen navigation channel, Hampshire, UK ($51^{\circ}02'58.9''\text{N } 1^{\circ}18'42.2''\text{W}$). The freshwater habitat from which fish were sourced averaged 15 m in width, and depths ranged from 0.34 m to 0.94 m. The watercourse is highly modified, with the combination of shallow-water (often < 1 m depth) and man-made solid banks, contributing to a complex acoustic environment.

Fish were transported to the University of Southampton's ICER facilities and gradually introduced to a holding net (0.78 m x 0.3 m x 0.62 m; water depth: 0.45 m; stocking density: 5.98 kg/ m^{-3}) within a tank (1.5 m x 1.0 m x 0.78 m; water depth: 0.68 m; mean temperature \pm s.e.: 13.7 ± 0.3 $^{\circ}\text{C}$) over a period of three hours. Minnows were acclimatised for five days prior to the start of the experiments, and water quality was monitored and maintained (NO_3^- : $< 50 \text{ mg L}^{-1}$; NO_2^- : $< 1 \text{ mg L}^{-1}$; NH_3 : 0; and pH: < 8.4). Fish were kept on a 14:10 h light:dark photoperiod cycle and fed daily with commercially available aquarium food until satiation. After each trial, fish were measured (standard length \pm MAD: 57.2 ± 4.4 mm) and weighed (wet mass \pm MAD: 2.8 ± 0.9 g). Differences (Kruskal-Wallis rank sum) in wet mass ($\chi^2 = 14.69$; *d.f.* = 4; $p < 0.01$) and standard

length ($\chi^2 = 11.54$; $d.f. = 4$; $p < 0.05$) were apparent between treatments. However, *post hoc* Dunn's test indicated deviations between treatments to only be for fish exposed to the 'SLOW' treatment (Table 5.1: Appendix B). Experiments were performed after review and approval by the University of Southampton's Animal Welfare and Ethical Review Board (Ethics ID: 25987).

5.2.2 Experimental set-up

Experiments were conducted within an acoustically isolated room, where trials were conducted in a physically segregated section (86 cm x 30.8 cm x 30.2 cm) of a still-water tank (300 cm x 30.8 cm x 30.2 cm; wall thickness: 1.2 cm), (Figure 5.1). Use of a still water tank-based approach allowed control over experimental conditions to ensure sound was the sole external stimuli of influence. Acoustic testing in a small tank is more appropriate for riverine freshwater species than marine fish, since the acoustic environment in a tank is closer to that of a shallow river than of typical marine environments (Tonolla *et al.*, 2010). That is not to suggest that even for these freshwater species that results from tank tests can be transferred directly to naturally occurring environments without further test or validation.

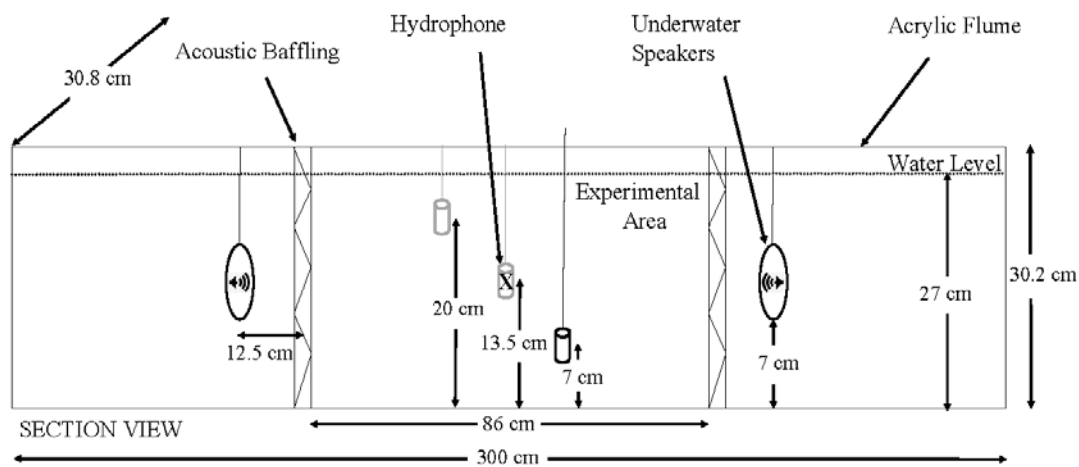


Figure 5.1: Schematic of experimental flume setup including the experimental area in which fish were exposed to acoustic stimuli. Hydrophone positions are shown for acoustic mapping at three water depths (7 cm; 13.5 cm; 20 cm), with "X" indicating the position at which sound pressure levels (RMS) (dB re 1 μ Pa) were standardised.

Two fully immersed speakers (Electro-Voice UW-30; maximal output 153 dB re 1 μ Pa at 1 m for 150 Hz, frequency response 0.1-10 kHz; Lubell Labs, Columbus, OH) were used to generate the sound field. Speakers were positioned at a fixed point in the middle of the water column, with

one behind each of two micro-mesh acoustic baffles at either end of the experimental arena (Figure 5.1). Water was maintained at a constant depth of 27 cm and replaced every ten trials to remove build-up of biological debris, or residual chemical alarm substance (“Schreckstoff”: Hasan, 2018). Tank water was left to settle overnight, allowing for a return to room temperature (mean \pm s.e.: 14.0 ± 0.17 ° C) and the release of gas bubbles which may influence the acoustic environment.

Fish within the experimental arena were visually isolated from the experimenter by plastic blackout sheeting. Light levels were maintained using a white background, attached to the outside of the experimental arena and lit from underneath by two PhotoSEL Photography bulbs (pure white full-spectrum flicker free; 85 W, 5000 lumen; SJT Commercial Ltd., UK). Consistent lighting throughout the trials allowed for an increased contrast of the fish for digital video recordings using a webcam (C920; HD 1080p; 30 frames per second; Logitech Pro, Switzerland) mounted overhead.

5.2.3 Sound stimuli and acoustic mapping

A sinewave frequency of 150 Hz has previously been observed to elicit changes in European minnow group behaviour (*e.g.* startle response, group swimming speed, shoal distribution), (Chapter 5), and as a result was subsequently chosen for this experiment. Sound samples were produced through the use of custom written MATLAB script (Release 2017a, The Mathworks, Inc., Natick, Massachusetts, United States). The signal was produced from a laptop computer via a DAQ (NI USB-6341; National Instruments, UK) and played from the underwater speakers through a ROTEL RA-920AX amplifier (75 W, frequency response range approx. 0.02-20 kHz; Rotel Europe, UK). Four acoustic treatments were used in the experiments to cover a range of inter-pulse (5 ms ramp-up/ down Hanning taper) spontaneous recovery times (Figure 5.2; Table 5.1). A ‘control’ of no sound (ambient noise: less than 80 dB re 1 μ Pa) was also tested, where an electrical signal was still sent to the speakers to avoid any potential confounding influences (*e.g.* electroreception). The sound pressure level (SPL), (RMS), calculated for the dominant frequency of treatment stimuli was standardised in the centre of the experimental arena (155 dB re 1 μ Pa). Note that although rms SPL was constant over any time window for which the sound was on (barring start-up transients in the first 5 ms), the total amount of acoustic energy delivered during a trial decreases as the off-time increases during a trial of fixed duration (as opposed to a trial that delivers a fixed number of pulses). A 1 s pulse duration was used for all pulsed exposures, and since sound travels approximately 1.5 km in this time, the pulse duration is sufficiently long to build up the same reverberant sound field in each case (Figure 5.2).

Table 5.1: Treatment parameters and acoustic conditions encountered by *Phoxinus phoxinus* in experimental trials conducted to assess their behavioural response and tolerance to tones differing in pulse repetition rate.

Treatment	<i>n</i> trials	Standardised tone SPL (RMS) (dB re 1 μ Pa)	Pulse Repetition Interval (s)	Pulse Repetition Rate (s^{-1})	Pulse duration (s)	Median fish standard length \pm MAD (mm)	Median fish wet mass \pm MAD (g)
CONTROL	10	n.a.	n.a.	n.a.	n.a.	58.0 \pm 8.9	2.8 \pm 1.3
CONTINUOUS	10	155	n.a.	n.a.	1.0	58.0 \pm 5.2	2.8 \pm 0.7
FAST	10	155	2.0	0.5	1.0	55.0 \pm 3.0	2.4 \pm 0.6
INTERMEDIATE	10	155	5.0	0.2	1.0	57.0 \pm 3.0	2.8 \pm 0.6
SLOW	10	155	10.0	0.1	1.0	59.5 \pm 8.2	3.3 \pm 1.5

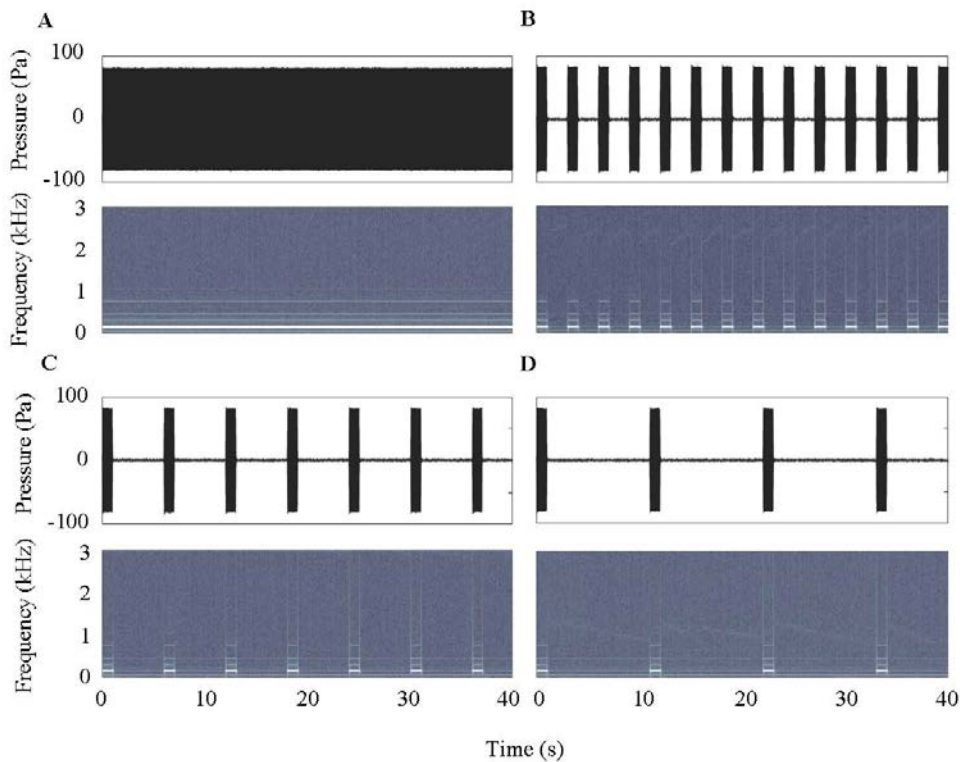


Figure 5.2: Waveforms and spectrograms ($\text{dB re } 1 \mu\text{Pa}^2 \text{ Hz}^{-1}$) showing temporal structure of acoustic treatment stimuli: **(A)** CONTINUOUS; **(B)** FAST (PRR: 0.5 s^{-1}); **(C)** INTERMEDIATE (PRR: 0.2 s^{-1}); and **(D)** SLOW (PRR: 0.1 s^{-1}), (sampling rate: 25.6 kHz; FFT 2048; overlap 50%; Hamming Window; frequency range 0 – 3 kHz).

In advance of conducting fish trials, the acoustic environment of the arena was quantified for the tonal stimuli (Figure 5.3). Acoustic intensities were measured at 306 positions (17 x 6 x 3 grid) using a hydrophone (Type: 4013; manufacturer-calibrated sensitivity -211 dB re: 1V μPa^{-1} , frequency response 0.01 Hz – 170 kHz; Teledyne RESON, Slangerup, Denmark) fixed to a customised rig, and connected to a hydrophone voltage amplifier (Type: A1001; 9 V; gain +40 dB, high pass filter 100 Hz; Etec, Frederiksværk, Denmark). The signal was recorded on a laptop via the DAQ, controlled using a custom written MATLAB script (sampling rate 25.6 kHz). A pistonphone (Type: 4229; Brüel & Kjær, UK) was used to ensure hydrophone calibration. Resulting SPLs were used to describe the sound-field within the tank across three different depths (Figure 5.3B). The particle acceleration component, a , was calculated based on:

$$a = -\frac{1}{\rho} \nabla P \quad (\text{Equation 5.1})$$

where P is the complex pressure amplitude and ρ is the ambient density.

As the pressure amplitude and phase were measured on a regular grid of points, from these measurements, the complex pressure amplitude at each was computed. The pressure gradient was approximated using finite differences in all three directions (x , y , and z). The particle acceleration was computed as the square root of the sum of the three directional components squared. Particle acceleration (dB re 1 mm s⁻²) for the centre depth (13.5 cm) of the tank was then mapped (Figure 5.3C and 5.3D).

The nature of the near-field conditions within a small tank relative to wavelength were responsible for highly complex and directionally variable conditions (Gray *et al.*, 2016). High levels of particle motion exist within small-tank set-ups, and in this experiment, a reduction in particle acceleration was recorded with increasing distance from the two speakers. It should be noted, however, that while acoustic intensity was standardised in the centre of the experimental arena, the left-hand speaker had a moderately stronger influence on the sound field. Acoustic intensities within the central region of the experimental arena were composed of higher SPLs and lower particle acceleration, an effect of interference from the directionally opposing speakers, or perhaps the result of a standing wave.

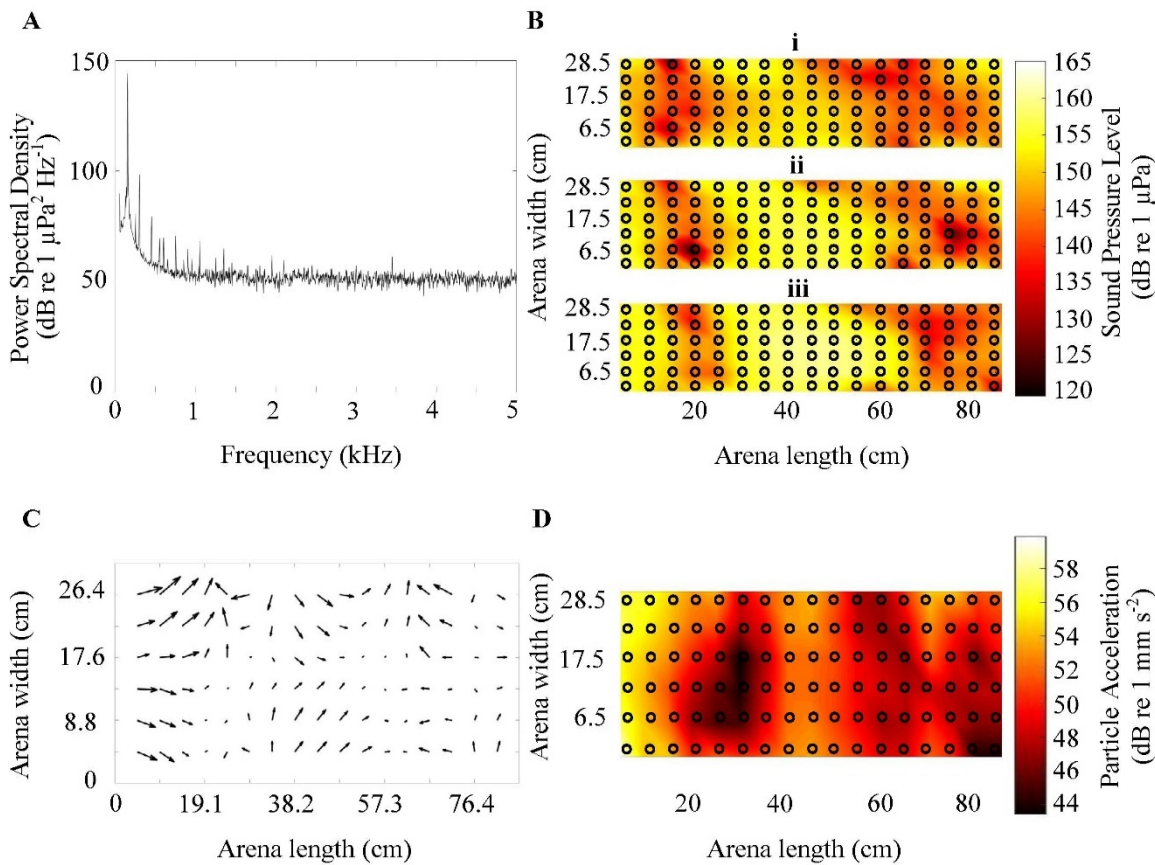


Figure 5.3: (A) Example power spectral density (dB re 1 $\mu\text{Pa}^2 \text{Hz}^{-1}$) of acoustic conditions within the experimental arena (sampling rate 25.6 kHz; FFT size 8192 (3 Hz bin width); overlap 91.5%; von Hann Window; frequency range 50-5000 Hz); (B) heat maps of sound pressure levels (SPL), (dB re 1 μPa), (150 Hz sinewave) for acoustic stimuli across three depths (i) 7 cm; (ii) 13.5 cm; and (iii) 20 cm; (C) quiver map indicating particle acceleration (dB re 1 mm s^{-2}) directionality at 13.5 cm depth; and (D) heat map of particle acceleration (dB re 1 mm s^{-2}) at 13.5 cm depth. *Note:* open circles indicate the location of the hydrophone when measuring the sound field.

5.2.4 Experimental protocol

A total of 50 trials were conducted, ten replicates for each treatment and control. Each trial lasted a total of 60 minutes, including a 20 minute acclimation period. After this time, an acoustic playback treatment was turned on for 20 minutes, projected simultaneously from two underwater speakers. Control groups of fish were tested under the same conditions, but without the acoustic playback stimuli. A random number generator was used to determine order of playback, thereby avoiding order effects. A final post-treatment period of 20 minutes was recorded after each treatment.

Each trial consisted of five naïve fish (total $n = 250$), introduced simultaneously as a group to the centre of the experimental arena. This avoided confounding influences of introduction order and spatial or viewing bias. At this point, the 60 minute video recording was then started. Each group of five fish was used once only.

5.2.5 Behavioural parameters and statistical analysis

Fish were tracked using a custom written MATLAB script. The mean shoal centre ($X_c(n)$) location (x, y axis) of groups of fish were taken for each frame. $X_c(n)$ was calculated as the position of the i th fish in the n th video frame (vector $\underline{X}_i(n) = (x_i(n), y_i(n))^t$), where $x_i(n)$ corresponds to the distance along the length of the tank, and $y_i(n)$ to the breadth, so as: $\underline{X}_c(n) = (x_c(n), y_c(n))^t = (\underline{X}_1(n) + \underline{X}_2(n) + \underline{X}_3(n) + \underline{X}_4(n) + \underline{X}_5(n))/5$. Group behaviour could then be calculated as: 1) group mean swimming speed ($m\ s^{-1}$), computed from $X_c(n)$ over time; 2) inter-individual distance (m), defined as the mean distance from $X_c(n)$, with measurements taken from the central point of each fish; and 3) orientation ($^\circ$), as the standard deviation of the angle of the fish compared to one another (lower orientation indicates greater alignment: Chapter 3, Table 3.1). This provided an output of 108 000 data points per variable calculated for each trial ($n = 50$).

As data failed to meet the assumptions of normality (Shapiro-Wilks test) and homoscedasticity (Levene's test), it was \log_{10} transformed to meet prerequisites for use in parametric analysis. Statistical analysis was performed with freeware programme RStudio (v 3.2.2: The R Foundation for Statistical Computing, Vienna, Austria, <http://www.r-project.org/>).

To assess whether group behaviour changed during the trials, repeated measures Analysis of Variance (ANOVAs) were performed. Treatment was allocated as a between-subjects factor, and time period as a within-subjects factor for group swimming speed, inter-individual distance and orientation. Time was divided into seven blocks of five-minute bins. Differences in behaviour over time were investigated between 'pre-' (five minutes immediately pre-stimuli), 'during-' (first; middle; and final five minutes during playback; Figure 5.4 and 5.5), and 'post-exposure' phases (first; middle; and final five minutes post-stimuli). Addition of a baseline control within the analyses increased the probability that any main effects would be outperformed by interaction effects. Subsequently, when these occurred, each treatment was separately tested for differences over time using repeated measures ANOVAs.

The univariate approach of repeated measures ANOVAs (sphericity) was assessed using Mauchly's test (Huynh and Mandeville, 1979). Greenhouse-Geisser corrections (Greenhouse and Geisser, 1959) were utilised for epsilon (ϵ) values less than 0.75; and Huynh-Feldt corrections (Huynh and

Feldt, 1976) for values greater than 0.75, when sphericity could not be assumed. When between factor effects were apparent, they were investigated using *post hoc* Bonferroni tests.

Treatment effects of each behavioural parameter were plotted as a ten second running t-statistic over time. An independent two-sample t-test with assumed equal variance was used to compare each treatment group ($n = 10$) to control “baseline” fish ($n = 10$). An alpha-level of 0.05 was chosen to indicate a significant influence of treatment. Note that owing to natural variation in fish behaviour, deviations may occur between treatment and control fish prior to the onset of an acoustic exposure. Using a four-point central moving average of the ten second running t-statistic, where an influence was observed within the first five minutes of acoustic exposure, the total duration from surpassing the significance threshold ($p < 0.05$) to pre-threshold recovery level ($p > 0.05$) of this influence, or ‘time to tolerate’ was calculated.

5.3 Results

5.3.1 Swimming speed

Swimming speed declined at the onset of acoustic stimuli for all treatments, reflective of a freezing behaviour, where most minnow groups exhibited temporary cessation of body movement (Figure 5.4). The three impulsive acoustic treatments (SLOW, INTERMEDIATE and FAST) induced a higher swimming speed over time in comparison to acclimated pre-exposure levels (Wilks’ Lambda = 0.4; $F_{3,61, 162.65} = 12.1$; $p < 0.01$; $\eta^2 = 0.21$). Groups exposed to CONTINUOUS tones, however, maintained a relatively consistent speed after the initial decline. Although changes in speed significantly differed from control groups of fish, the effects observed between treatments did not. An interaction between treatment and time did exist (Wilks’ Lambda = 0.39; $F_{11,32,162.65} = 2.2$; $p < 0.01$; $\eta^2 = 0.16$). Furthermore, the elevated swimming speed was observed to continue into the post-exposure phase, after termination of acoustic stimuli.

The INTERMEDIATE acoustic pulses were observed to induce the longest significant deviation from control group baseline speed, with time taken to develop a tolerance at the beginning of the sound exposure period taking 2 minutes 18 seconds ($p < 0.01$; Figure 5.4C). The same effect was observed in response to SLOW pulses, however, the greater shift in speed did not pass the arbitrary threshold for significance. Time taken to tolerate to acoustic stimuli also could not be quantified for CONTINUOUS and FAST treatments.

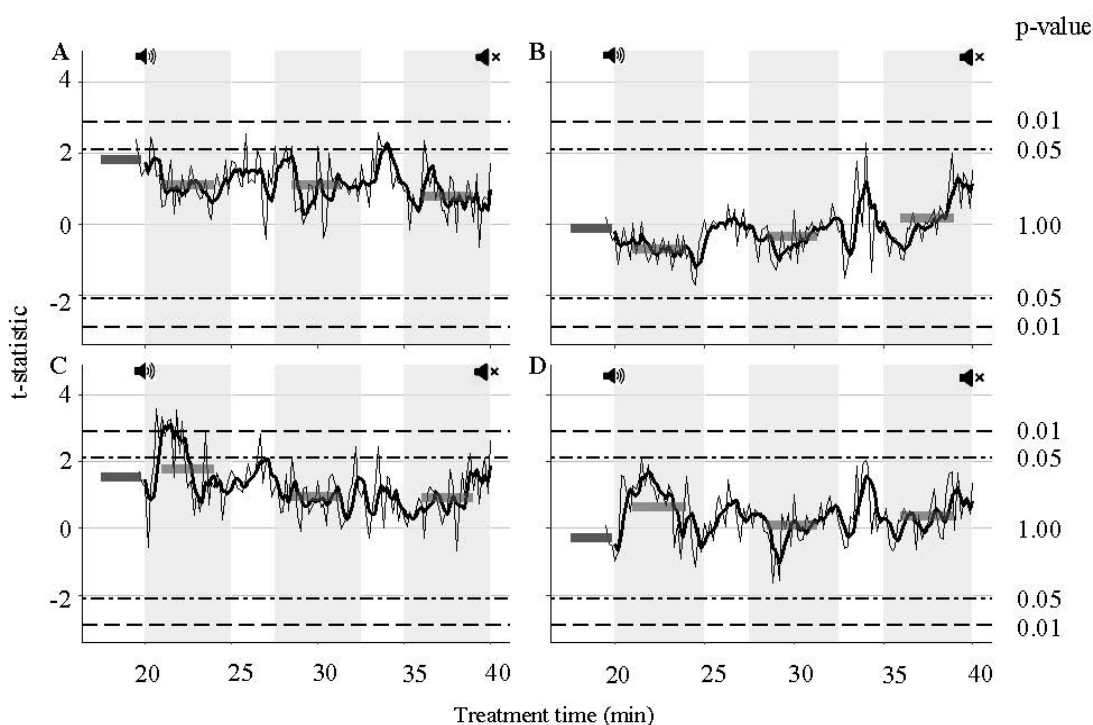




Figure 5.4: Change in speed (m s^{-1}) of European minnows exposed to **(A)** CONTINUOUS; **(B)** FAST; **(C)** INTERMEDIATE; and **(D)** SLOW pulse repetition rates, compared to baseline unexposed control fish groups. *Note:* Continuous thin solid line represents ten second running t-statistics; and the thicker solid line, a four-point central moving average of the ten second t-statistic (for assessment of tolerance). Horizontal dot-dashed lines indicate a cut-off at $p = 0.05$, and dashed lines a $p = 0.01$ for $\alpha = 0.05$ (in both directions). The four thick horizontal bars represent averages (one pre-exposure, and three during-exposure) over time of 5-minute bins (areas in grey represent blocks for repeated measures ANOVA assessing change in speed over time).  portrays sound on, and , sound off.

5.3.2 Inter-individual distance

In response to the onset of all acoustic treatments, fish shoals initially increased cohesion, displayed by a decrease in inter-individual distance, however this did not differ to the control fish (Figure 5.5). The distance between individuals gradually increased over time, with minnows spreading further apart from one another (Wilks' Lambda = 0.49; $F_{3,80, 171.15} = 8.2$; $p < 0.001$; $\eta^2 = 0.15$).

Minnows took longer to develop a tolerance to the INTERMEDIATE treatment, returning to baseline inter-individual distance after 2 minutes 18 seconds ($p < 0.01$; Figure 5.5C) of acoustic exposure. Inter-individual distance was also greater than control groups for minnows exposed to the SLOW treatment, with the change in behaviour returning to below significance thresholds

after 59 seconds ($p < 0.05$; Figure 5.5D). The influence of FAST and CONTINUOUS pulse repetitions on inter-individual distances were not large enough to interpret a 'time to tolerate'.

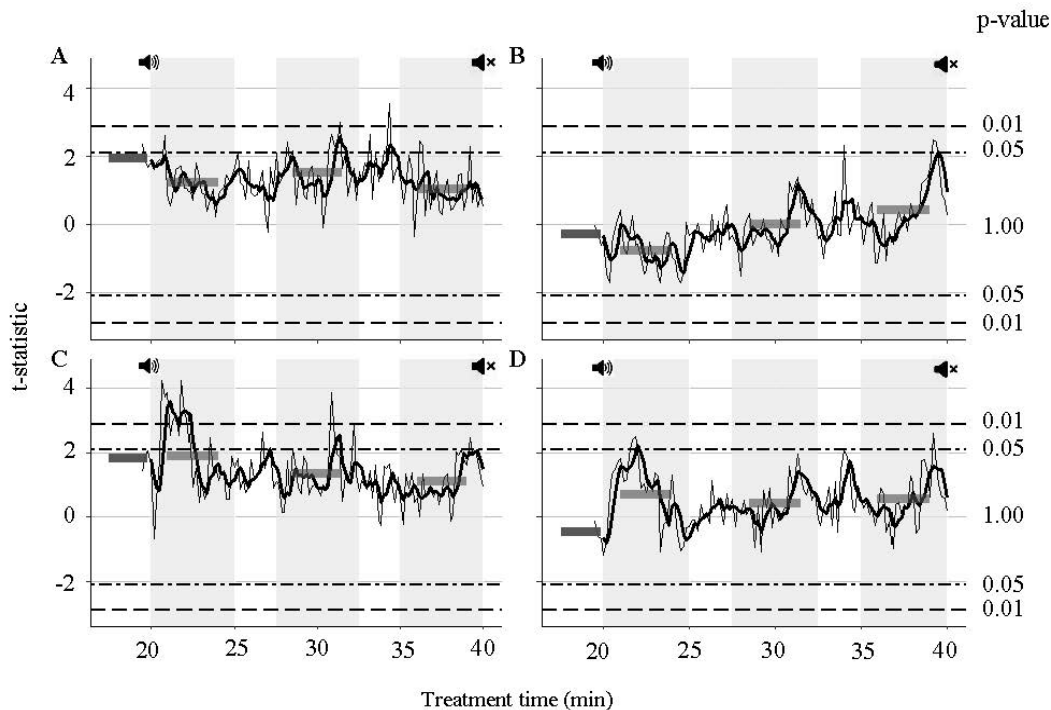




Figure 5.5: Change in inter-individual distance (m) of European minnows exposed to **(A)** CONTINUOUS; **(B)** FAST; **(C)** INTERMEDIATE; and **(D)** SLOW pulse repetition rates, compared to baseline unexposed control fish groups. *Note:* Continuous thin solid lines represent ten second running t-statistics; and the thicker solid line, a four-point central moving average of the ten second t-statistics (for assessment of tolerance). Horizontal dot-dashed lines indicate a cut-off at $p = 0.05$, and dashed lines a $p = 0.01$ for $\alpha = 0.05$ (in both directions). The four thick horizontal bars represent averages (one pre-exposure, and three during-exposure) over time of 5-minute bins (areas in grey represent blocks for repeated measures ANOVA assessing change in inter-individual distance over time).  portrays sound on, and , sound off.

5.3.3 Orientation

Although orientation did not change significantly over time, groups were observed to exhibit a decrease in orientation at the onset of stimuli, becoming more aligned with one another in comparison to control groups. Over the exposure period, individuals gradually became less commonly aligned, but again this effect was not significant. The observed effect was significant between treatments ($F_{4,45} = 4.05$; $p < 0.01$; $\eta^2 = 0.26$), with post hoc analysis indicating that fish

became less well aligned under FAST repetitions compared with those under the SLOW repetition treatment ($p < 0.01$). For this metric, however, the time taken to tolerate could not be quantified, since no significant changes from the control group were observed.

5.4 Discussion

This study investigated the group behaviour and tolerance of European minnows to tonal acoustic stimuli that differed with respect to pulse repetition rate (PRR). At the onset of all acoustic treatments, higher shoal swimming speed, lower inter-individual distance, and reduction in orientation, with fish becoming more aligned, was observed compared to control groups. European minnows have previously been observed to exhibit similar group behaviour in response to a low frequency (150 Hz) tonal stimuli (Chapter 5), and the observed behavioural changes are consistent with several other studies conducted on fish using varying broadband noise sources (*e.g.* Herbert-Read *et al.*, 2017a; McCormick *et al.*, 2018; Neo *et al.*, 2014). Notably, this study additionally observed that PRR influenced the time taken to tolerate to a tonal stimulus in freshwater fish shoals.

Changes of swimming speed among individuals within a group may be used by conspecifics to gather information on their surrounding environment (Harpaz *et al.*, 2017). Increases in swimming speed may indicate fright or anxiety associated with a perceived threat (*e.g.* predation risk: Neo *et al.*, 2014), and changes are highly correlated with alterations in group inter-individual distance and orientation (Herbert-Read *et al.*, 2017b; Kent *et al.*, 2019). An increase in inter-individual distance as observed over time during this study, may be costly, with isolated individuals more susceptible to predation (Handegard *et al.*, 2012). Noise can distract from the detection of an additional stimulus, and therefore reduce information sharing. For example, fathead minnow (*Pimephales promelas*) detection of a conspecific chemical alarm cue is reduced in the presence of anthropogenic noise (Hasan *et al.*, 2018). As for inter-individual distance, group orientation enables individuals to gain information from others (Harpaz *et al.*, 2017). For example, increased alignment among shoal members is linked to the detection of a predatory threat (Partridge, 1980; Herbert-Read *et al.*, 2017a). This behaviour was observed at the onset of all acoustic stimuli, but, group alignment rapidly decreased over time.

Impulsive anthropogenic noise induces greater initial and delayed behavioural changes in fish than continuous noise differing only in its temporal characteristics (PRR), (Neo *et al.*, 2014; 2015b; Shafiei Sabet *et al.*, 2015). In this study, INTERMEDIATE repetitions were observed to elicit the

greatest and longest lasting difference in response across all tested parameters in comparison to control fish. Minnows were least tolerant of this treatment, which induced an increased group swimming speed and inter-individual distance, and decreased alignment. This result is similar to those observed in marine studies that exposed European sea bass (*Dicentrarchus labrax*; Neo *et al.* 2014; 2015b) to broadband noise, in which an effect on inter-individual distance and swimming depth was recorded, but with no significant influence of pulse repetition interval on recovery to baseline behaviour. The present study tested a larger range of PRRs, and as predicted, found that groups exposed to INTERMEDIATE and SLOW repetitions took longer to return to baseline inter-individual distance. Additionally, INTERMEDIATE repetitions had the longest lasting impact on group swimming speed, indicative of the high correlations known to exist between these behaviours (Kent *et al.*, 2019). These observations are typical of some commonly described characteristics of habituation, whereby the more frequent a stimulation, the more rapid a decrement in response, provided an asymptote has been reached (Rankin *et al.*, 2009).

In this study, the magnitude of change in response to acoustic stimuli was observed to decrease over time. This reduction was described as an increase in tolerance, an instantaneously demonstrable behaviour, rather than habituation (Blumstein, 2016). To unequivocally demonstrate habituation, the same individual must repeatedly be tested over time and exhibit a diminished response (Bejder *et al.*, 2009). Alternative forms of sensory adaptation, such as a hearing threshold shift could also explain the return to baseline behaviour (Rankin *et al.*, 2009). While this explanation cannot be ruled out without the support of species-specific data, temporary threshold shifts (TTS) observed in closely related species (*e.g.* *Carassius auratus*; Smith *et al.*, 2004) suggest that louder (SPL), and longer durations of acoustic exposure would be required to induce TTS in minnows encountering a stimulus with the spectral and temporal attributes of those used in this study. Reductions in behavioural and physiological (*e.g.* ventilation rate: Nedelec *et al.*, 2016) responses to repeated anthropogenic noise exposure may act as a learned adaptive mechanism, allowing individuals to remain in an affected environment. In the absence of another paired predictive stimuli, or negative reinforcer (*e.g.* visual presence of a predator), tolerance and habituation are examples of single-stimulus learning, or irrelevant stimuli filtering (Rankin *et al.*, 2009; Blumstein, 2016). Given that multiple mechanisms are generally responsible for differing learning processes, dissociative learning may also occur in tandem (Rankin *et al.*, 2009). While such processes are beneficial in optimising the fitness of individuals reliant on, for instance, site-specific spawning grounds, on-the-other-hand, sustained or cumulative exposure to stressors is known to have physiological consequences. For example, overall fitness may be impacted in terms of growth, body condition, reproduction, predator-

avoidance or foraging behaviour (Nedelec *et al.*, 2015; Shafiei Sabet *et al.*, 2015). Furthermore, from a management perspective, a diminished response to a deployed stimulus could render acoustic guidance systems ineffective at reducing fish injury or mortalities.

This study employed a reductionist, tightly controlled approach using a small tank setup to provide a stable, easily modelled and reproducible acoustic field, in which the influence of confounding factors could be minimised. This approach ensured that the response of freshwater fish to sounds differing only in their temporal characteristics could be fundamentally addressed, prior to implementing any cost-heavy field studies. Sound stimuli generated within such a laboratory setup promote highly complex acoustic conditions, whereby a tank's small size, large impedance, wall material properties (influencing resonance frequencies), and sound speed differences between the water and surrounding air produce high levels of particle motion within the sound field that are understood to differ from large-scale "natural" aquatic environments (*e.g.* oceans or deep lakes), (Akamatsu *et al.*, 2002). Comparatively, the acoustic nature of rivers, shallow streams (sometimes < 1 m depth), or man-made channels where acoustic deterrents may be deployed are not well understood (Chapter 2.5).

While approaches are being taken to understand common acoustic patterns within physically or ecologically distinct river and shallow stream habitats (Tonolla *et al.*, 2010), the heterogeneous nature of these aquatic systems restricts the quantification of a "typical" natural riverine environment. Further experiments within well-controlled set-ups that better mimic 'real world' conditions (*e.g.* via use of an open-channel flume; see Chapter 7), and field trials to validate the results of these studies are therefore highly recommended to confirm the findings in settings where acoustic conditions reflect those that freshwater fish may more typically encounter, in combination with other confounding variables (*e.g.* seasonal flow), (Tonolla *et al.*, 2010). Additionally, this would allow for the investigation of response depletion to repeated exposures of a stimuli over time in an environment where animals have the option to swim away (Popper and Hastings, 2009b), subsequently better informing the development of appropriate acoustic deterrent technologies.

The PRRs tested during this study had consistent interval timings between each acoustic exposure, or regular pulse rates. Less predictable broadband noise signals using irregular pulse repetition intervals have been observed to have greater influence on habituation rate or anxiety reduced responses than regular pulse rate intervals in individual zebrafish (*Danio rerio*: Shafiei Sabet *et al.*, 2015). However, these results have yet to be replicated in experiments involving groups of fish, with inconsistent findings in both laboratory (zebrafish: Neo *et al.*, 2015a) and in-

situ field studies (European sea bass: Neo *et al.*, 2016). While it is hypothesised that the influence of group dynamics in these studies obscured any subtle influences of irregular PRR on group behaviour (Neo *et al.*, 2016), it was found not to be the case in this study with regular pulse rates.

This study highlights an effect of temporal variation (PRR) on the group behaviour and tolerance of a shoaling freshwater fish species. INTERMEDIATE PRRs were observed to induce a longer lasting shift in group behaviour from the baseline, across all behavioural parameters. The study adds to a growing body of evidence that indicates that intermittent sound has a stronger, and longer lasting impact on fish behaviour than continuous sound differing only in temporal structure. Results are promising for informing the development of more effective and sustainable acoustic deterrent systems. Further investigation in the field is required to validate technologies and better understand the longer-term effects of tolerance or habituation to sounds differing in bandwidth, entropy (*e.g.* tonal versus broadband) and temporal characteristics (regular/ irregular PRR and amplitude ramp-up).

CHAPTER 6 **Masking noise reduces the behavioural response of common carp (*Cyprinus carpio*) to an acoustic stimulus: application of Signal Detection Theory to fisheries management**

Anthropogenic noise is a globally prevalent pollutant of international concern, and may reduce the ability of fishes to detect, discriminate and respond to relevant acoustic cues. However, little information exists on the group behavioural responses of fish to targeted acoustic stimuli in the presence of high intensity environmental noise commonly experienced by fish in the wild, and with the potential to mask a signal of interest. In a controlled laboratory study, signal detection theory was used to investigate the coarse (startle response) and fine-scale (swimming speed, group cohesion and alignment) responses of common carp (*Cyprinus carpio*) shoals to pulsed tonal signals (170 Hz) differing only in their signal-to-noise ratio (low [LOW], intermediate [INT], or high [HIGH]) above either an ambient, or masking noise floor (fixed intensity Gaussian white noise: 120 – 3000 Hz). In comparison to independent control groups, fish exhibited a startle response, reduced their average swimming speed, increased group cohesion, and became more aligned in response to the onset of tonal stimuli under ambient noise conditions. The magnitude of change in response was typically greater the higher the signal-to-noise ratio. Under masked noise conditions, however, signal discriminability was reduced, with coarse-scale behavioural responses predominantly extinguished, and fine-scale responses suppressed but increasingly evident at higher signal-to-noise ratios. This chapter highlights the importance of understanding fish responses to acoustic signals under background environmental noise, which is ubiquitous in nature, but commonly overlooked. An appreciation of this topic is necessary to develop more effective freshwater fish conservation technologies (*e.g.* behavioural guidance systems), and to mitigate for the ecological implications of anthropogenic noise masking responses to biologically relevant acoustic cues.

6.1 Introduction

Most taxa obtain vital information from the acoustic signals transmitted between individuals (*e.g.* birds: Catchpole and Slater, 1995, anurans: Feng *et al.*, 2006, and insects: Nakano *et al.*, 2015) and those that emanate from abiotic features within their environment (*e.g.* flowing rivers: Amoser and Ladich, 2010, wind and rain: Swanson *et al.*, 1988). Varying over space and time, these acoustic patterns are responsible for the formation of local soundscapes (Pijanowski *et al.*, 2011; Sueur and Farina, 2015), and the signals themselves may be encoded with data concerning landscape structure (Farina, 2006), and population or community composition (Bayne *et al.*, 2008). The detection of the acoustic signals may elicit a contextually dependent behavioural response (Ellison *et al.*, 2011; Brintjes and Radford, 2013) with respect to habitat selection (Simpson *et al.*, 2005a), conspecific communication (sexual selection: Bass and McKibben, 2003, or competition: Amorim *et al.*, 2004), social aggregations (Moulton, 1960), or predator-prey interactions (Ward *et al.*, 2011). Sound is used by fish to facilitate a number of survival functions, and arises from a range of biological, abiotic and anthropogenic sources.

Global urbanisation has contributed to unwanted anthropogenic noise worldwide, and the negative impacts on fish species are widely recognised (Slabbekoorn *et al.*, 2010). Freshwater fish can sustain anatomical (*e.g.* ruptured swimbladders in Nile tilapia, *Oreochromis niloticus*: Halvorsen *et al.*, 2012a) and physiological damage (*e.g.* increased cortisol levels in Blacktail shiner, *Cyprinella venusta*: Crovo *et al.*, 2015) as a result of exposure to anthropogenic noise (Chapter 2.2), which can also drastically alter the behaviour of individuals and structural dynamics of groups (*e.g.* European minnows, *Phoxinus phoxinus*: Chapter 4). High intensity background noise can disrupt the ability of a fish to extract important biological information from their local soundscape. For instance, noise perturbs acoustic communication and subsequent spawning success of fish (*e.g.* in spotted, *Gobiusculus flavescens*, and painted gobies *Pomatoschistus pictus*: de Jong *et al.*, 2018), alters territorial behaviour (*e.g.* in red-mouthed gobies, *Gobius cruentatus*: Sebastianutto *et al.*, 2011), and disrupts orientation behaviour (*e.g.* in longspine cardinalfish, *Apogon doryssa*: Holles *et al.*, 2013). Background noise can limit anti-predator behaviour (*e.g.* in juvenile European eel, *Anguilla anguilla*: Simpson *et al.*, 2015), and weaken the response to chemical alarm cues (*e.g.* in fathead minnow, *Pimephales promelas*: Hasan *et al.*, 2018). While we are beginning to understand the influence of anthropogenic sources of sound across sensory modalities, there remains little information on how anti-predator-like responses of fish to acoustic stimuli is impacted by high intensity background noise.

An ability to detect, discriminate (d'), and respond to biologically relevant sounds is influenced by the signal-to-background-noise ratio (SNR). When energetic background, or masking noise, is of at least equal intensity to that of a signal, and within a critical frequency range (Scharf, 1970), it acts as a constraint to signal transmission (Ryan and Brenowitz, 1985; Rosa and Koper, 2018). These relationships are important components of Signal Detection Theory (SDT), that provides a framework to better understand the effects of masking on fish response to environmental stimuli (*e.g.* hydraulic gradients: Kemp *et al.*, 2012a; Kerr and Kemp, 2019; Chapter 2.6). From a fisheries management perspective, such an approach is two-fold. First, SDT may be applied to deliberately mask the effect of an unwanted environmental stimuli. For example, turbulence (hydrodynamic noise) has been used to distract fish from an accelerating velocity gradient (Kerr and Kemp, 2019). Alternatively, as in this study, SDT may be used to determine a SNR above a masking noise floor at which an acoustic signal induces a desired behavioural response. Field sites which necessitate fish guidance technologies to reduce injuries or mortalities (*e.g.* hydropower dams or weirs) are generally dominated by high-level background noise intensities (Miyamoto *et al.*, 1989; Schilt, 2007; Pedersen *et al.*, 2012; Johnson *et al.*, 2014), acting as a crucial constraint to acoustic signal transmission, and the subsequent response of a targeted species (Wiley, 1994). Understanding how fish respond to acoustic signals under masked noise conditions will assist in the development of more effective behavioural guidance systems and aid in conservation efforts to reduce the impacts of anthropogenic noise.

This laboratory based experimental study aimed to investigate whether high intensity background masking noise reduced the anti-predator-like response of a shoaling fish species to a tonal acoustic stimulus. Common carp (*Cyprinus carpio*) were selected as the model species because of their well-studied auditory sensitivity (Kojima *et al.*, 2005), and interest to fisheries management from both the perspective of conservation (IUCN red listed), (Freyhof and Kottelat, 2008a) and invasive species control (Vilizzi *et al.*, 2014; Crichingo *et al.*, 2016; Stuart and Conallin, 2018). Groups of five individuals were exposed to one of three different intensities (SPL) of an acoustic pure tone (170 Hz). A total of 400 fish were tested under either ambient or masking noise conditions across 80 independent trials. Fish were exposed to one of eight treatments, including a “masking” noise only, and ambient control. The study concentrated on coarse: a) startle response; and fine-scale behavioural metrics: b) mean group speed, c) cohesion, d) orientation, and e) signal detection, to quantify the magnitude of the anti-predator response exhibited when a tonal signal was deployed under ambient and masking noise conditions.

6.2 Materials and methods

6.2.1 Study species and husbandry

In March 2018, 420 juvenile common carp (*Cyprinus carpio*) were obtained from a hatchery fish supplier (DC Freshwater Fish, Surrey, UK). Fish were transported to the University of Southampton's ICER facilities in oxygenated plastic bags, containing water from the source aquaria. Survival during transportation was 100%. Fish were allowed a period of two hours before transferral to one of three indoor holding tanks (1.5 m x 1.0 m x 0.78 m; water depth: 0.68 m; stocking density: 1.21 kg/ m³; mean temperatures \pm s.e.: Tank 1: 9.9 \pm 1.5 ° C; Tank 2: 8.9 \pm 0.3 ° C; Tank 3: 9.1 \pm 0.3 ° C) where they acclimatised for three days prior to the start of the experiments. Water quality was monitored to ensure it remained below thresholds considered suboptimal (NO³⁻ : < 50 mg L⁻¹ ; NO²⁻ : < 1 mg L⁻¹ ; NH₃ : 0 ; and pH: < 8.4), and maintained using a submersible aerated pump in combination with partial water exchanges when necessary. Fish were held under a 12:12 h light:dark photoperiod cycle and provisioned daily with commercially available aquarium flaked food until satiation. On completion of each trial, fish were measured (standard length \pm s.e.: 68.3 \pm 0.8 mm) and weighed (wet mass \pm s.e.: 9.8 \pm 0.3 g). Differences (Kruskal-Wallis rank sum) in wet mass ($\chi^2 = 21.9$; *d.f.* = 7; *p* < 0.01) and standard length ($\chi^2 = 14.9$; *d.f.* = 7; *p* < 0.05) were apparent between treatments, however, a *post hoc* Dunn's test indicated deviations to only be for fish within the masking control treatment (Table 6.1: Appendix B). The study was approved by the University of Southampton's Animal Welfare and Ethical Review Board (Ethics ID: 40113.A1).

6.2.2 Experimental arena

Experiments were performed within an arena (86 cm x 30.8 cm x 30.2 cm), (Chapter 3.2; Chapter 4; Figure 4.1) housed inside an acoustically isolated room. Two fully immersed speakers (Electro-Voice UW-30; maximal output 153 dB re 1 μ Pa at 1 m for 150 Hz, frequency response 0.1-10 kHz; Lubell Labs, Columbus, OH) were used to generate the sound field. Each was suspended at a fixed point in the middle of the water column, one behind an acoustic baffle at either end of the arena. Water depth was kept constant at 27 cm. Every ten trials, water was replaced to minimise the build-up of biological debris or pheromones, and left to settle overnight and return to room temperature (mean \pm s.e.: 10.9 \pm 0.12 ° C).

The experimental arena was surrounded by a wooden frame covered in plastic blackout material to visually isolate the fish from the experimenter. Light levels were kept constant throughout the

trials using a white background that was attached to the outside of the experimental arena and lit from underneath using two PhotoSEL Photography bulbs (pure white full-spectrum flicker free; 85 W, 5000 lumen; SJT Commercial Ltd., UK). This created an increased contrast of the fish for digital video recordings using a webcam (C920; HD 1080p; 30 frames per second; Logitech Pro, Switzerland) mounted above the centre of the experimental arena.

6.2.3 Sound stimuli and acoustic mapping

Custom written MATLAB script (Release 2017a, The Mathworks, Inc., Natick, Massachusetts, United States) was used to produce sound samples. The signal was sent through a ProSound 200 power amplifier (50 W, frequency response range approx.: 0.02 – 20 kHz; London, UK), and on to the underwater speakers via a DAQ (NI USB-9174; National Instruments, U.K) connected to a laptop computer.

Test stimuli of 170 Hz (centred on the 1/3rd octave band: ~ 151 – 190 Hz) pulsed tones (one second ON: two seconds OFF) and masking broadband noise of 120 – 3000 Hz at a fixed intensity of 110 dB re 1 μ Pa (RMS) was chosen (Figure 6.1). Selected tonal stimuli were within known auditory sensitivities of common carp (100-3000 Hz, with lower thresholds observed in the range below 505 Hz: Kojima *et al.*, 2005). The masking noise was informed by field recordings conducted on 20th November 2017, at the Totnes Weir Hydro power plant on the River Dart, Devon (50°26'20.5"N 3°41'23.8"W). Noise samples were recorded for 1-minute, at 22 independent points using a hydrophone (Type 8105: manufacturer-calibrated sensitivity -205 dB re: 1V μ Pa⁻¹, frequency response 0.1 Hz – 160 kHz; Brüel & Kjær, Royston, U.K), connected to a charge amplifier (Type: 2635; Brüel & Kjær, Royston, U.K) and audio recorder (model: DR-100MKIII; .wav format, sampling rate 192 kHz; TASCAM, Weisbaden, Germany). Recordings taken from upstream and downstream of the turbine were analysed (dominant frequency range: 0-3 kHz; SPL (RMS): upstream of turbine 118.5 dB re 1 μ Pa; downstream 125.1 dB re 1 μ Pa).

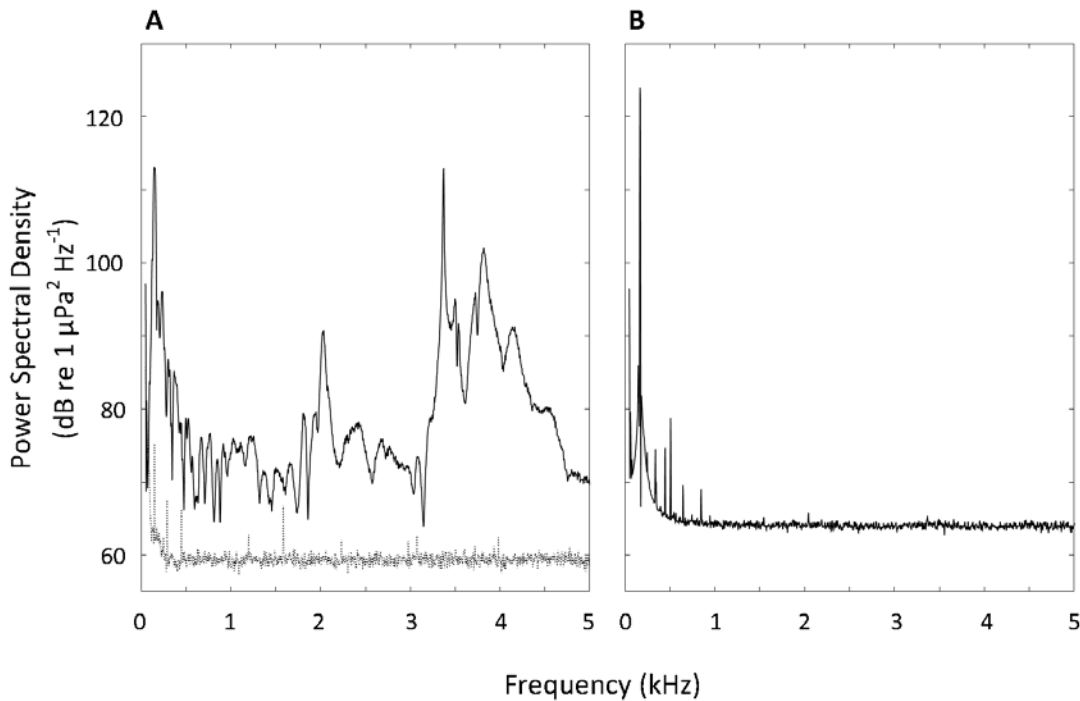


Figure 6.1: Example power spectral density (dB re 1 $\mu\text{Pa}^2 \text{Hz}^{-1}$) of acoustic conditions within the experimental area (sampling rate: 25.6 kHz; FFT size 8192 (3 Hz bin width), overlap 91.5%, von Hann Window, frequency range 50 – 5000 Hz) for **(A)** baseline ambient noise conditions (dotted line) with masking broadband noise (120 – 3000 Hz) conditions (solid line); and **(B)** 170 Hz tonal stimuli.

Artificial masking noise stimuli was created by digitally filtering Gaussian white noise, created at a sample rate of 12.8 kHz, and band-passed using an 8th order Butterworth filter. Acoustic intensity of the pulsed tone was played back at either a low (110 dB re 1 μPa), medium (121 dB re 1 μPa), or high (130 dB re 1 μPa) level, to replicate differing signal-to-noise ratios. To avoid lower frequency resonance issues with the underwater speakers during stimuli playback, a high pass filter was applied at 100 Hz. As spatial separation of a sound source can influence the effectiveness of a masker, noise and tonal stimuli were played back through both speakers (Fay, 1988). Eight acoustic treatments, including an ambient control of no sound (ambient noise: 82 dB re 1 μPa) were used in the experiments (Table 6.1). In the absence of any acoustic playback during the ambient control, an electrical signal was sent to the speakers to avoid any confounding influences of electroreception (Xu *et al.*, 2006). Sound pressure levels of all treatments were standardised in the centre of the experimental arena.

Table 6.1: Ambient and masking treatment parameters and abbreviations.

Treatment	Tone SPL (RMS) (dB re 1 μ Pa)	Abbreviation	<i>n</i> trials	Mean fish length \pm s.e. (mm)	Mean fish wet mass \pm s.e. (g)	
AMBIENT	Control	n.a.	'AMB-C'	10	66.2 \pm 1.9	8.7 \pm 0.8
	Low SPL	110	'AMB-LOW'	10	70.2 \pm 2.5	11.1 \pm 1.0
	Intermediate SPL	121	'AMB-INT'	10	65.4 \pm 2.0	8.5 \pm 0.7
	High SPL	130	'AMB-HIGH'	10	66.0 \pm 2.3	8.1 \pm 0.9
MASKING	Control	n.a.	'MASK-C'	10	74.3 \pm 1.2	11.8 \pm 0.6
	Low SPL	110	'MASK-LOW'	10	65.8 \pm 2.7	9.8 \pm 1.0
	Intermediate SPL	121	'MASK-INT'	10	69.7 \pm 1.9	9.9 \pm 0.7
	High SPL	130	'MASK-HIGH'	10	68.5 \pm 2.2	10.2 \pm 0.9

In advance of exposure, the acoustic environment was quantified for both tonal stimuli and masking noise. Intensity of masking noise was mapped both as broadband noise (120 – 3000 Hz) and additionally in the 1/3rd octave band to reflect the highly frequency selective nature of masking (Chapter 2.6). The 1/3rd octave band approximately represents the smallest band of frequencies which will simultaneously activate the natural auditory filters, causing perception interference to mask the tone (critical band). The hydrophone (Type: 4013; manufacturer-calibrated sensitivity -211 dB re: 1V μ Pa⁻¹, frequency response 0.01 Hz – 170 kHz; Teledyne RESON, Slangerup, Denmark) was connected to a voltage amplifier (Type: A1001; 9 V; gain +40 dB, high pass filter 100 Hz; Etec, Frederiksværk, Denmark) and fixed to a customised rig to measure acoustic intensities at 306 positions within the experimental arena. The signal was relayed through the DAQ and back to the laptop computer, from which custom written MATLAB script was used to control and record from the DAQ (sampling rate 25.6 kHz; FFT 1024, overlap 50%, Hann window). Resulting SPLs were used to describe the sound-field within the experimental arena across three different depths (Figure 6.2 and 6.3).

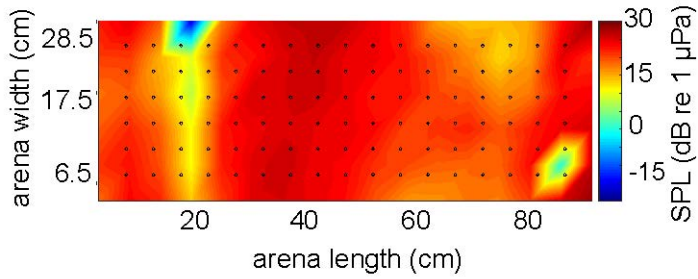


Figure 6.2: Insonified experimental arena showing sound pressure levels (RMS) (dB re 1 μ Pa) of the signal to 1/3rd octave band noise ratio (120-3000 Hz) at 13.5 cm depth.

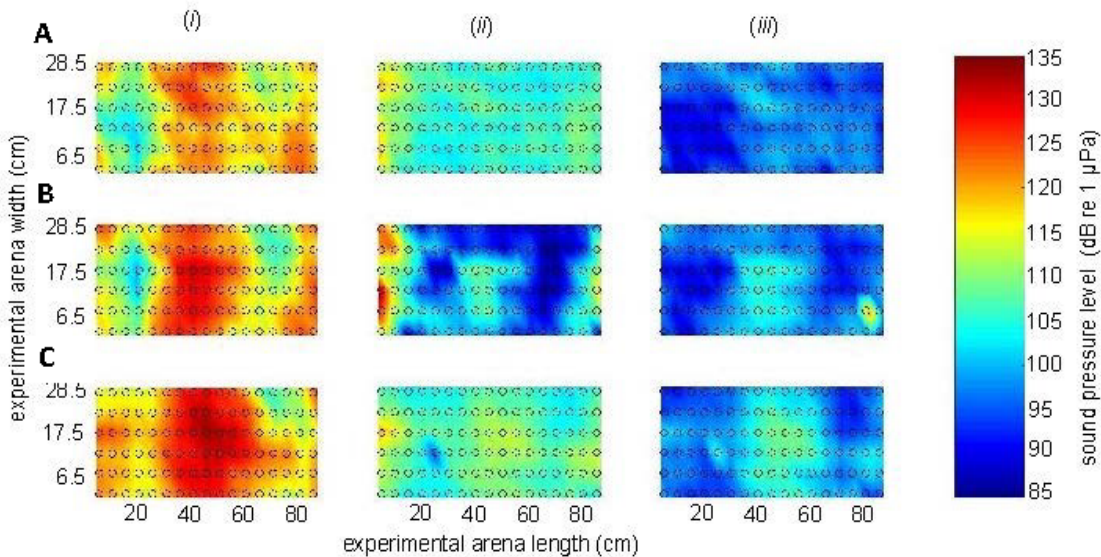


Figure 6.3: Sound Pressure Levels (RMS) (dB re 1 μ Pa) recorded at **(A)** 7 cm; **(B)** 13.5 cm; and **(C)** 20 cm water depth, for **(i)** 170 Hz (sinewave) tonal treatment; and 120 – 3000 Hz broadband masking noise recorded **(ii)** across the broadband frequency range, and **(iii)** within the 1/3rd octave noise band. *Note:* points indicate hydrophone matrix positioning.

The particle acceleration component, a , was calculated (Chapter 4 and 5) as:

$$a = -\frac{1}{\rho} \nabla P \quad (\text{Equation 6.1})$$

where P is the sound pressure, and ρ , the ambient density.

As the pressure signal was measured on a regular grid of points (306 positions: 17 x 6 x 3 grid), the pressure gradient could be computed from these measurements using a finite difference approach. The root mean square (RMS) of the pressure difference was evaluated independently in the x, y, and z direction. From here, the pressure gradient was obtained by dividing the distance between measurements. Based on Equation 6.1, the RMS particle acceleration was calculated in one direction by dividing by the water density. By combining RMS values in all three directions, the total RMS particle acceleration was finally determined. Results were expressed in decibels (dB re 1 mm s⁻²) and mapped for the central depth (13.5 cm) of the tank (Figure 6.4).

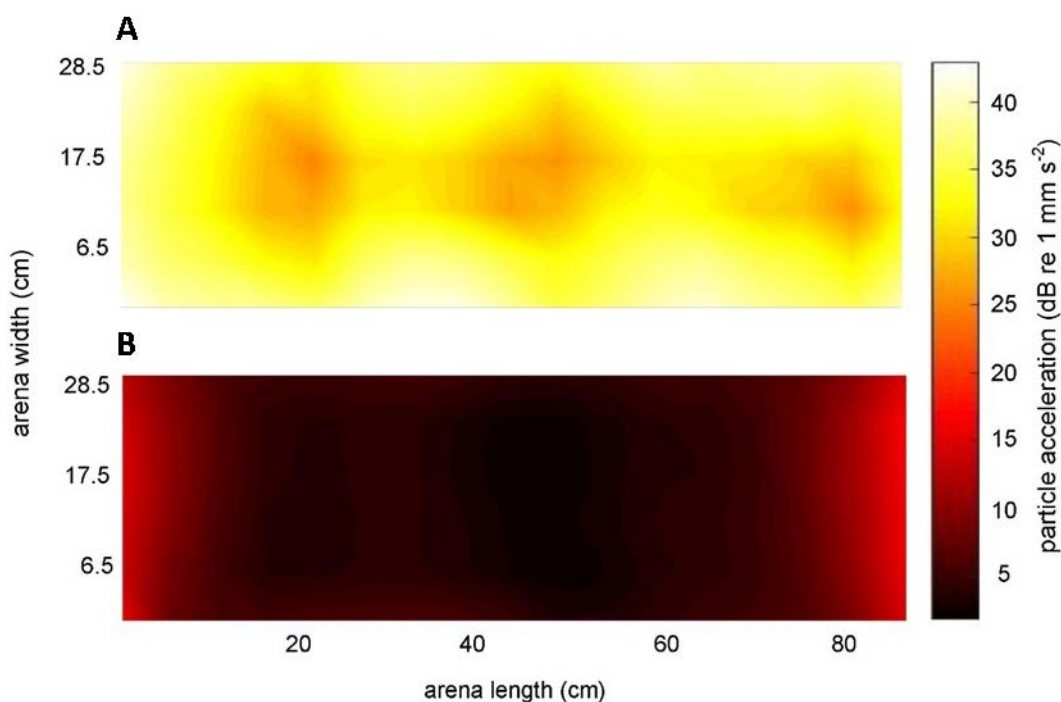


Figure 6.4: Heat maps of particle acceleration (dB re 1 mm s⁻²) measured at 13.5 cm depth for **(A)** 170 Hz sinewave tone; and **(B)** broadband noise (120 – 3000 Hz).

A small tank set-up allowed a carefully controlled reductionist approach to be adopted to minimise the influence of confounding factors, and provide a stable, reproducible acoustic field. As expected, owing to the nature of the near-field conditions relative to wavelength, particle motion was complex and highly variable in all directions (Gray *et al.*, 2016). This was not considered an issue as behavioural responses of carp, a pressure-sensitive otophysine species, to tonal stimuli under masked and ambient noise conditions at known SNR in the sound pressure domain, were the main parameters of interest.

The relationship between the pressure and particle motion components of sound is understood to differ between those observed for small tank setups and large-scale “natural” aquatic habitats (*e.g.* deep lakes or oceans). Owing to the small dimensions of the tank, the material properties of the walls (influencing resonance frequencies), and the sound speed differences between water and the surrounding air, high levels of particle motion are produced within the sound field (Akamatsu *et al.*, 2002). In contrast, the acoustic nature of shallow streams (commonly < 1 m depth), are more convoluted, and not well understood (Campbell *et al.*, 2019; Leighton *et al.*, 2019; Chapter 2.5). Nonetheless, results obtained from tank studies cannot be directly extrapolated to natural systems without further testing or validation.

6.2.4 Experimental protocol

A total of 80 trials were conducted, ten replicates for each treatment and control ($n = 400$). Each replicate consisted of five similar sized naïve fish, introduced simultaneously to the centre of the experimental arena. Each group of five carp was used once.

For masking treatments, carp were introduced to the experimental arena with the noise playback already projecting simultaneously from the two underwater speakers. Video recording began five minutes post-introduction. Each trial lasted a total of 50 minutes. This included a 30 minute acclimation period, determined to be sufficient based on pilot trial analyses, after which a tonal stimulus was presented for ten minutes (either in combination or absence of masking noise). To avoid order effects, a random number generator was used to determine order of playback. A final post-treatment period of ten minutes was included, where exposure to the tonal stimuli ceased.

6.2.5 Video tracking and behavioural parameters

Fish behaviour was analysed in respect to coarse-scale behaviour: a) a startle response, confirmed when a fish exhibited a c-start (full contraction of the body into a c-shape) at the onset of the tonal stimuli, followed by a clear swimming burst at a comparatively altered angle and direction

to the pre-startle behaviour (Bhandiwad *et al.*, 2013); and fine-scale behaviour (Chapter 3, Table 3.1): b) mean swimming speed (m s^{-1}), c) cohesion (m), and d) orientation ($^{\circ}$), (Neo *et al.*, 2015a; Herbert-Read *et al.*, 2017a).

For analysis of coarse-scale startle response, videos were played back in a randomly generated order. Presence or absence of a startle response at the onset of acoustic stimuli was determined via visual inspection of the videos, with the observer blind to treatment. The number of times at least one individual within a group exhibited a startle response to each consecutive tonal pulse from the onset of stimuli, without interruption, was also counted. This was classified as the number of “continuous startle responses”.

Using the principles of SDT, discriminability (d') and response criterion (C), were calculated with respect to observed startle responses under masked and ambient treatments. d' is calculated from the hit rate (HR) and false alarm rate (FAR), (Kemp *et al.*, 2012a; Kerr and Kemp, 2019) and is measured in standard deviation units (z-scores) for right-tail probabilities of the normal distribution, where:

$$d' = z(\text{HR}) - z(\text{FAR}) \quad (\text{Equation 6.2})$$

Standard corrections were performed on FAR ($1/(2N)$) when the true p-value was 0 ($z = \infty$), and for HR ($1-1/(2N)$) when the true p-value was 1 ($z = -\infty$) (Swets, 1996). The higher the d' value, the higher the level of signal discriminability. C assumes an equal probability of incorrect ‘false alarm’ or ‘miss’ responses (Stanislaw and Todorov, 1999; Wickens, 2002; Kerr and Kemp, 2019), and is a measure of response bias. At value 0, C is unbiased, with negative values skewed toward a ‘yes’ response, and positive, a ‘no’. Combined, these measures are used to produce a receiver operating characteristic (ROC) curve, showing whether an animal is capable of detecting a stimulus, and at what threshold the internal processes will also elicit a behavioural response (Kemp *et al.*, 2012a; Figure 6.5).

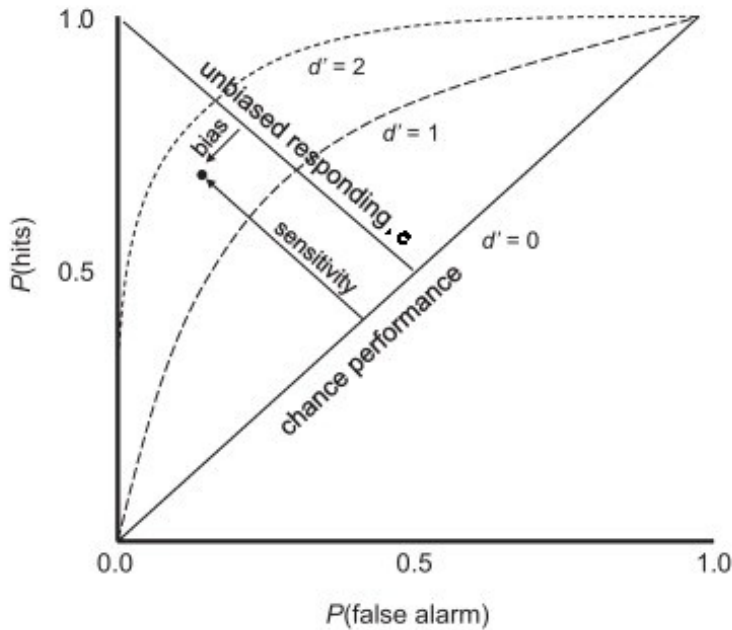


Figure 6.5: Example Receiver Operating Characteristic (ROC) curves for signals of differing strength (adapted from Kemp *et al.*, 2012a. Reproduced with the permission of Elsevier Ltd.). The stronger the signal, and/ or the more sensitive a subject, the more convex the ROC curve and the greater the value of d' . Where $d' = 0$, a response is deemed by chance. The line, **C**, intersecting all d' isolines represents an unbiased response. The filled circle represents a hypothetical response where d' is between 1.0 and 2.0, with a more conservative responding bias.

Fine-scale behaviour was investigated by tracking fish movements from video recordings using a custom written MATLAB script. Group mean of swimming speed, cohesion, and orientation were calculated, providing an output of 90 000 data points per variable for each fish group.

Low frequency tones have been observed to induce changes in cyprinid group cohesion (*e.g.* European minnow, *Phoxinus phoxinus*: Chapter 5), and therefore this parameter was used to determine fine-scale behaviour FAR and HR. Ninety-five percent confidence intervals (CI) for the slope in a linear least squares regression were calculated for each individual trial over the ten-minute acoustic “exposure” period, and compared to those performed across the control group average. A Studentised Breusch-Pagan test was used to test the homoscedasticity of each model. When a model could not be run without interference (*i.e.* presence of heteroscedasticity), bootstrapped estimates ($n = 1000$) were used to produce a variance robust standard error and bias corrected and accelerated confidence interval (BCa CI), (Efron and Tibshirani, 1993; Davison and Hinkley, 1997). A hit (during acoustic treatments), or false alarm (during ambient and masked

controls) was identified when a trial was determined to deviate from the “normative fit”, whereby either the upper bound trial CI was less than the lower bound of the weighted control treatment effect, or, the lower bound trial CI was higher than the weighted control treatment effects higher bound. The total number of correct (signal present: “hit”; signal absent: “correct non-response”), and incorrect responses (signal present: “miss”; signal absent: “false alarm”) could be used to calculate fine-scale behaviour discriminability and response criterion under ambient and masked treatments.

6.2.6 Statistical analysis

Statistical analysis was performed using freeware programme RStudio (v 3.2.2: The R Foundation for Statistical Computing, Vienna, Austria, <http://www.r-project.org/>).

Tests were conducted to assess whether data met the assumptions for normality (Shapiro Wilk) and homoscedasticity (Levene’s). To determine whether there were differences between treatments in the number of *startle responses* present at the onset of tonal stimuli, Kruskal-Wallis tests were performed across all treatments and the control to determine whether treatment influenced: 1) the number of undisturbed, continuous startle responses to the pulsed tonal stimuli, and 2) the total number of individuals within a group startling at the onset of tonal stimuli. The Dunn-Bonferroni *post hoc* method was conducted when differences between treatments were highlighted, providing a description of where and to what extent these occurred.

For analyses of *group speed*, *cohesion*, and *orientation*, data points (30 frames per second) were averaged (mean) to 1 second outputs. The median, and median absolute deviation (MAD) were calculated over 30 second time periods. To determine if the presence of masking noise alone had an influence on behaviour, Wilcoxon rank sum tests were conducted for the 30 second medians of AMB-C and MASK-C for a total of 50 minutes. After determining no difference (Figure 6.6), each treatment condition was separately compared to AMB-C using the same method. This was completed for all three behavioural parameters, producing three sets of comparative running p-values. These allowed for differences in behaviour between control and treatment groups to be quantified during the ten-minute tonal-exposure period. Finally, the total proportion of time the comparative p-value remained < 0.05 during the tonal-exposure period was calculated per treatment and behaviour. This allowed for the assessment of differences across ambient and noise treatments for each behavioural parameter through the use of chi-square contingency tables.

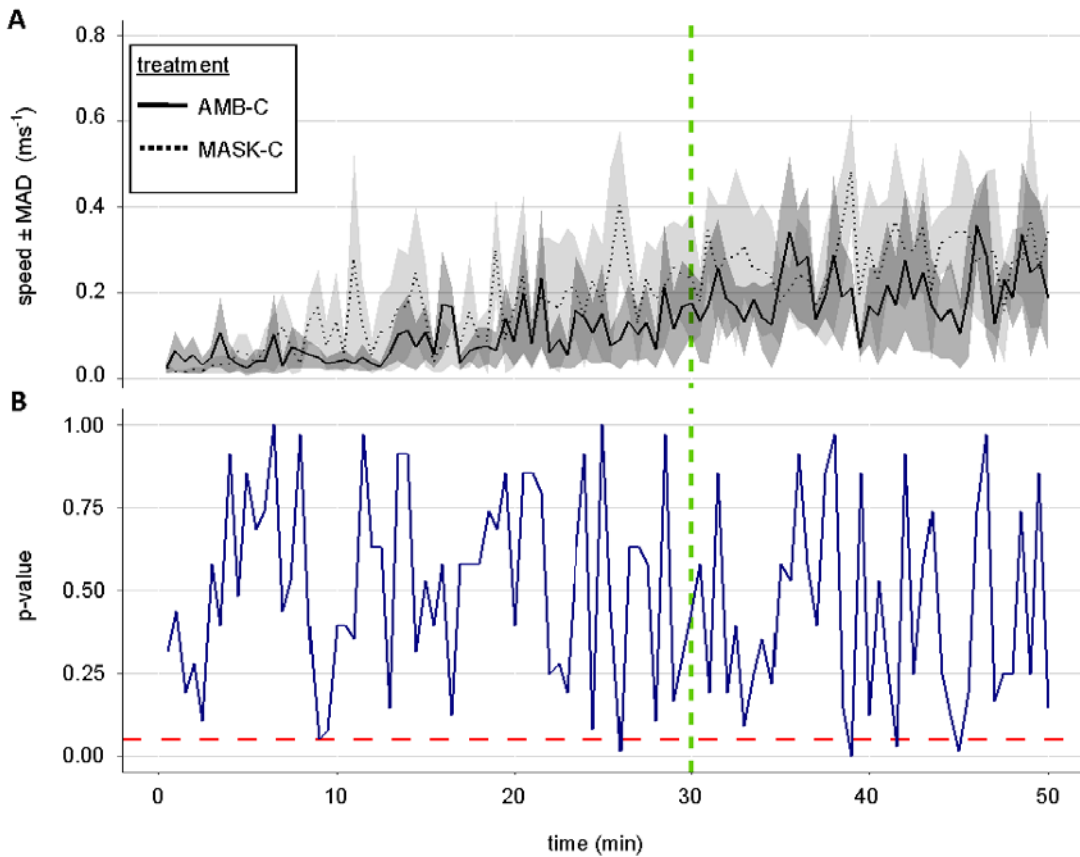


Figure 6.6: (A) Example comparison of median group swimming speeds \pm MAD (median absolute deviation) of five common carp ($n = 10$ per condition) over time for ambient (AMB-C: solid line) and masked (MASK-C: dot-dashed line) control conditions, with (B) running p-values (Wilcoxon rank sum test) indicating no differences in swimming speed between ambient and masked control conditions over 30 second median time frames. *Note:* Horizontal red dot-dashed line indicates cut-off level of significance ($p < 0.05$: below the line). Vertical green dashed lines indicate end of acclimation period.

6.3 Results

6.3.1 Startle response

Fish startled at the onset of tonal stimuli under all ambient treatment SNRs (Figure 6.7). The greater the intensity of the signal, the more fish within a group startled on the initial tone (Figure 6.6: $\chi^2_3 = 30.88$; $p < 0.01$). AMB-HIGH elicited the highest number of startles from individuals at the onset (median $_{(IQR)}$: 5 $_{(0)}$), followed by AMB-INT (median $_{(IQR)}$: 2.5 $_{(1)}$), then AMB-LOW (median $_{(IQR)}$: 2 $_{(1.75)}$). More intense tones also stimulated a greater number of continuous startle responses

under ambient treatments (Figure 6.8: $\chi^2_3 = 31.64$; $p < 0.01$). For masked treatments, no startle responses were observed at the onset of acoustic stimuli asides from one individual MASK-INT outlier.

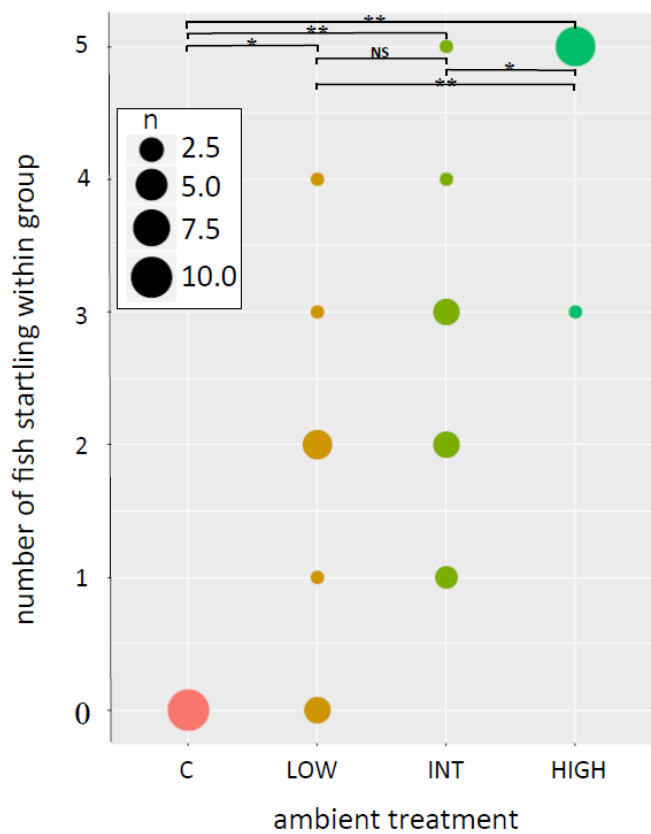


Figure 6.7: Number of individuals within a group of five common carp exhibiting a startle response at the onset of tonal stimuli (Kruskal-Wallis rank sum test: $\chi^2 = 30.88$; $d.f. = 3$; $p < 0.01$). Note: Three different acoustic intensity (RMS) treatments shown: AMB-LOW (110 dB re 1 μ Pa), AMB-INT (121 dB re 1 μ Pa), and AMB-HIGH (130 dB re 1 μ Pa).

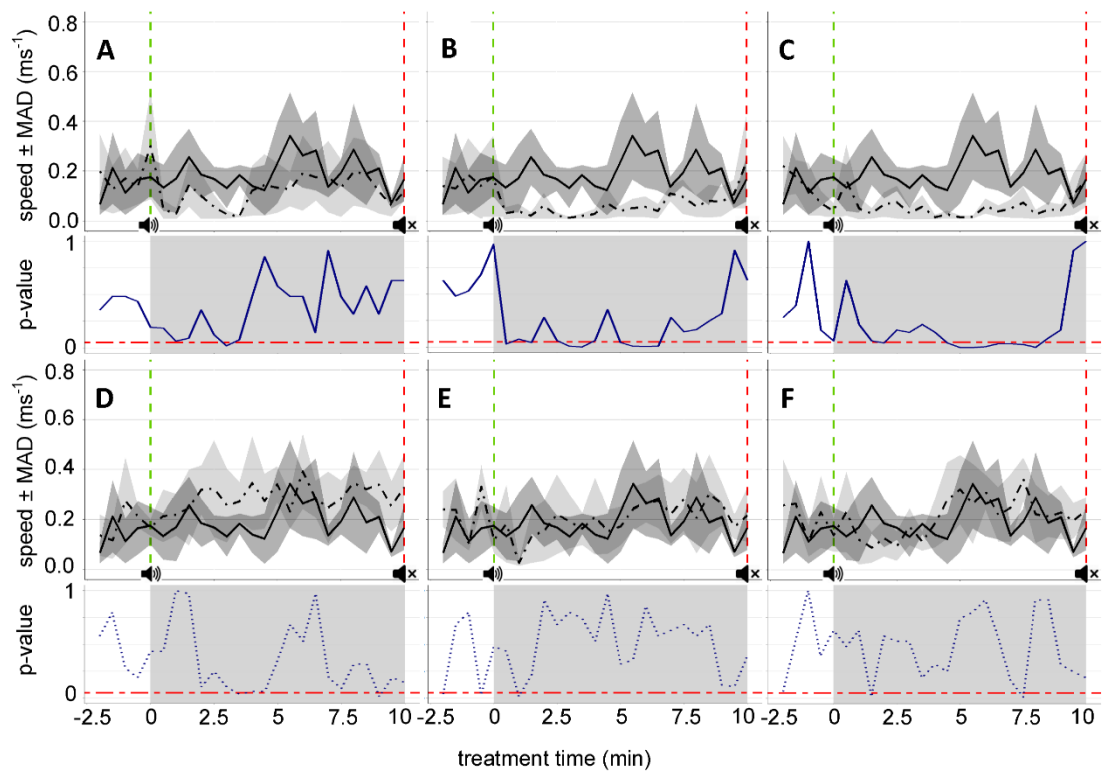


Figure 6.9: Median swimming speed \pm MAD (median absolute deviation) for groups ($n = 10$ per condition) of five common carp over time during ambient control (AMB-C: solid line) and treatment (dot-dashed line) conditions: **(A)** AMB-LOW; **(B)** AMB-INT; **(C)** AMB-HIGH; **(D)** MASK-LOW; **(E)** MASK-INT; and **(F)** MASK-HIGH; alongside running p-values (Wilcoxon rank sum test) indicating differences in swimming speed between AMB-C and treatment over 30 second median time frames. *Note:* Horizontal red dot-dashed line indicates cut-off level of significance ($p < 0.05$). Vertical green dashed lines \llcorner indicate start of the tonal exposure period and vertical red dashed lines \llcorner^* , the end.

6.3.3 Cohesion

Under masked treatments, differences in cohesion were observed between treatments ($\chi^2_2 = 86.87$; $p < 0.001$), with groups exhibiting increased cohesion for a higher proportion of time under greater acoustic treatment intensities (Figure 6.10). Group cohesion increased under MASK-LOW after 2.5 minutes ($Z = 2.04$; $p < 0.05$; Figure 6.10D), and did so for 20% of the stimuli exposure. Increases in group cohesion were observed in response to MASK-INT after 0.5 minutes ($Z = 2.19$; $p < 0.05$; Figure 6.10E), lasting 60% of the exposure. MASK-HIGH incurred differences

after 0.5 minutes ($Z = 2.19$; $p < 0.05$; Figure 6.10F), and group cohesion increased for 85% of the tonal stimuli exposure. For ambient treatments, group cohesion increased when carp were exposed to tonal stimuli. After 1.5 minutes of exposure to AMB-LOW, the distance between individuals reduced in comparison to the baseline ($Z = -2.49$; $p < 0.05$; Figure 6.10A). For AMB-INT, the increase in cohesion began after 0.5 minutes ($Z = -3.09$; $p < 0.01$; Figure 6.10B), and continued for 90% of the stimuli exposure. Groups exposed to AMB-HIGH also increased cohesion after 0.5 minutes ($Z = -3.40$; $p < 0.001$; Figure 6.10C), lasting for 80% of the exposure period. There were, however, no differences in group cohesion between the ambient treatments as all groups spent a similar proportion of time in a significantly different state to the control.

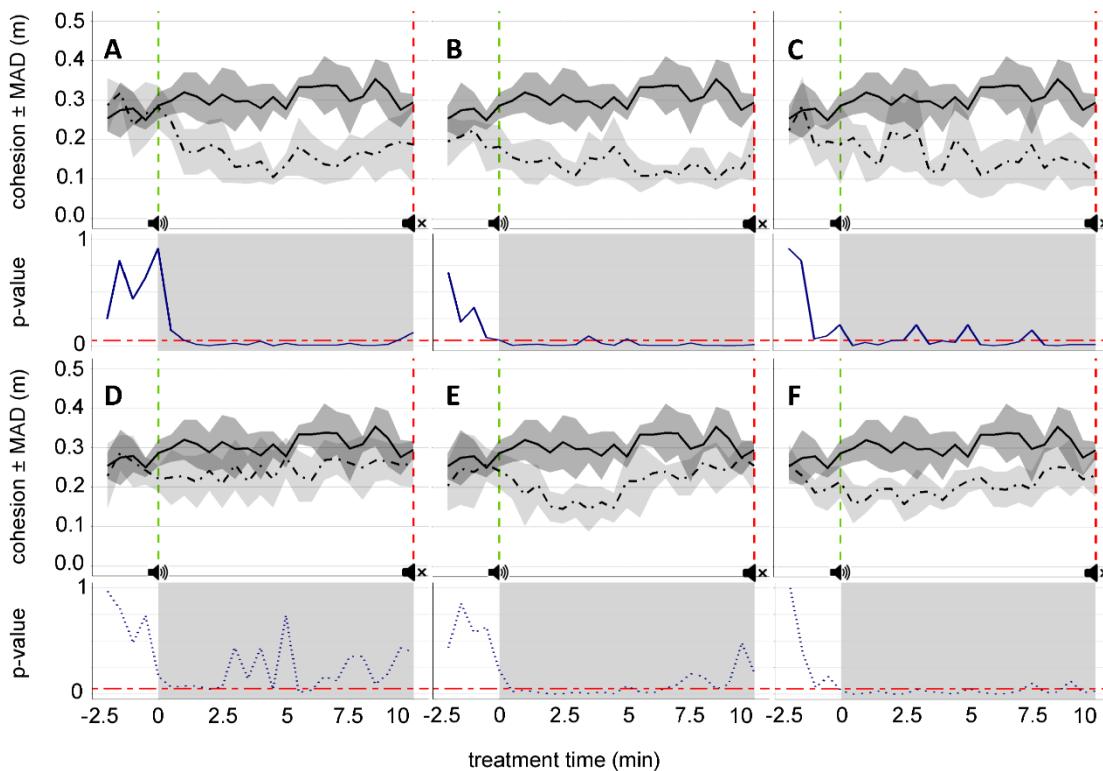




Figure 6.10: Median group cohesion \pm MAD (median absolute deviation) for groups ($n = 10$ per condition) of five common carp over time during ambient control (AMB-C: solid line) and treatment (dot-dashed line) conditions: **(A)** AMB-LOW; **(B)** AMB-INT; **(C)** AMB-HIGH; **(D)** MASK-LOW; **(E)** MASK-INT; and **(F)** MASK-HIGH; alongside running p-values (Wilcoxon rank sum test) indicating differences in group cohesion between AMB-C and treatment over 30 second median time frames. *Note:* Horizontal red dot-dashed line indicates cut-off level of significance ($p < 0.05$). Vertical green dashed lines  indicate start of the tonal exposure period and vertical red dashed lines , the end.

6.3.4 Orientation

Differences in orientation were observed between groups exposed to masked treatments ($\chi^2_2 = 17.81$; $p < 0.001$). Individuals were observed to become more aligned in response to tonal stimuli. However, there was no linear relationship with acoustic intensity (Figure 6.11). Groups experiencing MASK-LOW decreased group orientation after 1 minute exposure ($Z = 3.40$; $p < 0.001$), lasting 25% of the time. For MASK-INT, alignment significantly increased from the baseline after 3 minutes ($Z = 2.57$; $p < 0.01$), but this only lasted for 0.5 minutes. Finally, MASK-HIGH groups increased alignment after 30 seconds ($Z = 2.79$; $p < 0.01$) and did so over 25% of the exposure period. Under all ambient treatments, median group orientation initially decreased in response to tonal stimuli as individuals became more aligned with one another, however, quickly returned to baseline. For AMB-HIGH, this secondary shift in orientation involved fish decreasing their alignment in comparison to control groups. Group orientation differed from the baseline for AMB-INT and AMB-HIGH, but not for AMB-LOW (Figure 6.11D). AMB-INT groups reduced orientation after 6 minutes of exposure to tonal stimuli for a total of 0.5 minutes ($Z = 2.65$; $p < 0.01$; Figure 6.11E). For AMB-HIGH groups, reduced orientation was observed after 4 minutes ($Z = 2.19$; $p < 0.05$; Figure 6.11F), and lasted for 10% of the exposure. Group orientation differed between the ambient treatments ($\chi^2_2 = 8.05$; $p < 0.05$), with individuals reducing alignment at greater acoustic intensity.

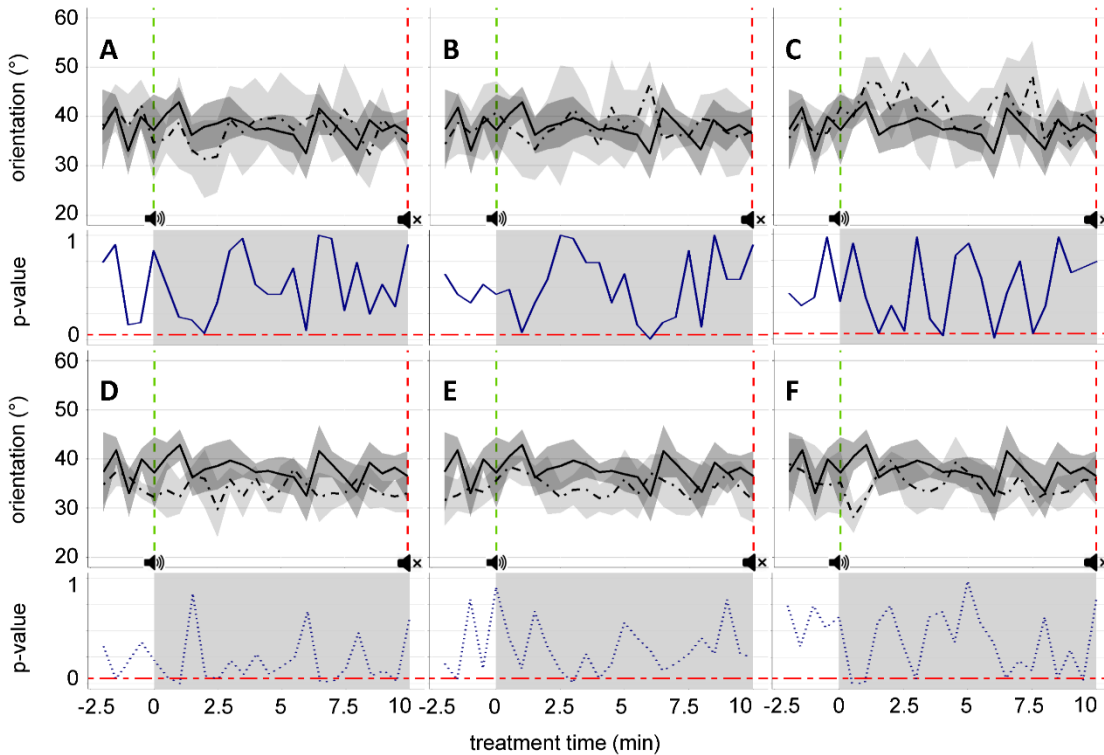


Figure 6.11: Median group orientation \pm MAD (median absolute deviation) for groups ($n=10$ per condition) of five carp over time during ambient control (AMB-C: solid line) and treatment (dot-dashed line) conditions: **(A)** AMB-LOW; **(B)** AMB-INT; **(C)** AMB-HIGH; **(D)** MASK-LOW; **(E)** MASK-INT; and **(F)** MASK-HIGH; alongside running p-values (Wilcoxon Rank Sum Test) indicating differences in group orientation between AMB-C and treatment over 30 second averaged (median) time frames. *Note:* Horizontal red dot-dashed line indicates cut off level of significance ($p < 0.05$). Vertical green dashed lines indicate start of the tonal exposure period and vertical red dashed lines, the end.

6.3.5 Signal detection

Signal discriminability under masked treatments for coarse-scale behaviour (startle response) was relatively similar (MASK-LOW: $d' = 0$; MASK-INT: $d' = 0.36$; MASK-HIGH: $d' = 0$; Figure 6.12A). Response criterion was positive and similar under MASK-LOW ($C = 1.64$), MASK-INT ($C = 1.46$), and MASK-HIGH ($C = 1.64$) treatments (Figure 6.12A), indicating a general bias in which fish would not startle under masked treatments. Comparatively, the signal discriminability for fine-scale behaviour (group cohesion) under masked treatments was greater for MASK-INT ($d' = 1.37$) and MASK-HIGH ($d' = 1.10$). Discriminability for MASK-LOW ($d' = 0$) remained the same (Figure 6.12B). The fine-scale response criterion was positive, reasonably unbiased, and similar for MASK-INT

($C = 0.16$) and MASK-HIGH ($C = 0.29$). Fine-scale response criterion for MASK-LOW ($C = 0.84$) indicated that responses were more conservative, and less likely for this treatment (Figure 6.12B; Table 6.2; Appendix C).

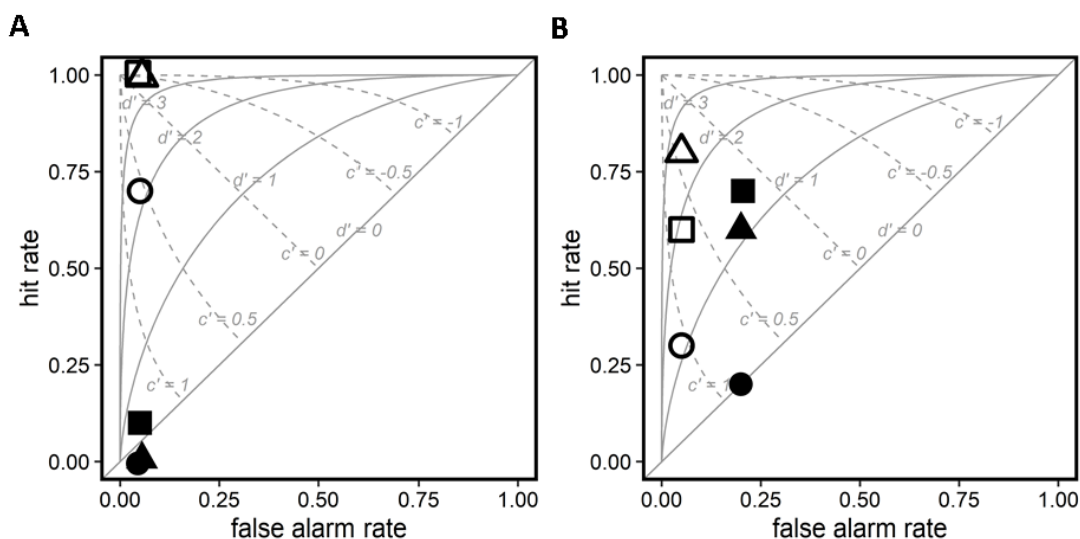


Figure 6.12: Receiver-operating characteristics (ROC) plot of hit rate against false-alarm rate for masked (●, ■, ▲) and ambient (○, □, △) treatment (A) coarse-scale (startle response); and (B) fine-scale (group cohesion) behavioural responses of *Cyprinus carpio* to onset of a tonal acoustic stimuli at -LOW (●, ○); -INT (■, □); and -HIGH (▲, △) signal-to-noise ratio (SNR). *Note:* Light grey lines indicate reference discriminability ($d' = 0, 1, 2, 3$), with an increase in d' representing a greater signal discriminability. Dashed lines show response criterion ($C = -1, -0.5, 0, 0.5, 1$), with an increase in c representing a greater bias toward responding.

Signal discriminability for coarse-scale behaviour was pronounced under ambient treatments and was greater for higher SNR (AMB-LOW: $d' = 2.17$; AMB-INT and HIGH: $d' = 3.29$). Response criterion was positive, reasonably unbiased, and the same for AMB-INT and AMB-HIGH ($C = 5.55e^{-16}$), (Figure 6.12A). For AMB-LOW ($C = 0.56$), the response criterion was slightly more conservative. When investigating fine-scale behaviour, discriminability was again more prominent under ambient treatments, and a clear linear relationship with acoustic intensity was observed. The greater the SNR, the greater the fine-scale discriminability (AMB-LOW: $d' = 1.12$; AMB-INT: $d' = 1.90$; AMB-HIGH: $d' = 2.49$). In general, response criterion for fine-scale behaviour were more conservative than for coarse-scale behaviour. Criterion remained reasonably unbiased for AMB-INT and AMB-HIGH ($C = 0.70$; and $C = 0.40$ respectively), whereas the increase in AMB-LOW

($C = 1.08$) indicated a greater bias towards not responding for this treatment (Figure 6.12B; Table 6.3; Appendix C).

Table 6.2: False alarm (FAR) and hit rates (HR) for trial groups exposed to 170 Hz tonal stimuli under masked noise treatments determined through the calculation of linear least squares regression models. Note: Grey shading indicates that a trial (01-10) deviated from the group “normative fit” (regression line equation: $y = 0.304 - 4.8 \times 10^{-6} x$; \pm s.e. = $\pm 2.14 \times 10^{-5}$; CI [-4.69×10^{-5} ; 3.73×10^{-5}]) and was classed as a “false alarm” (incorrect response for control) or “hit” (correct response for treatments). A \diamond next to 95% confidence intervals indicates the use of BCa CI.

<u>MASK-C</u>	Trial no°									
(FAR = 0.2)	01	02	03	04	05	06	07	08	09	10
Lower CI	-5.15 $\times 10^{-4} \diamond$	1.22 x 10^{-4}	-2.72 x 10^{-5}	-3.98 x 10^{-5}	-1.39 x 10^{-5}	-8.97 x 10^{-5}	-1.44 x 10^{-4}	-1.26 x 10^{-4}	-1.03 x 10^{-4}	-3.05 x 10^{-5}
Upper CI	-2.43 x $10^{-4} \diamond$	2.82 x 10^{-4}	8.07 x 10^{-5}	1.81 x 10^{-4}	1.41 x 10^{-4}	6.19 x 10^{-5}	7.28 x 10^{-5}	4.36 x 10^{-5}	1.20 x 10^{-4}	1.30 x 10^{-4}
<u>MASK-LOW</u>										
(HR = 0.2)	01	02	03	04	05	06	07	08	09	10
Lower CI	4.15 x 10^{-5}	-6.03 x 10^{-5}	-4.11 x $10^{-5} \diamond$	3.32 x 10^{-5}	-5.48 $\times 10^{-5} \diamond$	-1.14 x $10^{-4} \diamond$	-1.77 x 10^{-5}	-5.08 x 10^{-5}	2.90 x 10^{-5}	9.49 x 10^{-5}
Upper CI	2.64 x 10^{-4}	1.35 x 10^{-4}	1.58 x $10^{-4} \diamond$	1.80 x 10^{-4}	9.73 x $10^{-5} \diamond$	1.05 x $10^{-4} \diamond$	1.43 x 10^{-4}	1.46 x 10^{-4}	1.84 x 10^{-4}	2.85 x 10^{-4}
<u>MASK-INT</u>										
(HR = 0.7)	01	02	03	04	05	06	07	08	09	10
Lower CI	-1.60 x 10^{-4}	4.90 x 10^{-5}	6.62 x $10^{-5} \diamond$	9.41 x $10^{-5} \diamond$	1.01 x $10^{-4} \diamond$	-1.20 x 10^{-4}	-9.51 x 10^{-5}	9.72 x 10^{-5}	1.31 x 10^{-4}	1.39 x 10^{-4}
Upper CI	9.85 x 10^{-5}	2.50 x 10^{-4}	3.15 x $10^{-4} \diamond$	3.03 x $10^{-4} \diamond$	2.97 x $10^{-4} \diamond$	8.32 x 10^{-5}	1.26 x 10^{-4}	2.50 x 10^{-4}	3.79 x 10^{-4}	3.84 x 10^{-4}
<u>MASK-HIGH</u>										
(HR = 0.6)	01	02	03	04	05	06	07	08	09	10
Lower CI	-9.77 x 10^{-5}	-1.40 x 10^{-4}	-4.26 x 10^{-5}	1.30 x 10^{-4}	6.36 x 10^{-5}	1.59 x 10^{-4}	-9.34 x 10^{-5}	6.64 x 10^{-5}	6.94 x 10^{-5}	1.08 x 10^{-4}
Upper CI	7.39 x 10^{-5}	1.21 x 10^{-5}	1.24 x 10^{-4}	3.42 x 10^{-4}	2.52 x 10^{-4}	3.22 x 10^{-4}	9.56 x 10^{-5}	2.76 x 10^{-4}	2.36 x 10^{-4}	2.67 x 10^{-4}

Table 6.3: False alarm (FAR) and hit rates (HR) for trial groups exposed to 170 Hz tonal stimuli under ambient noise treatments determined through the calculation of linear least squares regression models. Note: Grey shading indicates that a trial (01-10) deviated from the group “normative fit” (regression line equation: $y = 0.217 + 3.84 \times 10^{-5} x$; \pm s.e. = $\pm 2.04 \times 10^{-5}$; CI [-1.78 $\times 10^{-6}$; 7.85 $\times 10^{-5}$]) and was classed as a “false alarm” (incorrect response for control) or “hit” (correct response for treatments). A \diamond next to 95% confidence intervals indicates the use of BCa CI.

AMB-C (FAR = 0.0)	Trial no°									
	01	02	03	04	05	06	07	08	09	10
Lower CI	-1.24 x 10 ⁻⁵	-7.22 x 10 ⁻⁵	-7.46 x 10 ⁻⁵	-1.12 x 10 ⁻⁴	-2.05 x 10 ⁻⁴	-1.19 x 10 ⁻⁵	1.53 x 10 ⁻⁵	-1.15 x 10 ⁻⁴	3.03 x 10 ⁻⁵	-1.67 x 10 ⁻⁴
Upper CI	1.55 x 10 ⁻⁴	1.34 x10 ⁻⁴	2.06 x 10 ⁻⁴	1.19 x 10 ⁻⁴	2.93 x 10 ⁻⁵	2.26 x10 ⁻⁴	2.14 x 10 ⁻⁴	1.09 x 10 ⁻⁴	2.18 x 10 ⁻⁴	8.04 x 10 ⁻⁵
AMB-LOW										
(HR = 0.3)	01	02	03	04	05	06	07	08	09	10
Lower CI	-1.30 x 10 ⁻⁴	-2.33 x 10 ⁻⁴ \diamond	-5.44 x 10 ⁻⁵	-1.80 x 10 ⁻⁴	-2.00 x 10 ⁻⁴	-1.55 x 10 ⁻⁴ \diamond	-3.05 x 10 ⁻⁴ \diamond	3.17 x 10 ⁻⁴	-8.74 x 10 ⁻⁵ \diamond	5.23 x 10 ⁻⁵
Upper CI	4.98 x 10 ⁻⁵	-1.42 x 10 ⁻⁵ \diamond	6.16 x 10 ⁻⁵	3.31 x 10 ⁻⁵	8.50 x 10 ⁻⁵	-4.58 x 10 ⁻⁵ \diamond	-9.58 x 10 ⁻⁵ \diamond	5.45 x 10 ⁻⁴	1.39 x 10 ⁻⁴ \diamond	2.94 x 10 ⁻⁴
AMB-INT										
(HR = 0.6)	01	02	03	04	05	06	07	08	09	10
Lower CI	-5.13 x 10 ⁻⁵ \diamond	-1.50 x 10 ⁻⁴	-4.37 x 10 ⁻⁵	-1.40 x 10 ⁻⁴	5.13 x 10 ⁻⁵	-2.03 x 10 ⁻⁴ \diamond	1.84 x 10 ⁻⁴	-2.30 x 10 ⁻⁴	-1.20 x 10 ⁻⁴	-9.34 x 10 ⁻⁵
Upper CI	1.56 x 10 ⁻⁴ \diamond	-1.61 x 10 ⁻⁵	1.54 x 10 ⁻⁴	1.37 x 10 ⁻⁵	2.98 x 10 ⁻⁴	-1.16 x 10 ⁻⁵ \diamond	4.24 x 10 ⁻⁴	-6.66 x 10 ⁻⁵	-4.28 x 10 ⁻⁵	4.37 x 10 ⁻⁶
AMB-HIGH										
(HR = 0.8)	01	02	03	04	05	06	07	08	09	10
Lower CI	-4.00 x 10 ⁻⁴	-1.50 x 10 ⁻⁴	-2.50 x 10 ⁻⁴	-9.40 x 10 ⁻⁵	-4.12 x 10 ⁻⁴ \diamond	-1.98 x 10 ⁻⁴ \diamond	1.49 x 10 ⁻⁴ \diamond	-2.40 x 10 ⁻⁴	-2.00 x 10 ⁻⁴	1.71 x 10 ⁻⁴
Upper CI	-6.11 x 10 ⁻⁵	2.77 x 10 ⁻⁵	-3.03 x 10 ⁻⁵	5.90 x 10 ⁻⁵	-5.65 x 10 ⁻⁵ \diamond	-4.55 x 10 ⁻⁵ \diamond	3.37 x 10 ⁻⁴ \diamond	-5.58 x 10 ⁻⁵	-6.30 x10 ⁻⁵	4.97 x 10 ⁻⁴

6.4 Discussion

This research chapter investigated coarse and fine-scale behavioural responses of common carp to acoustic tonal stimuli that differed in intensity (SPL), under ambient and masking noise conditions. Groups tested under ambient background noise displayed changes in their collective behaviour in response to the onset of tonal stimuli when compared to control groups. Behavioural adjustments were consistent with previous studies investigating group responses of fish to varying broadband noise sources (*e.g.* European sea bass, *Dicentrarchus labrax*: Herbert-Read *et al.*, 2017; Neo *et al.*, 2014), and low frequency (150 Hz) tonal stimuli (*e.g.* European minnow, *Phoxinus phoxinus*: Chapter 4 and 5). Observed changes included a discernible startle response, a decline in swimming speed, reduced orientation, and an increase in group cohesion. The magnitude of departure from control group behaviour was typically larger at higher SNRs, suggesting a linear relationship with acoustic intensity. Under masking noise conditions, however, responses at the onset of tonal stimuli were lower when compared with ambient treatments, with startles absent under all SNR treatments. Masking also suppressed the fine-scale responses (swim speed, group cohesion and orientation), although they increased at higher SNRs.

Startles are commonly observed in response to perceived threats, in which the fish contracts its body before exhibiting distinct burst swimming in an altered direction to its pre-startle trajectory and increased swimming speed (Domenici and Blake, 1997; Nedelec *et al.*, 2015). Under ambient noise, all acoustic treatments elicited a startle response in one or more subject fish. Furthermore, with increasing acoustic intensity, a greater number of fish within a group were observed to startle at the onset of tonal stimuli. A similar effect has been reported for groups of European sea bass in response to relatively louder single strike exposure levels (SEL_{SS} : 122 – 158 dB re 1 $\mu Pa^2 s$) of impulsive pile driving sound playback, with increasing SEL_{SS} observed to provoke an initial startle response in a greater number of schools (Kastelein *et al.*, 2017). In this study, more intense tones also instigated more continuous startles by at least one individual fish within a group. Akin to studies which have investigated startle behaviour among groups of fish using a range of anthropogenic sound sources (*e.g.* underwater gun firings: Wardle *et al.*, 2001; pulse white noise; Neo *et al.*, 2015; pure tone sinewaves: Kastelein *et al.*, 2008; Chapter 4), the coarse-scale behaviour exhibited by individuals was observed to return to “baseline” after relatively few repeated acoustic exposures. Conversely, under acoustically masked conditions, no startle responses were observed (except on one occasion), and signal discriminability was lower. A highly positive response criterion was exhibited, suggesting an overall reduced likelihood of startling, even for the higher SNRs. While contrary to information available on threshold-to-noise ratios in

common carp (*e.g.* auditory evoked potential [AEP]: Amoser and Ladich, 2005; or auditory brainstem response [ABR] audiograms and psychoacoustic experimentation: Kojima *et al.*, 2005), it is understood that data on hearing thresholds will vary, most likely due to variation in acoustic conditions between studies. Furthermore, the absolute sensitivity of the auditory system must be considered in conjunction with the ability of a fish to discriminate or make informative sense of a signal when masked by a background noise (Fay, 2011). While the startle response is a useful behavioural parameter, indicative of a response to a perceived threat (Domenici and Blake, 1997), other internal non-locomotor processes (*e.g.* motivation to escape; behavioural phenotype) may determine the responsiveness of an individual to an acoustic stimulus (Kemp *et al.*, 2012a; Jolles *et al.*, 2020).

To better understand shoal behaviour in response to acoustic stimuli, a more in-depth quantifiable analysis of fine-scale behaviour was conducted. Under ambient noise treatments, group swimming speed was observed to decline during experimentation, and may indicate a fear or anxiety-like behaviour, corresponding to an increased risk, or perception of threat (Neo *et al.*, 2014). A trade-off exists with increasing group activity (*e.g.* swimming speed); increased movement to supplement resource acquisition also elevates the encounter rate, or detection by predators (Anholt *et al.*, 2000). Changes in swimming speed among individuals are highly associated with adjustments in group cohesion and orientation (Kent *et al.*, 2019), and may be used by conspecifics within a group to obtain second-hand information regarding the surrounding environment (Harpaz *et al.*, 2017). An increase in group cohesion, as observed over time during this study, may be highly beneficial, reducing risk through the effects of dilution (Lehtonen and Jaatinen, 2016), confusion (Landeau and Terborgh, 1986), or attack abatement (*i.e.* through risk dilution or swamping of predator functional responses), (Turner and Pitcher, 1986; Pitcher and Parrish, 1993), and thereby leaving fewer individuals isolated or susceptible to predation. At higher SNR, the shift in inter-individual distance was observed to last for longer durations. These continued fine-scale behavioural responses under ambient noise conditions suggested the effects of tolerance, or motor fatigue, not to be an issue for the tonal stimuli tested during this study (Chapter 5). Comparable to group cohesion, orientation similarly provisions information sharing, and an increase in this behaviour among shoal members denotes the detection of a predatory threat (Herbert-Read *et al.*, 2017a). During experimentation, this behaviour was detected at the onset of all tonal stimuli, but rapidly declined over time, with the greatest reduction observed at the highest SNR.

The addition of noise may mask or distract from the detection or response to a stimulus (Fletcher, 1940), a factor frequently overlooked, for instance, in the design and deployment of acoustic

deterrent systems (A. Fewings, Environment Agency, pers com). In this study, fine-scale signal discriminability was greater, and response criterion were less conservative than for coarse-scale startle responses to masked treatments. Nevertheless, added background noise reduced overall fine-scale signal discriminability, with the diminished response to tonal stimuli reflected through a negligible deviation in swimming speed and group alignment from control groups. In contrast, changes in inter-individual distance were significantly suppressed, although groups were observed to increase cohesion in response to tones at higher SNRs under masked noise. Other researchers have also used controlled laboratory studies to examine the response of carp to sound sources within a fisheries management context (*e.g.* bighead carp, *Hypophthalmichthys nobilis*: Taylor *et al.*, 2005; Vetter *et al.*, 2017). Many behavioural experiments are typically performed under relatively quiet laboratory conditions (*e.g.* up to 80 dB re 1 μ Pa: common carp: Zielinski *et al.*, 2014), which do not reflect the higher level noise intensities that exist in the wild (Amoser and Ladich, 2005; Wysocki and Ladich, 2005b). While little data exists in regard to background noise in freshwater habitats (*e.g.* rivers, streams and small lakes: Amoser and Ladich, 2010; Tonolla *et al.*, 2010; Putland and Mensinger, 2020; anthropogenic activity: Amoser *et al.*, 2004; Holt and Johnston, 2015; weirs or hydropower facilities: Johnson *et al.*, 2014; Miyamoto *et al.*, 1989), ambient levels in rivers can be higher (below 100 Hz) than those arising at sea (Hawkins and Johnstone, 1978) where masking has been confirmed to occur even under relatively quiet conditions (Chapman, 1973; Chapman and Hawkins, 1973). Wysocki and Ladich (2005b) noted that although earlier studies have addressed the issue of environmental noise and masking in individual fishes (*e.g.* avoidance conditioning: comet goldfish, *Carassius auratus*; pinfish, *Lagodon rhomboides*; and African mouthbreeder, *Tilapia macrocephala*: Tavalga, 1974; cardiac rhythm or respiratory suppression: cod, *Gadus morhua*; Atlantic salmon, *Salmo salar*; goldfish: Buerkle, 1968; Hawkins and Johnstone, 1978; Fay, 1983), data acquisition of sound detection in fishes is also frequently obtained in the absence of an environmentally representative noise floor. For example, Tavalga (1974) found that individual goldfish required a SNR of approximately 22 dB (re 1 μ Pa) above the masking floor to initiate an avoidance response. Using SDT, this research study similarly observed fine-scale signal discriminability in shoals of carp to increase under the MASK-INT and MASK-HIGH treatments, at SNRs of 11 and 20 dB (re 1 μ Pa) respectively. While it cannot be discerned from this experiment whether fish were responding to auditory information obtained by themselves as an individual, or via the behavioural cues of other fish, it is highly probable that these results reflect the physiological and phenotypic variability among shoal members (Kemp *et al.*, 2012a; Jolles *et al.*, 2020; see Chapter 8.3). Many migratory fish species are known to socially aggregate, and therefore the collective behavioural responses to masked acoustic stimuli is an important topic that warrants further investigation. This will assist in the

design of more effective behavioural deterrent systems to reduce economic and ecological costs associated with invasive species (Pimentel *et al.*, 2000a; Weber and Brown, 2009), or prevent hydropower associated mortalities in native regions (*e.g.* barotrauma: Brown *et al.*, 2014). Moreover, with globally rising levels of impactful anthropogenic noise (Slabbekoorn *et al.*, 2010), data on the ability of fishes to extract important biological information from their local soundscape is required to mitigate for any associated ecological implications (Pijanowski *et al.*, 2011), including the conservation of keystone species.

Masking noise in this study was informed by upstream audio recordings of a micro hydropower plant, and artificial experimental noise therefore had a constant power spectral density (broadband limited random noise), whereby the intensity across frequencies remained equal. It is however important to note that anthropogenic and natural noise sources are often non-random in structure, or “comodulated”; containing temporally complex fluctuations in amplitude that are correlated across certain frequency ranges (Nelken *et al.*, 1999; Branstetter and Finneran, 2008; Trickey *et al.*, 2010; Bee and Vélez, 2018). This study made use of a reductionist small tank setup that provided a stable, reproducible and easily modelled acoustic field. While tank-based studies allow for careful control of confounding factors and provide precursory data for follow-on modelling or field studies (Slabbekoorn, 2016), they are not without their limitations. To better understand the impact of masking noise on group behavioural responses of fish to target acoustic stimuli, results from complimentary methodologies should be combined to ensure ecological validation (*e.g.* Simpson *et al.*, 2016; Ferrari *et al.*, 2018). This may be particularly pertinent for studies investigating the influence of masking noise, as differing environmental conditions have been observed to induce different results in the auditory detection pressure thresholds of more generalist hearing salmonids (*e.g.* *Salmo salar*: Hawkins and Johnstone, 1978).

This research provides evidence of an effect of masking on the coarse and fine-scale behavioural discriminability of a socially shoaling species to tonal acoustic stimuli. Coarse-scale responses were absent, whereas fine-scale group cohesion was significantly suppressed, but increasingly discriminable at higher SNR. This experiment further stresses the need for future studies to better consider background environmental noise when investigating and interpreting the behavioural responses of fishes to an acoustic stimulus of interest (Popper *et al.*, 2020). Results are promising for advising the development of more effective behavioural guidance systems, however, further work is required to understand the impacts of noise on the collective behaviour of fish. For instance, as fish may be better adapted to mitigate for the impact of non-randomly structured noise, the comodulated masking release phenomenon (Hall *et al.*, 1984; Klink *et al.*, 2010; Fay, 2011) could theoretically be exploited when deploying more bespoke acoustic deterrents and

would be an interesting avenue for further investigation. Alternatively, when combined with other stimuli (*e.g.* velocity gradients), the impact of masking on behavioural responses may differ dependent on the uni- or multimodal effect of such stimuli on fish sensory systems (Hasan *et al.*, 2018; Kerr and Kemp, 2019) and warrants future exploration.

CHAPTER 7 **The influence of underwater sound on the upstream route choice of common roach (*Rutilus rutilus*) under different water velocities**

Underwater sound may provide a useful conservation tool to guide the movements of fish away from dangerous areas. Acoustic stimuli have been used to manipulate the swimming paths of cyprinids under still water and low velocity ($< 0.1 \text{ m s}^{-1}$) laboratory conditions, but its effectiveness under different velocities has yet to be tested. Using an open-channel flume, this study quantified the route choice and response of upstream moving common roach (*Rutilus rutilus*) shoals to an acoustic stimulus under three water velocity conditions ('low' [0.16 m s^{-1}], 'intermediate' [0.33 m s^{-1}], or 'high' [0.45 m s^{-1}]). Groups of three fish were offered a choice of route under either an acoustic treatment in which a sound signal (170 Hz pulsed tone) was presented at the entrance to one of two passage routes or, a control where both routes remained "quiet" (ambient noise only). Mean group cohesion was higher and time taken to move upstream and select a channel was greater during the sound treatments compared to the control trials. Shoals more frequently displayed a route switch behaviour prior to selecting the quiet channel in the presence of a tonal stimulus. Velocity had little influence on group behaviour, but discriminability of the acoustic signal and overall efficacy with which fish were deterred from the treatment channel was greatest under the intermediate and high velocities. This study illustrates the importance of understanding the response of fish to acoustic signals in the presence of ancillary abiotic factors and will assist the development of more effective acoustic guidance systems.

7.1 Introduction

River connectivity is necessary to facilitate water-mediated energy, sediment transportation (Deegan, 1993; Atkinson *et al.*, 2019), and movements of aquatic organisms (Northcote, 1978; Jones *et al.*, 2020). Nevertheless, more than two thirds of large rivers are no longer free flowing (Grill *et al.*, 2019) and therefore these environments are considered among the most threatened and modified on the planet (Dudgeon *et al.*, 2006). Widespread development of in-river

infrastructure (*e.g.* dams or weirs) for the provisioning of societal services (*e.g.* flood reduction, energy production, irrigation) has detrimentally impacted freshwater ecosystems (Malmqvist and Rundle, 2002). Alteration to flow disrupts the transfer of sediment and nutrients (Petts and Gurnell, 2005; Bizzi *et al.*, 2015), changes the chemistry and temperature of the water (Meißner *et al.*, 2018), affects the structure of river communities (Carpenter-Bundhoo *et al.*, 2020), and blocks life-cycle essential fish migrations (Northcote, 1978; Duarte *et al.*, 2020). River barriers may be the largest threat to all migratory fish, with freshwater populations plummeting in highly urbanised regions (*e.g.* 93% decline in Europe since 1970) where fragmentation impedes movement between critical habitats (WWF, 2020). While the environmental impact of large hydropower (dams typically above 10 – 15 m high) is well recognised, smaller infrastructure (*e.g.* gauging weirs, small-scale or low head hydropower) is commonly overlooked. This is despite early 19th century development of weirs to facilitate (now decommissioned) water mills (Downward and Skinner, 2005; Garcia de Leaniz, 2008), and more recent endeavours to exploit small-scale opportunities (≤ 10 MW) for hydropower expansion across Europe (Kelly-Richards *et al.*, 2017; Manzano-Agugliaro *et al.*, 2017).

Europe houses the world's most fragmented river landscape, with approximately 864 thousand low-head (< 2 m) structures cumulatively impacting river connectivity (Belletti *et al.*, 2020). Small structures may delay, or block access to upstream habitats that are essential for reproduction, feeding, and refuge purposes (Kubečka *et al.*, 1997). Additionally, delay at structures may deplete energy reserves, reduce migratory motivation (Nyqvist *et al.*, 2017), and leave congregating fish more susceptible to predation (Lucas *et al.*, 2009). Such impacts may be particularly problematic for potamodromous fish (*e.g.* Cyprinids: Ovidio *et al.*, 2017) as individuals may need to pass structures on multiple occasions to facilitate life essential activities (Piper *et al.*, 2018).

Furthermore, these species are abundant in lowland systems that are prime real estate for small-hydropower scheme development (Piper *et al.*, 2018). High water velocities that are common at low-head barriers often exceed the swimming capabilities of many fish species, thereby limiting or delaying upstream fish passage (Armstrong *et al.*, 2004). It is therefore necessary to develop appropriate mitigation tools to reduce the environmental impacts caused by these structures and effectively re-establish habitat connectivity.

A wide range of fish passage structures, or 'fishways' (*e.g.* vertical slot, Denil, pool-and-weir, nature-like) have been designed to restore river connectivity and facilitate upstream movement of fish (Schilt, 2007; Bunt *et al.*, 2012). While fishways are commonly constructed to match the physiological swimming capabilities (*e.g.* maximum sustained swimming speed) of target species, unsuccessful passage or delay to migration still occurs when individuals fail to completely ascend

a fishway or are unable to initially detect the attraction flow of a fishway entrance (Schilt, 2007; Cooke and Hinch, 2013). To improve overall passage, behavioural guidance systems may be installed to repel fish from undesirable areas and guide them towards preferred routes (Schilt, 2007). For example, acoustic stimuli may be used to maximise attraction efficiencies and increase river connectivity during the upstream migration of native species (Lange *et al.*, 2018; Wilkes *et al.*, 2018). The biological relevance of sound to fish (*e.g.* in navigation: Simpson *et al.*, 2005a; predator avoidance: Ward *et al.*, 2011; mate selection: Mann and Lobel, 1997; conspecific interactions and male competition: Salas *et al.*, 2018) and recorded response of many species to man-made noise (Slabbekoorn *et al.*, 2010), supports the use of acoustics as an effective stimulus in such technologies (Popper and Carlson, 1998). While laboratory studies have investigated the response of cyprinids (*e.g.* silver carp, *Hypophthalmichthys molitrix*: Vetter *et al.*, 2015; Murchy *et al.*, 2017; bighead carp, *Hypophthalmichthys nobilis*: Taylor *et al.*, 2005; Murchy *et al.*, 2017; Vetter *et al.*, 2017; common carp, *Cyprinus carpio*: Zielinski *et al.*, 2014; straight-mouth nase, *Pseudochondrostoma duriense* and Iberian barbel, *Luciobarbus bocagei*: Jesus *et al.*, 2019a) to sound stimuli within a fisheries management context (*e.g.* control range expansion of invasive species), responses are generally considered under controlled still-water or low velocity environments (*e.g.* 0.05 m s^{-1} : Zielinski *et al.*, 2014; 0.07 m s^{-1} : Jesus *et al.*, 2019a) and do not consider how differing velocity regimes may have an effect on observed responses.

This laboratory based study investigated whether an acoustic stimulus could be used to guide a group of upstream moving cyprinid fish into a channel, using a route choice experimental design. Groups of three individuals were exposed to ambient noise (the control) or a tonal acoustic stimulus (170 Hz of 1 second pulse duration) under one of three water velocities ('low' [0.16 m s^{-1}], 'intermediate' [0.33 m s^{-1}], or 'high' [0.45 m s^{-1}]). A total of 405 fish were tested across 135 independent trials. Common roach (*Rutilus rutilus*) were selected as a model species as they are a highly rheophilic, shoaling species of cyprinid (Christensen and Persson, 1993; Eklöv and Persson, 1995), with a widespread local distribution and good hearing sensitivity (Amoser *et al.*, 2004). This study quantified: (1) the influence of underwater sound on cyprinid group behaviour (group cohesion [m], latency time [sec], passage time [sec]); (2) the initial group response (*no observable response, reaction, rejection, or route switch*) when approaching a channel; (3) whether the presence of an acoustic stimulus influences the route selection of groups when compared with the performance of control groups; and (4) Signal Detection Theory (SDT) as a framework to determine the influence of water velocity on the ability of fish to detect, discriminate (d') and appropriately respond (C : response criterion, or 'bias') to an acoustic stimulus (Kemp *et al.*, 2012a; Kerr and Kemp, 2019; Chapters 2.6 and 6).

7.2 Materials and methods

7.2.1 Study species and husbandry

In April 2019, common roach (*Rutilus rutilus*) were collected by a licensed fisheries consultant (Fisheries Solutions) using a seine net (5 mm micro-mesh) from Caddington Lake, Bedfordshire, U.K. (51°52'08.0"N 0°27'11.1"W). Roach were selected as a model species owing to their widespread distribution across Europe and western Asia. They are highly rheophilic cyprinid fishes, and a freshwater partial migrant (spawning migration: April-May: Kestemont *et al.*, 1999), with burst swim speeds akin to many potamodromous non-salmonids (Clough and Turnpenny, 2001). Fish were transported on three separate days to the University of Southampton's International Centre for Ecohydraulics Research (ICER) in a well-aerated transport container (average temperature: 12.8 °C; survival: 99.2%). Upon arrival at ICER facilities, roach were acclimated over a period of 1 hour before final transferal to one of two holding tanks (1.5 m x 1.0 m x 0.8 m; water depth: 0.68 m; mean \pm standard error [s.e.] temperatures: 14.95 \pm 0.11 °C and 14.94 \pm 0.1 °C; maximum stocking density: 4.49 kg/m³). Roach were left to acclimatise to captive conditions for 5 days prior to the start of the experiments. Water quality was maintained by a fully automated UV filtered (Cl⁻; PO₄³⁻; NO₃⁻) mains water supply and ammonia remover (Hydra Stream 2 Inline Filter, Ocean Free, Singapore), and monitored to ensure optimum thresholds were adhered to (NO₃⁻ : < 50 mg L⁻¹ ; NO₂⁻ : < 1 mg L⁻¹ ; NH₃ : 0 ; and pH: < 8.4). Fish were kept on a 12:12 h light:dark photoperiod cycle, and fed daily to satiation with a mix of commercially available aquarium flaked and pelleted food. After each trial, fish were weighed (wet mass \pm median absolute deviation [MAD]: 34.3 \pm 9.4 g) and measured (standard length \pm MAD.: 123.0 \pm 10.5 mm). Body metrics of individuals did not differ between treatments (Kruskal-Wallis rank sum test: wet mass: $\chi^2 = 5.6$; *d.f.* = 5; *p* = 0.34; standard length: $\chi^2 = 6.3$; *d.f.* = 5; *p* = 0.28: Appendix B). All experiments were conducted with the approval of the University of Southampton's Animal Welfare and Ethical Review Board (Ethics ID: 48067).

7.2.2 Experimental zone

Trials were performed within a 3 m 'experimental zone' of an indoor recirculating flume (model HM 161: GUNT, Hamburg: 16 m long; 0.6 m wide; 0.8 m depth) at ICER facilities (Boldrewood Innovation Campus). A 100 mm thick polycarbonate flow straightener (7mm diameter tubular porosity) and fine mesh (12 mm spacing) wire screen were placed at the upstream and downstream extent of the experimental zone, respectively. A flow channel divider (100 cm x 20

cm; Figure 7.1) was installed directly downstream of the upstream barrier and was centrally positioned perpendicular to the flow, along the flume channel floor (Figure 7.2). This separated the end of the experimental zone into two equally sized channels (20 cm width each), provisioning fish with a route choice decision: either left or right from the perspective of an upstream swimming group of fish. An acclimation holding pen, where fish were placed prior to a trial commencing, was located 140 cm downstream of the channel divider. The pen comprised of a three-sided wooden frame (50 cm x 43.8 cm x 75.5 cm) wrapped in micromesh (2 mm diameter) material and was positioned centrally in the flume channel. A rope-pulley operated release gate was rigged directly above the unimpeded upstream face of the pen. Upon release, fish could swim into the experimental zone at their own volition.

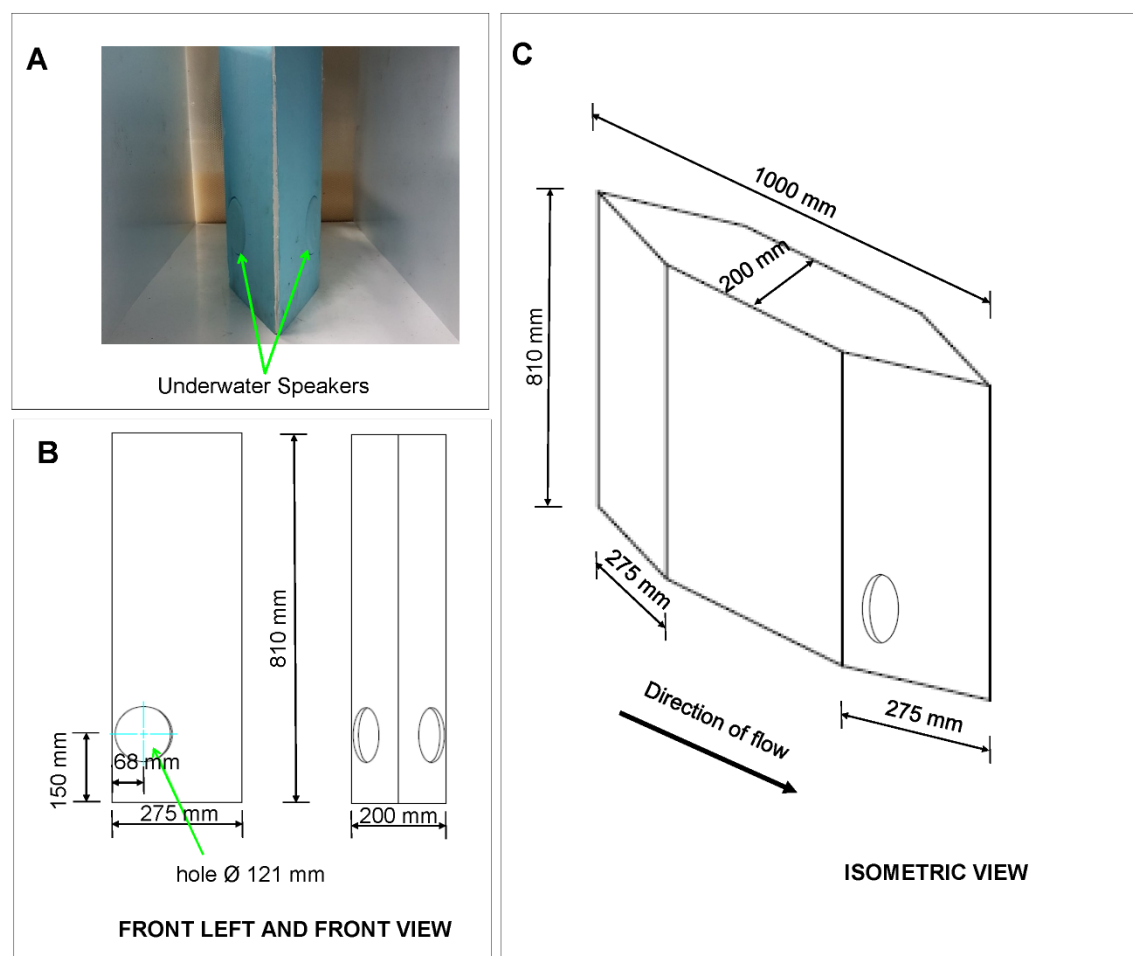


Figure 7.1: (A) Underwater speakers built into customised channel divider; and (B) front left, front; and (C) isometric views of high-density polystyrene foam flow channel divider.

The sound field was generated through two speakers (Electro-Voice UW-30; maximal output 153 dB re 1 μ Pa at 1 m for 150 Hz, Lubell Labs, Columbus, OH, USA) which were embedded into the front left- and righthand sides of the flow channel divider (Figure 7.1), made of high-density polystyrene foam. The speakers were fully immersed and held in place 8.95 cm from the floor of the flume. During trials, flume water was maintained at a constant depth of 30 cm and at a temperature (\pm s.e.) of 16.6 ± 0.1 °C.

In-air background SPLs were monitored through the use of a hand-held recorder (Mini Sound Level Meter N33GJ; measuring level range: 40 – 130 dB; accuracy: ± 3.5 dB @ 1 kHz, 94 dB under reference conditions; frequency weighting: dB(C); frequency response: 0.315-8 kHz; Maplin, Rotherham, UK) to ensure standardised ambient room conditions across treatments (averaged SPL of 50.7 dB re 20 μ Pa). Fish were visually isolated from the experimenter using a plastic frame, draped with white-sheeting material which surrounded the entire experimental zone. Light levels were monitored through the use of a hand-held light meter (Precision Gold N76C; 12 V; measuring range reference level @ 200 lux; accuracy: ± 5 %rdg + 10 dgts (< 10, 000 lux), calibrated to standard incandescent lam, 2856 k; repeatability ± 2 %; temperature characteristic: ± 0.1 %/ °C; Maplin, Rotherham, UK). Consistent lighting (mean \pm s.e.: 33.95 ± 0.4 LUX) during trials, in combination with white plastic sheeting affixed to the interior of the flume walls and floor, allowed for good contrast between the fish and base of the flume for digital video recordings and tracking using a webcam (C920; HD 1080p; 30 frames per second; Logitech Pro, Switzerland) mounted 2.6 m above the centre of the experimental zone. Two additional webcams were installed to monitor fish behaviour. The first surveilled the acclimation holding pen, while the second camera was attached to the top of the rope-pulley operated release gate. This provided an additional high-viewing angle of the upstream experimental zone.

7.2.3 Flow regimes and velocity mapping

Fish responses were assessed under one of three velocities, 'low,' 'intermediate,' or 'high' (Table 7.1) that were selected to be within either the maximal burst or sustained swimming speeds of common roach (Clough and Turnpenny, 2001). Water depth was maintained at 30 cm by adjusting the height of the downstream overshoot weir and altering the discharge of two centrifugal pumps, dependent on the trial velocity condition. The flume was set at an inclination slope gradient of 0.2% during all trials.

Prior to exposing fish to experimental conditions, water velocities in the experimental zone were quantified (Figure 7.2). In total, 355 positions were measured (34 x 11 grid) using an acoustic

Doppler velocimeter (ADV: Vectrino+, Nortek AS, Norway: sample frequency: 50 Hz, sample volume: 0.31 cm³, record length: 60 s) at a single depth, where pre-trial experiments indicated fish to mainly occupy and where the best approximate average vertical flow velocity can be achieved (60% depth: Herschy, 2002).

Table 7.1: Water velocity conditions and measurements of controlled confounding variables.

Water velocity condition	Approach velocity median \pm MAD (m s⁻¹)	Sub-channel maximum velocity (m s⁻¹)	Flow discharge (m³ s⁻¹)	Flume water temperature mean \pm s.e. (°C)	Light levels mean \pm s.e. (LUX)	In-air ambient noise intensity harmonic mean (dB re 20 μPa)
Low	0.07 \pm 0.01	0.16	0.018	16.5 \pm 0.11	33.3 \pm 0.2	49.6
Intermediate	0.16 \pm 0.01	0.33	0.037	16.4 \pm 0.11	33.8 \pm 0.2	51.1
High	0.22 \pm 0.01	0.45	0.050	17.0 \pm 0.13	33.9 \pm 0.2	52.3

Mean velocity (U), was calculated from the filtered (maximum/ minimum threshold filter: Cea *et al.*, 2007) ADV data corresponding to the simultaneously recorded values of x , y , and z in space:

$$U = \sqrt{\bar{u}^2 + \bar{v}^2 + \bar{w}^2} \quad (\text{Equation 7.1})$$

where, \bar{u} , \bar{v} , and \bar{w} denote the time-averaged mean of the longitudinal, lateral and vertical components (m s⁻¹) respectively. The mean velocity was mapped per velocity condition using interpolated colourplots in MATLAB (Release 2015b, The Mathworks, Inc., Natick, Massachusetts, USA). To ensure consistency throughout experiments, water velocity was measured at a fixed location prior to each trial using an electromagnetic flow meter (model 801 EM Flow Meter: Valeport, UK).

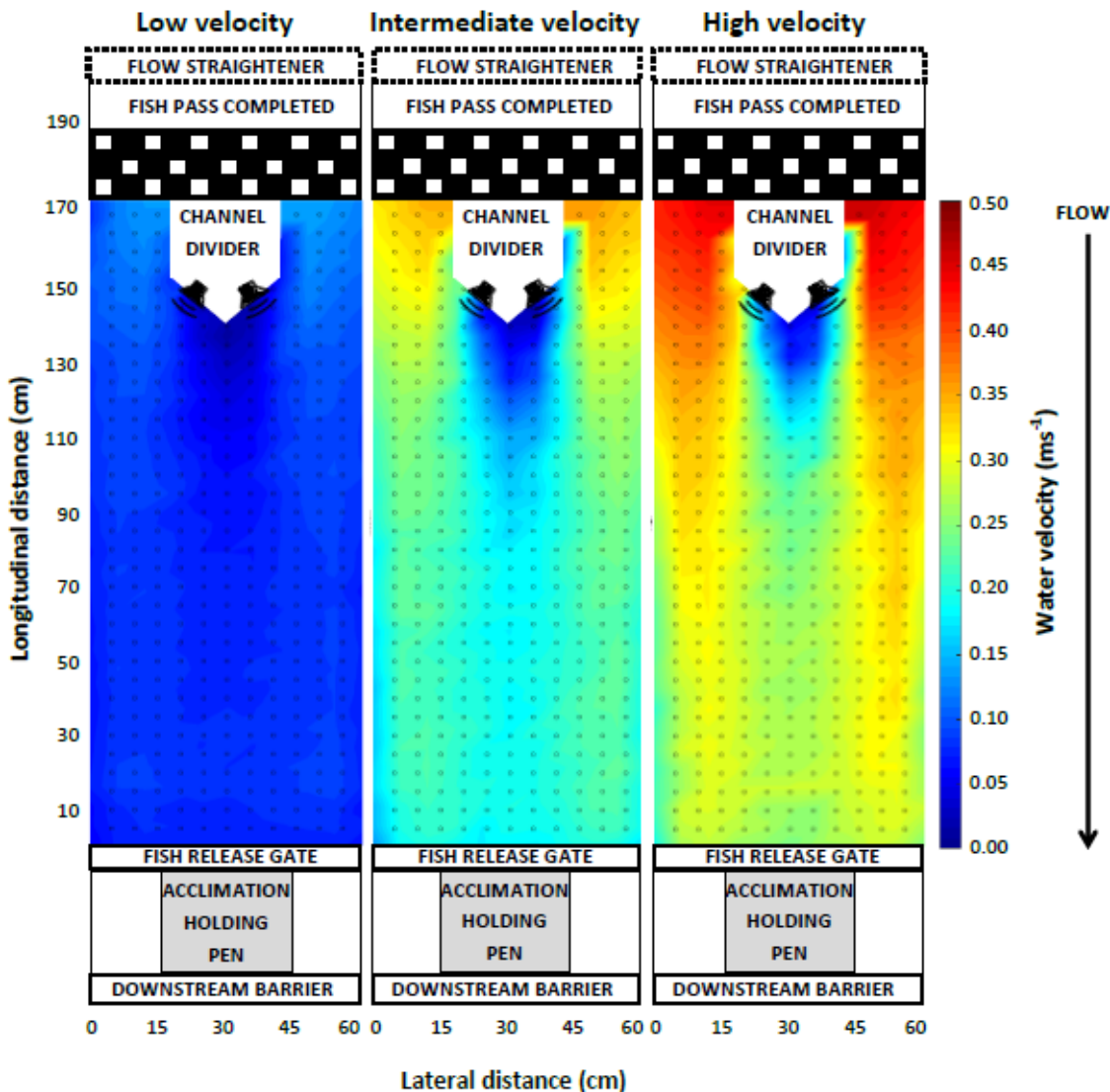


Figure 7.2: Experimental flume set-up with water velocity (m s^{-1}) shown for low, intermediate and high conditions (readings taken at 60% water depth). *Note:* grey points indicate ADV matrix positioning.

7.2.4 Acoustic stimuli and mapping

Sound samples were produced using a custom written MATLAB script on a laptop computer. A USB connected DAQ (NI USB-6241,; National Instruments, UK) converted the digital to analog signal, and output was transmitted through a ProSound 200 power amplifier (50 W, frequency response range approx.: 0.02 – 20 kHz; London, UK), and on to the underwater speakers. Use of differing velocity conditions required changes in the driving rate of the flume hydraulic pump system, and therefore background ambient noise differed between low (110 dB re 1 μPa),

intermediate (107 dB re 1 μPa), and high (112 dB re 1 μPa) flow conditions (Figure 7.3A). To account for these differences, and to replicate background ambient noise levels informed by field recordings at a low-head hydro-power plant (River Dart, Devon, UK: 50°26'20.5"N 3°41'23.8"W; Chapter 6), a standardised artificial masking noise was deployed through both underwater speakers (per velocity: $n = 15$) during control conditions (Figure 7.3B). Masking noise was created using digitally filtered Gaussian white noise (120-3000 Hz), constructed at a sample rate of 25.6 kHz and designed at a fixed intensity of 115 dB re 1 μPa (RMS); the band-pass filter used was a 6th order Butterworth filter. A high-pass filter was applied at 100 Hz to prevent lower frequency resonance issues with the underwater speakers during acoustic playback. SPL was standardised centrally in front of each speaker, 10 cm laterally from the flume wall, and 158 cm longitudinally from the fish release gate.

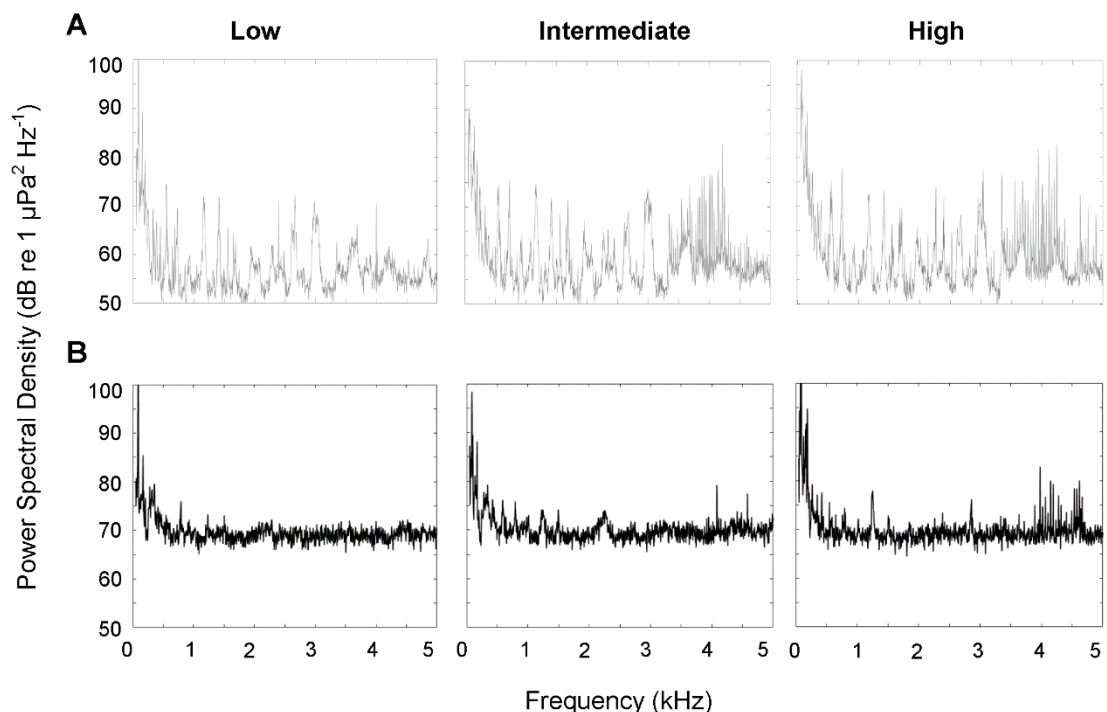


Figure 7.3: Power spectral densities (dB re 1 $\mu\text{Pa}^2 \text{ Hz}^{-1}$) of ambient noise conditions in the experimental zone (sampling rate: 25.6 kHz; FFT 8192; overlap 91.5%; Hanning window; frequency range 50-5000 Hz) under low, intermediate and high velocities **(A)** before (grey lines); and **(B)** after standardisation (black lines) using an artificial masking noise floor.

The acoustic treatment consisted of 170 Hz pulsed tones (one second ON: two seconds OFF; 5 ms ramp-up/ down Hanning taper) played back at 145 dB re 1 μPa (RMS); a signal-to-noise ratio (SNR) of 30 dB above the simultaneously projected artificial masking noise floor (Figure 7.4). Selected

tonal stimuli was within known auditory sensitivities of common roach (100 – 4000 Hz, with lower thresholds observed in the range below 500 Hz: Amoser *et al.*, 2004), and sinewave frequencies of 150 Hz and 170 Hz have previously been observed to elicit changes in cyprinid group behaviour (European minnow, *Phoxinus phoxinus*; and common carp, *Cyprinus carpio*, respectively; Chapter 4, 5 and 6). Playback of noise was emitted from both underwater speakers, while pulsed tones were played through one speaker only, with order of side pseudorandomised throughout trials (per velocity condition: $n_{\text{total}} = 30$; $n_{\text{right}} = 15$; $n_{\text{left}} = 15$).

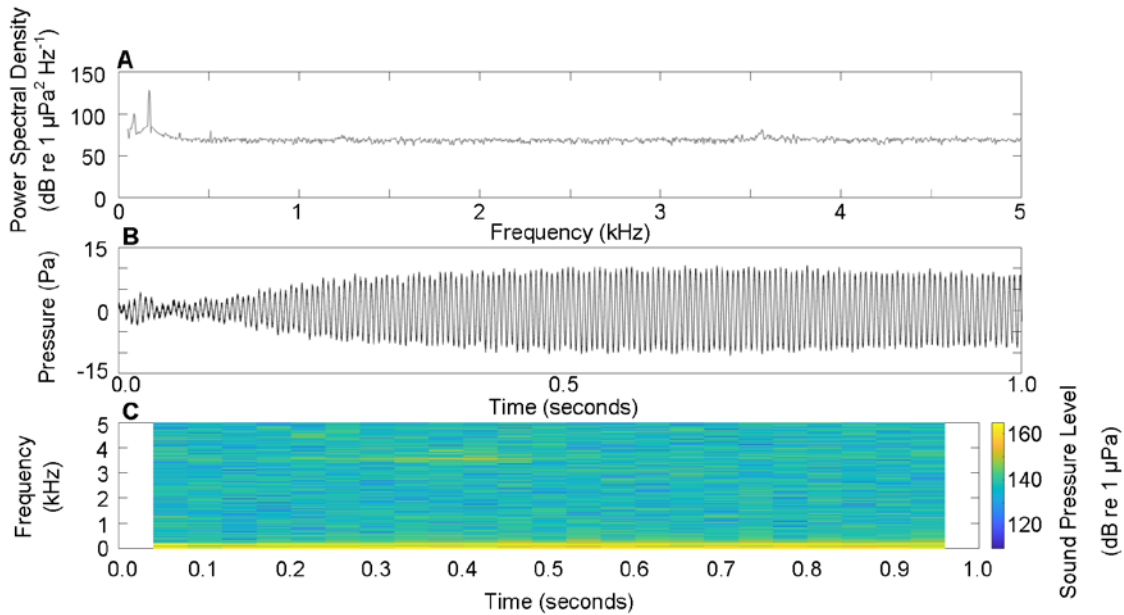


Figure 7.4: (A) Example power spectral density (dB re 1 $\mu\text{Pa}^2 \text{Hz}^{-1}$); (B) waveform; and (C) spectrogram (dB re 1 $\mu\text{Pa}^2 \text{Hz}^{-1}$) of acoustic treatment conditions (170 Hz pulsed tone at SNR 30 dB above 120-3000 Hz broadband noise floor) within the experimental zone (sampling rate: 25.6 kHz; FFT 8192; overlap 91.5%; Hanning window; frequency range 50-5000 Hz).

In advance of running trials, the acoustic environment within the arena was quantified for all treatments and the harmonic mean calculated across all three velocity conditions and at three water depths (7.5 cm; 15 cm; and 22.5 cm). A total of 1092 measurements were taken (34 x 11 x 3 grid) using a hydrophone (Type: TC4013: manufacturer-calibrated sensitivity -211 dB re: 1V μPa^{-1} , frequency response 0.01 Hz – 170 kHz, Teledyne RESON, Slangerup, Denmark) mounted to a depth gauge on a guide rail, and connected to a pre-amplifier (Type: EC6081: 9V; gain +40 dB, high pass filter 100 Hz, Teledyne RESON, Slangerup, Denmark). This was connected to the data acquisition device (DAQ), where the signal was sent to a laptop computer, from which custom

written MATLAB script was used to control and record from the DAQ (sampling rate 25.6 kHz; FFT 1024, overlap 50%, Hanning window). The spatial distribution of the flume sound-field was described using the resulting sound pressure levels (SPL) calculated as the root mean squared (RMS), (Figure 7.5A).

Measures of particle acceleration (m s^{-2}), a , were calculated for the tonal stimulus and background masking noise as the difference in pressure (*e.g.* measured along the x-axis) between two hydrophone points with:

$$a_x = (p_1 - p_2) / \rho d \quad (\text{Equation 7.2})$$

where, $p_1 - p_2$ is the pressure difference measured along the x-axis; d , is the distance between the hydrophones (m); ρ is the density of freshwater (998.4 kg/m^3 at 18.3°C), (Kinsler *et al.*, 1982).

Measurements were taken along three orthogonal axes (x, y, and z) and combined to give a single particle acceleration using:

$$a = \sqrt{a_x^2 + a_y^2 + a_z^2} \quad (\text{Equation 7.3})$$

Results were expressed in decibels ($\text{dB re } 1 \text{ mm s}^{-2}$) and mapped as the harmonic mean across all three depths for the intermediate water velocity condition (Figure 7.5B).

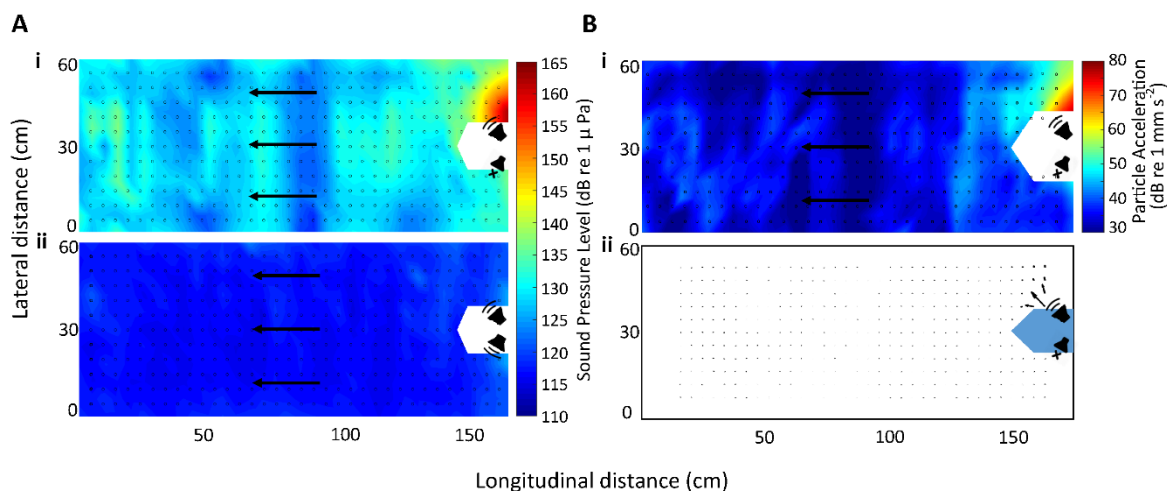


Figure 7.5: Acoustic conditions shown as **(A)** sound pressure level (SPL), ($\text{dB re } 1 \mu\text{Pa}$), (average of three depths: 7 cm; 13.5 cm; 20 cm and velocities: low, intermediate, and high – each treatment was standardised at $145 \text{ dB re } 1 \mu\text{Pa} \sim 15 \text{ cm}$ from the active speaker) for: **(i)** 170 Hz tonal stimulus (left speaker shown in example); and **(ii)** 120-3000 Hz broadband noise floor; and **(B)** particle acceleration level ($\text{dB re } 1 \text{ mm s}^{-2}$), (average of three depths) for 170 Hz tonal stimulus portrayed as: **(i)** heat map; and **(ii)** quiver map indicating directionality. *Note:* Tonal stimulus acoustic field portrayed as left-hand speaker example and open circles indicate hydrophone matrix positioning. Three parallel black arrows display the direction of flow.

7.2.5 Experimental protocol

A total of 135 trials were conducted between 20th April and 24th May 2019 (Table 7.2) and took place from 0800 to 2000 hours, daily. This was deemed appropriate as it was within the peak reproductive migratory season for roach (April-May: Vøllestad and L'Abée-Lund, 1987; Prchalová *et al.*, 2006) where upstream movement typically occurs during daylight hours (Prchalová *et al.*, 2006). For each replicate, three similar sized naïve fish (total $n = 405$) were netted from the holding tank and transported to the test flume in a container (26 L capacity) of water (10 L). Fish were then transferred as a group into the centre of the acclimation holding pen to avoid the confounding influences of introduction order, or spatial bias. At this stage, all three webcam recordings commenced.

Groups were left to acclimate to the pre-running velocity condition for 15 minutes, after which the acoustic treatment started playing through the speakers. Fish were allowed to acclimate for a further 15 minutes (30 minutes total acclimation) before the release gate was opened by the experimenter using a rope-pulley system from a visually isolated workstation. The gate remained open for the remainder of the trial and fish were free to leave the acclimation area at their own volition.

Table 7.2: Treatment parameters and acoustic conditions encountered by *Rutilus rutilus* in experimental trials conducted to assess group behavioural responses to masked tones under differing water velocities.

Acoustic treatment	Velocity condition	Sample size (n)	Standard length median \pm MAD (mm)	Wet mass median \pm MAD (g)
		135	123.0 \pm 10.5	34.3 \pm 9.4
Control (simulated background noise)	Low	15	118.0 \pm 10.4	31.3 \pm 10.7
	Intermediate	15	126.0 \pm 17.8	39.4 \pm 18.5
	High	15	123.0 \pm 16.3	33.3 \pm 12.9
Simulated background noise + pulsed tone	Low	30 total (15 right: 15 left)	125.0 \pm 21.5	38.6 \pm 21.4
	Intermediate	30 total (15 right: 15 left)	125.5 \pm 15.6	36.0 \pm 13.4
	High	30 total (15 right: 15 left)	127.0 \pm 14.8	37.4 \pm 13.6

Assigning playback to a group was determined per velocity using an online random number generator. The order of velocity conditions tested was randomised and was alternated every five days to avoid confounding influence of season, or other order effects. Each group of three fish was used once only. A trial was considered complete either after ≥ 2 fish had successfully completed passage as a group, or, two hours had elapsed, at which point video recordings ceased.

7.2.6 Behavioural parameters and statistical analysis

Fish movements were tracked from video recordings using a custom written MATLAB script. Mean shoal centre ($X_c(n)$) location (x, y axis) was taken for each frame (see Chapter 3.6; Table 3.1). Group behaviour was then calculated from video tracking data as (1) *group cohesion* (m), (2) *latency time* (sec) and (3) *passage time* (sec), (Table 7.3). Data failed to meet assumptions of normality and variance, which were investigated using Shapiro-Wilk and Levene's tests, respectively. Therefore, a two-way bootstrapped ANOVA was performed to assess the influence of sound treatment and velocity on *group cohesion*, *latency time*, and *passage time*. Such an approach uses estimators that are robust to both violations of assumptions and outliers (Wilcox, 2011). Bootstrapped ($n = 5000$) pairwise comparisons were conducted *post hoc* as required.

The initial group response of roach upon first entry to the route choice decision area (Figure 7.6) were categorised as *no observable response*, *reaction*, *rejection*, or *route switch* (Table 7.3; Vowles and Kemp, 2021). A multinomial logistic regression model and likelihood ratio statistic (Type II sum of squares method) were used to determine whether sound treatment and velocity influenced the initial behavioural response. Backwards selection was implemented to achieve a minimal adequate model using the Akaike information criterion (AIC) estimator.

To determine whether route choice (treatment or control channel; Table 7.3) deviated from an expected (50:50) frequency during the sound treatment trials, a goodness-of-fit (χ^2) test was performed.

Using the principles of Signal Detection Theory, discriminability (d') and response criterion (C), were calculated with respect to passage outcome in response to the 170 Hz tonal sound treatment under low, intermediate, and high velocity conditions. Four possible outcomes were determined relative to the initial acoustic experience (*i.e.* whether initial approach was to the active speaker or quiet channel): *Hit*, *Miss*, *Correct non-response*, *False alarm* (Table 7.3; Chapter 6.2.5; Kemp *et al.*, 2012a).

In 24% of trials individuals were observed to startle in response to the opening of the fish release gate, traverse the channel in isolation (*i.e.* as opposed to a group of ≥ 2 fish), or spawning interactions took place within mixed-sex groups (*e.g.* territorial infighting). Such behaviours were deemed not to be in response to the test conditions and were therefore not included in the final analyses. All statistical analysis was performed conducted in RStudio (v 3.2.2: The R Foundation for Statistical Computing, Vienna, Austria, <http://www.r-project.org/>).

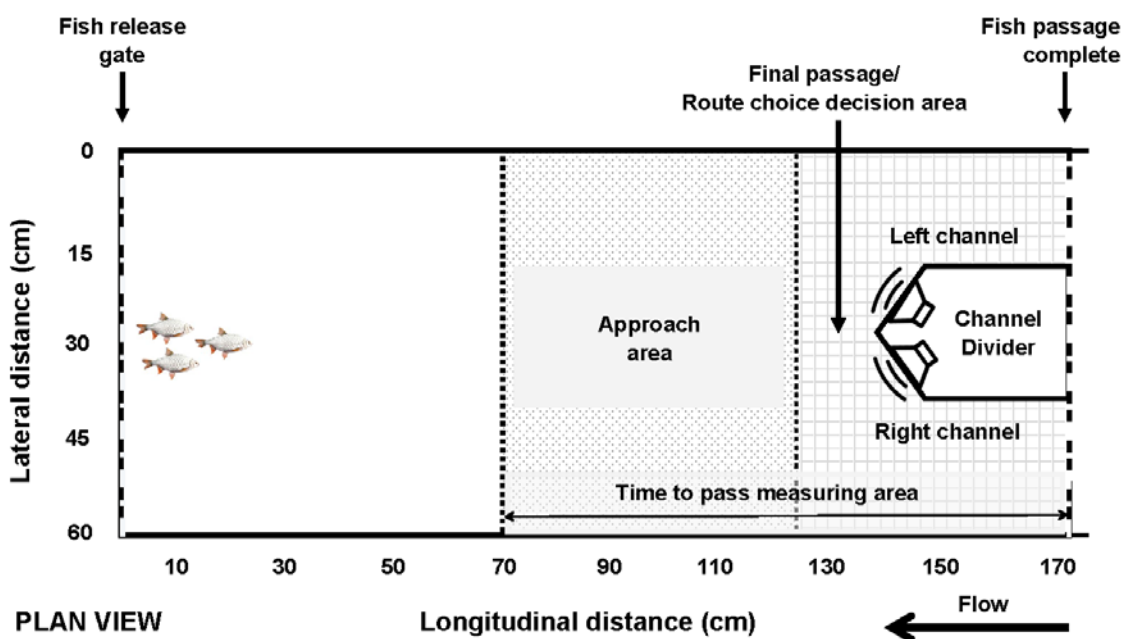


Figure 7.6: Experimental zone within indoor recirculating flume. A custom-built flow channel divider made of high-density polystyrene foam was installed centrally at the upstream end of the zone, providing fish with a route choice decision. The crossed and meshed sections represent the approach and final passage areas, respectively. The two zones combined represent the area for which “passage time” was measured.

Table 7.3: Metrics used to assess the group behaviour of common roach (*Rutilus rutilus*) in response to playback of a 170 Hz tonal stimulus, under low, intermediate and high velocity conditions.

Group Behaviour	Definition	Statistical Analyses
Group cohesion (m)	Average inter-individual distance (m) during final time to pass. Defined as the mean distance from $(X_c(n))$, with measurements taken at the centre point of each fish	Two-way bootstrapped ANOVA ($n = 5000$)
Latency time (sec)	Time from fish release gate opened (Figure 7.6), to first whole body fish length exiting acclimation holding pen	
Passage time (sec)	Time from first whole fish body length entering approach area for the final time, to last whole fish body length completing passage	
Initial response	One of four outcomes upon first entry to route choice decision area, categorised with increasing magnitude of hierarchy of response (1-4)	
1. No observable response	Entrance into route choice decision area (Figure 7.6) without alteration to movement behaviour (e.g. swimming trajectory or speed of upstream movement)	Multinomial logistic regression model and likelihood-ratio statistic
2. Reaction	Explore, delay, change in swimming kinematics (e.g. acceleration or startle response)	
3. Rejection	180 ° turn in body position from positive to negative rheotaxis followed by a downstream movement for at least one body length	
4. Route switch	Altered swimming trajectory: movement from one side of the flume to the other prior to route selection	
Route choice	Fish complete passage via sound treatment or control channel (Figure 7.6)	χ^2 goodness-of-fit statistic
Signal detection	One of four outcomes applied to Signal Detection Theory	
Hit	Group initially approaching active speaker changes trajectory to complete passage via “quieter” channel	Signal discriminability (d') is measured in standard deviation units (z-scores) for right-tail probabilities of the normal distribution, where: $d' = z(\text{Hit Rate}) - z(\text{False Alarm Rate})$
Miss	Group initially approaching active speaker persists to complete passage via active speaker channel	
Correct non-response	Group initially approaching inactive speaker persists to complete passage via “quieter” channel	
False alarm	Group initially approaching inactive speaker changes trajectory to complete passage via active speaker channel	

7.3 Results

7.3.1 Group cohesion

Group cohesion (m) was influenced by sound treatment (two-way bootstrapped ANOVA: $p < 0.001$; Figure 7.7A), with groups exposed to a 170 Hz tonal stimulus reducing the inter-individual distance between shoal members in comparison to control groups. Velocity did not influence group cohesion ($p = 0.35$), and no interaction effect was observed ($p = 0.35$).

7.3.2 Latency time

Latency to exit the gate (sec) during each trial was influenced by sound treatment (two-way bootstrapped ANOVA: $p < 0.001$; Figure 7.7B), but not velocity ($p = 0.09$). An interaction effect ($p < 0.05$) was also observed, however, *post hoc* analysis did not identify any significant pairwise comparisons. Groups under low and intermediate velocity conditions reduced their latency time during sound treatments relative to “quiet” control trials (low: $p = 0.15$; intermediate: $p = 0.14$), while the opposite affect was observed for those exposed to high velocity conditions (mean latency time of 16.2 sec and 216.2 sec under the control and treatment conditions, respectively: Figure 7.7B), ($p = 0.08$).

7.3.3 Passage time

Passage time (sec) was influenced by sound treatment (two-way bootstrapped ANOVA: $p < 0.001$; Figure 7.7C), with treatment groups taking longer to pass than under control trials. A linear relationship with velocity ($p < 0.05$) was observed, with groups taking longer to pass, the higher the water velocity. An interaction effect was also observed ($p < 0.05$), indicating effects to be for the high velocity condition, but further *post hoc* analysis determined this to be non-significant ($p = 0.08$).

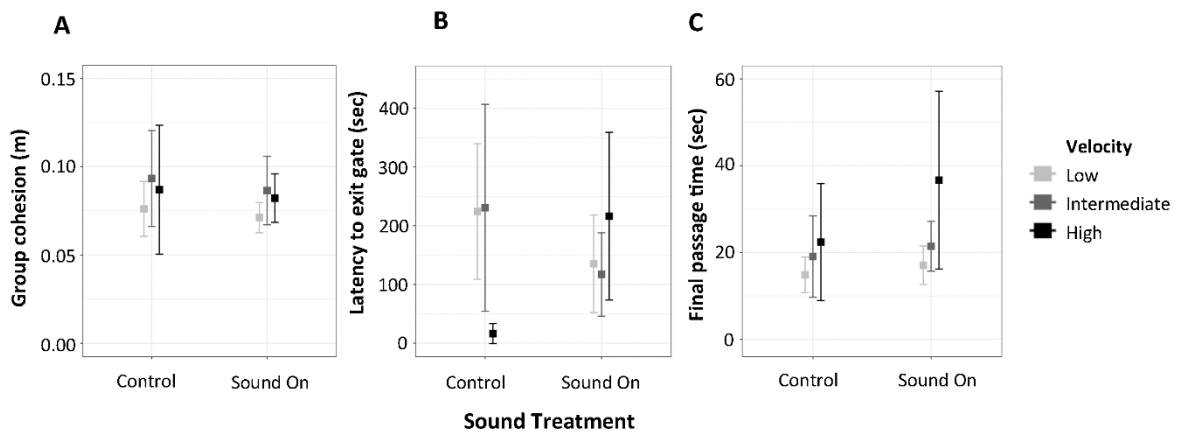


Figure 7.7: Mean (\pm s.e.) **(A)** group cohesion (m), **(B)** latency time (sec); and **(C)** passage time (sec) of common roach approaching a 170 Hz pulsed tonal stimulus under low, intermediate, and high velocity conditions.

7.3.4 Initial response

Upon first entry to the choice area, initial group response was influenced by sound treatment ($\chi^2_3 = 16.12$; $p < 0.01$; Figure 7.8) with roach increasing the ratio of reactions (9.42; $CI = 2.60, 34.09$), rejections (8.99; $CI = 1.96, 41.28$), and route switch behaviours (10.43; $CI = 2.13, 51.09$) in comparison to control groups. The effect of sound treatment was also dependent on the channel side of approach (*i.e.* active vs inactive speaker; $\chi^2_6 = 19.91$; $p < 0.01$; Figure 7.8; Appendix D). Fish groups were observed to increase expression of a route switching behaviour by a ratio of 10.73 ($CI = 1.91, 60.43$; $p < 0.01$) upon approaching the channel with the active speaker when compared to control groups. Velocity did not influence the initial behavioural response ($\chi^2_6 = 3.65$; $p = 0.72$).

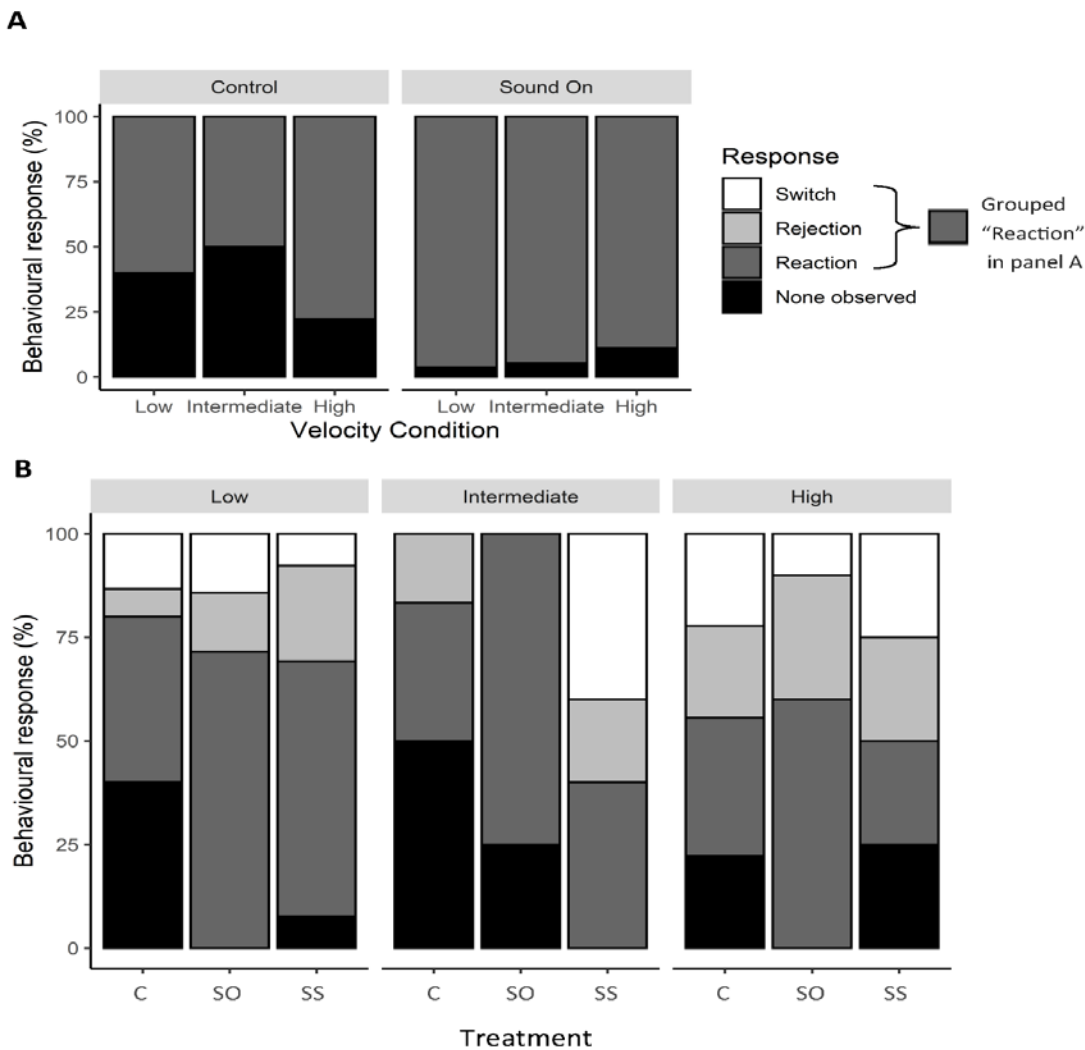


Figure 7.8: Initial response of groups of three upstream moving common roach (*Rutilus rutilus*) within the route choice decision area as they encountered one test channel (SS: Same as speaker) playing back a 170 Hz pulsed tone (one second ON: two seconds OFF) at 145 dB re 1 μ Pa (RMS), or a “quieter” channel (SO: Opposite speaker) with no tonal playback. Side of playback (right or left) was randomised throughout trials. Under the control treatment (C), both channels were “quiet”. **(A)** Difference in initial *reaction vs none observed* between control and sound treatment conditions under low, intermediate and high velocity conditions; and **(B)** difference in initial response (*none observed, reaction, rejection, route switch*) relative to the channel approached (control, opposite speaker, same as speaker) at different velocities.

7.3.5 Channel selected

Selection of channel passage during control trials did not differ from 0.5 as expected under control (absence of 170 Hz tone) conditions ($\chi^2 = 0.00$; $d.f. = 1$; $p = 1$; Figure 7.9). However, when provided the option of either a “quiet” or treatment (170 Hz tone) channel, the route selected deviated from expectation ($\chi^2 = 4.27$; $d.f. = 1$; $p < 0.05$; Figure 7.9), with more groups completing passage via the “quieter” channel (58.33%, 66.67% and 66.67% during low, intermediate, and high velocity conditions, respectively).

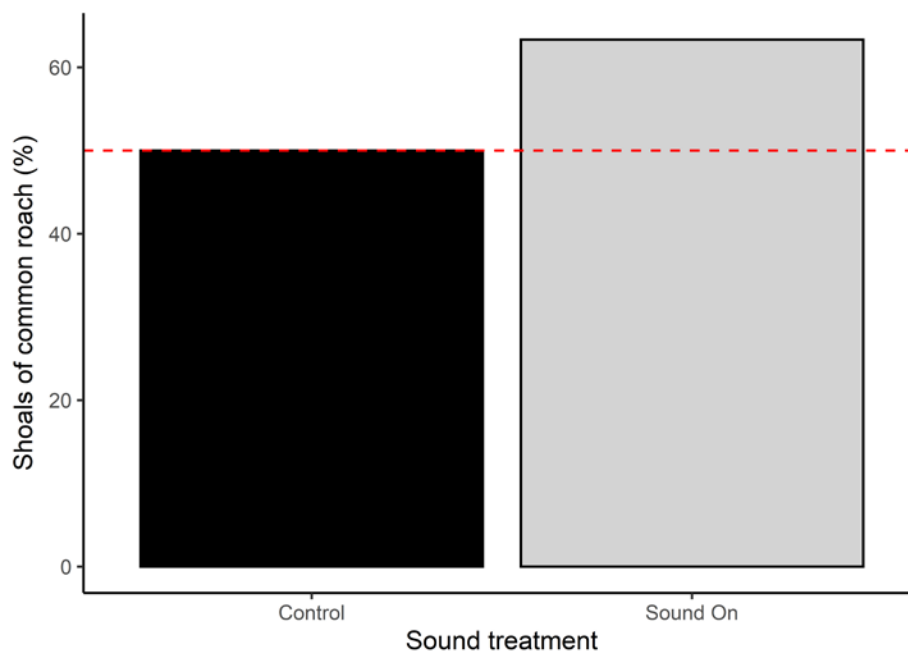


Figure 7.9: Percent of common roach (*Rutilus rutilus*) that selected the “quieter” control channel over the treatment (sound on) channel while swimming upstream in an experimental flume. The dashed line indicates an expected 50% frequency, where the null hypothesis states that underwater sound has no influence on channel selection.

7.3.6 Signal detection

Signal discriminability was two times greater under intermediate ($d' = 0.86$) and high ($d' = 0.84$) velocity conditions in comparison to the low velocity ($d' = 0.43$), (Figure 7.10). Response criterion was positive for the low velocity ($C = 0.82$), indicating a general bias in which fish were less likely to respond to the underwater sound treatment. Comparatively, response criterion for the intermediate ($C = 0.00$) and high ($C = 0.10$) velocities were relatively unbiased (Figure 7.10).

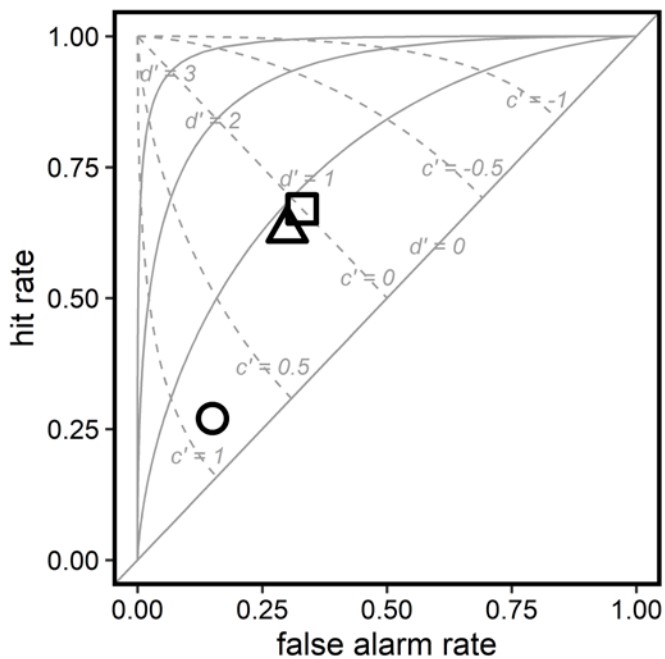


Figure 7.10: Receiver-operating characteristics (ROC) plot of hit rate against false-alarm rate for shoals of three common roach (*Rutilus rutilus*) encountering a 170 Hz tonal stimulus under low (○), intermediate (□), and high (△) velocity conditions. *Note:* Light grey lines indicate reference discriminability ($d' = 0, 1, 2, 3$), where an increase in d' indicates a greater signal discriminability. Dashed lines show response criterion ($C = -1, -0.5, 0, 0.5, 1$), where an increase in c represents a greater bias toward responding.

7.4 Discussion

This study investigated the group response and guidance of upstream moving cyprinids to an acoustic stimulus, under differing water velocities ('low', 'intermediate', 'high'). When exposed to a 170 Hz tonal stimulus, groups were observed to change their collective behaviour in comparison to control groups. Behavioural changes reflected those observed in previous studies investigating group and individual responses of fish to low frequency tonal stimuli (e.g. European minnow, *Phoxinus phoxinus* to 150 Hz: Chapter 4 and 5; and common carp, *Cyprinus carpio* to 170 Hz: Chapter 6) and broadband noise sources (e.g. European sea bass, *Dicentrarchus labrax*: Herbert-Read *et al.*, 2017a; common goby, *Pomatoschistus microps*: Blom *et al.*, 2019). Roach increased group cohesion, altered their latency to exit an acclimation area, and took longer to complete passage into a divided section of an experimental flume under sound treatment conditions. In the presence of the tonal stimulus, shoals were observed to perform more route switches upon approaching the active speaker channel and completed passage via the "quieter" channel more often than control groups. Furthermore, while changes in velocity had little effect on roach group behaviour, the signal discriminability and subsequent effectiveness of the acoustic stimulus was greater for intermediate and high velocity conditions.

Changes in group cohesion may be used by conspecifics within a group to derive information about their local environment (Harpaz *et al.*, 2017). In this study, an increase in group cohesion, alongside a reduction in the overall variability of this behaviour was observed when fish were exposed to a 170 Hz acoustic stimulus, when compared to control groups. Comparable observations have been reported in work conducted under still water conditions in which group cohesion in shoaling minnows (e.g. 150 Hz tonal stimuli: Chapter 5; and 60 – 2000 Hz random broadband noise: Short *et al.*, 2020) and common carp (e.g. 170 Hz tonal stimuli: Chapter 6) initially increased when exposed to an acoustic stimulus. The response to underwater sound was consistent across all three water velocities whereby flow condition did not influence group cohesion. Similar observations to this study have been reported in experimental work conducted on wild schools of tropical damselfish (*Chromis viridis*) that suggests group cohesion may be maintained across a range of local flow conditions (Nadler *et al.*, 2018). This is beneficial from a fisheries management perspective if it results in fewer individuals being left isolated when using underwater sound to steer shoals toward more desirable passage routes, regardless of flow conditions. Even so, in addition to increasingly altered flow regimes, greater understanding of the influence of other fluctuating abiotic factors on the group response of cyprinids to underwater sound stimuli is needed. For example, human induced elevations in water turbidity (*i.e.*

eutrophication and sedimentation from agricultural practices, urbanisation, and deforestation) may degrade the visual environment for fish. This has been shown to reduce group cohesion in a number of fish species (*e.g.* guppy, *Poecilia reticulata*: Kimbell and Morrell, 2015; three-spined stickleback, *Gasterosteus aculeatus*: Chamberlain and Ioannou, 2019), and could act synergistically, antagonistically or additively with sound, potentially influencing its effectiveness in guiding fish.

Man-made sound is well documented for its propensity to induce behavioural changes that are commonly described as indicators of stress in fish (Sopinka *et al.*, 2016). In this study, roach shoals were observed to alter their latency time to leave an acclimation area in response to the 170 Hz tonal stimulus. Contrary to studies investigating the influence of anthropogenic noise on fish behaviour (*e.g.* increased latency to activity: Blom *et al.*, 2019), treatment fish groups took less time to exit the acclimation area in comparison to control groups, and were quick to explore the experimental zone. While an effect of velocity on latency time was not observed, when considering the high velocity condition, control groups were quicker to emerge, but took longer to forgo refuge in the presence of a tonal stimulus. Passage time was also influenced by the presence of underwater sound, with shoals taking longer to pass into one of two channels of equal width in comparison to control groups. Time to pass was also influenced by velocity condition, with fish taking longer to pass, the higher the velocity. Although the resulting increase in passage time may extend the total exposure time to an acoustic stimulus and potentially influence the subsequent response, no interaction effect between sound treatment and velocity was observed for this behaviour. The difference in absolute values of latency and passage times between control and sound treatment groups were small, as was the scale over which these differences were observed (1 - 2 m). From a management perspective, it is important these results are validated using site-specific field trials to determine whether water velocity influences the efficacy of fishways fitted with acoustic guidance technology designed to improve attraction efficiency.

Underwater sound has successfully been used to reduce the encroachment of cyprinids into undesirable areas within still and low water velocity experimental set-ups (*e.g.* Murchy *et al.*, 2017; Jesus *et al.*, 2019a). In this study, a 170 Hz tonal stimulus was observed to influence the initial response and final channel selection by groups of roach under varying flow conditions. In contrast to control groups, when one of the channels was insonified, roach were observed to increase the ratio of group reactions (*route switch, rejection, or reaction*). Importantly, treatment groups displayed a tenfold increase in the expression of a route switching behaviour after initially approaching the active speaker channel. More groups were observed to complete passage via the

“quiet” channel in response to the sound treatment, with most shoals (80.9%) taking one to two approaches into the route choice decision area (range: 1 – 6 approaches) prior to passing. Projection of the pulsed deterrent used in this experiment was uninterrupted throughout the trials and terminated only after shoals had completed passage. An impulsive acoustic stimulus was selected as it is understood to induce greater initial and delayed behavioural changes in fish when compared to continuous sound differing only in temporal characteristic (Neo *et al.*, 2014; 2015b), and should therefore reduce the influence of any short-term behavioural tolerance (Chapter 5). Nevertheless, this study did not test for the effects of tolerance or longer-term habituation to stimulus presentation. Prior to field implementation, future studies must address how repeated or cumulative exposure to an acoustic stimulus under varying flow conditions may deplete any observed response to sound over time, thus ensuring long term effectiveness of acoustic guidance systems.

Understanding the response of cyprinids to underwater sound is necessary to develop effective acoustic deterrents. However, it is imperative that we also recognise how differing water velocities may influence the ability of fish to detect, discriminate (*d*) and appropriately respond (*C*) to an acoustic stimulus. Using SDT, this study found signal discriminability of the acoustic stimulus to be two times greater, and the response to be less conservatively biased (*i.e.* more likely to respond) under intermediate and high velocity conditions, when compared to low velocity responses. Zielinski *et al.* (2014) described comparable correlations in common carp, where the combined influence of hydrodynamic and acoustic stimuli generated by bubble curtains were responsible for greater reductions in passage, when compared to acoustic speaker arrays in isolation. Under acoustically near field conditions, the ability of a fish to detect the local flow fields (*i.e.* the particle motion component) of sound and localise an acoustic source (Webb *et al.*, 2008a) may be amplified with increasing water velocities, potentially owing to the added stimulation of pertinent sensory mechanisms. The mechanosensory lateral line system plays a key role in interpreting regional differences in water flow across differing sections of a fish’s body, and under certain conditions, may also be stimulated by sound (Montgomery *et al.*, 2000; Webb *et al.*, 2008a). Similarly, it has also been hypothesised that in addition to hearing, the detection of whole-body accelerations by the sensory hair cells of the inner ear may also provide additional information regarding the presence of a velocity gradient (Kerr and Kemp, 2019). It should be noted that the three water velocities deployed during this study were low fluctuating and tightly controlled. In contrast, less predictable, or more turbulent conditions could have a masking effect on fish behaviour (*e.g.* spatial positions, energetic costs), or response to sound, and requires further investigation.

This study highlights a synergistic effect of water velocity on the group behavioural response of common roach to underwater sound. A 170 Hz tonal stimulus was observed to steer groups of fish away from an insonified channel, and was more discriminable by shoals experiencing the intermediate or high velocity conditions. The study adds to a growing body of evidence that indicates acoustic stimuli to be a useful tool in the freshwater management of cyprinid fishes. Given the range of hydraulic conditions found within rivers, it is recommended that further laboratory and field testing be implemented to understand the implications of these findings. This study demonstrates the need for more work investigating the combined effects of abiotic factors on the response of fish to underwater sound. Such research will help to inform the development of more effective and sustainable acoustic deterrent systems and may also assist in conservation efforts to reduce the negative impacts of anthropogenic noise.

CHAPTER 8 Thesis discussion

Natural underwater sound has clear ecological relevance to most, if not all fish species. Yet the globally rising levels of anthropogenic noise and its negative impacts on fish are recognised as cause for concern (Slabbekoorn *et al.*, 2010). The biological relevance of sound to fish and observed responses to man-made noise, support the use of acoustics as a tool in behavioural guidance systems. These technologies are designed to facilitate the passage of native migratory species and direct them away from anthropogenic hazards, as well as to control the spread of invasive species (Popper and Carlson, 1998). Interest in the use of sound to control the movement of fish has been ongoing for approximately 80 years (Burner and Moore, 1962), and deterrents have been tested across a range of species that are negatively impacted by freshwater barriers to migration (*e.g.* hydropower dams, weirs). Nevertheless, mixed results exist between laboratory and field testing, and efficacies of field deployed acoustic deterrents are rarely higher than 50% (Putland and Mensinger, 2019). Many acoustic guidance systems have been developed based on the audiograms of a target species, however, neglect to consider many factors that are critical to improving such technologies. Crucial elements that require investigation include: 1) behavioural strategies (*e.g.* group-living species); 2) the response of fish to differing acoustic characteristics of a stimulus (*e.g.* signal complexity, pulse repetition rate); 3) system longevity (*e.g.* owing to behavioural tolerance or habituation); and 4) site-specific constraints (*e.g.* background noise, fluctuations in water velocity). The research conducted as part of this thesis addressed these knowledge gaps and advances our fundamental understanding of the group behavioural responses of fish to anthropogenic noise, alongside its application to improving acoustic guidance technologies. This chapter discusses the key findings of this research, including limitations and benefits of the methods used, and provides suggestions for future work.

8.1 Rising underwater sound levels and impacts on freshwater fishes

The hearing mechanisms of fish are dominated by particle motion sensors, but certain groups of fishes are also capable of detecting sound pressure (Popper and Fay, 2011; Putland *et al.*, 2019). The ability to do so runs along a graded continuum, with Otophysan fishes (64% of freshwater species; Nelson *et al.*, 2016), including Cyprinidae, making extensive use of the sound pressure

component (Putland *et al.*, 2019). The evolutionary success and dominance of cyprinids within lowland systems, may be attributed to the shared presence of the Weberian apparatus that connects the swimbladder to the inner ear (Briggs, 2005). This apparatus provides great selective value within the freshwater habitats of this fish family, as it permits an acute auditory reception of the local soundscape (Ladich and Popper, 2004; Amoser and Ladich, 2005). Cyprinids are an important component of fish communities, and owing to their enhanced auditory sensitivities, may prove to be particularly sensitive to the global rise of underwater sound levels (Pieniasek *et al.*, 2020). The results of the meta-analysis in Chapter 2.2 of this thesis support this theory. They indicate that an overwhelming proportion of studies (87.7% of *dataset1*; 90.2% of *dataset2*) have found anthropogenic noise to negatively impact fish. These negative effects alter fish anatomy (*e.g.* hearing loss: Smith *et al.*, 2006), physiology (*e.g.* ontogeny: Nedelec *et al.*, 2015) and behaviour (*e.g.* predator avoidance: Simpson *et al.*, 2015), and have a greater impact on juvenile and adult fish, compared to larvae and eggs. Importantly, results also indicated that noise negatively impacts most fish species, regardless of environment, but the degree of impact is greatest among freshwater fish. This has implications for legislation covering aquatic noise mitigation, which currently exhibits a predominantly marine-centric focus (*e.g.* Marine Strategy Framework Directive). In order to mitigate against the pervasive impacts of this transboundary pollutant of international concern, strategies must become enshrined among terrestrial (including freshwater) protected area legislation, in addition to well-integrated marine policies and protections (Buxton *et al.*, 2017). It is recommended that the impact of anthropogenic noise on freshwater ecosystems warrants further investigation.

8.2 Group responses to underwater sound

Many migratory species employ group-living social structures that have numerous benefits for the individual (*e.g.* mating: Fox *et al.*, 2015; foraging: Day *et al.*, 2001; reduction of energy expenditure: Hemelrijk *et al.*, 2015; or predator avoidance: Larsson, 2009; Handegard *et al.*, 2012). While it is understood that human driven disturbance affects the behaviour and physiology of individual fish, less is known about how acoustic signals influence group behaviour in fish. Previous studies have investigated the group responses of marine fish species to sound (*e.g.* tuna, *Thunnus thynnus*: Sarà *et al.*, 2007; and sea bass, *Dicentrarchus labrax*: Herbert-Read *et al.*, 2017a) and observed alterations to collective behaviour, with shoals spreading further apart in response to an acoustic stimulus. In contrast, research conducted in this thesis quantified the group behavioural changes of freshwater cyprinids in response to underwater sound and described increases in group cohesion. European minnow (*Phoxinus phoxinus*: Chapter 5),

common carp (*Cyprinus carpio*: Chapter 6), and common roach (*Rutilus rutilus*: Chapter 7) were all observed to reduce the inter-individual distance between conspecifics in response to an acoustic stimulus. This increase in group cohesion may be highly beneficial, as it facilitates information sharing, and leaves fewer individuals isolated or susceptible to predation (*e.g.* through risk dilution or swamping of predator functional responses: Turner and Pitcher, 1986; Pitcher and Parrish, 1993: see Chapter 2.3, Table 2.4). Additionally, as observed in Chapter 7, it is apparent that the collective response of cyprinid shoals to underwater sound may be maintained across a range of velocity conditions. Field sites where acoustic guidance systems are deployed commonly experience a range of flow regimes. Preservation of group cohesion in response to acoustic stimuli under such conditions is important to ensure that fish guidance technologies do not delay migration, or counteractively isolate individuals by leaving them more susceptible to predation, or reducing the migratory success of grouping individuals exploiting the net energetic (*e.g.* reduction of drag: Svendsen *et al.*, 2003) and directional decision-making benefits (*i.e.* owing to individual directional uncertainties: Larkin and Walton, 1969; Simons, 2004).

Group swimming speed was also used to quantify the collective behavioural response of fishes to sound in Chapters 4, 5 and 6. Swimming speed is a measure of activity, and, as observed in this body of work, typically declines as perceived risk increases (Anholt *et al.*, 2000). Decreases in swimming speed may be interpreted as a beneficial tactic to enhance information transfer among individuals (Herbert-Read *et al.*, 2011; Miller *et al.*, 2013), and similar responses to acoustic stimuli have been observed in juvenile European sea bass (*Dicentrarchus labrax*: Herbert-Read *et al.*, 2017a). By contrast, an earlier study that also used the freshwater European minnow under a similar experimental set-up to the one used in Chapters 4, 5 and 6 of this thesis (see Chapter 3.2), found no difference between the group swimming speeds of control and acoustically treated shoals (Short *et al.*, 2020). Reported differences in swimming behaviour may reflect the use of an alternative experimental design, or acoustic stimuli (broadband filtered random Gaussian noise between 60-2000 Hz pulsed for 2 sec On, 1 sec OFF; central tank SPL \sim 110 dB re 1 μ Pa @ 400 Hz), however, a myriad of reasons could explain the differences in results reported between studies, and warrants further investigation.

8.3 Context specific responses and acoustic stimuli characteristics

Owing to the large diversity in characteristics of human induced noise (*i.e.* frequency, sound pressure level, particle velocity or acceleration, and temporal waveform), understanding context dependent inter- and intra-specific variation in response to differing sound types is necessary for

the development of environmental impact assessments and subsequent mitigation policies. Chapter 4 investigated how the collective behaviour of European minnow is influenced by signals of differing complexity, under low (150 Hz) and high (2200 Hz) frequencies, and is one of the first studies to intricately quantify spatial avoidance behaviour of freshwater fish to an acoustic stimulus. Shoals of European minnow exposed to low frequency acoustic stimuli were observed to spend more time in areas of lower acoustic intensity, than expected under control conditions. However, further work is required to refine the approach taken, including quantification of spatial avoidance behaviour in the particle motion domain, and under field settings where fish have the option to swim away. While other recent studies have observed broadband noise (*e.g.* outboard motor Hp 4-stroke engine: Vetter *et al.*, 2017) and sweep-up stimulus (*e.g.* repeated sine sweep up to 2 kHz: Jesus *et al.*, 2019a) to elicit a stronger behavioural response in cyprinids than pure tone stimuli, conversely, this study observed simple sinewave tones to induce a detectable collective response more frequently than complex signals. It should be noted that differences in behavioural response may be on account of the use of octave band noise centred around a focal frequency of interest (*i.e.* 150 Hz or 2200 Hz), rather than broadband stimuli encompassing a wider frequency spectrum. Further work is required to better understand the specific components of broadband stimuli that are responsible for negatively impacting fish, and whether certain acoustic characteristics may differentially impact behaviour (*e.g.* increase or decrease in group cohesion). Such information may assist in mitigating against the effects of noise pollution on behaviour and other fish population dynamics (*e.g.* via regulations on use of certain boat engine types: McCormick *et al.*, 2019).

Alternative explanations for the variation in results between acoustic impact studies conducted on the same species could indicate seasonal shifts in behaviour. Hearing sensitivities in fish have been observed to decrease with water temperature (Codarin *et al.*, 2009; Papes and Ladich, 2011), and year-round variability in ambient noise has been observed in many temperate streams (Amoser and Ladich, 2010) and small freshwater lakes (Putland and Mensinger, 2020). Changes in behaviour exhibited by sexually mature individuals during the breeding season may increase freshwater fish (*e.g.* European minnow) susceptibility to predation, and might also explain the differences between studies (Museth *et al.*, 2003). If seasonality does have an impact on baseline hearing thresholds or general behavioural responses of freshwater fish to acoustic stimuli, this may add a further level of complexity when considering conservational management, and therefore mandates future investigation. For instance, seasonal trials (*e.g.* January, April, July, October) using a replicable tank-based or *in situ* set-up could be conducted repeatedly over the course of a four to five year experimental period. This would allow for an investigation of the

group behavioural responses of a cyprinid subject species to a known acoustic stimulus across seasons, and factoring in annual variation. Experiments should be accompanied by long-term acoustic and environmental (*e.g.* temperature, flow regime) monitoring and mapping of the subject species natural habitat. Better understanding the seasonal responses of freshwater fishes to acoustic stimuli is necessary for adaptive management of anthropogenic noise, *i.e.* whether the aquatic environment should be 'quieter' at certain times of the year to protect a specific species of concern, and also to ensure maximal efficacies of acoustic guidance systems during target species peak migratory periods.

Group swimming speed is highly correlated with other behaviours, including polarisation. An increase in group orientation in response to the detection of a predatory threat is similarly used by individuals to gain information and copy the movement decisions of conspecifics (Herbert-Read *et al.*, 2017a; Ginnaw *et al.*, 2020). Alterations to group orientation in response to acoustic stimuli were reported in Chapters 4, 5 and 6 of this body of work, although results varied between studies. The lesser than expected responses observed for this parameter using minnows in Chapters 5 and 6 mirror shoal interaction rules previously described in groups of mosquitofish (*Gambusia holbrooki*), whereby group alignment may be achieved through an alternative mechanism that does not involve the orientation of a neighbour (Herbert-Read *et al.*, 2011). The magnitude of this response may be species dependent, and could also vary with factors including environmental setting, or group size (Shelton *et al.*, 2015). To better understand noise-induced behavioural syndromes, such as how adoption of group alignment may be contextually dependent (Herbert-Read *et al.*, 2011), further investigation is still required.

Larger groups of fish may be better equipped to solve cognitive tasks in comparison to smaller groups, or lone individuals (Ioannou, 2017). Nevertheless, owing to the acoustic scattering properties of a fish swimbladder (or any other air bubble), an increase in shoal size may influence a localised acoustic field (*e.g.* reduce speed of sound through a shoal: Dolder, 2014) and the sensory experience of individual fish (Rogers *et al.*, 2016). Recent work by Short *et al.* (2020) reported group responses to underwater sound as less variable than those of individuals, suggesting that individual fish gather sensory information from the behavioural cues exhibited by others. It would be useful to study: 1) whether this collective behavioural response differs among larger groups of fish (> 5 individuals); and 2) if the acoustic field is influenced by an increasing presence, range of sizes, or spatial distribution of swimbladders. Experimental subjects used during this body of work were euthanised to reduce the limit of contamination to wild populations. In line with the principles of the 3Rs, some individuals from each study were repurposed, whereby swimbladder dissections were performed, and morphological details

recorded. All studies within this body of work conformed to UK legal requirements (Animals [Scientific Procedures] Act 1986) and were approved by the University of Southampton's Ethics and Research Governance Office. In the future, this swimbladder dataset could be applied to the development of swimbladder resonance models or contribute to answering the above questions.

8.4 Behavioural mechanisms, field constraints and acoustic masking

Understanding the behavioural mechanisms that support fish responses to acoustic deterrents is important to inform sustainable management strategies (Blumstein, 2016). Acoustic deterrents may need to be deployed for extended durations and must remain effective over time (*i.e.* ranging from days, to longer exposure periods). Experiments on marine species have noted that temporal structure (*e.g.* pulse repetition rate, ramp-up) plays an important role in the recovery rate of fish to an acoustic stimulus (Neo *et al.*, 2014; Neo *et al.*, 2015b). Chapter 5 investigated the influence of pulse repetition rate on group behaviour and tolerance of the freshwater European minnow and found the longest lasting responses to tonal sequences when shoals were exposed to the intermediate (0.2 s^{-1}) pulse rate treatment. The observed reduction over time in Chapter 5 was, however, considered an instantaneously demonstrable behaviour, rather than habituation (Blumstein, 2016). To confirm habituation, the same individual must be repeatedly tested over time, and display a diminished response (Bejder *et al.*, 2009). Akin to other studies, this body of work (Chapters 4, 5, 6 and 7) investigated single sampling periods, and therefore the latter issue of habituation still remains understudied. Less predictable irregular pulse repetition intervals have been observed to have a greater influence on the habituation rate of individual fish (zebrafish: *Danio rerio*: Shafiei Sabet *et al.*, 2015) than the regular pulse repetition rates used in Chapter 5. Collective responses of fish to acoustic stimuli with irregular pulse repetition rates warrants further investigation, as do group responses to multi-signal stimuli (*e.g.* changing the acoustic stimulus at random over time). Addressing these knowledge gaps will be critical to developing sustainable acoustic deterrent technologies and will require longer-term laboratory and field monitoring studies.

Site-specific constraints, such as the background ambient noise levels at target locations, are another commonly overlooked factor in the deployment of acoustic deterrent systems. In addition to using signal frequencies within the auditory range of a target species, the sound pressure level of a used device must be discriminable from the local soundscape (*i.e.* loud enough to be detected and induce a desired response), but not so loud as to cause hearing damage (*e.g.* temporary: Smith *et al.*, 2004b, or permanent threshold shifts: Popper and Fay, 2011). For most

fish species, in order for a signal to be discriminable, hearing studies suggest it to be at least 10 dB above a noise floor (Buerkle, 1968; Amoser and Ladich, 2005). Chapter 6 used Signal Detection Theory (also see Chapter 2.6) to determine an appropriate signal-to-noise ratio (SNR) above a masking noise floor at which a tonal acoustic signal would induce a desirable behavioural response in common carp. Using fine-scale behavioural analysis, the group behavioural responses of fish to the pulsed 170 Hz tone were observed to be more discernible, the higher the SNR (> 10 dB). While this work provides evidence that the ambient sound level of an environment can mask the response of a socially shoaling species to a tonal deterrent, or biologically relevant cue, as earlier noted, differences in the response of cyprinids to tonal and more complex broadband acoustic stimuli have been reported. It is important to also consider how deployment of the latter may be masked by background noise. Complex signals may be harder to detect than those with sound energy concentrated within a narrower frequency range (Pohl *et al.*, 2009), and therefore the ability of fish to discriminate and respond to specific acoustic components, or signal types within the presence of a background noise, warrants further exploration.

Similar to many psychoacoustic experiments investigating the physiological abilities of fishes to detect a signal within a background noise (*e.g.* Buerkle, 1968; Tavalga, 1974; Fay and Coombs, 1983; Wysocki and Ladich, 2005), Chapter 6 deployed the use of broadband limited random (Gaussian) noise as a masker. Experimental masking noise therefore had a constant power spectral density, whereby the intensity across frequencies remained equal. In this study, masking noise was informed by upstream audio recordings of a micro hydro power plant. It is however important to note that other anthropogenic and natural noise sources are non-random in structure, or “comodulated”, containing temporally complex fluctuations in amplitude that are correlated across certain frequency ranges (Nelken *et al.*, 1999; Branstetter and Finneran, 2008; Bee and Vélez, 2018). Comodulation of different frequency bands in background noise has been observed to facilitate the detection of tones for a range of vertebrate species (*e.g.* humans, *Homo sapiens*: Hall *et al.*, 1984; European starlings, *Sturnus vulgaris*: Klump and Langemann, 1995; mice, *Mus musculus*: Klink *et al.*, 2010; Mongolian gerbils, *Meriones unguiculatus*: Klump *et al.*, 2001; bottlenose dolphins, *Tursiops truncatus*: Branstetter and Finneran, 2008; Cope’s gray treefrogs, *Hyla chrysoscelis*: Bee and Vélez, 2018; and goldfish, *Carassius auratus*: Fay, 2011), and reduce the detection threshold relative to Gaussian maskers. As fish may be better evolutionarily adapted to mitigate for the impact of comodulated noise, this phenomenon could theoretically be exploited (*e.g.* through the addition of flanking noise bands to reduce SNRs) when deploying more bespoke acoustic deterrents, and would be an interesting avenue for further investigation.

8.5 Benefits and limitations of experimental approach

Experiments performed in Chapters 4, 5, and 6, all deployed a reductionist approach, using a stable, homogenous, and reproducible acoustic field within a still-water small tank set-up. This approach allowed for the careful control of confounding factors and provides valuable reference data for complimentary modelling or field studies (Rice *et al.*, 2010; Slabbekoorn *et al.*, 2016). While most tank based fish experiments describe the acoustic pressure field using an averaged power spectral density plot, they often only provide one reading from the centre of the tank, and thereby sample at too few spatial points to capture the complexity of the sound field that the fish may encounter (Leighton *et al.*, 2019). For a more representative and replicable portrayal of the acoustic field, this body of work measured pressure amplitude and phase along a regular grid of points, at 5 cm increments and across three depths. From here, the sound field was intricately described by high-resolution acoustic maps in both the sound pressure (dB re 1 μ Pa) and particle acceleration (dB re 1 mm s^{-2}) domains. Of course, no approach is without its limitations, and it has long been argued that the nature of near-field conditions within a small tank, relative to acoustic wavelength, do not fully replicate more “real world” environments (Akamatsu *et al.*, 2002; Gray *et al.*, 2016). Nonetheless, a recent study on freshwater fish provides evidence that acoustic tank studies may give rise to more natural behaviours than previously given credence (Pieniasek *et al.*, 2020). Pieniasek *et al.* (2020) reported consistent results between fish exposed to noise in the laboratory and those independently introduced to the same sound stimuli (boat noise: 80 – 10 000 Hz at 160 dB re 1 μ Pa) under experimental field conditions. Although conditions within small tanks are far removed from many marine species “natural” aquatic environments, testing acoustic stimuli under such set-ups may produce an acoustic environment more akin to extremely variable, shallow-watered and highly modified riverine field conditions (Leighton *et al.*, 2019). Despite the long-standing debate regarding tank acoustic experiments, laboratory studies may be more relatable to certain freshwater field settings than previously assumed. However, further work is required to better understand the complexities of freshwater soundscapes. While laboratory studies cannot fully reflect the natural behaviour of fish in the wild, they are appropriate for more controlled experiments that provide insight into approximate responses, and may be applicable to broader community-level effects (Pieniasek *et al.*, 2020). Results obtained from Chapters 4, 5, and 6 provided an improved fundamental understanding of fish group responses to underwater sound, and were used to inform the acoustic conditions deployed during the more applied experimental set-up in Chapter 7.

The use of a large open-channel flume in Chapter 7 permitted the use of hydrodynamic cues that were more representative of lotic field conditions, and allowed fish to display more natural compensatory behaviours (*e.g.* burst and glide swimming: Tudorache *et al.*, 2007). Following on from Chapter 6, the use of Signal Detection Theory (SDT: see Chapter 2.6) was also employed in Chapter 7 to quantify the ability of a shoal to detect and respond to acoustic signals under differing velocity conditions. By dissociating the influence of discriminability from bias (*i.e.* the probability of eliciting a response upon detection of a signal), SDT is more accurate than commonly used percentage attraction, deflection, or hit rate (in isolation) metrics, which fail to consider the importance of bias. SDT is therefore beneficial, as it provides both a biologically meaningful performance indicator of decision making, and quantifies the effectiveness of behavioural guidance devices (Kemp *et al.*, 2012a). To the author's knowledge, the experiment conducted in Chapter 7 is the first to investigate the effect of water velocity on the group behavioural response of cyprinids to underwater sound. Behavioural changes in response to a pulsed low frequency tone reflected those observed under still water conditions (*e.g.* increase in group cohesion: Chapters 4, 5, and 6), and the tone was also observed to influence the initial response and final channel selection by groups of roach. Additionally, the signal discriminability and effectiveness of the acoustic stimulus was found to be greater with increasing water velocities. Understanding how water velocity may influence the ability of fish to detect, discriminate and appropriately respond to sound is necessary to develop effective acoustic deterrents.

8.6 Future validation of studies and practical applications

As alluded to earlier in Chapter 7, this experimental study made use of tightly controlled, low fluctuating water velocities that will differ to less predictable turbulent conditions that are frequently encountered in the wild. It would therefore be ideal to validate the work conducted in the laboratory (Chapters 4, 5, 6, and 7) and test the efficacies of acoustic stimuli on a much larger, and longer-term scale, that could also address issues previously discussed regarding habituation (*e.g.* BACI [Before-after-control-impact] acoustic telemetry studies to track fish movements). For example, acoustic guidance systems could be installed in the field (either in isolation, or in conjunction with physical guide screens) adjacent to hydropower stations, or weirs with an available fishway, and would allow for the consideration of more variable and turbulent hydrodynamic conditions. Acoustic and hydrodynamic conditions should be intricately mapped (see Chapters 4, 5, 6, 7) on a seasonal basis, both in advance of and post-installation, and site-specific environmental characteristics should be appropriately modelled into the system design

(*e.g.* influence of bathymetry on bottom and surface reflections). This will ensure a comprehensive understanding of target location specificities, giving fish adequate time to respond to a deployed signal (*i.e.* device positioning relative to water velocity and desired route of passage), and to achieve adequate SNRs and minimal destructive interference of the sound field (Putland and Mensinger, 2019).

Alternatively, when the primary goal is to restrict invasive species, rather than reduce fish mortalities or assist passage of native species, deterrents require strategic placement to prevent further spread (*e.g.* at population bottlenecks such as locks or dams: Putland and Mensinger, 2019) and provide managers the opportunity to isolate, remove, or eradicate problematic fish species (*e.g.* common carp in U.S.A. or Australia). Biological invasions are drastically increasing because of human induced global change including increased temperatures and transportation networks (Assessment, 2005; Fenoglio *et al.*, 2016). Invasive species are a key cause of biodiversity loss (Cardinale *et al.*, 2012; Tittensor *et al.*, 2014) and ecosystem alteration (Simberloff *et al.*, 2013), contributing substantially to ecological, economical and societal costs worldwide (Lowe *et al.*, 2000). Freshwater ecosystems are particularly susceptible to the establishment of aquatic invasive species as native communities are highly vulnerable to biotic exchange (Sala *et al.*, 2000). These environments also house a greater biodiversity per unit area than their respective marine and terrestrial ecosystems (Sala *et al.*, 2000; Dudgeon *et al.*, 2006). Therefore, damage to the ecological health of a freshwater ecosystem has a direct impact on natural capital availability which many human societies depend upon (*e.g.* drinking water, sanitation, renewable energy potential, minerals, agricultural irrigation, fish, transportation, recreation), (Strayer, 2010). It is paramount that more effective strategies, including fit for purpose acoustic or alternative non-physical barriers, be established to reduce these detrimental impacts.

The programme of research presented in this thesis focused on understanding the impact of underwater sound on the group behavioural responses of cyprinids and its applications to improving fish acoustic guidance technologies. Other sensory cues have also been used to modify fish behaviour (*e.g.* light, electricity, bubbles, hydrodynamics: see Chapter 1; Figure 1.1) and have been discussed in detail in other work (Noatch and Suski, 2012). However, it is important that responses to these cues are understood not only in isolation, but, as touched upon in Chapter 7, also in a multimodal context (*e.g.* bubbles and sound: Zielinski *et al.*, 2014) to improve the effectiveness of deterrents or reduce the impacts of habituation. Equally, responses to alternative stimuli require further investigation to mitigate against the cumulative impacts of other emerging threats to freshwater ecosystems, including; light pollution, decline or excess of limiting nutrients,

toxic contaminants, changing climates, and expanding hydropower (Reid *et al.*, 2019). For instance, while acoustics may be used to target commercially viable fish species of interest and increase habitat connectivity following hydropower expansion, it is equally necessary to consider the influence of novel underwater sound on non-target aquatic or terrestrial species (*e.g.* alteration to life-essential feeding or reproductive behaviour: Shafiei Sabet *et al.*, 2015; Maxwell *et al.*, 2018) and community level impacts prior to installation of acoustic deterrent systems. Owing to species diversity and target location variability, a “one size fits all” approach does not exist. Subsequently, commercially available technologies will need to be adapted to cater to pre-assessed individual locations, and systems installed on a bespoke basis (*e.g.* transducer array size and positioning, SNRs, multi-signal capacities, seasonal or diurnal use) to ensure that they are fit for purpose and do not inadvertently result in economic or ecological damage.

8.7 Scientific contributions and conclusions

The research reported in this thesis was conducted in pursuit of better quantifying group behavioural responses of cyprinid fishes to acoustic stimuli to aid conservation efforts, and the development of acoustic deterrent or guidance systems. To realise these aims, five research objectives were identified (also see Chapter 1.1). Conclusions drawn from this body of research, and original contributions to existing knowledge and thinking, have been presented below in relation to each objective:

Objective 1: *Review current literature and highlight research trends and bias and identify knowledge gaps that may assist in understanding how fish respond to sound.*

A literature review, including a quantitative meta-analysis (Chapter 2), highlighted the negative impacts of anthropogenic noise on fish. Unwanted man-made sound was found to alter anatomy, physiology and behaviour, with the greatest impact observed in adult and juvenile fish. Despite the noise impact problem tending to attract a marine-centric viewpoint, it is freshwater fish species which were found to be more affected, therefore raising questions surrounding current policy approaches. The literature review and meta-analysis data search revealed knowledge gaps that were later addressed as research questions in subsequent experimental Chapters 4, 5, 6, and 7. Topics that warranted investigation included: the impact of noise on collective fish behaviour; fish behavioural response to differing acoustic stimulus characteristics (*e.g.* signal complexity, pulse repetition rate); acoustic tolerance or habituation; acoustic masking and behavioural

responses to acoustic stimuli of differing signal-to-noise ratios; and finally, the influence of additional cross-modal stimuli on fish response to sound.

Original contributions from Objective 1 include:

- A subset of the literature review (Chapter 2) was presented, by invitation, at a national conference:
 - *“Towards the development of a globally effective behavioural guidance system for use in fish passage systems.”* SMMPG Conference “Sea Lines of Communication: Discovery”, University of Southampton, UK, November 2016
- Results of the meta-analysis (Chapter 2) were presented (as a poster) at a national conference:
 - *“Using sound to save fish: development of an “acoustic scarecrow” for use in freshwater fisheries management and conservation.”* Student Conference on Conservation Science (SCCS), University of Cambridge, UK, March 2018
- Two conference papers have been published from parts of the literature review (Chapter 2):
 - **Currie (2016).** *Towards the development of a globally effective behavioural guidance system for use in fish passage systems.* In: Sea Lines of Communication Discovery. University of Southampton Press. (ISBN: 9780854329960)
 - Leighton, **Currie et al. (2019).** Analogies in contextualizing human response to airborne ultrasound and fish response to acoustic noise and deterrents. *Proceedings of Meetings on Acoustics.* **37(1)**, 010014. doi:10.1121/2.0001260
- In addition, a paper summarising the findings of the meta-analysis (Chapter 2) is in the final preparation stage for submission to the journal *Fish and Fisheries*, as:
 - **Currie, H.A.L. et al.** Impacts of anthropogenic noise on fish across freshwater and marine habitats: a meta-analysis.

Objective 2: *Assess how the complexity of acoustic stimuli influences the group behavioural responses of fish in a highly controlled and well measured experimental environment.*

Objective 2 was met through novel contributions to science, produced by experimental research (Chapter 4) investigating the collective behavioural responses of European minnow to signals of differing acoustic complexity (simple tone or complex octave band noise) and frequency (low: 150 Hz; or high: 2200 Hz). High resolution video tracking in combination with fine scale acoustic mapping was used to quantify the group behaviour of fish and found low frequency sinewave

tones to have the greatest influence on behaviour. Shoals were also observed to exhibit spatial avoidance behaviour in response to the low frequency treatments. This work advances our understanding of the influence of anthropogenic noise on the spatial distribution and social dynamics within groups of fish and has applications in the development of behavioural guidance systems.

Outputs from Objective 2 include:

- The results of experimental Chapter 4 have been presented at three national conferences:
 - *“Behavioural response of European minnow to acoustic stimuli: Future investigation and potential applications (poster presentation).”* Sustainability in Action, University of Southampton, UK, November 2016
 - *“Towards the development of a globally effective behavioural guidance system for use in fish passage systems.”* SMMPG Conference “Sea Lines of Communication: Discovery”, University of Southampton, UK, November 2016
 - *“Using sound to save fish: development of an “acoustic scarecrow” for use in freshwater fisheries management and conservation (poster presentation).”* Student Conference on Conservation Science (SCCS), University of Cambridge, UK, March 2018
- They have also been presented at one international conference:
 - *“Group behavioural response of cyprinids to artificial acoustic stimuli: implications for fisheries management.”* Fish Passage 2018: International conference on river connectivity, Albury, New South Wales, Australia, December 2018
- Additionally, a paper summarising these findings has been published:
 - **Currie et al. (2021)**. Collective behaviour of the European minnow (*Phoxinus phoxinus*) is influenced by signals of differing acoustic complexity. *Behavioural Processes*. **189**, 104416. doi:10.1016/j.beproc.2021.104416.

Objective 3: *Assess how temporal characteristics of an acoustic stimulus influence the rate of behavioural tolerance in fish groups.*

The experimental research in Chapter 5 addressed Objective 3 through a laboratory study that built on work previously conducted in marine species of fish. Chapter 5 investigated the influence of temporal characteristics on group behaviour and tolerance of a freshwater shoaling fish. The

magnitude of response and the time taken to develop a behavioural tolerance to treatments, or return to baseline behaviour, differed according to pulse repetition rate. Groups displayed the longest lasting response to the intermediate pulse rate of 0.2 s^{-1} . The study used a novel analytical method (running t-statistic over time) to add to our understanding on short-term, or instantaneously demonstrable behavioural recovery to anthropogenic sound. This work highlights the need to better disentangle the fundamental properties of sound (*e.g.* regular or irregular pulse interval timings) which are responsible for inducing negative behavioural changes in fish. This work also calls for longer-term studies that directly address the issue of habituation, which could render acoustic guidance technologies ineffective.

The results of experimental Chapter 5 have been published as:

- **Currie et al. (2020)**. Group behavioral response and tolerance of European minnow (*Phoxinus phoxinus*) to tones of differing pulse repetition rate. *Journal of the Acoustical Society of America*. **147**, 1709-1718. doi: 10.1121/10.0000910

Objective 4: *Utilise Signal Detection Theory to assess the influence of background masking noise on group behavioural responses to acoustic stimuli.*

Although background noise is ubiquitous in nature, it is commonly overlooked when mitigating for the ecological implications of anthropogenic noise masking responses to biologically relevant cues. Chapter 6 advanced our understanding on the impact of high intensity environmental noise on the group behavioural response of fish to a targeted acoustic stimulus. Signal Detection Theory (SDT) was used to investigate coarse and fine-scale responses of common carp. SDT acts as a biologically meaningful performance indicator that not only considers signal discriminability, but also equates the importance of bias (*i.e.* the probability of eliciting a response upon detection of a signal). The magnitude of response to acoustic stimuli was typically greater, the higher the signal-to-noise ratio under ambient noise conditions. However, signal discriminability was significantly reduced under masked noise conditions, with the change in response more accurately identified using fine-scale behavioural quantification. Results should be applied to the development of more effective behavioural guidance systems, which should be installed after appropriate evaluation of location specific acoustic properties and environmental impact.

Novel contributions to existing knowledge and thinking from Objective 4 include:

- The results of experimental Chapter 6 have been presented at three international conferences, and were due to be presented at a fourth (suspended due to COVID-19):
 - “Group behavioural response of cyprinids to artificial acoustic stimuli: implications for fisheries management.” Fish Passage 2018: International conference on river connectivity, Albury, New South Wales, Australia, December 2018
 - “Group behavioural responses of juvenile common carp (*Cyprinus carpio*) to pulsed tonal stimuli in the presence of masking noise.” 5th International conference on the effects of noise on aquatic life, The Hague, The Netherlands, July 2019
 - “Group behavioural response of cyprinids to pulsed tonal stimuli in the presence of masking noise: application of signal detection theory.” Animal Behaviour Live, Virtual Conference, August 2020
 - “Application of Signal Detection Theory to understand the anti-predator responses of cyprinids to masked acoustic signals in still and flowing water.” FSBI Symposium 2020: Fish in a Dynamic World, Nottingham Trent University, UK, 2020 (Postponed, abstract accepted)
- Results from Chapter 6 have also been published as a conference paper:
 - **Currie et al. (2019)**. Group behavioral responses of juvenile common carp (*Cyprinus carpio*) to pulsed tonal stimuli in the presence of masking noise. *Proceedings of Meetings on Acoustics*. **37(1)**, 010008. doi: 10.1121/2.0001180
- A paper based on the results from Chapter 6 is in the final preparation stage for submission to the journal, *Proceedings of the Royal Society B: Biological Sciences*, entitled:
 - **Currie et al.** Masking noise reduces the anti-predator response of common carp (*Cyprinus carpio*) to an acoustic stimulus: application of Signal Detection Theory to fisheries management.

Objective 5: *Assess the manipulation of upstream migrating cyprinid group behaviour using acoustic stimuli under different experimentally controlled water velocities.*

Previous studies have successfully manoeuvred cyprinids away from undesirable areas using underwater sound, under still water and low velocity conditions. Chapter 7 used a route choice experimental set-up within an open-channel flume and built upon the findings of Chapters 4, 5, and 6, to address Objective 5. This laboratory study was the first to illustrate how higher water velocities that are more commonly encountered by fish in the wild can influence the group response of upstream moving cyprinids to an acoustic stimulus. Shoals were observed to more

commonly switch routes prior to selecting an acoustically “quiet” channel in the presence of a 170 Hz tonal stimulus and the discriminability of a signal increased under intermediate and high velocity conditions. The study highlights the importance of considering ancillary abiotic factors when addressing fish response to underwater sound. More studies investigating the combined effects of abiotic factors on the acoustic response of fish, including increasingly turbulent conditions, would be a valuable area for future research.

Outputs from Objective 5 include:

- The results of experimental Chapter 7 have been presented at one international conference:
 - “*Group behavioural response of cyprinids to pulsed tonal stimuli in the presence of masking noise: application of signal detection theory.*” Animal Behaviour Live, Virtual Conference, August 2020
- Additionally, they were due to be presented, at one national (by invitation *) and one international (abstract accepted) conference (suspended due to COVID-19):
 - “*Application of Signal Detection Theory to understand the anti-predator responses of cyprinids to masked acoustic signals in still and flowing water.*” FSBI Symposium 2020: Fish in a Dynamic World, Nottingham Trent University, UK, 2020 (Postponed)
 - “*Determining fish response to acoustics: on the road to behavioural deterrents.*” 13th Power Industry Cooling Water Specialists (PICWS) network conference, University of Southampton, UK, 2020 (Postponed) *
- A paper based on the results from Chapter 7 is in preparation for submission to the journal *Ecological Engineering*, as:
 - **Currie et al.** The influence of underwater sound on the upstream route choice of common roach (*Rutilus rutilus*) under different water velocities.

The research conducted in this thesis is of benefit to scientists working in a diverse range of fields (e.g. animal behaviour, aquatic ecology, bioacoustics). Key outputs will be of use to fisheries managers and policy makers seeking to better understand the impacts of anthropogenic underwater sound on freshwater fish or apply acoustic guidance technologies for the improvement of fish passage, or invasive species control. The main findings and novel contributions to science brought about as a result of this research will aid in the conservation of vulnerable fish species and benefit the promotion of productive, resilient ecosystems that will benefit local economies and wider society.

APPENDIX A Meta-analysis Literature

Table A1: Studies included in dataset1. *Note:* Two aligned vertical asterisks denote that the study was included in final dataset2 effect size meta-analysis calculation.

Study	Title	Journal	Study Species	Species Category (Laboratory or Field Study)	Life-stage Tested	Analysed Parameter(s)	Noise Stimuli Type(s)	Effect of Noise
Alderks and Sisneros, 2013	Development of the acoustically evoked behavioral response in larval plainfin midshipman fish, <i>Porichthys notatus</i>	<i>PLOS ONE</i> . 8, e82182.	Plainfin midshipman (<i>Porichthys notatus</i> , Batrachoididae)	Marine (Laboratory)	Larvae	Behavioural	White Noise & Tonal Frequencies	Yes
Amoser and Ladich, 2003 ‡	Diversity in noise-induced temporary hearing loss in otophysine fishes	<i>J. Acoust. Soc. Am.</i> 113, 2170-2179.	Goldfish (<i>Carassius auratus</i> , Cyprinidae)	Freshwater (Laboratory)	Adult	Anatomical	White Noise	Yes
Amoser and Ladich, 2003 ‡	Diversity in noise-induced temporary hearing loss in otophysine fishes	<i>J. Acoust. Soc. Am.</i> 113, 2170-2179.	Pictus catfish (<i>Pimelodus pictus</i> , Pimelodidae)	Freshwater (Laboratory)	Adult	Anatomical	White Noise	Yes
Anderson et al., 2011 ‡	Sound, stress, and seahorses: The consequences of a noisy environment to animal health	<i>Aquaculture</i> . 311, 129-138.	Lined seahorse (<i>Hippocampus erectus</i> , Syngnathidae)	Marine (Laboratory)	Adult	¹ Behavioural & ² Physiological	Aquaculture Ambient Noise	Yes ^{1,2}

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Andersson et al., 2007	Swimming behavior of roach (<i>Rutilus rutilus</i>) and three-spined stickleback (<i>Gasterosteus aculeatus</i>) in response to wind power noise and single-tone frequencies	<i>Ambio.</i> 36 , 636-638.	Three-spined stickleback (<i>Gasterosteus aculeatus</i> , Gasterosteidae)	Euryhaline (Laboratory)	Adult	Behavioural	Wind Power Noise	Yes
Andersson et al., 2007	Swimming behavior of roach (<i>Rutilus rutilus</i>) and three-spined stickleback (<i>Gasterosteus aculeatus</i>) in response to wind power noise and single-tone frequencies	<i>Ambio.</i> 36 , 636-638.	Roach (<i>Rutilus rutilus</i> , Cyprinidae)	Euryhaline (Laboratory)	Adult	Behavioural	Wind Power Noise	Yes
Andrews et al., 2014	Identification of a gene set to evaluate the potential effects of loud sounds from seismic surveys on the ears of fishes: a study with <i>Salmo salar</i>	<i>J. Fish. Biol.</i> 84 , 1793-1819.	Atlantic salmon (<i>Salmo salar</i> , Salmonidae)	Euryhaline (Laboratory)	Adult	Physiological	Airgun Noise	Yes
Banner and Hyatt, 1973	Effects of noise on eggs and larvae of two estuarine fishes	<i>T. Am. Fish. Soc.</i> 102 , 134-136.	Sheepshead minnow (<i>Cyprinodon variegatus</i> , Cyprinodontidae)	Freshwater (Laboratory)	Larvae	Anatomical	Aquaculture Ambient Noise	Yes
Banner and Hyatt, 1973	Effects of noise on eggs and larvae of two estuarine fishes	<i>T. Am. Fish. Soc.</i> 102 , 134-136.	Longnose killifish (<i>Fundulus similis</i> , Fundulidae)	Freshwater (Laboratory)	Larvae	Anatomical	Aquaculture Ambient Noise	Yes
Belanger et al., 2010	The effect of stimulus type and background noise on hearing abilities of the round goby <i>Neogobius melanostomus</i>	<i>J. Fish Biol.</i> 77 , 1488-1504.	Round goby (<i>Neogobius melanostomus</i> , Gobiidae)	Euryhaline (Laboratory)	Adult	Anatomical	White Noise	Yes

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Berthe and Lecchini, 2016	Influence of boat noises on escape behaviour of white-spotted eagle ray <i>Aetobatus ocellatus</i> at Moorea Island (French Polynesia)	<i>Comptes Rendus Biologies.</i> 339 , 99-103.	White-spotted eagle ray (<i>Aetobatus ocellatus</i> , Myliobatidae)	Marine (Free Field)	Adult	Behavioural	Motor Boat Engine Noise	Yes
Bhandiwad et al., 2013	Auditory sensitivity of larval zebrafish (<i>Danio rerio</i>) measured using a behavioral prepulse inhibition assay	<i>J. Exp. Biol.</i> 216 , 3504-3513.	Zebrafish (<i>Danio rerio</i> , Cyprinidae)	Freshwater (Laboratory)	Larvae	Behavioural	Tonal Frequencies	Yes
Blaxter and Hoss, 1981	Startle response in herring: the effect of sound stimulus frequency, size of fish and selective interference with the acoustico-lateralis system	<i>J. Mar. Biol. Assoc.</i> 61 , 871-879.	Atlantic herring (<i>Clupea haerengus</i> , Clupeidae)	Marine (Laboratory)	^a Larvae & ^b Juvenile	Behavioural	Tonal Frequencies	Yes ^{a,b}
Blaxter et al., 1981	Sound and startle responses in herring shoals	<i>J. Mar. Biol. Assoc.</i> 61 , 851 - 869.	Atlantic herring (<i>Clupea haerengus</i> , Clupeidae)	Marine (Laboratory)	^a Juvenile & ^b Adult	Behavioural	Tonal Frequencies	Yes ^{a,b}
Bruintjes et al., 2016[‡]	Rapid recovery following short-term acoustic disturbance in two fish species	<i>R. Soc. Open Sci.</i> 3 , 150686.	European eel (<i>Anguilla anguilla</i> , Anguillidae)	Euryhaline (Laboratory)	Juvenile	¹ Behavioural & ² Physiological	Ship Engine Noise	Yes ^{1,2}
Bruintjes et al., 2016[‡]	Rapid recovery following short-term acoustic disturbance in two fish species	<i>R. Soc. Open Sci.</i> 3 , 150686.	European sea bass (<i>Dicentrarchus labrax</i> , Moronidae)	Euryhaline (Laboratory & Field Enclosure)	Juvenile	Physiological	Ship Engine Noise	Yes

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Bruintjes and Radford, 2014	Chronic playback of boat noise does not impact hatching success or post-hatching larval growth and survival in a cichlid fish	<i>PeerJ.</i> 2 , e594.	Daffodil cichlid (<i>Neolamprologus pulcher</i> , Cichlidae)	Freshwater (Laboratory)	Juvenile	Physiological	Motor Boat Engine Noise	No
Bruintjes and Radford, 2013	Context-dependent impacts of anthropogenic noise on individual and social behaviour in a cooperatively breeding fish	<i>Anim. Behav.</i> 85 , 1343-1349.	Daffodil cichlid (<i>Neolamprologus pulcher</i> , Cichlidae)	Freshwater (Laboratory)	Adult	Behavioural	Motor Boat Engine Noise	Yes
Bui et al., 2013 *	Group behavioural responses of Atlantic salmon (<i>Salmo salar</i> L.) to light, infrasound and sound stimuli	<i>PLOS ONE.</i> 8 , e63696.	Atlantic salmon (<i>Salmo salar</i> , Salmonidae)	Euryhaline (Laboratory)	Juvenile	Behavioural	Tonal Frequencies	Yes
Buscaino et al., 2010 *	Impact of an acoustic stimulus on the motility and blood parameters of European sea bass (<i>Dicentrarchus labrax</i> L.) and gilthead sea bream (<i>Sparus aurata</i> L.)	<i>Mar. Environm. Res.</i> 69 , 136-142.	European sea bass (<i>Dicentrarchus labrax</i> , Moronidae)	Euryhaline (Field Enclosure)	Juvenile	¹ Behavioural & ² Physiological	Simulated Ship Engine Noise	Yes ^{1,2}
Buscaino et al., 2010 *	Impact of an acoustic stimulus on the motility and blood parameters of European sea bass (<i>Dicentrarchus labrax</i> L.) and gilthead sea bream (<i>Sparus aurata</i> L.)	<i>Mar. Environm. Res.</i> 69 , 136-142.	Gilthead sea bream (<i>Sparus aurata</i> , Sparidae)	Marine (Field Enclosure)	Juvenile	¹ Behavioural & ² Physiological	Simulated Ship Engine Noise	Yes ^{1,2}

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Caiger et al., 2012 ‡	Chronic low-intensity noise exposure affects the hearing thresholds of juvenile snapper	<i>Mar. Ecol. Progr. Ser.</i> 466 , 225-232.	Pink snapper (<i>Pagrus auratus</i> , Sparidae)	Marine (Laboratory)	Juvenile	Anatomical	Aquaculture Ambient Noise	Yes
Casper et al., 2012	Recovery of barotrauma injuries in chinook salmon, <i>Oncorhynchus tshawytscha</i> from exposure to pile driving sound	<i>PLOS ONE.</i> 7 , e39593.	Chinook salmon (<i>Oncorhynchus tshawytscha</i> , Salmonidae)	Euryhaline (Laboratory)	Juvenile	Anatomical	Pile Driving Noise	Yes
Casper et al., 2013a	Recovery of barotrauma injuries resulting from exposure to pile driving sound in two sizes of hybrid striped bass	<i>PLOS ONE.</i> 8 , e73844.	Hybrid striped bass (white bass <i>Morone chrysops</i> , Moronidae * striped bass <i>Morone saxatilis</i> , Moronidae)	Euryhaline (Laboratory)	Adult	Anatomical	Pile Driving Noise	Yes
Casper et al., 2017	Onset of barotrauma injuries related to number of pile driving strike exposures in hybrid striped bass	<i>J. Acoust. Soc. Am.</i> 141 , 4380-4387.	Hybrid striped bass (white bass <i>Morone chrysops</i> , Moronidae * striped bass <i>Morone saxatilis</i> , Moronidae)	Euryhaline (Laboratory)	Adult	Anatomical	Pile Driving Noise	Yes
Celi et al., 2016 ‡	Vessel noise pollution as a human threat to fish: assessment of the stress response in gilthead sea bream (<i>Sparus aurata</i> , Linnaeus 1758)	<i>Fish. Physiol. Biochem.</i> 42 , 631-641.	Gilthead sea bream (<i>Sparus aurata</i> , Sparidae)	Marine (Laboratory)	Adult	Physiological	Motor Boat & Ship Engine Noise	Yes
Codarin et al., 2009 ‡	Effects of ambient and boat noise on hearing and communication in three fish species living in a marine protected area (Miramare, Italy)	<i>Mar. Poll. Bull.</i> 58 , 1880-1887.	Mediterranean damselfish (<i>Chromis chromis</i> , Pomacentridae)	Marine (Laboratory)	Adult	Anatomical	Motor Boat Engine Noise	Yes

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Codarin et al., 2009 ‡	Effects of ambient and boat noise on hearing and communication in three fish species living in a marine protected area (Miramare, Italy)	<i>Mar. Poll. Bull.</i> 58 , 1880-1887.	Red-mouthed goby (<i>Gobius cruentatus</i> , Gobiidae)	Marine (Laboratory)	Adult	Anatomical	Motor Boat Engine Noise	No
Codarin et al., 2009	Effects of ambient and boat noise on hearing and communication in three fish species living in a marine protected area (Miramare, Italy)	<i>Mar. Poll. Bull.</i> 58 , 1880-1887.	Brown meagre (<i>Sciaena umbra</i> , Sciaenidae)	Marine (Laboratory)	Adult	Anatomical	Motor Boat Engine Noise	Yes
Cott et al., 2012	Impacts of river-based air gun seismic activity on Northern Fishes	<i>Adv. Exp. Med. Biol.</i> 730 , 367-369.	Broad whitefish (<i>Coregonus nasus</i> , Salmonidae)	Freshwater (Field Enclosure)	Adult	¹ Anatomical & ² Physiological & ³ Behavioural	Airgun Noise	No ^{1,2,3}
Cott et al., 2012	Impacts of river-based air gun seismic activity on Northern Fishes	<i>Adv. Exp. Med. Biol.</i> 730 , 367-369.	Lake chub (<i>Couesius plumbeus</i> , Cyprinidae)	Freshwater (Field Enclosure)	Adult	¹ Anatomical & ² Physiological & ³ Behavioural	Airgun Noise	Yes ¹
Cott et al., 2012	Impacts of river-based air gun seismic activity on Northern Fishes	<i>Adv. Exp. Med. Biol.</i> 730 , 367-369.	Northern pike (<i>Esox lucius</i> , Esocidae)	Freshwater (Field Enclosure)	^a Juvenile & ^b Adult	¹ Anatomical & ² Physiological & ³ Behavioural	Airgun Noise	Yes ^{1b}
Crovo et al., 2015 ‡	Stress and Auditory Responses of the Otophysan Fish, <i>Cyprinella venusta</i> , to Road Traffic Noise	<i>PLOS ONE.</i> 10 , e0137290.	Blacktail shiner (<i>Cyprinella venusta</i> , Cyprinidae)	Freshwater (Laboratory)	Adult	¹ Anatomical & ² Physiological	Road Traffic Noise	Yes ^{1,2}
Davidson et al., 2009 ‡	The effects of aquaculture production noise on the growth, condition factor, feed conversion, and survival of rainbow trout, <i>Oncorhynchus mykiss</i>	<i>Aquaculture.</i> 288 , 337-343.	Rainbow trout (<i>Oncorhynchus mykiss</i> , Salmonidae)	Euryhaline (Laboratory)	Juvenile	¹ Anatomical & ² Physiological	Aquaculture Ambient Noise	No ^{1,2}

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Debusschere et al., 2016	Acoustic stress responses in juvenile sea bass <i>Dicentrarchus labrax</i> induced by offshore pile driving	<i>Environ. Pollut.</i> 208 , 747-757.	European sea bass (<i>Dicentrarchus labrax</i> , Moronidae)	Euryhaline (Laboratory & Field Enclosure)	Juvenile	Physiological	Pile Driving Noise	Yes
Debusschere et al., 2014	In Situ Mortality Experiments with Juvenile Sea Bass (<i>Dicentrarchus labrax</i>) in Relation to Impulsive Sound Levels Caused by Pile Driving of Windmill Foundations	<i>PLOS ONE.</i> 9 , e109280	European sea bass (<i>Dicentrarchus labrax</i> , Moronidae)	Euryhaline (Field Enclosure)	Larvae	Physiological	Pile Driving Noise	No
de Jong et al., 2018	Noise can affect acoustic communication and subsequent spawning success in fish	<i>Environ. Pollut.</i> 237 , 814-823.	Two-spotted goby (<i>Gobiusculus flavescens</i> , Gobiidae)	Marine (Laboratory)	Adult	Behavioural	Broadband Noise	Yes
de Jong et al., 2018	Noise can affect acoustic communication and subsequent spawning success in fish	<i>Environ. Pollut.</i> 237 , 814-823.	Painted goby (<i>Pomatoschistus pictus</i> , Gobiidae)	Marine (Laboratory)	Adult	Behavioural	Broadband Noise	Yes
Doksæter et al., 2012	Behavior of captive herring exposed to naval sonar transmissions (1.0 - 1.6 kHz) throughout a yearly cycle	<i>J. Acoust. Soc. Am.</i> 131 , 1632-1342.	Atlantic herring (<i>Clupea harengus</i> , Clupeidae)	Marine (Field Enclosure)	Adult	Behavioural	Motor Boat Engine Noise	Yes
Doksæter et al., 2009	Behavioral responses of herring (<i>Clupea harengus</i>) to 1–2 and 6–7 kHz sonar signals and killer whale feeding sounds	<i>J. Acoust. Soc. Am.</i> 125 , 554-564.	Atlantic herring (<i>Clupea harengus</i> , Clupeidae)	Marine (Field Enclosure)	Adult	Behavioural	Sonar	No

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Everley et al., 2016	Pile-driving noise impairs antipredator behavior of the European sea bass <i>Dicentrarchus labrax</i>	<i>Adv. Exp. Med. Biol.</i> 875 , 273-279.	European sea bass (<i>Dicentrarchus labrax</i> , Moronidae)	Euryhaline (Laboratory)	Juvenile	Behavioural	Pile Driving Noise	Yes
Ferrari et al., 2018 ‡	School is out on noisy reefs: the effect of boat noise on predator learning and survival of juvenile coral reef fishes	<i>Proc. R. Soc. Lond. B.</i> 285 , 20180033	Ambon damselfish (<i>Pomacentrus amboinensis</i> , Pomacentridae)	Marine (Laboratory & Free Field)	Juvenile	Behavioural	Motor Boat Engine Noise	Yes
Fewtrell and McCauley, 2012	Impact of air gun noise on the behaviour of marine fish and squid	<i>Mar. Poll. Bull.</i> 64 , 984-993.	Pink snapper (<i>Pagrus auratus</i> , Sparidae)	Marine (Field Enclosure)	Adult	Behavioural	Airgun Noise	Yes
Fewtrell and McCauley, 2012	Impact of air gun noise on the behaviour of marine fish and squid	<i>Mar. Poll. Bull.</i> 64 , 984-993.	White trevally (<i>Pseudocaranx dentex</i> , Carangidae)	Marine (Field Enclosure)	Adult	Behavioural	Airgun Noise	Yes
Filiciotto et al., 2013 ‡	Effect of acoustic environment on gilthead sea bream (<i>Sparus aurata</i>): Sea and onshore aquaculture background noise	<i>Aquaculture.</i> 414 , 36-45.	Gilthead sea bream (<i>Sparus aurata</i> , Sparidae)	Marine (Laboratory)	Adult	¹ Anatomical & ² Physiological	Aquaculture Ambient Noise	Yes ^{1,2}
Filiciotto et al., 2017	Impact of aquatic acoustic noise on oxidative status and some immune parameters in gilthead sea bream <i>Sparus aurata</i> (Linnaeus, 1758) juveniles	<i>Aquacult. Res.</i> 48 , 1895-1903	Gilthead sea bream (<i>Sparus aurata</i> , Sparidae)	Marine (Laboratory)	Juvenile	Physiological	Aquaculture Ambient Noise	Yes

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Goetz et al., 2015	Do pingers cause stress in fish? An experimental tank study with European sardine, <i>Sardina pilchardus</i> (Walbaum, 1792) (Actinopterygii, Clupeidae), exposed to a 70 kHz dolphin pinger	<i>Hydrobiologia.</i> 749 , 83-96.	European pilchard (<i>Sardina pilchardus</i> , Clupeidae)	Euryhaline (Laboratory)	Adult	¹ Behavioural & ² Physiological	Acoustic Pinger	Yes ^{1,2}
Gutscher et al., 2011*	Effects of aquarium and pond noise on hearing sensitivity in an otophysine fish	<i>Bioacoustics.</i> 20 , 117-136.	Goldfish (<i>Carassius auratus</i> , Cyprinidae)	Freshwater (Laboratory)	Adult	Anatomical	Aquaculture Ambient Noise	Yes
Halvorsen et al., 2013	Effects of low-frequency naval sonar exposure on three species of fish	<i>J. Acoust. Soc. Am.</i> 134 , EL205-EL210.	Channel catfish (<i>Ictalurus punctatus</i> , Ictaluridae)	Freshwater (Field Enclosure)	Adult	Anatomical	Sonar	Yes
Halvorsen et al., 2013	Effects of low-frequency naval sonar exposure on three species of fish	<i>J. Acoust. Soc. Am.</i> 134 , EL205-EL210.	Largemouth bass (<i>Micropterus salmoides</i> , Centrarchidae)	Freshwater (Field Enclosure)	Adult	Anatomical	Sonar	No
Halvorsen et al., 2013	Effects of low-frequency naval sonar exposure on three species of fish	<i>J. Acoust. Soc. Am.</i> 134 , EL205-EL210.	Yellow perch (<i>Perca flavescens</i> , Percidae)	Freshwater (Field Enclosure)	Adult	Anatomical	Sonar	No
Halvorsen et al., 2012a	Effects of exposure to pile-driving sounds on the lake sturgeon, Nile tilapia and hogchoker	<i>Proc. R. Soc. Lond. B.</i> 279 , 4705-4714.	Lake sturgeon (<i>Acipenser fulvescens</i> , Acipenseridae)	Freshwater (Laboratory)	Adult	Anatomical	Pile Driving Noise	Yes
Halvorsen et al., 2012a	Effects of exposure to pile-driving sounds on the lake sturgeon, Nile tilapia and hogchoker	<i>Proc. R. Soc. Lond. B.</i> 279 , 4705-4714.	Nile tilapia (<i>Oreochromis niloticus</i> , Cichlidae)	Freshwater (Laboratory)	Adult	Anatomical	Pile Driving Noise	Yes

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Halvorsen et al., 2012a	Effects of exposure to pile-driving sounds on the lake sturgeon, Nile tilapia and hogchoker	<i>Proc. R. Soc. Lond. B.</i> 279 , 4705-4714.	Hogchoker (<i>Trinectes maculatus</i> , Achiridae)	Euryhaline (Laboratory)	Adult	Anatomical	Pile Driving Noise	No
Halvorsen et al., 2012b	Threshold for Onset of Injury in Chinook Salmon from Exposure to Impulsive Pile Driving Sounds	<i>PLOS ONE.</i> 7 , e38968.	Chinook salmon (<i>Oncorhynchus tshawytscha</i> , Salmonidae)	Euryhaline (Laboratory)	Juvenile	Anatomical	Pile Driving Noise	Yes
Halvorsen et al., 2012c*	Effects of mid-frequency active sonar on hearing in fish	<i>J. Acoust. Soc. Am.</i> 131 ,599-607.	Channel catfish (<i>Ictalurus punctatus</i> , Ictaluridae)	Freshwater (Field Enclosure)	Juvenile	Anatomical	Sonar	Yes
Halvorsen et al., 2012c*	Effects of mid-frequency active sonar on hearing in fish	<i>J. Acoust. Soc. Am.</i> 131 ,599-607.	Rainbow trout (<i>Oncorhynchus mykiss</i> , Salmonidae)	Euryhaline (Field Enclosure)	Juvenile	Anatomical	Sonar	No
Handegard et al., 2015	The reaction of a captive herring school to playbacks of a noise-reduced and a conventional research vessel	<i>Can. J. Fish. Aquat. Sci.</i> 72 , 491-499.	Atlantic herring (<i>Clupea harengus</i> , Clupeidae)	Marine (Field Enclosure)	Adult	Behavioural	Ship Engine Noise	Yes
Hasan et al., 2018*	A cross-modal effect of noise: the disappearance of the alarm reaction of a freshwater fish	<i>Animal Cogn.</i> 21 , 419-424.	Fathead minnow (<i>Pimephales promelas</i> , Cyprinidae)	Freshwater (Laboratory)	Adult	Behavioural	Motor Boat Engine Noise	Yes
Hastings et al., 2008	The effects of seismic airgun noise on the hearing sensitivity of tropical reef fishes at Scott Reef, Western Australia	<i>Proceedings of the Institute of Acoustics..</i> 30 , 102-109.	Green chromis (<i>Chromis veridis</i> , Pomacentridae)	Marine (Field Enclosure)	Adult	Anatomical	Airgun Noise	No

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Hastings et al., 2008	The effects of seismic airgun noise on the hearing sensitivity of tropical reef fishes at Scott Reef, Western Australia	<i>Proceedings of the Institute of Acoustics.</i> 30 , 102-109.	Bluestripe seaperch (<i>Lutjanus kasmira</i> , Lutjanidae)	Marine (Field Enclosure)	Adult	Anatomical	Airgun Noise	No
Hastings et al., 2008	The effects of seismic airgun noise on the hearing sensitivity of tropical reef fishes at Scott Reef, Western Australia	<i>Proceedings of the Institute of Acoustics.</i> 30 , 102-109.	Pinecone soldierfish (<i>Myripristis murdjan</i> , Holocentridae)	Marine (Field Enclosure)	Adult	Anatomical	Airgun Noise	No
Hastings et al., 2008	The effects of seismic airgun noise on the hearing sensitivity of tropical reef fishes at Scott Reef, Western Australia	<i>Proceedings of the Institute of Acoustics.</i> 30 , 102-109.	Sabre squirrelfish (<i>Sargocentron spiniferum</i> , Holocentridae)	Marine (Field Enclosure)	Adult	Anatomical	Airgun Noise	No
Hastings et al., 1996	Effects of low-frequency underwater sound on hair cells of the inner ear and lateral line of the teleost fish <i>Astronotus ocellatus</i>	<i>J. Acoust. Soc. Am.</i> 99 , 1759 - 1766.	Oscar (<i>Astronotus ocellatus</i> , Cichlidae)	Freshwater (Laboratory)	Adult	Anatomical	Tonal Frequencies	Yes
Herbert-Read et al., 2017a	Anthropogenic noise pollution from pile-driving disrupts the structure and dynamics of fish shoals	<i>Proc. R. Soc. Lond. B.</i> 284 , 20171627.	European sea bass (<i>Dicentrarchus labrax</i> , Moronidae)	Euryhaline (Laboratory)	Juvenile	Behavioural	Pile Driving Noise	Yes
Holles et al., 2013	Boat noise disrupts orientation behaviour in a coral reef fish	<i>Mar. Ecol. Progr. Ser.</i> 485 , 295-300.	Longspine cardinalfish (<i>Apogon doryssa</i> , Apogonidae)	Marine (Field Enclosure)	Larvae	Behavioural	Motor Boat Engine	Yes

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Holt and Johnston, 2014 ‡	Evidence of the Lombard effect in fishes	<i>Behav. Ecol.</i> 25 , 819-826.	Blacktail shiner (<i>Cyprinella venusta</i> , Cyprinidae)	Freshwater (Laboratory)	Adult	Behavioural	White Noise	Yes
Johansson et al., 2016	Stress response and habituation to motorboat noise in two coastal fish species in the Bothnian sea	<i>Adv. Exp. Med. Biol.</i> 875 , 513-521.	Roach (<i>Rutilus rutilus</i> , Cyprinidae)	Euryhaline (Field Enclosure)	Juvenile	Physiological	Motor Boat Engine Noise	No
Johansson et al., 2016	Stress response and habituation to motorboat noise in two coastal fish species in the Bothnian sea	<i>Adv. Exp. Med. Biol.</i> 875 , 513-521.	Eurasian perch (<i>Perca fluviatilis</i> , Percidae)	Freshwater (Field Enclosure)	Juvenile	Physiological	Motor Boat Engine Noise	Yes
Jung and Swearer, 2011	Reactions of temperate reef fish larvae to boat sound	<i>Aquat. Conserv. Mar. Freshw. Ecosyst.</i> 21 , 389-396.	Australian anchovy (<i>Engraulis australis</i> , Engraulidae)	Marine (Field Enclosure)	Larvae	Behavioural	Motor Boat Engine Noise	No
Jung and Swearer, 2011	Reactions of temperate reef fish larvae to boat sound	<i>Aquat. Conserv. Mar. Freshw. Ecosyst.</i> 21 , 389-396.	Three-by-two garfish (<i>Hemiramphus robustus</i> , Hemiramphidae)	Marine (Field Enclosure)	Larvae	Behavioural	Motor Boat Engine Noise	No
Kane et al., 2010 ‡	Exposure of fish to high-intensity sonar does not induce acute pathology	<i>J. Fish Biol.</i> 76 , 1825-1840.	Channel catfish (<i>Ictalurus punctatus</i> , Ictaluridae)	Freshwater (Field Enclosure)	Adult	Physiological	Sonar	No
Kane et al., 2010 ‡	Exposure of fish to high-intensity sonar does not induce acute pathology	<i>J. Fish Biol.</i> 76 , 1825-1840.	Hybrid sunfish (<i>Lepomis</i> sp., Centrarchidae)	Freshwater (Field Enclosure)	Adult	Physiological	Sonar	No
Kane et al., 2010 ‡	Exposure of fish to high-intensity sonar does not induce acute pathology	<i>J. Fish Biol.</i> 76 , 1825-1840.	Rainbow trout (<i>Oncorhynchus mykiss</i> , Salmonidae)	Euryhaline (Field Enclosure)	Adult	Physiological	Sonar	No

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Kastelein et al., 2008	Startle response of captive North Sea fish species to underwater tones between 0.1 and 64 kHz	<i>Mar. Environ. Res.</i> 65 , 369-377.	European eel (<i>Anguilla anguilla</i> , Anguillidae)	Euryhaline (Laboratory)	Juvenile	Behavioural	Tonal Frequencies	No
Kastelein et al., 2008	Startle response of captive North Sea fish species to underwater tones between 0.1 and 64 kHz	<i>Mar. Environ. Res.</i> 65 , 369-377.	Thicklip grey mullet (<i>Chelon labrosus</i> , Mugilidae)	Marine (Laboratory)	Juvenile	Behavioural	Tonal Frequencies	Yes
Kastelein et al., 2008	Startle response of captive North Sea fish species to underwater tones between 0.1 and 64 kHz	<i>Mar. Environ. Res.</i> 65 , 369-377.	Atlantic herring (<i>Clupea haerengus</i> , Clupeidae)	Marine (Laboratory)	Adult	Behavioural	Tonal Frequencies	Yes
Kastelein et al., 2008	Startle response of captive North Sea fish species to underwater tones between 0.1 and 64 kHz	<i>Mar. Environ. Res.</i> 65 , 369-377.	European sea bass (<i>Dicentrarchus labrax</i> , Moronidae)	Euryhaline (Laboratory)	Juvenile	Behavioural	Tonal Frequencies	Yes
Kastelein et al., 2008	Startle response of captive North Sea fish species to underwater tones between 0.1 and 64 kHz	<i>Mar. Environ. Res.</i> 65 , 369-377.	Atlantic cod (<i>Gadus morhua</i> , Gadidae)	Marine (Laboratory)	Juvenile	Behavioural	Tonal Frequencies	No
Kastelein et al., 2008	Startle response of captive North Sea fish species to underwater tones between 0.1 and 64 kHz	<i>Mar. Environ. Res.</i> 65 , 369-377.	Atlantic pollack (<i>Pollachius pollachius</i> , Gadidae)	Marine (Laboratory)	Juvenile	Behavioural	Tonal Frequencies	No

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Kastelein et al., 2008	Startle response of captive North Sea fish species to underwater tones between 0.1 and 64 kHz	<i>Mar. Environ. Res.</i> 65 , 369-377.	Horse mackerel (<i>Trachurus trachurus</i> , Carangidae)	Marine (Laboratory)	Juvenile	Behavioural	Tonal Frequencies	Yes
Kastelein et al., 2008	Startle response of captive North Sea fish species to underwater tones between 0.1 and 64 kHz	<i>Mar. Environ. Res.</i> 65 , 369-377.	Whiting-pout (<i>Trisopterus luscus</i> , Gadidae)	Marine (Laboratory)	Adult	Behavioural	Tonal Frequencies	Yes
Kastelein et al., 2007	Effects of acoustic alarms, designed to reduce small cetacean bycatch in gillnet fisheries, on the behaviour of North Sea fish species in a large tank	<i>Mar. Environ. Res.</i> 64 , 160-180.	European sea bass (<i>Dicentrarchus labrax</i> , Moronidae)	Euryhaline (Laboratory)	Adult	Behavioural	Acoustic Pinger	Yes
Kastelein et al., 2007	Effects of acoustic alarms, designed to reduce small cetacean bycatch in gillnet fisheries, on the behaviour of North Sea fish species in a large tank	<i>Mar. Environ. Res.</i> 64 , 160-180.	Thicklip grey mullet (<i>Chelon labrosus</i> , Mugilidae)	Marine (Laboratory)	Adult	Behavioural	Acoustic Pinger	Yes
Kastelein et al., 2007	Effects of acoustic alarms, designed to reduce small cetacean bycatch in gillnet fisheries, on the behaviour of North Sea fish species in a large tank	<i>Mar. Environ. Res.</i> 64 , 160-180.	Atlantic herring (<i>Clupea haerengus</i> , Clupeidae)	Marine (Laboratory)	Adult	Behavioural	Acoustic Pinger	Yes

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Kastelein et al., 2007	Effects of acoustic alarms, designed to reduce small cetacean bycatch in gillnet fisheries, on the behaviour of North Sea fish species in a large tank	<i>Mar. Environ. Res.</i> 64 , 160-180.	Atlantic cod (<i>Gadus morhua</i> , Gadidae)	Marine (Laboratory)	Adult	Behavioural	Acoustic Pinger	No
Kastelein et al., 2007	Effects of acoustic alarms, designed to reduce small cetacean bycatch in gillnet fisheries, on the behaviour of North Sea fish species in a large tank	<i>Mar. Environ. Res.</i> 64 , 160-180.	Whiting-pout (<i>Trisopterus luscus</i> , Gadidae)	Marine (Laboratory)	Adult	Behavioural	Acoustic Pinger	No
Ladich and Schulz-Mirbach, 2013 ‡	Hearing in Cichlid Fishes under Noise Conditions	<i>PLOS ONE.</i> 8 , e57588.	Orange chromide (<i>Etroplus maculatus</i> , Cichlidae)	Freshwater (Laboratory)	Adult	Anatomical	White Noise	Yes
Ladich and Schulz-Mirbach, 2013 ‡	Hearing in Cichlid Fishes under Noise Conditions	<i>PLOS ONE.</i> 8 , e57588.	Slender lionhead cichlid (<i>Steatocranus tinanti</i> , Cichlidae)	Freshwater (Laboratory)	Adult	Anatomical	White Noise	Yes
Liu et al., 2013 ‡	Ship noise-induced temporary hearing threshold shift in the Chinese sucker <i>Myxocyprinus asiaticus</i> (Bleeker, 1864)	<i>J. Appl. Ichtyol.</i> 29 , 1416-1422.	Chinese sucker (<i>Myxocyprinus asiaticus</i> , Catostomidae)	Freshwater (Laboratory)	Adult	Anatomical	Ship Engine Noise	Yes
Liu et al., 2018	Sound shock response in larval zebrafish: A convenient and high-throughput assessment of auditory function	<i>Neurotoxicol. Teratol.</i> 66 , 1-7.	Zebrafish (<i>Danio rerio</i> , Cyprinidae)	Freshwater (Laboratory)	Larvae	Behavioural	Broadband Noise	Yes

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Maxwell et al., 2018 *	Does motor noise from recreational boats alter parental care behaviour of a nesting freshwater fish?	<i>Aquat. Conserv. Mar. Freshw. Ecosyst.</i> 28 , 969-978.	Largemouth bass (<i>Micropterus salmoides</i> , Centrarchidae)	Freshwater (Free Field)	Adult	Behavioural	Motor Boat Engine Noise	Yes
McCauley et al., 2003 *	High intensity anthropogenic sound damages fish ears	<i>J. Acoust. Soc. Am.</i> 113 , 638-642.	Pink snapper (<i>Pagrus auratus</i> , Sparidae)	Marine (Field Enclosure)	Adult	Anatomical	Airgun Noise	Yes
McCormick et al., 2018 *	Effect of elevated CO ₂ and small boat noise on the kinematics of predator-prey interactions	<i>Proc. R. Soc. Lond. B.</i> 285 , 20172650	Damselfish (<i>Pomacentrus wardi</i> , Pomacentridae)	Marine (Laboratory)	Juvenile	Behavioural	Motor Boat Engine Noise	No
McCormick et al., 2018 *	Effect of elevated CO ₂ and small boat noise on the kinematics of predator-prey interactions	<i>Proc. R. Soc. Lond. B.</i> 285 , 20172650	Brown dottyback (<i>Pseudochromis fuscus</i> , Pseudochromidae)	Marine (Laboratory)	Adult	Behavioural	Motor Boat Engine Noise	No
McLaughlin and Kunc, 2015	Changes in the acoustic environment alter the foraging and sheltering behaviour of the cichlid <i>Amititlania nigrofasciata</i>	<i>Behav. Process.</i> 116 , 75-79.	Convict cichlid (<i>Amititlania nigrofasciata</i> , Cichlidae)	Freshwater (Laboratory)	Adult	Behavioural	Ship Engine Noise	Yes
Nedelec et al., 2016 *	Repeated exposure to noise increases tolerance in a coral reef fish	<i>Environ. Pollut.</i> 216 , 428-436.	Threespot dascyllus (<i>Dascyllus trimaculatus</i> , Pomacentridae)	Marine (Laboratory)	Juvenile	¹ Behavioural & ² Physiological	Motor Boat Engine Noise	Yes ^{1,2}
Nedelec et al., 2015	Impacts of regular and random noise on the behaviour, growth and development of larval Atlantic cod (<i>Gadus morhua</i>)	<i>Proc. R. Soc. Lond. B.</i> 282 , 20151943.	Atlantic cod (<i>Gadus morhua</i> , Gadidae)	Marine (Laboratory)	Larvae	¹ Behavioural & ² Physiological	Ship Engine Noise	Yes ^{1,2}

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Nedwell et al., 2006	An investigation into the effects of underwater piling noise on salmonids	<i>J. Acoust. Soc. Am.</i> 120 , 2550-2554.	Brown trout (<i>Salmo trutta</i> , Salmonidae)	Freshwater (Field Enclosure)	Adult	¹ Behavioural & ² Physiological	Pile Driving Noise	No ^{1,2}
Neo et al., 2016	Sound exposure changes European seabass behaviour in a large outdoor floating pen: Effects of temporal structure and a ramp-up procedure	<i>Environ. Pollut.</i> 214 , 26-34.	European sea bass (<i>Dicentrarchus labrax</i> , Moronidae)	Euryhaline (Field Enclosure)	Juvenile	Behavioural	Brown Noise	Yes
Neo et al., 2015a ‡	Behavioral changes in response to sound exposure and no spatial avoidance of noisy conditions in captive zebrafish	<i>Front. Behav. Neurosci.</i> 9 , 28.	Zebrafish (<i>Danio rerio</i> , Cyprinidae)	Freshwater (Laboratory)	Adult	Behavioural	White Noise	Yes
Neo et al., 2015b ‡	Impulsive sounds change European seabass swimming patterns: Influence of pulse repetition interval	<i>Mar. Poll. Bull.</i> 97 , 111-117.	European sea bass (<i>Dicentrarchus labrax</i> , Moronidae)	Euryhaline (Laboratory)	Juvenile	Behavioural	Brown Noise	Yes
Neo et al., 2014	Temporal structure of sound affects behavioural recovery from noise impact in European seabass	<i>Biol. Cons.</i> 178 , 65-73.	European sea bass (<i>Dicentrarchus labrax</i> , Moronidae)	Euryhaline (Laboratory)	Adult	Behavioural	Brown Noise	Yes
Nichols et al., 2015 ‡	Intermittent Noise Induces Physiological Stress in a Coastal Marine Fish	<i>PLOS ONE.</i> 10 , e0139157.	Giant kelpfish (<i>Heterostichus rostratus</i> , Clinidae)	Marine (Laboratory)	Juvenile	Physiological	Motor Boat Engine Noise	Yes

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Papoutsoglou et al., 2015 ‡	Gilthead seabream (<i>Sparus auratus</i>) response to three music stimuli (Mozart – “Eine Kleine Nachtmusik,” Anonymous – “Romanza,” Bach – “Violin Concerto No. 1”) and white noise under recirculating water conditions	<i>Fish Physiol. Biochem.</i> 41 , 219-232.	Gilthead seabream (<i>Sparus auratus</i> , Sparidae)	Marine (Laboratory)	Juvenile	Physiological	Classical Music & White Noise	Yes
Papoutsoglou et al., 2013 ‡	Effect of musical stimuli and white noise on rainbow trout (<i>Oncorhynchus mykiss</i>) growth and physiology in recirculating water conditions	<i>Aquacult. Eng.</i> 55 , 16-22.	Rainbow trout (<i>Oncorhynchus mykiss</i> , Salmonidae)	Euryhaline (Laboratory)	Adult	Physiological	Classical Music & White Noise	Yes
Papoutsoglou et al., 2007 ‡	Effect of Mozart's music (Romanze-Andante of "Eine Kleine Nacht Musik", sol major, K525) stimulus on common carp (<i>Cyprinus carpio</i> L.) physiology under different light conditions	<i>Aquacult. Eng.</i> 36 , 61-72.	Common carp (<i>Cyprinus carpio</i> , Cyprinidae)	Freshwater (Laboratory)	Juvenile	Physiological	Classical Music	Yes
Pearson et al., 1992	Effects of sounds from a geophysical survey device on behavior of captive rockfish (<i>Sebastes</i> spp.)	<i>Can. J. Fish. Aquat. Sci.</i> 49 , 1343-1356.	Black rockfish (<i>Sebastes melanops</i> , Sebastidae)	Marine (Field Enclosure)	Adult	Behavioural	Airgun Noise	Yes

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Pearson et al., 1992	Effects of sounds from a geophysical survey device on behavior of captive rockfish (<i>Sebastes</i> spp.)	<i>Can. J. Fish. Aquat. Sci.</i> 49 , 1343-1356.	Vermilion rockfish (<i>Sebastes miniatus</i> , Sebastidae)	Marine (Field Enclosure)	Adult	Behavioural	Airgun Noise	Yes
Pearson et al., 1992	Effects of sounds from a geophysical survey device on behavior of captive rockfish (<i>Sebastes</i> spp.)	<i>Can. J. Fish. Aquat. Sci.</i> 49 , 1343-1356.	Blue rockfish (<i>Sebastes mystinus</i> , Sebastidae)	Marine (Field Enclosure)	Adult	Behavioural	Airgun Noise	Yes
Pearson et al., 1992	Effects of sounds from a geophysical survey device on behavior of captive rockfish (<i>Sebastes</i> spp.)	<i>Can. J. Fish. Aquat. Sci.</i> 49 , 1343-1356.	Olive rockfish (<i>Sebastes serranoides</i> , Sebastidae)	Marine (Field Enclosure)	Adult	Behavioural	Airgun Noise	Yes
Picciulin et al., 2010*	In situ behavioural responses to boat noise exposure of <i>Gobius cruentatus</i> (Gmelin, 1789; fam. Gobiidae) and <i>Chromis chromis</i> (Linnaeus, 1758; fam. Pomacentridae) living in a Marine Protected Area	<i>J. Exp. Mar. Biol. Ecol.</i> 386 , 125-132.	Mediterranean damselfish (<i>Chromis chromis</i> , Pomacentridae)	Marine (Free Field)	Adult	Behavioural	Motor Boat & Ship Engine Noise	Yes
Picciulin et al., 2010*	In situ behavioural responses to boat noise exposure of <i>Gobius cruentatus</i> (Gmelin, 1789; fam. Gobiidae) and <i>Chromis chromis</i> (Linnaeus, 1758; fam. Pomacentridae) living in a Marine Protected Area	<i>J. Exp. Mar. Biol. Ecol.</i> 386 , 125-132.	Red-mouthed goby (<i>Gobius cruentatus</i> , Gobiidae)	Marine (Free field)	Adult	Behavioural	Motor Boat & Ship Engine Noise	Yes

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Popper et al., 2016	Effects of exposure to the sound from seismic airguns on pallid sturgeon and paddlefish	<i>PLOS ONE</i> . 11 , e0159486.	Pallid sturgeon (<i>Scaphirhynchus albus</i> , Acipenseridae)	Freshwater (Field Enclosure)	Juvenile	Anatomical	Airgun Noise	No
Popper et al., 2016	Effects of exposure to the sound from seismic airguns on pallid sturgeon and paddlefish	<i>PLOS ONE</i> . 11 , e0159486.	Paddlefish (<i>Polyodon spathula</i> , Polyodontidae)	Freshwater (Field Enclosure)	Juvenile	Anatomical	Airgun Noise	No
Popper et al., 2007	The effects of high-intensity, low-frequency active sonar on rainbow trout	<i>J. Acoust. Soc. Am.</i> 122 , 623-635.	Rainbow trout (<i>Oncorhynchus mykiss</i> , Salmonidae)	Euryhaline (Field Enclosure)	Adult	Anatomical	Sonar	Yes
Popper et al., 2005 ‡	Effects of exposure to seismic airgun use on hearing of three fish species	<i>J. Acoust. Soc. Am.</i> 117 , 3958-3971.	Broad whitefish (<i>Coregonus nasus</i> , Salmonidae)	Freshwater (Field Enclosure)	Adult	Anatomical	Airgun Noise	No
Popper et al., 2005 ‡	Effects of exposure to seismic airgun use on hearing of three fish species	<i>J. Acoust. Soc. Am.</i> 117 , 3958-3971.	Lake chub (<i>Couesius plumbeus</i> , Cyprinidae)	Freshwater (Field Enclosure)	Adult	Anatomical	Airgun Noise	Yes
Popper et al., 2005 ‡	Effects of exposure to seismic airgun use on hearing of three fish species	<i>J. Acoust. Soc. Am.</i> 117 , 3958-3971.	Northern pike (<i>Esox Lucius</i> , Esocidae)	Freshwater (Field Enclosure)	Adult	Anatomical	Airgun Noise	Yes
Poulton et al., 2017	Combined impacts of elevated CO ₂ and anthropogenic noise on European sea bass (<i>Dicentrarchus labrax</i>)	<i>ICES J. Mar. Sci.</i> 74(4) , 1230-1236.	European sea bass (<i>Dicentrarchus labrax</i> , Moronidae)	Euryhaline (Laboratory)	Juvenile	¹ Behavioural & ² Physiological	Pile Driving Noise	Yes ²

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Purser and Radford, 2011 ✳	Acoustic Noise Induces Attention Shifts and Reduces Foraging Performance in Three-Spined Sticklebacks (<i>Gasterosteus aculeatus</i>)	<i>PLOS ONE</i> . 6 , e17478.	Three-spined stickleback (<i>Gasterosteus aculeatus</i> , Gasterosteidae)	Euryhaline (Laboratory)	Adult	Behavioural	White Noise	Yes
Purser et al., 2016	Condition-dependent physiological and behavioural responses to anthropogenic noise	<i>Physiol. Behav.</i> 155 , 157-161.	European eel (<i>Anguilla anguilla</i> , Anguillidae)	Euryhaline (Laboratory)	Juvenile	¹ Behavioural & ² Physiological	Ship Engine Noise	Yes ^{1,2}
Radford et al., 2016 ✳	Repeated exposure reduces the response to impulsive noise in European seabass	<i>Glob. Change Biol.</i> 22 , 3349-3360.	European sea bass (<i>Dicentrarchus labrax</i> , Moronidae)	Euryhaline (Laboratory)	Juvenile	Physiological	Pile Driving Noise & Airgun Noise	Yes
Shafiei Sabet et al., 2015 ✳	The effect of temporal variation in sound exposure on swimming and foraging behaviour of captive zebrafish	<i>Anim. Behav.</i> 107 , 49-60.	Zebrafish (<i>Danio rerio</i> , Cyprinidae)	Freshwater (Laboratory)	Adult	Behavioural	White Noise	Yes
Shafiei Sabet et al., 2016 ✳	Behavioural responses to sound exposure in captivity by two fish species with different hearing ability	<i>Anim. Behav.</i> 116 , 1-11.	Zebrafish (<i>Danio rerio</i> , Cyprinidae)	Freshwater (Laboratory)	Adult	Behavioural	White Noise	Yes
Shafiei Sabet et al., 2016 ✳	Behavioural responses to sound exposure in captivity by two fish species with different hearing ability	<i>Anim. Behav.</i> 116 , 1-11.	Lake Victoria Cichlid (<i>Haplochromis piceatus</i> , Cichlidae)	Freshwater (Laboratory)	Adult	Behavioural	White Noise	Yes

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Scholik and Yan, 2002a	Effects of boat engine noise on the auditory sensitivity of the fathead minnow, <i>Pimephales promelas</i>	<i>Environm. Biol. Fish.</i> 63 , 203-209.	Fathead minnow (<i>Pimephales promelas</i> , Cyprinidae)	Freshwater (Laboratory)	Adult	Anatomical	Motor Boat Engine Noise	Yes
Scholik and Yan, 2002b *	The effects of noise on the auditory sensitivity of the bluegill sunfish, <i>Lepomis macrochirus</i>	<i>Comp. Biochem. Phys. A.</i> 133 , 43-52.	Bluegill sunfish (<i>Lepomis macrochirus</i> , Centrarchidae)	Freshwater (Laboratory)	Juvenile	Anatomical	White Noise	No
Scholik and Yan, 2001 *	Effects of underwater noise on auditory sensitivity of a cyprinid fish	<i>Hear. Res.</i> 152 , 17-24.	Fathead minnow (<i>Pimephales promelas</i> , Cyprinidae)	Freshwater (Laboratory)	Adult	Anatomical	White Noise	Yes
Schuck and Smith, 2009 *	Cell proliferation follows acoustically-induced hair cell bundle loss in the zebrafish sacculle	<i>Hear. Res.</i> 253 , 67-76.	Zebrafish (<i>Danio rerio</i> , Cyprinidae)	Freshwater (Laboratory)	Adult	Anatomical	Tonal Frequencies	Yes
Sebastianutto et al., 2011 *	How boat noise affects an ecologically crucial behaviour: the case of territoriality in <i>Gobius cruentatus</i> (Gobiidae)	<i>Environm. Biol. Fish.</i> 92 , 207-215.	Red-mouthed goby (<i>Gobius cruentatus</i> , Gobiidae)	Marine (Laboratory)	Adult	Behavioural	Motor Boat Engine Noise	Yes
Sierra-Flores et al., 2015 *	Stress response to anthropogenic noise in Atlantic cod <i>Gadus morhua</i> L.	<i>Aquacult. Eng.</i> 67 , 67-76.	Atlantic cod (<i>Gadus morhua</i> , Gadidae)	Marine (Laboratory)	Adult	Physiological	Broadband Noise	Yes
Simpson et al., 2016a	Small-boat noise impacts natural settlement behavior of coral reef fish larvae	<i>Adv. Exp. Med. Biol.</i> 875 , 1041-1048.	Ambon damsel (<i>Pomacentrus amboinensis</i> , Pomacentridae)	Marine (Free Field)	Larvae	Behavioural	Motor Boat Engine Noise	Yes

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Simpson et al., 2016b ‡	Anthropogenic noise increases fish mortality by predation	<i>Nat. Comm.</i> 7 , 10544.	Ambon damselfish (<i>Pomacentrus amboinensis</i> , Pomacentridae)	Marine (Laboratory & Free Field)	Juvenile	¹ Behavioural & ² Physiological	Motor Boat Engine Noise	Yes ^{1,2}
Simpson et al., 2016b	Small-boat noise impacts natural settlement behavior of coral reef fish larvae	<i>Adv. Exp. Med. Biol.</i> 875 , 1041-1048.	Nagasaki damsel (<i>Pomacentrus nagasakiensis</i> , Pomacentridae)	Marine (Free Field)	Larvae	Behavioural	Motor Boat Engine Noise	Yes
Simpson et al., 2015 ‡	Anthropogenic noise compromises antipredator behaviour in European eels	<i>Glob. Change Biol.</i> 21 , 586-593.	European eel (<i>Anguilla anguilla</i> , Anguillidae)	Euryhaline (Laboratory & Field Enclosure)	Larvae	¹ Behavioural & ² Physiological	Ship Engine Noise	Yes ^{1,2}
Simpson et al., 2010	Behavioral plasticity in larval reef fish: orientation is influenced by recent acoustic experiences	<i>Behav. Ecol.</i> 21 , 1098-1105.	Ambon damselfish (<i>Pomacentrus amboinensis</i> , Pomacentridae)	Marine (Field Enclosure)	Larvae	Behavioural	Tonal Frequencies	Yes
Simpson et al., 2010	Behavioral plasticity in larval reef fish: orientation is influenced by recent acoustic experiences	<i>Behav. Ecol.</i> 21 , 1098-1105.	Charcoal damsel (<i>Pomacentrus brachialis</i> , Pomacentridae)	Marine (Field Enclosure)	Larvae	Behavioural	Tonal Frequencies	Yes
Simpson et al., 2010	Behavioral plasticity in larval reef fish: orientation is influenced by recent acoustic experiences	<i>Behav. Ecol.</i> 21 , 1098-1105.	Lemon damsel (<i>Pomacentrus moluccensis</i> , Pomacentridae)	Marine (Field Enclosure)	Larvae	Behavioural	Tonal Frequencies	Yes
Simpson et al., 2010	Behavioral plasticity in larval reef fish: orientation is influenced by recent acoustic experiences	<i>Behav. Ecol.</i> 21 , 1098-1105.	Nagasaki damsel (<i>Pomacentrus nagasakiensis</i> , Pomacentridae)	Marine (Field Enclosure)	Larvae	Behavioural	Tonal Frequencies	Yes

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Simpson et al., 2005	Response of embryonic coral reef fishes (Pomacentridae: Amphiprion spp.) to noise	<i>Mar. Ecol. Progr. Ser.</i> 287 , 201-208.	Red saddleback anemonefish (<i>Amphiprion ephippium</i> , Pomacentridae)	Marine (Laboratory)	Embryo	Physiological	Tonal Frequencies	Yes
Simpson et al., 2005	Response of embryonic coral reef fishes (Pomacentridae: Amphiprion spp.) to noise	<i>Mar. Ecol. Progr. Ser.</i> 287 , 201-208.	Australian clownfish (<i>Amphiprion rubrocinctus</i> , Pomacentridae)	Marine (Laboratory)	Embryo	Physiological	Tonal Frequencies	Yes
Smith et al., 2006 ‡	Anatomical and functional recovery of the goldfish (<i>Carassius auratus</i>) ear following noise exposure	<i>J. Exp. Biol.</i> 209 , 4193-4202.	Goldfish (<i>Carassius auratus</i> , Cyprinidae)	Freshwater (Laboratory)	Adult	Anatomical	White Noise	Yes
Smith et al., 2004a	Acoustical stress and hearing sensitivity in fishes: does the linear threshold shift hypothesis hold water?	<i>J. Exp. Biol.</i> 207 , 3591-3602.	Nile tilapia (<i>Oreochromis niloticus</i> , Cichlidae)	Freshwater (Laboratory)	Adult	Anatomical	White Noise	Yes
Smith et al., 2004a	Acoustical stress and hearing sensitivity in fishes: does the linear threshold shift hypothesis hold water?	<i>J. Exp. Biol.</i> 207 , 3591-3602.	Goldfish (<i>Carassius auratus</i> , Cyprinidae)	Freshwater (Laboratory)	Adult	Anatomical	White Noise	Yes
Smith et al., 2004b ‡	Noise-induced stress response and hearing loss in goldfish (<i>Carassius auratus</i>)	<i>J. Exp. Biol.</i> 207 , 427-435.	Goldfish (<i>Carassius auratus</i> , Cyprinidae)	Freshwater (Laboratory)	Adult	¹ Anatomical & ² Physiological	White Noise	Yes ^{1,2}

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Song et al., 2008	The inner ears of Northern Canadian freshwater fishes following exposure to seismic air gun sounds	<i>J. Acoust. Soc. Am.</i> 124 , 1360-1366.	Broad whitefish (<i>Coregonus nasus</i> , Salmonidae)	Freshwater (Field Enclosure)	Adult	Anatomical	Airgun Noise	No
Song et al., 2008	The inner ears of Northern Canadian freshwater fishes following exposure to seismic air gun sounds	<i>J. Acoust. Soc. Am.</i> 124 , 1360-1366.	Lake chub (<i>Couesius plumbeus</i> , Cyprinidae)	Freshwater (Field Enclosure)	Adult	Anatomical	Airgun Noise	No
Song et al., 2008	The inner ears of Northern Canadian freshwater fishes following exposure to seismic air gun sounds	<i>J. Acoust. Soc. Am.</i> 124 , 1360-1366.	Northern pike (<i>Esox Lucius</i> , Esocidae)	Freshwater (Field Enclosure)	Adult	Anatomical	Airgun Noise	No
Spiga et al., 2012	Effects of short- and long-term exposure to boat noise on cortisol levels in juvenile fish	<i>Adv. Exp. Med. Biol.</i> 730 , 251-253.	Red drum (<i>Sciaenops ocellatus</i> , Sciaenidae)	Marine (Laboratory)	Juvenile	Physiological	Motor Boat Engine Noise	Yes
Spiga et al., 2012	Effects of short- and long-term exposure to boat noise on cortisol levels in juvenile fish	<i>Adv. Exp. Med. Biol.</i> 730 , 251-253.	Spotted sea trout (<i>Cynoscion nebulosus</i> , Sciaenidae)	Marine (Laboratory)	Juvenile	Physiological	Motor Boat Engine Noise	Yes
Vasconcelos et al., 2007 ‡	Effects of ship noise on the detectability of communication signals in the Lusitanian toadfish	<i>J. Exp. Biol.</i> 210 , 2104-2112.	Lusitanian toadfish (<i>Halobatrachus didactylus</i>)	Marine (Laboratory)	Adult	Anatomical	Ship Engine Noise	Yes

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Vazzana et al., 2017 ‡	Noise elicits hematological stress parameters in Mediterranean damselfish (<i>Chromis chromis</i> , perciformes): A mesocosm study	<i>Fish Shellfish Immunol.</i> 62 , 147-152.	Mediterranean Damselfish (<i>Chromis chromis</i> , Batrachoididae)	Marine (Field Enclosure)	Adult	Physiological	Tonal Frequencies	Yes
Vetter et al., 2017	Acoustic deterrence of bighead carp (<i>Hypophthalmichthys nobilis</i>) to a broadband sound stimulus	<i>J. Great Lakes Res.</i> 43 , 163-171.	Bighead carp (<i>Hypophthalmichthys nobilis</i> , Cyprinidae)	Freshwater (Laboratory)	Adult	Behavioural	Broadband Noise	Yes
Vetter et al., 2015	Acoustical deterrence of Silver Carp (<i>Hypophthalmichthys molitrix</i>)	<i>Biol. Invasions</i> 17 , 3383-3392.	Silver Carp (<i>Hypophthalmichthys molitrix</i> , Cyprinidae)	Freshwater (Laboratory)	Adult	Behavioural	Broadband Noise	Yes
Voellmy et al., 2014a ‡	Acoustic noise reduces foraging success in two sympatric fish species via different mechanisms	<i>Anim. Behav.</i> 89 , 191-198.	Three-spined stickleback (<i>Gasterosteus aculeatus</i> , Gasterosteidae)	Euryhaline (Laboratory)	Adult	Behavioural	Ship Engine Noise	Yes
Voellmy et al., 2014a ‡	Acoustic noise reduces foraging success in two sympatric fish species via different mechanisms	<i>Anim. Behav.</i> 89 , 191-198.	European minnow (<i>Phoxinus phoxinus</i> , Cyprinidae)	Freshwater (Laboratory)	Adult	Behavioural	Ship Engine Noise	Yes
Voellmy et al., 2014b	Increased Noise Levels Have Different Impacts on the Anti-Predator Behaviour of Two Sympatric Fish Species	<i>PLOS ONE.</i> 9 , e102946.	Three-spined stickleback (<i>Gasterosteus aculeatus</i> , Gasterosteidae)	Euryhaline (Laboratory)	Adult	Behavioural	Ship Engine Noise	Yes

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Voellmy et al., 2014b	Increased Noise Levels Have Different Impacts on the Anti-Predator Behaviour of Two Sympatric Fish Species	<i>PLOS ONE</i> , 9 , e102946.	European minnow (<i>Phoxinus phoxinus</i> , Cyprinidae)	Freshwater (Laboratory)	Adult	Behavioural	Ship Engine Noise	No
Wagner et al., 2015	The effect of seismic waterguns on the inner ears of round goby	<i>J. Great. Lake. Res.</i> 41 , 1191-1196.	Round goby (<i>Neogobius melanostomus</i> , Gobiidae)	Euryhaline (Field Enclosure)	Adult	Anatomical	Watergun Noise	No
Wilson and Dill, 2002*	Pacific herring respond to simulated odontocete echolocation sounds	<i>Can. J. Fish. Aquat. Sci.</i> 59 , 542-553.	Pacific Herring (<i>Clupea pallasii</i> , Clupeidae)	Marine (Laboratory)	Adult	Behavioural	Simulated Broadband Clicks	Yes
Wilson et al., 2011	Directional escape behavior in allis shad (<i>Alosa alosa</i>) exposed to ultrasonic clicks mimicking an approaching toothed whale	<i>J. Exp. Biol.</i> 214 , 22-29.	Allis shad (<i>Alosa alosa</i> , Clupeidae)	Euryhaline (Laboratory)	Adult	Behavioural	Simulated Broadband Clicks	Yes
Wysocki and Ladich, 2005a*	Effects of noise exposure on click detection and the temporal resolution ability of the goldfish auditory system	<i>Hear. Res.</i> 201 , 27-36.	Goldfish (<i>Carassius auratus</i> , Cyprinidae)	Freshwater (Laboratory)	Adult	Anatomical	White Noise	Yes
Wysocki and Ladich, 2005b	Hearing in fishes under noise conditions	<i>JARO</i> , 6 , 28-36.	Goldfish (<i>Carassius auratus</i> , Cyprinidae)	Freshwater (Laboratory)	Adult	Anatomical	White Noise	Yes
Wysocki and Ladich, 2005b	Hearing in fishes under noise conditions	<i>JARO</i> , 6 , 28-36.	Lined Raphael Catfish (<i>Platydoras costatus</i> , Doradidae)	Freshwater (Laboratory)	Adult	Anatomical	White Noise	Yes

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Wysocki and Ladich, 2005b ‡	Hearing in fishes under noise conditions	<i>JARO</i> , 6 , 28-36.	Pumpkinseed sunfish (<i>Lepomis gibbosus</i> , Centrarchidae)	Freshwater (Laboratory)	Adult	Anatomical	White Noise	No
Wysocki et al., 2007	Effects of aquaculture production noise on hearing, growth, and disease resistance of rainbow trout <i>Oncorhynchus mykiss</i>	<i>Aquaculture</i> , 272 , 687-697.	Hybrid rainbow*steelhead trout (<i>Oncorhynchus mykiss</i> , Salmonidae)	Euryhaline (Laboratory)	Juvenile	¹ Anatomical & ² Physiological	Aquaculture Ambient Noise	No ^{1,2}
Wysocki et al., 2006 ‡	Ship noise and cortisol secretion in European freshwater fishes	<i>Biol. Cons.</i> 128 , 501-508.	Wild common carp (<i>Cyprinus carpio</i> , Cyprinidae)	Freshwater (Laboratory)	Adult	Physiological	Ship Engine Noise	Yes
Wysocki et al., 2006 ‡	Ship noise and cortisol secretion in European freshwater fishes	<i>Biol. Cons.</i> 128 , 501-508.	Gudgeon (<i>Gobio gobio</i> , Cyprinidae)	Freshwater (Laboratory)	Adult	Physiological	Ship Engine Noise	Yes
Wysocki et al., 2006 ‡	Ship noise and cortisol secretion in European freshwater fishes	<i>Biol. Cons.</i> 128 , 501-508.	European perch (<i>Perca fluviatilis</i> , Percidae)	Freshwater (Laboratory)	Adult	Physiological	Ship Engine Noise	Yes
Zeddies et al., 2012	Local acoustic particle motion guides sound-source localization behavior in the plainfin midshipman fish, <i>Porichthys notatus</i>	<i>J. Exp. Biol.</i> 215 , 152-160.	Plainfin midshipman (<i>Porichthys notatus</i> , Batrachoididae)	Marine (Laboratory)	Adult	Behavioural	Tonal Frequencies	Yes
Zeddies et al., 2010	Sound source localization by the plainfin midshipman fish, <i>Porichthys notatus</i>	<i>J. Acoust. Soc. Am.</i> 127 , 3104-3113.	Plainfin midshipman (<i>Porichthys notatus</i> , Batrachoididae)	Marine (Laboratory)	Adult	Behavioural	Tonal Frequencies	Yes

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Zielinski and Sorensen, 2017	Silver, bighead, and common carp orient to acoustic particle motion when avoiding a complex sound	<i>PLOS ONE</i> . 12(6) , e0180110.	Bighead carp (<i>Hypophthalmichthys nobilis</i> , Cyprinidae)	Freshwater (Laboratory)	Juvenile	Behavioural	Motor Boat Engine Noise	Yes
Zielinski and Sorensen, 2017	Silver, bighead, and common carp orient to acoustic particle motion when avoiding a complex sound	<i>PLOS ONE</i> . 12(6) , e0180110.	Common carp (<i>Cyprinus carpio</i> , Cyprinidae)	Freshwater (Laboratory)	Juvenile	Behavioural	Motor Boat Engine Noise	Yes
Zielinski and Sorensen, 2017	Silver, bighead, and common carp orient to acoustic particle motion when avoiding a complex sound	<i>PLOS ONE</i> . 12(6) , e0180110.	Silver Carp (<i>Hypophthalmichthys molitrix</i> , Cyprinidae)	Freshwater (Laboratory)	Juvenile	Behavioural	Motor Boat Engine Noise	Yes

APPENDIX B Fish measurement and experimental condition variation

Table B1: Experiment I: One-Way ANOVAs † and Kruskal-Wallis rank sum tests ψ between treatments showing: minnow total length ($p = 0.72$; $F_{1,4} = 0.52$); standard length ($p = 0.79$; $F_{1,4} = 0.43$); fork length ($p = 0.69$; $F_{1,4} = 0.55$); wet mass ($p = 0.84$; $F_{1,4} = 0.35$); experimental flume water temperature ($\chi^2 = 9.12$; $d.f. = 4$; $p = 0.06$); background in-air ambient noise intensity ($\chi^2 = 13.57$; $d.f. = 4$; $p < 0.05$).

<i>Treatment</i>	Mean total length ± s.e. (mm)	Mean standard length ± s.e. (mm)	Mean fork length ± s.e. (mm)	Mean wet mass ± s.e. (g)	Median experimental flume water temperature ± MAD (°C)	Median in-air background ambient noise intensity ± MAD (dB re 20 μPa)
<i>All Combined</i>	61.1 ± 0.5 †	51.6 ± 0.4 †	56.6 ± 0.5 †	2.1 ± 0.1 †	18.3 ± 0.4 ψ	36.0 ± 2.9 ψ
<i>Control</i>	61.9 ± 1.0 †	52.3 ± 0.9 †	57.5 ± 0.9 †	2.1 ± 0.1 †	18.3 ± 0.6 ψ	36.0 ± 1.5 ψ
<i>SINE_150</i>	59.9 ± 1.0 †	50.9 ± 0.9 †	55.5 ± 1.0 †	1.9 ± 0.1 †	18.0 ± 0.6 ψ	36.0 ± 0.7 ψ
<i>SINE_2200</i>	61.6 ± 1.1 †	52 ± 0.9 †	57.1 ± 0.9 †	2.1 ± 0.1 †	18.4 ± 0.4 ψ	38.0 ± 5.9 ψ
<i>NOISE_150</i>	61.2 ± 1.3 †	51.8 ± 1.0 †	56.6 ± 1.1 †	2.2 ± 0.1 †	18.3 ± 0.8 ψ	34.5 ± 4.4 ψ
<i>NOISE_2200</i>	60.6 ± 1.1 †	52.2 ± 0.9 †	56.4 ± 0.9 †	2.1 ± 0.1 †	18.3 ± 0.3 ψ	38.0 ± 5.9 ψ

Appendix B

Table B2: Experiment II: Kruskal-Wallis rank sum tests between treatments showing: minnow total length ($\chi^2 = 13.0$; $d.f. = 4$; $p < 0.05$); standard length ($\chi^2 = 11.5$; $d.f. = 4$; $p < 0.05$); fork length ($\chi^2 = 14.8$; $d.f. = 4$; $p < 0.01$); wet mass ($\chi^2 = 14.7$; $d.f. = 4$; $p < 0.01$); experimental flume water temperature ($\chi^2 = 4.7$; $d.f. = 4$; $p = 0.31$); background in-air ambient noise intensity ($\chi^2 = 16.6$; $d.f. = 4$; $p < 0.01$). Although differences were observed, *post hoc* (Dunn's test with Benjamini-Hochberg adjusted p -value method) analysis indicated the only difference for fish size and mass to be between PRRO.5 and PRRO.2. Difference in background in-air ambient noise intensity was only between PRRO.5 with the control and continuous treatments.

<i>Treatment</i>	Median total length \pm MAD (mm)	Median standard length \pm MAD (mm)	Median fork length \pm MAD (mm)	Median wet mass \pm MAD (g)	Median experimental flume water temperature \pm MAD ($^{\circ}$ C)	Median in-air background ambient noise intensity \pm MAD (dB re 20 μ Pa)
<i>All Combined</i>	68.0 \pm 5.9	57.0 \pm 4.4	63.0 \pm 4.4	2.8 \pm 0.9	13.9 \pm 1.1	39.0 \pm 5.9
<i>Control</i>	68.0 \pm 8.9	58.0 \pm 8.9	64.0 \pm 8.9	2.8 \pm 1.3	14.1 \pm 1.6	40.5 \pm 2.9
<i>CONTINUOUS</i>	68.5 \pm 5.2	58.0 \pm 5.2	63.0 \pm 5.2	2.8 \pm 0.7	14.1 \pm 1.1	40.5 \pm 3.0
<i>FAST</i>	66.0 \pm 3.0	55.0 \pm 3.0	60.0 \pm 3.0	2.4 \pm 0.6	14.0 \pm 0.4	35.0 \pm 3.0
<i>INTERMEDIATE</i>	68.0 \pm 4.4	57.0 \pm 3.0	63.0 \pm 3.0	2.8 \pm 0.6	13.6 \pm 0.7	36.0 \pm 3.7
<i>SLOW</i>	70.0 \pm 8.9	59.5 \pm 8.2	65.0 \pm 8.9	3.3 \pm 1.5	13.7 \pm 0.9	34.5 \pm 2.2

Appendix B

Table B3: Experiment III: Kruskal-Wallis rank sum tests between treatments showing: carp total length ($\chi^2 = 15.4$; $d.f. = 7$; $p < 0.05$); standard length ($\chi^2 = 14.9$; $d.f. = 7$; $p < 0.05$); fork length ($\chi^2 = 14.8$; $d.f. = 7$; $p < 0.05$); wet mass ($\chi^2 = 21.9$; $d.f. = 7$; $p < 0.01$); and experimental flume water temperature ($\chi^2 = 17.2$; $d.f. = 7$; $p < 0.05$). Although differences were observed, *post hoc* (Dunn's test with Benjamini-Hochberg adjusted *p*-value method) analysis indicated the only difference for fish size to be for MASK-NOISE fish, and no differences were observed for water temperature.

<i>Treatment</i>	Median total length \pm MAD (mm)	Median standard length \pm MAD (mm)	Median fork length \pm MAD (mm)	Median wet mass \pm MAD (g)	Median experimental flume water temperature \pm MAD ($^{\circ}$ C)
All Combined	85.0 \pm 21.5	69.0 \pm 17.8	75.0 \pm 19.3	8.7 \pm 6.4	10.8 \pm 1.2
AMB-C	77.5 \pm 14.1	63.0 \pm 11.9	69.0 \pm 13.3	6.3 \pm 3.9	10.6 \pm 1.3
MASK-C	90.0 \pm 9.6	73.0 \pm 7.4	80.0 \pm 8.9	10.8 \pm 4.5	10.7 \pm 1.4
AMB-LOW	88.0 \pm 22.2	70.5 \pm 20.0	78.0 \pm 19.3	9.5 \pm 8.5	11.0 \pm 0.8
AMB-INT	78.5 \pm 22.9	64.5 \pm 15.6	70.0 \pm 17.8	7.4 \pm 5.6	11.5 \pm 0.7
AMB-HIGH	79.0 \pm 17.0	64.5 \pm 14.8	69.5 \pm 16.3	6.3 \pm 3.9	10.9 \pm 1.3
MASK-LOW	79.0 \pm 32.6	64.0 \pm 27.4	71.0 \pm 29.7	7.3 \pm 7.8	10.7 \pm 1.3
MASK-INT	91.0 \pm 18.5	75.0 \pm 13.3	80.5 \pm 14.1	10.2 \pm 6.2	10.6 \pm 0.4
MASK-HIGH	88.5 \pm 22.9	72.0 \pm 19.3	80.0 \pm 22.2	10.0 \pm 7.9	10.8 \pm 1.5

Appendix B

Table B4: Experiment IV: One-Way ANOVAs † and Kruskal-Wallis rank sum tests ψ between treatments showing: fish total length ($\chi^2 = 7.7$; $d.f. = 5$; $p = 0.176$); standard length ($\chi^2 = 6.3$; $d.f. = 5$; $p = 0.28$); fork length ($\chi^2 = 7.12$; $d.f. = 5$; $p = 0.21$); wet mass ($\chi^2 = 5.6$; $d.f. = 5$; $p = 0.34$); experimental flume water temperature ($p = 0.24$; $F_{5,90} = 1.39$); background light levels ($p = 0.88$; $F_{5,90} = 0.35$); background in-air ambient noise intensity ($p < 0.01$; $F_{5,90} = 3.31$). Differences were observed, *post hoc* (Tukey Honest Significant Difference †) for background in-air noise intensity, however only between the low velocity under control conditions, and the high velocity under the sound treatment ($p < 0.05$).

<i>Acoustic Treatment</i>	<i>Velocity Regime</i>	<i>Median velocities ± MAD (m s⁻¹)</i>	<i>Median total length ± MAD (mm)</i>	<i>Median standard length ± MAD (mm)</i>	<i>Median fork length ± MAD (mm)</i>	<i>Median wet mass ± MAD (g)</i>	<i>Mean experimental flume water temperature ± s.e. (°C)</i>	<i>Mean background light levels ± s.e. (LUX)</i>	<i>Mean in-air background ambient noise intensity ± s.e. (dB re 20 µPa)</i>
<i>All Combined</i>		n.a.	150.0 ± 13.0 ψ	123.0 ± 10.5 ψ	135.0 ± 11.0 ψ	34.3 ± 9.4 ψ	16.6 ± 0.1 †	33.95 ± 0.4 †	50.7 ± 0.2 †
<i>Background noise (control)</i>	<i>Low</i>	0.07 ± 0.01 ψ	145.0 ± 13.3 ψ	118.0 ± 10.4 ψ	130.0 ± 11.9 ψ	31.3 ± 10.7 ψ	16.6 ± 0.2 †	33.70 ± 0.2 †	49.9 ± 0.2 †
	<i>Intermediate</i>	0.16 ± 0.01 ψ	156.0 ± 20.8 ψ	126.0 ± 17.8 ψ	140.0 ± 17.8 ψ	39.4 ± 18.5 ψ	16.4 ± 0.2 †	33.81 ± 0.2 †	51.7 ± 0.2 †
	<i>High</i>	0.22 ± 0.01 ψ	148.0 ± 19.3 ψ	123.0 ± 16.3 ψ	135.0 ± 19.3 ψ	33.3 ± 12.9 ψ	17.1 ± 0.2 †	33.84 ± 0.3 †	52.4 ± 0.1 †
<i>Background noise + tone</i>	<i>Low</i>	0.08 ± 0.01 ψ	155.0 ± 28.2 ψ	125.0 ± 21.5 ψ	139.0 ± 23.7 ψ	38.6 ± 21.4 ψ	16.4 ± 0.2 †	33.83 ± 0.1 †	49.6 ± 0.18 †
	<i>Intermediate</i>	0.16 ± 0.0 ψ	151.0 ± 16.3 ψ	125.5 ± 15.6 ψ	138.5 ± 16.3 ψ	36.0 ± 13.4 ψ	16.3 ± 0.1 †	33.81 ± 0.2 †	50.9 ± 0.1 †
	<i>High</i>	0.23 ± 0.0 ψ	154.5 ± 15.6 ψ	127.0 ± 14.8 ψ	140.0 ± 14.8 ψ	37.4 ± 13.6 ψ	16.9 ± 0.1 †	33.96 ± 0.2 †	52.3 ± 0.1 †

APPENDIX C False alarm (FAR) and hit rate (HR) for fine-scale behaviour

Table C1: False alarm (FAR) and hit rates (HR) for trial groups exposed to 170 Hz tonal stimuli under masked noise treatments determined through the calculation of linear least squares regression models. Note: Grey shading indicates that a trial (01-10) deviated from the group “normative fit” (regression line equation: $y = 0.304 - 4.8 \times 10^{-6} x$; \pm s.e. = $\pm 2.14 \times 10^{-5}$; CI [-4.69 $\times 10^{-5}$; 3.73 $\times 10^{-5}$]) and was classed as a “false alarm” (incorrect response for control) or “hit” (correct response for treatments). Models failing to meet assumptions of homoscedasticity, underwent bootstrapped estimates ($n = 1000$) to produce a variance robust standard error and bias corrected and accelerated confidence interval (BCa CI).

	Regression line equations ($y = mx + c$)	\pm s.e.	\pm variance robust s.e.	CI Lower	CI Upper	BCa CI Lower	BCa CI Upper
Masking Control	$0.304 - 4.8 \times 10^{-6} x$	2.14×10^{-5}	n.a.	-4.69×10^{-5}	3.73×10^{-5}	n.a.	n.a.
MASK-C (FAR = 0.2)							
01	$1.130 - 3.79 \times 10^{-4} x$	n.a.	6.79×10^{-5}	n.a.	n.a.	-5.15×10^{-4}	-2.43×10^{-4}
02	$-0.137 + 2.02 \times 10^{-4} x$	3.99×10^{-5}	n.a.	1.22×10^{-4}	2.82×10^{-4}	n.a.	n.a.
03	$0.065 + 2.68 \times 10^{-5} x$	2.70×10^{-5}	n.a.	-2.72×10^{-5}	8.07×10^{-5}	n.a.	n.a.
04	$0.180 + 7.06 \times 10^{-5} x$	5.52×10^{-5}	n.a.	-3.98×10^{-5}	1.81×10^{-4}	n.a.	n.a.
05	$0.155 + 6.38 \times 10^{-5} x$	3.88×10^{-5}	n.a.	-1.39×10^{-5}	1.41×10^{-4}	n.a.	n.a.
06	$0.270 - 1.39 \times 10^{-5} x$	3.79×10^{-5}	n.a.	-8.97×10^{-5}	6.19×10^{-5}	n.a.	n.a.
07	$0.426 - 3.56 \times 10^{-5} x$	5.42×10^{-5}	n.a.	-1.44×10^{-4}	7.28×10^{-5}	n.a.	n.a.
08	$0.402 - 4.10 \times 10^{-5} x$	4.23×10^{-5}	n.a.	-1.26×10^{-4}	4.36×10^{-5}	n.a.	n.a.
09	$0.319 + 8.29 \times 10^{-6} x$	5.56×10^{-5}	n.a.	-1.03×10^{-4}	1.20×10^{-4}	n.a.	n.a.
10	$0.229 + 4.97 \times 10^{-5} x$	4.01×10^{-5}	n.a.	-3.05×10^{-5}	1.30×10^{-4}	n.a.	n.a.

MASK-LOW
(HR = 0.2)

01	$-0.045 + 1.53 \times 10^{-4} x$	5.57×10^{-5}	n.a.	4.15×10^{-5}	2.64×10^{-4}	n.a.	n.a.
02	$0.177 + 3.75 \times 10^{-5} x$	4.89×10^{-5}	n.a.	-6.03×10^{-5}	1.35×10^{-4}	n.a.	n.a.
03	$0.153 + 5.84 \times 10^{-5} x$	n.a.	4.97×10^{-5}	n.a.	n.a.	-4.11×10^{-5}	1.58×10^{-4}
04	$0.103 + 1.06 \times 10^{-4} x$	3.66×10^{-5}	n.a.	3.32×10^{-5}	1.80×10^{-4}	n.a.	n.a.
05	$0.143 + 2.13 \times 10^{-5} x$	n.a.	3.80×10^{-5}	n.a.	n.a.	-5.48×10^{-5}	9.73×10^{-5}
06	$0.236 - 4.49 \times 10^{-6} x$	n.a.	5.49×10^{-5}	n.a.	n.a.	-1.14×10^{-4}	1.05×10^{-4}
07	$0.160 + 6.27 \times 10^{-5} x$	4.02×10^{-5}	n.a.	-1.77×10^{-5}	1.43×10^{-4}	n.a.	n.a.
08	$0.057 + 4.78 \times 10^{-5} x$	4.93×10^{-5}	n.a.	-5.08×10^{-5}	1.46×10^{-4}	n.a.	n.a.
09	$-0.049 + 1.06 \times 10^{-4} x$	3.87×10^{-5}	n.a.	2.90×10^{-5}	1.84×10^{-4}	n.a.	n.a.
10	$-0.140 + 1.90 \times 10^{-4} x$	4.75×10^{-5}	n.a.	9.49×10^{-5}	2.85×10^{-4}	n.a.	n.a.

MASK-INT
(HR = 0.7)

01	$0.307 - 3.01 \times 10^{-5} x$	6.43×10^{-5}	n.a.	-1.60×10^{-4}	9.85×10^{-5}	n.a.	n.a.
02	$-0.167 + 1.50 \times 10^{-4} x$	5.03×10^{-5}	n.a.	4.90×10^{-5}	2.50×10^{-4}	n.a.	n.a.
03	$-0.186 + 1.91 \times 10^{-4} x$	n.a.	6.22×10^{-5}	n.a.	n.a.	6.62×10^{-5}	3.15×10^{-4}
04	$-0.163 + 1.99 \times 10^{-4} x$	n.a.	5.22×10^{-5}	n.a.	n.a.	9.41×10^{-5}	3.03×10^{-4}
05	$-0.168 + 1.99 \times 10^{-4} x$	n.a.	4.91×10^{-5}	n.a.	n.a.	1.01×10^{-4}	2.97×10^{-4}
06	$0.207 - 1.79 \times 10^{-5} x$	5.06×10^{-5}	n.a.	-1.20×10^{-4}	8.32×10^{-5}	n.a.	n.a.
07	$0.197 + 1.52 \times 10^{-5} x$	5.51×10^{-5}	n.a.	-9.51×10^{-5}	1.26×10^{-4}	n.a.	n.a.
08	$-0.183 + 1.74 \times 10^{-4} x$	3.82×10^{-5}	n.a.	9.72×10^{-5}	2.50×10^{-4}	n.a.	n.a.
09	$-0.339 + 2.55 \times 10^{-4} x$	6.18×10^{-5}	n.a.	1.31×10^{-4}	3.79×10^{-4}	n.a.	n.a.
10	$-0.288 + 2.62 \times 10^{-4} x$	6.13×10^{-5}	n.a.	1.39×10^{-4}	3.84×10^{-4}	n.a.	n.a.

MASK-HIGH (HR = 0.6)							
01	$0.234 - 1.19 \times 10^{-5} x$	4.29×10^{-5}	n.a.	-9.77×10^{-5}	7.39×10^{-5}	n.a.	n.a.
02	$0.308 - 6.35 \times 10^{-5} x$	3.78×10^{-5}	n.a.	-1.40×10^{-4}	1.21×10^{-5}	n.a.	n.a.
03	$0.114 + 4.05 \times 10^{-5} x$	4.16×10^{-5}	n.a.	-4.26×10^{-5}	1.24×10^{-4}	n.a.	n.a.
04	$-0.216 + 2.36 \times 10^{-4} x$	5.29×10^{-5}	n.a.	1.30×10^{-4}	3.42×10^{-4}	n.a.	n.a.
05	$-0.149 + 1.58 \times 10^{-4} x$	4.71×10^{-5}	n.a.	6.36×10^{-5}	2.52×10^{-4}	n.a.	n.a.
06	$-0.274 + 2.40 \times 10^{-4} x$	4.08×10^{-5}	n.a.	1.59×10^{-4}	3.22×10^{-4}	n.a.	n.a.
07	$0.160 + 1.09 \times 10^{-6} x$	4.72×10^{-5}	n.a.	-9.34×10^{-5}	9.56×10^{-5}	n.a.	n.a.
08	$-0.140 + 1.71 \times 10^{-4} x$	5.23×10^{-5}	n.a.	6.64×10^{-5}	2.76×10^{-4}	n.a.	n.a.
09	$-0.081 + 1.53 \times 10^{-4} x$	4.17×10^{-5}	n.a.	6.94×10^{-5}	2.36×10^{-4}	n.a.	n.a.
10	$-0.205 + 1.87 \times 10^{-4} x$	3.97×10^{-5}	n.a.	1.08×10^{-4}	2.67×10^{-4}	n.a.	n.a.

Appendix C

Table C2: False alarm (FAR) and hit rates (HR) for trial groups exposed to 170 Hz tonal stimuli under ambient noise treatments determined through the calculation of linear least squares regression models. Note: Grey shading indicates that a trial (01-10) deviated from the group “normative fit” (regression line equation: $y = 0.217 + 3.84 \times 10^{-5} x$; \pm s.e. = $\pm 2.04 \times 10^{-5}$; CI [-1.78 $\times 10^{-6}$; 7.85 $\times 10^{-5}$]) and was classed as a “false alarm” (incorrect response for control) or “hit” (correct response for treatments). Models failing to meet assumptions of homoscedasticity, underwent bootstrapped estimates (n = 1000) to produce a variance robust standard error and bias corrected and accelerated confidence interval (BCa CI).

	Regression line equations ($y = mx + c$)	\pm s.e.	\pm variance robust s.e.	CI Lower	CI Upper	BCa CI Lower	BCa CI Upper
Ambient Control	$0.217 + 3.84 \times 10^{-5} x$	2.04×10^{-5}	n.a.	-1.78×10^{-6}	7.85×10^{-5}	n.a.	n.a.
AMB-C							
(FAR = 0.0)							
01	$0.057 + 7.12 \times 10^{-5} x$	4.18×10^{-5}	n.a.	-1.24×10^{-5}	1.55×10^{-4}	n.a.	n.a.
02	$0.224 + 3.08 \times 10^{-5} x$	5.15×10^{-5}	n.a.	-7.22×10^{-5}	1.34×10^{-4}	n.a.	n.a.
03	$0.101 + 6.58 \times 10^{-5} x$	7.02×10^{-5}	n.a.	-7.46×10^{-5}	2.06×10^{-4}	n.a.	n.a.
04	$0.267 + 3.34 \times 10^{-6} x$	5.77×10^{-5}	n.a.	-1.12×10^{-4}	1.19×10^{-4}	n.a.	n.a.
05	$0.508 - 8.77 \times 10^{-5} x$	5.85×10^{-5}	n.a.	-2.05×10^{-4}	2.93×10^{-5}	n.a.	n.a.
06	$0.081 + 1.07 \times 10^{-4} x$	5.95×10^{-5}	n.a.	-1.19×10^{-5}	2.26×10^{-4}	n.a.	n.a.
07	$0.110 + 1.15 \times 10^{-4} x$	4.98×10^{-5}	n.a.	1.53×10^{-5}	2.14×10^{-4}	n.a.	n.a.
08	$0.336 - 2.93 \times 10^{-6} x$	5.61×10^{-5}	n.a.	-1.15×10^{-4}	1.09×10^{-4}	n.a.	n.a.
09	$0.093 + 1.24 \times 10^{-4} x$	4.70×10^{-5}	n.a.	3.03×10^{-5}	2.18×10^{-4}	n.a.	n.a.
10	$0.390 - 4.33 \times 10^{-5} x$	6.18×10^{-5}	n.a.	-1.67×10^{-4}	8.04×10^{-5}	n.a.	n.a.

Appendix C

AMB-LOW (HR = 0.3)	$0.375 - 3.85 \times 10^{-5} x$	4.41×10^{-5}	n.a.	-1.30×10^{-4}	4.98×10^{-5}	n.a.	n.a.
01							
02	$0.398 - 1.24 \times 10^{-4} x$	n.a.	5.47×10^{-5}	n.a.	n.a.	-2.33×10^{-4}	-1.42×10^{-5}
03	$0.106 + 3.59 \times 10^{-6} x$	2.90×10^{-5}	n.a.	-5.44×10^{-5}	6.16×10^{-5}	n.a.	n.a.
04	$0.321 - 7.26 \times 10^{-5} x$	5.28×10^{-5}	n.a.	-1.80×10^{-4}	3.31×10^{-5}	n.a.	n.a.
05	$0.334 - 5.93 \times 10^{-5} x$	7.21×10^{-5}	n.a.	-2.00×10^{-4}	8.50×10^{-5}	n.a.	n.a.
06	$0.356 - 1.00 \times 10^{-4} x$	n.a.	2.73×10^{-5}	n.a.	n.a.	-1.55×10^{-4}	-4.58×10^{-5}
07	$0.554 - 2.00 \times 10^{-4} x$	n.a.	5.22×10^{-5}	n.a.	n.a.	-3.05×10^{-4}	-9.58×10^{-5}
08	$-0.710 + 4.31 \times 10^{-4} x$	5.68×10^{-5}	n.a.	3.17×10^{-4}	5.45×10^{-4}	n.a.	n.a.
09	$0.212 + 2.6 \times 10^{-5} x$	n.a.	5.67×10^{-5}	n.a.	n.a.	-8.74×10^{-5}	1.39×10^{-4}
10	$-0.156 + 1.73 \times 10^{-4} x$	6.04×10^{-5}	n.a.	5.23×10^{-5}	2.94×10^{-4}	n.a.	n.a.
<hr/>							
AMB-INT (HR = 0.6)							
01	$0.006 + 5.26 \times 10^{-5} x$	n.a.	5.19×10^{-5}	n.a.	n.a.	-5.13×10^{-5}	1.56×10^{-4}
02	$0.305 - 8.46 \times 10^{-5} x$	3.42×10^{-5}	n.a.	-1.50×10^{-4}	-1.61×10^{-5}	n.a.	n.a.
03	$0.025 + 5.49 \times 10^{-5} x$	4.93×10^{-5}	n.a.	-4.37×10^{-5}	1.54×10^{-4}	n.a.	n.a.
04	$0.256 - 6.44 \times 10^{-5} x$	3.90×10^{-5}	n.a.	-1.40×10^{-4}	1.37×10^{-5}	n.a.	n.a.
05	$-0.210 + 1.74 \times 10^{-4} x$	6.15×10^{-5}	n.a.	5.13×10^{-5}	2.98×10^{-4}	n.a.	n.a.
06	$0.549 - 1.07 \times 10^{-4} x$	n.a.	4.79×10^{-5}	n.a.	n.a.	-2.03×10^{-4}	-1.16×10^{-5}
07	$-0.427 + 3.04 \times 10^{-4} x$	5.99×10^{-5}	n.a.	1.84×10^{-4}	4.24×10^{-4}	n.a.	n.a.
08	$0.516 - 1.49 \times 10^{-4} x$	4.12×10^{-5}	n.a.	-2.30×10^{-4}	-6.66×10^{-5}	n.a.	n.a.
09	$0.312 - 7.98 \times 10^{-5} x$	1.85×10^{-5}	n.a.	-1.20×10^{-4}	-4.28×10^{-5}	n.a.	n.a.
10	$0.206 - 4.45 \times 10^{-5} x$	2.44×10^{-5}	n.a.	-9.34×10^{-5}	4.37×10^{-6}	n.a.	n.a.

Appendix C

AMB-HIGH (HR = 0.8)							
01	$0.746 - 2.30 \times 10^{-4} x$	8.43×10^{-5}	n.a.	-4.00×10^{-4}	-6.11×10^{-5}	n.a.	n.a.
02	$0.452 - 6.22 \times 10^{-5} x$	4.49×10^{-5}	n.a.	-1.50×10^{-4}	2.77×10^{-5}	n.a.	n.a.
03	$0.482 - 1.38 \times 10^{-4} x$	5.36×10^{-5}	n.a.	-2.50×10^{-4}	-3.03×10^{-5}	n.a.	n.a.
04	$0.155 - 1.75 \times 10^{-5} x$	3.82×10^{-5}	n.a.	-9.40×10^{-5}	5.90×10^{-5}	n.a.	n.a.
05	$0.676 - 2.34 \times 10^{-4} x$	n.a.	8.89×10^{-5}	n.a.	n.a.	-4.12×10^{-4}	-5.65×10^{-5}
06	$0.396 - 1.22 \times 10^{-4} x$	n.a.	3.80×10^{-5}	n.a.	n.a.	-1.98×10^{-4}	-4.55×10^{-5}
07	$-0.371 + 2.43 \times 10^{-4} x$	n.a.	4.70×10^{-5}	n.a.	n.a.	1.49×10^{-4}	3.37×10^{-4}
08	$0.503 - 1.50 \times 10^{-4} x$	4.72×10^{-5}	n.a.	-2.40×10^{-4}	-5.58×10^{-5}	n.a.	n.a.
09	$0.349 - 1.33 \times 10^{-4} x$	3.50×10^{-5}	n.a.	-2.00×10^{-4}	-6.30×10^{-5}	n.a.	n.a.
10	$-0.442 + 3.34 \times 10^{-4} x$	8.13×10^{-5}	n.a.	1.71×10^{-4}	4.97×10^{-4}	n.a.	n.a.

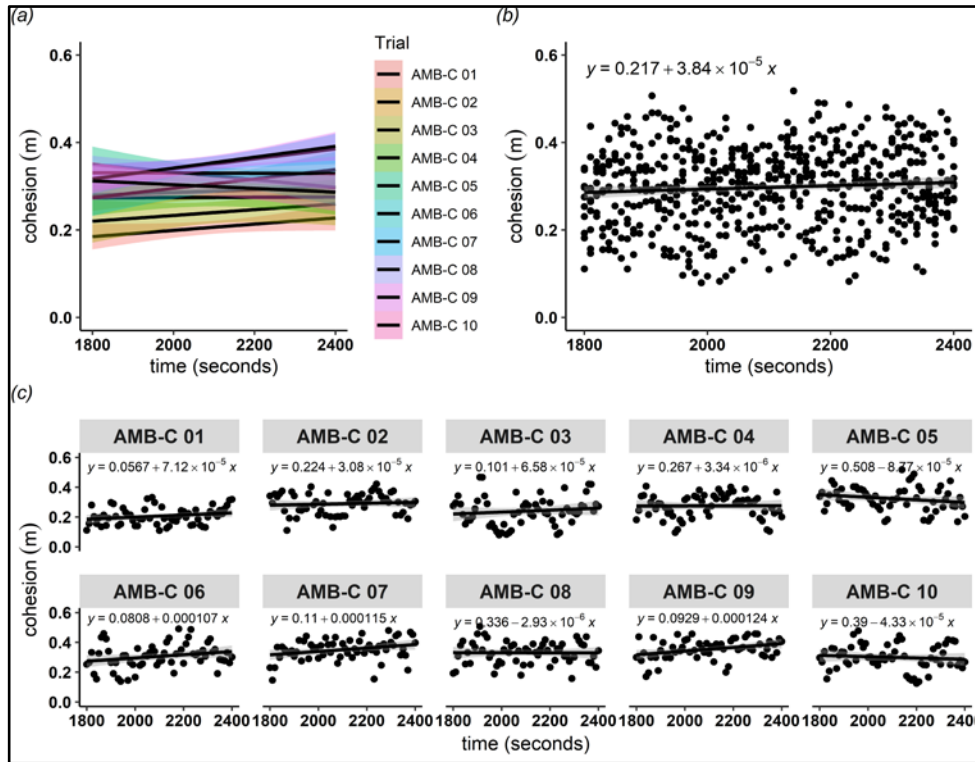


Figure C1: Group cohesion (m) over time (seconds) shown as **(A)** all individual ambient control trials; **(B)** mean ambient control; and **(C)** individual ambient control trials with regression line equation.

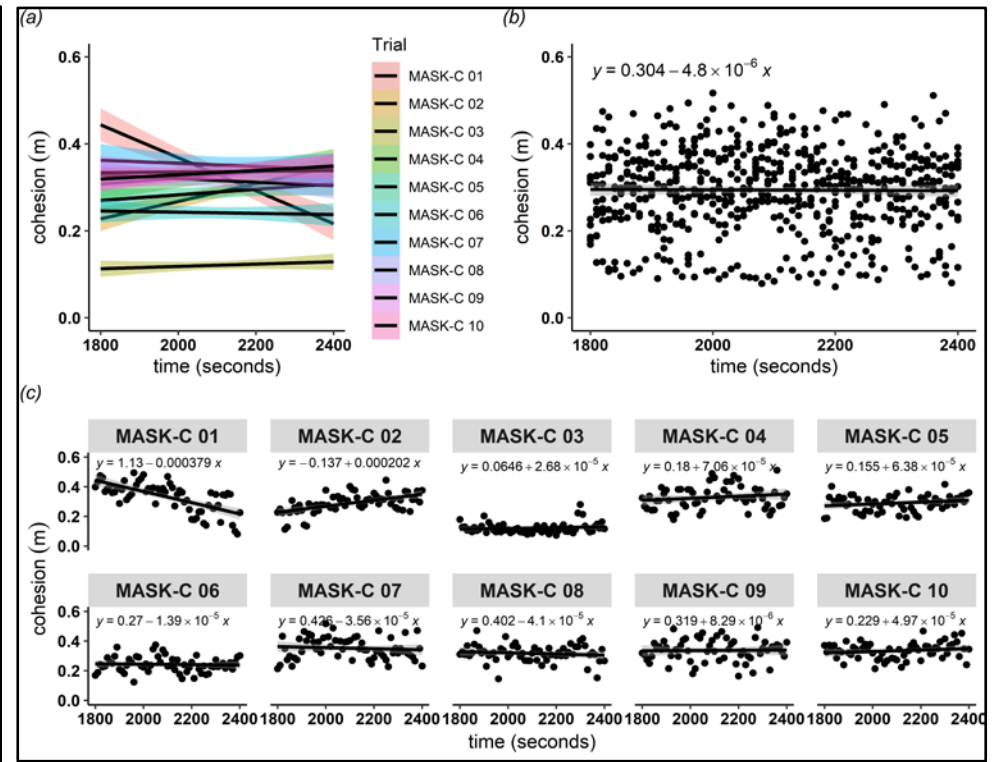


Figure C2: Group cohesion (m) over time (seconds) shown as **(A)** all individual masking control trials; **(B)** mean masking control; and **(C)** individual masking control trials with regression line equation.

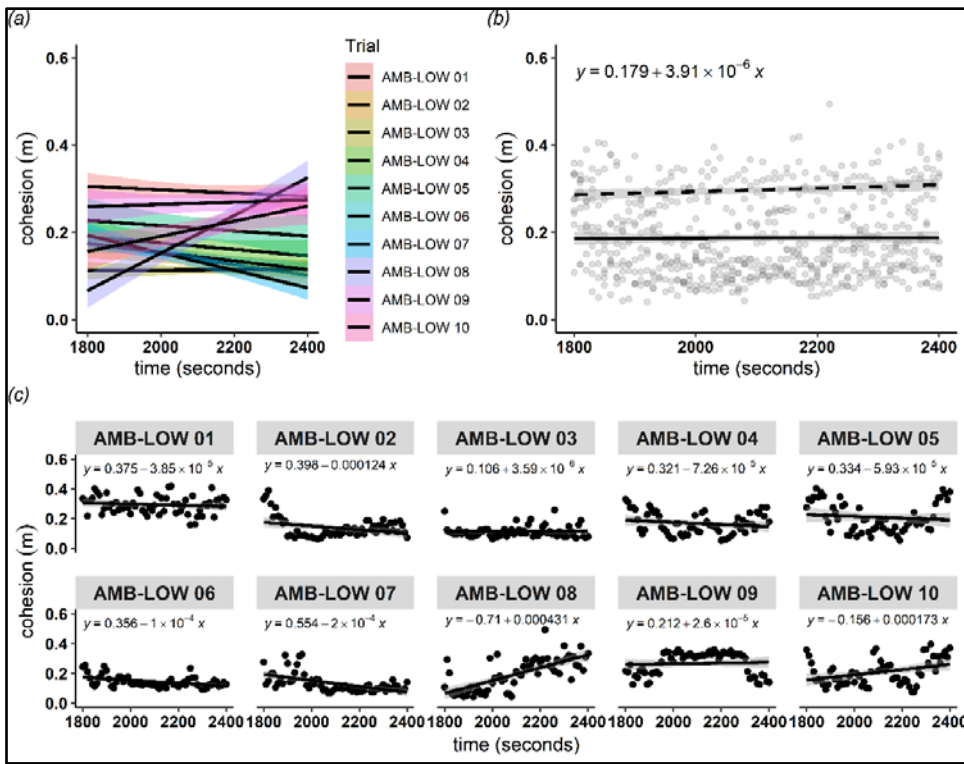


Figure C3: Group cohesion (m) over time (seconds) shown as (A) all individual AMB-LOW trials; (B) mean AMB-LOW (solid line) and mean ambient control (dashed line); and (C) individual AMB-LOW trials with regression line equation.

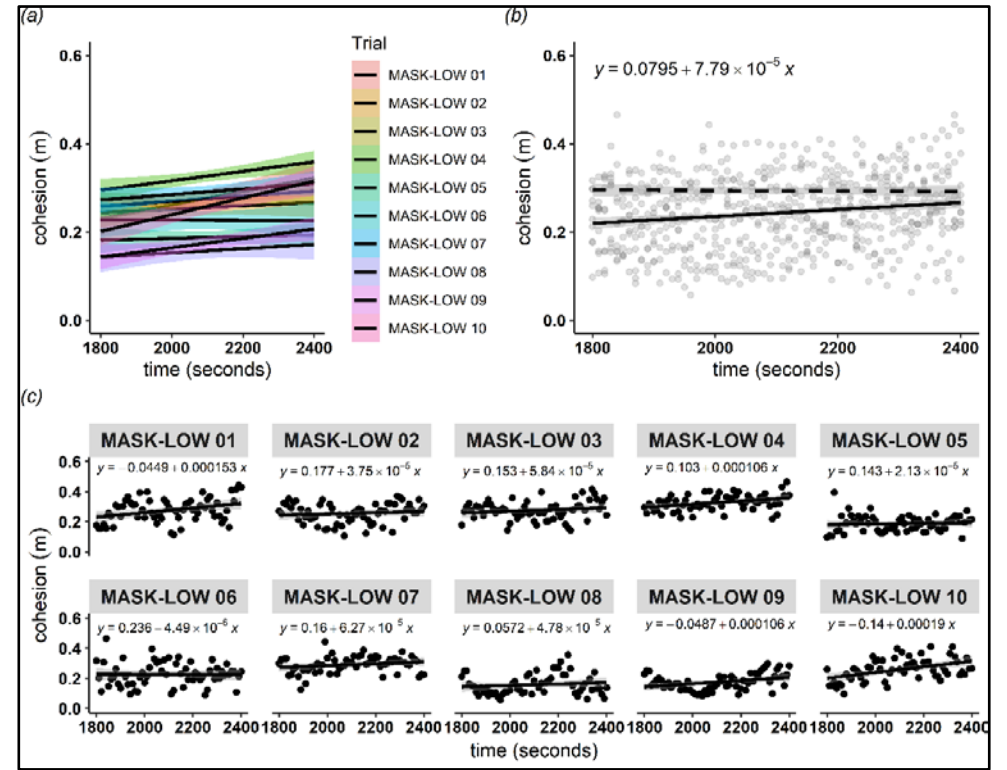


Figure C4: Group cohesion (m) over time (seconds) shown as (A) all individual MASK-LOW trials; (B) mean MASK-LOW (solid line) and mean masking control (dashed line); and (C) individual MASK-LOW trials with regression line equation.

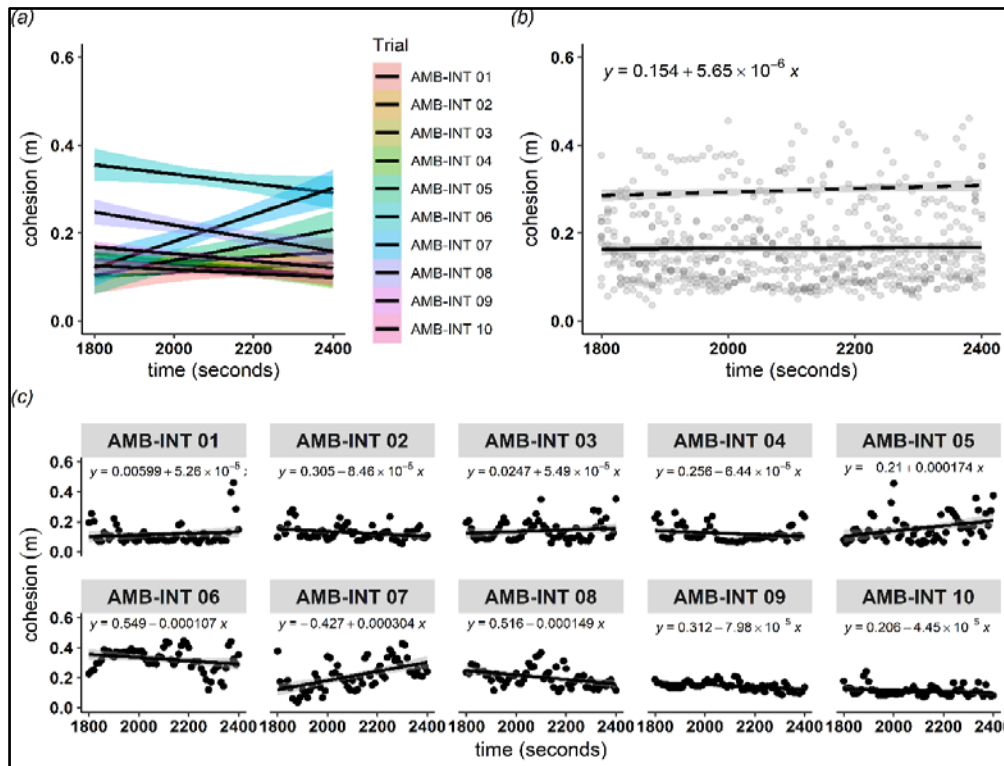


Figure C5: Group cohesion (m) over time (seconds) shown as (A) all individual AMB-INT trials; (B) mean AMB-INT (solid line) and mean ambient control (dashed line); and (C) individual AMB-INT trials with regression line equation.

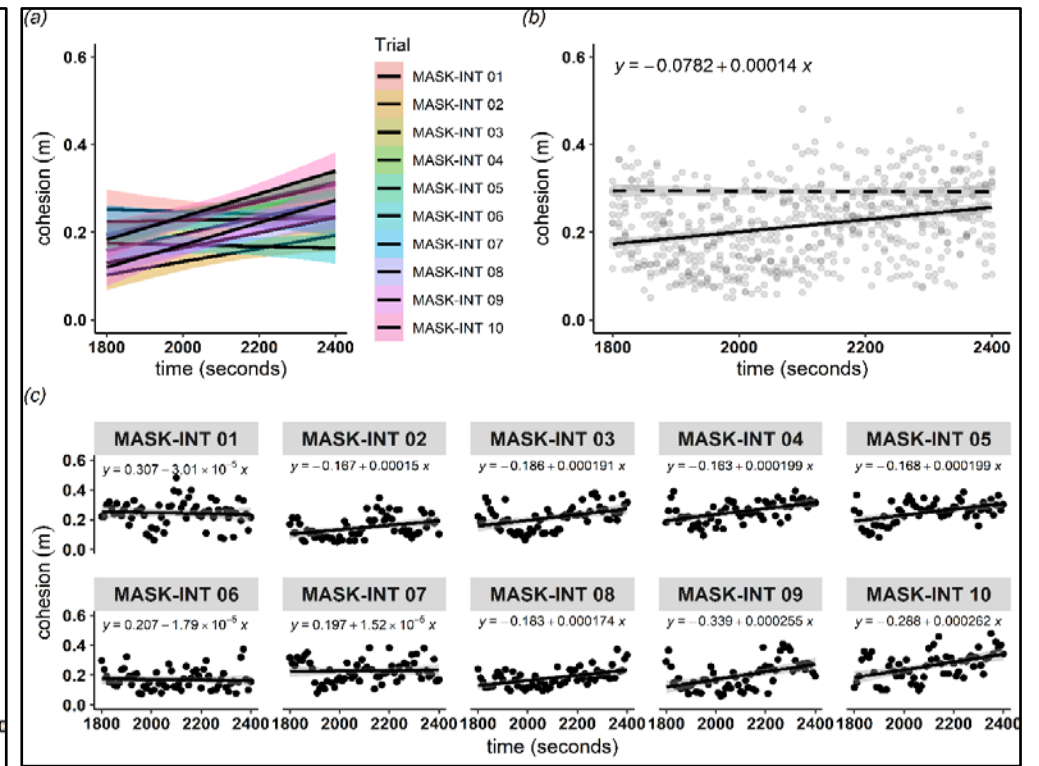


Figure C6: Group cohesion (m) over time (seconds) shown as (A) all individual MASK-INT trials; (B) mean MASK-INT (solid line) and mean ambient control (dashed line); and (C) individual MASK-INT trials with regression line equation.

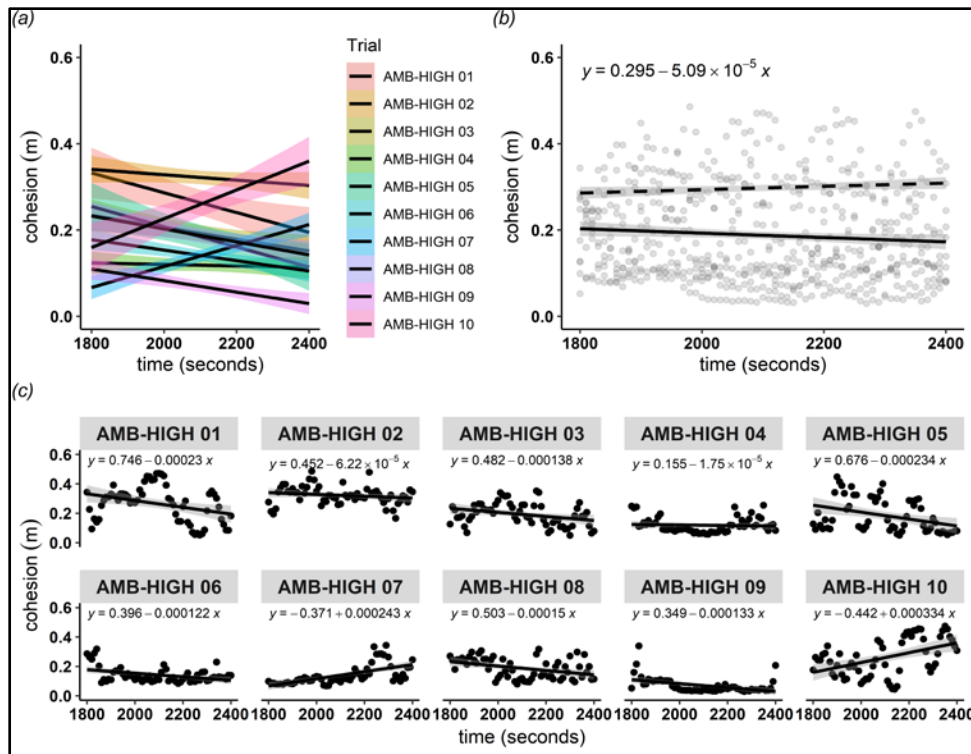


Figure C7: Group cohesion (m) over time (seconds) shown as **(A)** all individual AMB-HIGH trials; **(B)** mean AMB-HIGH (solid line) and mean ambient control (dashed line); and **(C)** individual AMB-HIGH trials with regression line equation.

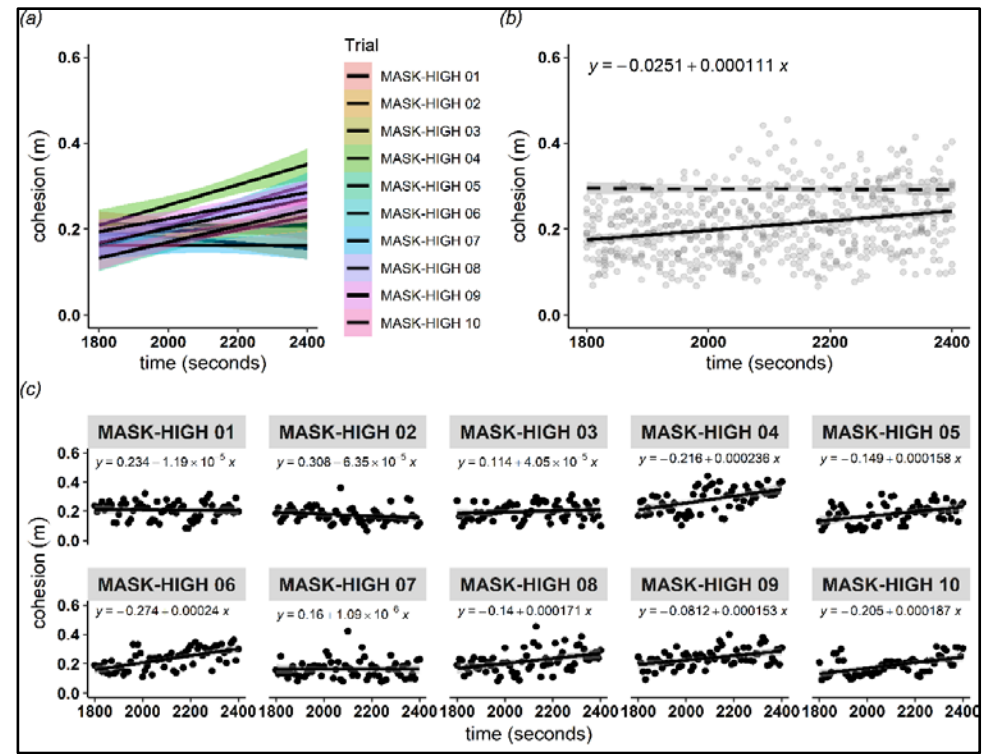


Figure C8: Group cohesion (m) over time (seconds) shown as **(A)** all individual MASK-HIGH trials; **(B)** mean MASK-HIGH (solid line) and mean ambient control (dashed line); and **(C)** individual MASK-HIGH trials with regression line equation.

APPENDIX D Statistical tables

Table D1: Initial group response of common roach (*Rutilus rutilus*) exposed to control (no sound) and 170 Hz pulsed tones across velocity conditions (“low”, “intermediate”, and “high”).

Fish exposed to the sound treatment initially entered the route choice decision area on the same side as the active speaker, or could approach the “quieter” channel on the opposite side. Roach were observed to initially display a *switch*, *rejection*, or *reaction* behaviour, or exhibited no response during treatment trials in comparison to control groups. Note: A multinomial regression model and likelihood ratio test statistic was used to determine the influence of sound treatment (by side) and velocity on initial behavioural response. * indicates significance of $p < 0.05$; ** indicates significance of $p < 0.01$; and *** indicates significance of $p < 0.001$.

INITIAL BEHAVIOURAL RESPONSE	Wald χ^2 test: Side: $\chi^2_6 = 19.91$; $p < 0.01$ ** Velocity: $\chi^2_6 = 3.31$; $p = 0.77$			Cox and Snell, pseudo $R^2 = 0.21$					
	Incidence rate ratio (\pm s.e.)	<u>SWITCH</u> exp(Lower: Upper 95% CI)	p -value (z- score)	Incidence rate ratio (\pm s.e.)	<u>REJECTION</u> exp(Lower: Upper 95% CI)	p -value (z- score)	Incidence rate ratio (\pm s.e.)	<u>REACTION</u> exp(Lower: Upper 95% CI)	p -value (z- score)
Side: Opposite speaker	9.94 (1.30)	0.78, 126.07	0.08 (1.77)	12.44 (1.22)	1.13, 136.69	< 0.05 * (2.06)	19.50 (1.10)	2.24, 169.41	< 0.01 ** (2.69)
Side: Same as speaker	10.73 (0.88)	1.91, 60.43	< 0.01 ** (2.69)	7.92 (0.87)	1.45, 43.16	< 0.05 * (2.39)	5.95 (0.74)	1.38, 25.58	< 0.05 ** (2.40)
Velocity: Intermediate	1.09 (0.87)	0.20, 5.97	0.92 (0.10)	0.83 (0.86)	0.15, 4.49	0.83 (-0.22)	0.63 (0.70)	0.16, 2.46	0.50 (-0.67)
Velocity: High	1.73 (0.94)	0.27, 10.96	0.56 (0.58)	1.95 (0.89)	0.34, 11.14	0.45 (0.75)	0.73 (0.79)	0.15, 3.46	0.69 (-0.39)
Constant (Intercept)	0.24 (0.76)	0.05, 1.05	0.06 (-1.90)	0.31	0.08, 1.23	0.10 (-1.66)	1.16 (0.52)	0.42, 3.22	0.77 (0.29)

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