Swimming bass under pounding bass : fish response to sound exposure

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CHAPTER 1
General Introduction

Acoustic world of fish

Fish live in a world that is not silent. On the contrary, they experience an acoustic world that is brimming with sounds, produced by natural processes, such as winds and surges, and by various aquatic animals, from invertebrates to mammals[1,2]. Fish can hear low frequency sounds (typically below 4 kHz) and make use of them[3]. For example, they may use sounds in their environment as a guide to navigate among different habitats[4–6]. They may also use sounds generated by their predators and prey to avoid or locate them[7,8]. Moreover, some fish species produce calls to repel competitors or attract potential mates[9–11]. Since the underwater world contains a large amount of acoustic information, which propagates more effectively underwater than information in other sensory modalities, fish depend considerably on sounds for survival.

Due to their dependence on sounds, fish may be particularly sensitive to changes in their acoustic world. Since the 1900s, the acoustic world of fish has been altered by a new prominent sound source: human activities[12]. These activities include commercial shipping, offshore construction, sonar exploration, seismic shootings and underwater explosions, which generate a cacophony of high-intensity sounds. At close range, these sounds may damage the auditory tissue of fish[13,14] or deafen them temporarily[15,16]. When fish are further away from the sound source, more moderate sounds they experience may mask important acoustic cues[17,18]. Moreover, the sounds may also alter the behaviour of the fish, changing their swimming patterns[19], disrupting spawning activities[20] and impairing territorial defence[21]. Furthermore, sound exposure may reduce fish efficacy in foraging[22,23] and avoiding predators[24,25]. There are currently growing concerns that these changes may threaten the health of fish stocks and eventually disrupt the stability of ecosystems (Fig. 1).

Challenges in understanding behavioural impacts

In order to regulate man-made sound productions and mitigate behavioural impacts, regulators and developers need to be able to assess potential impacts effectively. The assessments of the severity of behavioural impacts are not straightforward and are often problematic. For example, current guidelines predict severity based on the sound level and the duration of an exposure, using several standard metrics, such as sound pressure level (SPL) and sound exposure level (SEL)[26,27]. Although such metrics have been shown to correlate with physical injuries and temporary hearing loss[13,14], they may not be adequate in assessing behavioural impacts. These metrics do not sufficiently account for variation in relevant acoustic features, such as the temporal structure of sound exposure. The temporal variation in diverse man-made sounds are reflected in their intermittency, pulse shape, pulse repetition interval and interval regularity (Fig. 2). Since the temporal characteristics of sounds can be perceived by fish to gather important information about their environment[28,29], fish may be particularly sensitive to specific acoustic features. This feature-dependent sensitivity may in turn determine their susceptibility to certain sound exposures.

Behavioural studies on sound impacts can sometimes carry implications that are difficult to assess because of generalisation uncertainties inherent to different experimental approaches. These approaches can be divided into three categories: 1) laboratory, 2) field and 3) semi-natural, each with their pros and cons[30–32] (Fig. 3). For example, indoor tank set-ups enable researchers to control and manipulate experimental conditions to examine causal relationships between behavioural changes and specific factors of interest. However, these studies may not

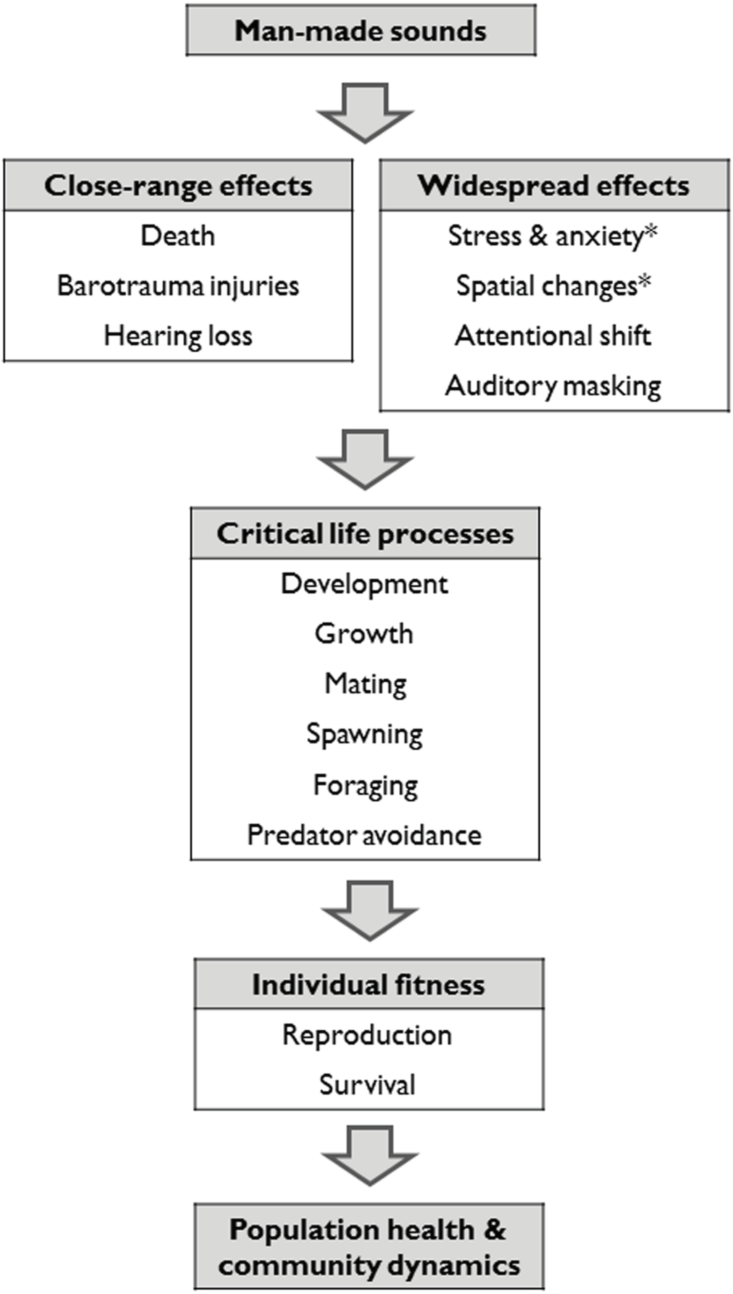


Fig. 1 Diagram showing the different potential effects of man-made sounds. Asterisks (*) indicate the effects that are examined in this thesis.

reflect the acoustic fields in natural waters and the behavioural changes observed may differ considerably from wild fish. On the other hand, field studies on free-ranging fish can provide direct evidence of behavioural impacts. However, such outdoor studies, when properly replicated and controlled, can be exceedingly costly and logistically challenging. Bridging the laboratory and field approaches, a semi-natural approach may be an optimal compromise, as it offers some control over the experimental design while keeping the experimental setting natural. Nonetheless, for proper interpretation of findings, it is crucial to determine which sound impacts are generalisable among these approaches and which are not. To test for generalisability, these approaches should be compared directly using the same experimental design and study species. Such comparisons will provide insights into the underlying mechanisms of the impacts, which are instrumental to devising mitigating strategies.

Translating findings from behavioural research to management decisions can be tricky, since animal behaviour is inherently complex (Fig. 1). Behavioural complexity is often reflected in highly variable behavioural read-outs, which can be due to personality differences among individuals, as well as context-dependent behavioural response[33]. For example, behavioural phenotypes of fish (e.g. bold vs shy) may determine their responsiveness towards an acoustic stressor. In addition, fish response towards sound exposure may be modulated by various factors, such as time of day, temperature, light level and tide condition. Moreover, the behavioural changes may be permanent or temporary. The persistence of these changes needs to be examined, because fish may recover from or habituate to sound exposure. The behavioural recovery may be influenced by some acoustic or ecological factors, and carry management implications[34]. Furthermore, the implications of behavioural studies are sometimes difficult to ascertain because some behavioural changes may not directly indicate fitness consequences. However, these behavioural changes may reflect physiological stress or compromised energetics, which may in turn affect growth and reproduction, but these effects still need to be demonstrated.

Scope of the thesis

This thesis was part of a larger project entitled 'The effects of underwater noise on fish and marine mammals in the North Sea', funded by the Dutch National Ocean and Coastal Research Programme (NWO-ZKO). The project consisted of three subprojects with complementary aims: 1) generating sound maps to understand the distribution and composition of sounds in the North Sea, 2) relating the distribution of man-made sounds to the distribution of marine mammals and their exploitation of natural resources, and 3) assessing experimentally the impacts of different types of man-made sounds on fish behaviour. The latter was my project and I collaborated with Őzkan Sertlek from the first project to determine the relevant man-made sounds and acoustic parameters to be tested, and collaborated with Geert Aarts from the second project to understand the distributional relationship between fish and their predators, marine mammals under sound exposure.

In this thesis, I used the European seabass (*Dicentrarchus labrax*) as a model species (Fig. 4). European seabass are a very good model species to represent fish in the North Sea, since their ecology and hearing ability are generally similar to many other important commercial fishes, such as cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), whiting (*Merlangius merlangus*) and pollock (*Pollachius pollachius*)[35]. Like these species, European seabass live and feed near

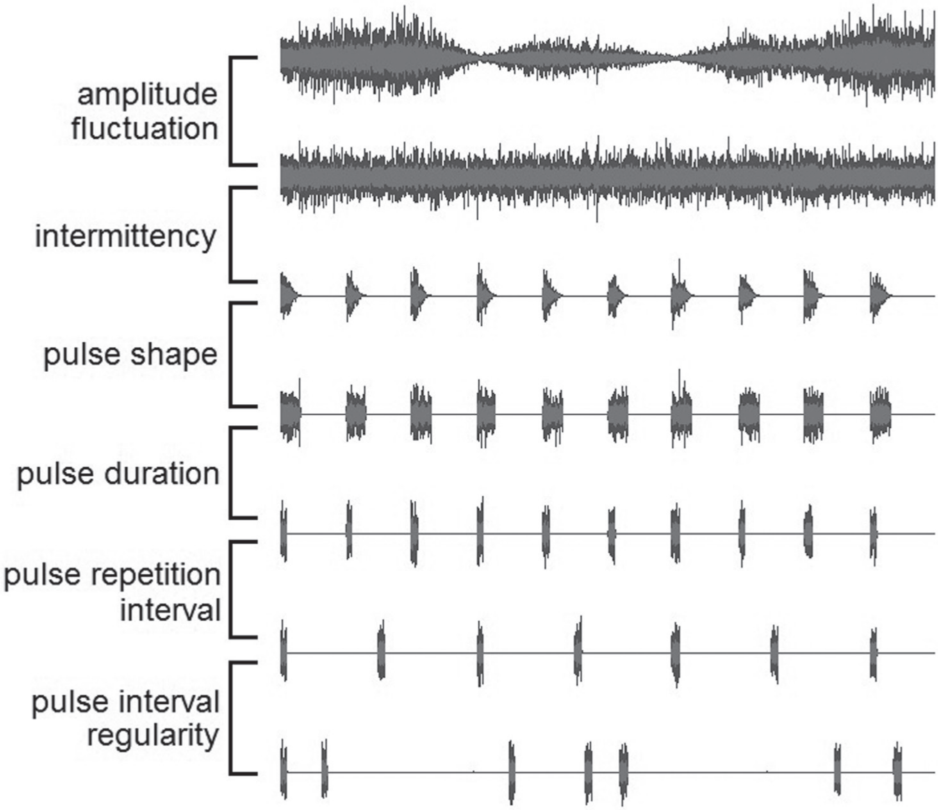


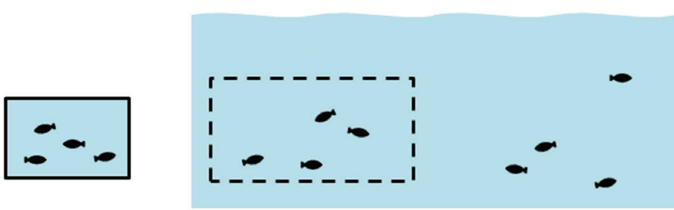
Fig. 2 Comparisons between acoustic waveforms showing different temporal parameters.

the sea bottom. They hear best below 1000 Hz using their otoliths and aided by the presence of swim bladder, without other accessory hearing apparatus[35–37]. Based on their auditory morphology, they possibly perceive both sound pressure and particle motion, although the latter component may be perceptually more dominant3. The fish are economically important and are widely farmed in Europe. They occur naturally throughout most of European coasts, including the North Sea, the Mediterranean Sea and the Black Sea[38]. Since these waters are full of human activities, the fish experience a great deal of man-made sounds. They are sensitive to man-made sounds and are known to respond with clear movement changes36. With the rise of underwater noise pollution, as well as the increasing pressure from commercial fishing[39], European seabass may suffer negative consequences that could disrupt the fish stocks.

Using hatchery-reared European seabass, I looked into how their swimming patterns changed upon sound exposure and how the changes could be associated with stress and anxiety. Next, I examined relevant acoustic parameters that contribute to noise impacts. More specifically, I focused on the influence of the temporal structure of sound. I teased apart different temporal parameters with a bottom-up approach, in which I artificially generated sound treatments that differed only in the parameters of interest, while keeping all other acoustic conditions the same. With this approach, I was able to conduct behavioural assays that revealed the relative impact strengths of different acoustic parameters. My findings have important implications for assessing noise impacts and devising exposure schemes.

In addition, I used the same experimental design to conduct experiments both in an indoor basin as well as an outdoor floating pen. The basin set-up offered much control of the experimental conditions to reveal high-resolution behavioural changes and potential impact differences caused by the temporal structure of sound. On the other hand, the semi-natural set-up offered more natural acoustic conditions and behavioural response, while allowing me to examine how noise impact may be influenced by other environmental factors, such as temperature, tide and time of day. By comparing findings from these two approaches, I demonstrated the generalisability of the behavioural changes. Moreover, the comparison may also provide insights into the underlying mechanisms of noise-induced behavioural changes.

This thesis contains six chapters. This general introduction chapter (chapter 1) is followed by two indoor experiments (chapter 2 & 3), two outdoor experiments (chapter 4 & 5), and a general discussion (chapter 6). **Chapter 2** examines how European seabass change their swimming patterns in an indoor basin upon sound exposure, and how sound intermittency and amplitude fluctuation affect the behavioural recovery. **Chapter 3** describes how the pulse repetition interval of impulsive sounds affects the immediate and delayed behavioural changes of European seabass. **Chapter 4** assesses the efficacy of a ‘ramp-up’ procedure and the influence of sound intermittency and pulse interval regularity in a semi-natural setting, while comparing findings with the two previous indoor basin studies. **Chapter 5** demonstrates if European seabass habituate to repeated sound exposures and whether sound exposure at night affects fish differently than during the day. **Chapter 6** summarises findings from previous chapters and provides guidelines for future research.



	Laboratory	Semi-natural	Field
Acoustic validity	LOW	HIGH	HIGH
Behavioural validity	LOW	MEDIUM	HIGH
Generalisability	LOW	MEDIUM	HIGH
Controllability	HIGH	MEDIUM	LOW
Replicability	HIGH	MEDIUM	LOW
Practicability	HIGH	MEDIUM	LOW

Fig. 3 Comparisons among three categories of experimental approaches: laboratory, semi-natural and field [adjusted after 32].

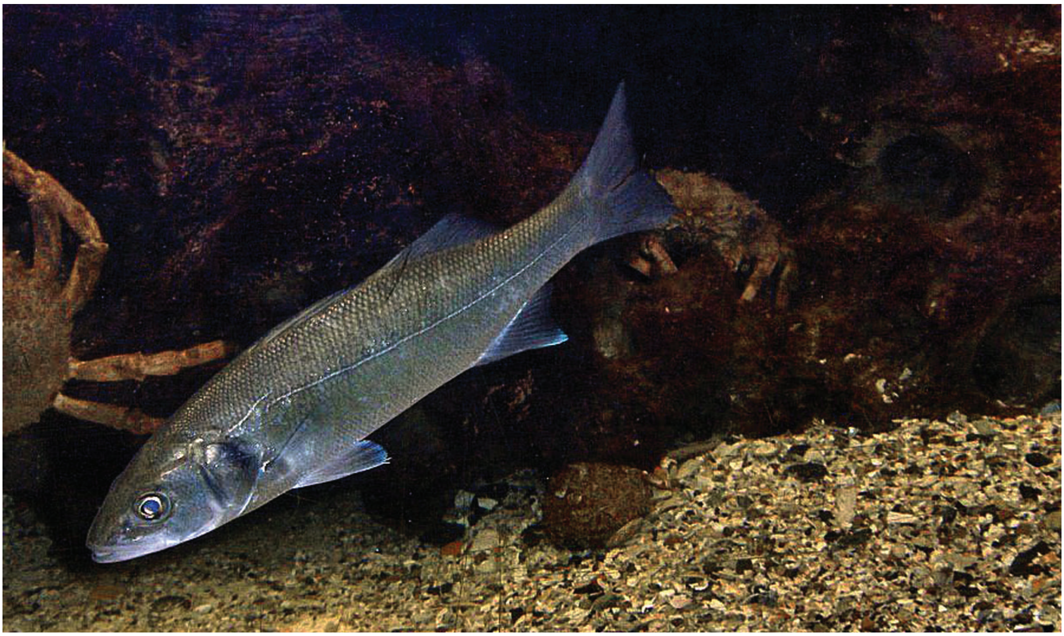


Fig. 4 European seabass (*Dicentrarchus labrax*).

References

1 Popper, A. N. & Hastings, M. C. *Integr. Zool.* **4**, 43–52 (2009).

2 Kennedy, E. V. *et al. J. Exp. Mar. Bio. Ecol.* **395**, 85–92 (2010).

3 Popper, A. N. & Fay, R. *R. Hear. Res.* **273**, 25–36 (2011).

4 Radford, C. A. *et al. Coral Reefs* **30**, 295–305 (2011).

5 Simpson, S. D. *et al. Science* **308**, 221 (2005).

6 Simpson, S. D. *et al. Mar. Ecol. Prog. Ser.* **276**, 263–268 (2004).

7 Holt, D. E. & Johnston, C. E. *Anim. Behav.* **82**, 529–534 (2011).

8 Ward, D. et al. *J. Exp. Biol*. **214**, 2641–8 (2011).

9 Amorim, M. *in Commun. fishes Vol 1* (Ladich, F. *et al*) 71–105 (Science Publishers, 2006).

10 Verzijden, M. N. *et al. Behav. Ecol.* **21**, 548–555 (2010).

11 Ladich, F. *Mar. Freshw. Behav. Physiol.* **29**, 87–108 (1997).

12 Knudsen, V. *et al. J. Mar. Res.* **7**, 410–429 (1948).

13 Halvorsen, M. B. *et al. Proc. R. Soc. B Biol. Sci.* **279**, 4705–14 (2012).

14 Halvorsen, M. B. *et al. PLoS One* **7**, e38968 (2012).

15 Popper, A. N. *et al. J. Acoust. Soc. Am.* **122**, 623–35 (2007).

16 Popper, A. N. *et al. J. Acoust. Soc. Am.* **117**, 3958–3971 (2005).

17 Vasconcelos, R. O. *et al. J. Exp. Biol.* **210**, 2104–12 (2007).

18 Codarin, A. *et al. Mar. Pollut. Bull.* **58**, 1880–1887 (2009).

19 Slotte, A. *et al. Fish. Res.* **67**, 143–150 (2004).

20 Boussard, A. *in Proc. 2nd Br. Freshw. Fish. Conf.* (O'Hara, K. & Barr, C. D.) 188–388 (University of Liverpool, 1981).

21 Sebastianutto, L. *et al. Environ. Biol. Fishes* **92**, 207–215 (2011).

22 Purser, J. & Radford, A. N. *PLoS One* **6**, e17478 (2011).

23 Voellmy, I. K. *et al. Anim. Behav*. **89**, 191–198 (2014).

24 Voellmy, I. K. *et al. PLoS One* **9**, e102946 (2014).

25 Simpson, S. D. *et al. Glob. Chang. Biol.* **21**, 586–593 (2015).

26 Popper, A. N. *et al. Sound Exposure Guidelines for Fishes and Sea Turtles: A Technical Report prepared by ANSI-Accredited Standards Committee S3/SC1 and registered with ANSI.* Springer (2014).

27 Hawkins, A. D. *et al. Rev. Fish Biol. Fish.* **25**, 39–64 (2014).

28 Marvit, P. & Crawford, J. D. *J. Acoust. Soc. Am.* **108**, 1819–25 (2000).

29 Wysocki, L. & Ladich, *F. Hear. Res.* **169**, 36–46 (2002).

30 Calisi, R. M. & Bentley, G. E. *Horm. Behav.* **56**, 1–10 (2009).

31 Brewer, M. *in Handb. Res. methods Soc. Personal. Psychol.* (Reis, H. & Judd, C.) 3–16 (Cambridge University Press, 2000).

32 Slabbekoorn, H. *in Eff. noise Aquat. life, Budapest Conf. Proc.* (Popper, A. N. & Hawkins, A. D.) (Elseviers, 2014).

33 Conrad, J. L. *et al. J. Fish Biol*. **78**, 395–435 (2011).

34 Slabbekoorn, H. *et al. Trends Ecol. Evol.* **25**, 419–27 (2010).

35 Bouton, N. *et al. Hearing and water column use in North Sea fishes : a review to serve exploration of variation in exposure to vessel sounds among species and species groups. IBL-report for TNO for the EU SONIC-project.* (2015).

36 Kastelein, R. A. *et al. Mar. Environ. Res.* **65**, 369–77 (2008).

37 Lovell, J. M. *The hearing abilities of the bass, Dicentrarchus labrax. Technical report commissioned by ARIA Marine Ltd. for the European Commission Fifth Framework Programme.* Project Reference: Q5AW-CT-2001-01896. (2003).

38 Frimodt, C. *Illustrated Multilingual Guide to the World's Commercial Warmwater Fish* (Wiley-Blackwell, 1995).
39 ICES. *ICES Advice on fishing opportunities, catch, and effort. Celtic Seas and Greater North Sea Ecoregions. Book 5.* (2015).