

The Effects of Seismic Surveys on Marine Zooplankton

Emilie Hernes Vereide

Dissertation presented for the degree of
Philosophiae Doctor (Ph.D.)

2024



Department of Biosciences
Faculty of Mathematics and Natural Sciences
University of Oslo

and

Ecosystem Acoustics Group
Institute of Marine Research

© **Emilie Hernes Vereide, 2024**

*Series of dissertations submitted to the
Faculty of Mathematics and Natural Sciences, University of Oslo
No. 2749*

ISSN 1501-7710

All rights reserved. No part of this publication may be
reproduced or transmitted, in any form or by any means, without permission.

Cover: UiO.

Print production: Graphic center, University of Oslo.

Preface

Embarking on the journey to accomplish a great task and uncovering something novel for the very first time has been an immense honor and a profound privilege.

First and foremost, I would like to thank my main supervisor, Karen de Jong. Thank you for your guidance from the very beginning. For your honesty, patience, and knowledge. You have challenged and supported me through drafts, late nights in the laboratory, and everything in between. Thank you for the opportunity - for seeing and believing in me.

Furthermore, thank you to Josefin Titelman, Anne Christine Utne Palm, and Mette Dalgaard Agersted for your supervision. Without your input, help, and support, this thesis would not have existed.

Thank you to the Ecosystem Acoustics Group at the Institute of Marine Research for the discussions, support, and cups of coffee. Special thanks to Lise Doksaeter Sivle, Tonje Nesse Forland, Kate McQueen, Howard Browman, and Babak Khodabandeloo for the needed advice and help.

To everyone involved in the ZoopSeis project, thank you for the initiative to create this project. Thank you for three incredible years - I have enjoyed every second.

To Marina Mihaljevic, thank you for keeping up with me. Without you, I would still be counting copepods in the North Sea. I would also like to thank Saskia Kühn. For the discussions, the unique support and for being my fellow sound and copepod enthusiast.

I would also like to thank my family. For your unconditional support, for replacing my late-night cold dinners with an actual meal, and for your help. This would not have been possible without you.

To all my friends in academia, thank you for turning bad drafts and days into a laugh and for your continuous support. To all my friends outside academia, thank you for reminding me that there is a life on the other side. To remind me of that life, sometimes— is more than copepods. Without you, I would have given up after the introduction.

Finally, I would like to thank the twenty-something-year-old version of me who was curious enough to pursue this. (We did it).

Now. Let us dive into it.

Content

Preface.....	3
Content.....	5
List of publications.....	7
Sammendrag.....	9
Summary.....	11
1 Introduction.....	15
1.1 Anthropogenic underwater noise.....	15
1.2 Seismic surveys.....	16
1.3 Effects of seismic surveys on marine life.....	18
1.4 Zooplankton and seismic surveys.....	20
2 Aims and research questions.....	23
3 Research methodology.....	24
3.1 Sound and pressure exposures.....	24
3.2 Study animals.....	25
3.3 Experimental approach and study endpoints.....	26
4 Summary of results.....	29
5 Discussion.....	32
5.1 Potential airgun characteristics causing damage.....	32
5.2 Rapid pressure drop associated with airgun blasts.....	33
5.3 Variations in zooplankton responses.....	35
5.4 Ecological relevance.....	39
6 Conclusions and future recommendations.....	42
7 Acknowledgements.....	43
References.....	45

List of publications

Paper I

Vereide, E. H., Kühn, S. (2023). Effects of Anthropogenic Noise on Marine Zooplankton. In: Popper, A. N., Sisneros, J., Hawkins, A. D., Thomsen, F. (eds) The Effects of Noise on Aquatic Life. Springer, Cham. https://doi.org/10.1007/978-3-031-10417-6_63-1

Paper II

Sivle, L. D., Vereide, E. H., de Jong, K., Forland, T. N., Dalen, J., Wehde, H. (2021). Effects of Sound from Seismic Surveys on Fish Reproduction, the Management Case from Norway. Journal of Marine Science and Engineering. 2021, 9, 436. <https://doi.org/10.3390/jmse9040436>

Paper III

Vereide, E. H., Khodabandeloo, B., de Jong, K. The copepod *Acartia* sp. is more sensitive to a rapid pressure drop associated with seismic airguns than *Calanus* sp. Marine Ecology Progress Series. 2024 March Vol. 730: 15–30. <https://doi.org/10.3354/meps14515>

Paper IV

Vereide E. H., Mihaljevic M., Browman H. I., Fields D. M., Agersted M. D., Titelman J., de Jong K. (2023). Effects of airgun discharges used in seismic surveys on development and mortality in nauplii of the copepod *Acartia tonsa*. Environmental Pollution. 2023 Jun 15;327:121469. <https://doi.org/10.1016/j.envpol.2023.121469>

Paper V

Vereide, E. H., Utne Palm, A. C., Titelman, J., Pedersen, G., Strand, E., Mihaljevic, M., Kühn, S., Altin, D., Thorsen, A., Campillo, L., Fields, D. M., Khodabandeloo, B., de Jong, K. Zooplankton mortality and distribution around a seismic survey (*Manuscript*).

Throughout the thesis, the publications will be referred to as papers **I**, **II**, **III**, **IV**, and **V**.

Sammendrag

Denne avhandlingen beskriver og utforsker påvirkningen av seismiske undersøkelser på dyreplankton. Avhandlingen fokuserer primært på effektene på dødelighet i dyreplankton, men ser også på subletale effekter som adferd og utvikling. Videre ser avhandlingen på hvilke egenskaper i seismiske luftkanoner som kan forårsake potensiell skade, og belyser mulighetene for artsspesifikke effekter. Ved å adressere kunnskapshull fra tidligere forskning gjennom to litteraturstudier, integrerer avhandlingen nye funn fra mindre laboratorieeksperimenter til omfattende feltstudier. Gjennom bruk av ulike metoder og undersøkelser av forskjellig dyreplankton, bidrar forskningen med ny innsikt i hvordan seismiske luftkanoner kan påvirke dyreplankton. Spesielt belyser avhandlingen artsspesifikke effekter fra seismiske luftkanoner og identifiserer egenskaper som har potensial til å forårsake skade på dyreplankton.

Artikkel I gjennomgår tidligere studier som undersøker effektene av menneskeskapt undervannsstøy på dyreplankton. Artikkelen oppsummerer funn om dødelige og subletale effekter, og fremhever variasjoner i lydtkilder, eksperimentell design og endepunkter. Av de inkluderte studiene, fokuserer majoriteten på meroplankton og endepunkter knyttet til utvikling og dødelighet. Artikkelen fremhever også kunnskapshull fra tidligere forskning, og trekker frem forslag til videre studier.

Artikkel II fokuserer på hvordan vitenskapelige fremskritt har påvirket Norges forvaltning og rådgivning av seismiske undersøkelser og deres inkorporering i nye forskningsprosjekter. Artikkelen gjennomgår litteraturen om seismiske undersøkelser og deres påvirkning på marint liv, hovedsakelig fisk, pattedyr og dyreplankton, og fremhever Norges kunnskapsbaserte tilnærming til forvaltning.

Artikkel III undersøker effekten av et raskt trykkfall, en karakteristikk ved eksponering av seismiske luftkanoner, på to takson av hoppekreps, *Acartia* sp. og *Calanus* sp. Et hydrostatisk trykkfall ble simulert (~2 bar) og resulterte i høyere dødelighetsrate hos trykkeksponerte *Acartia* sp. sammenlignet med kontroller. Dødelighetsraten hos *Calanus* sp. økte kun etter 5 t. Studien avdekket at et raskt trykkfall kan påvirke dødeligheten og adferden i dyreplankton negativt. Videre viste den at *Acartia* sp. er mer sårbar enn *Calanus* sp., noe som antyder potensielle taksonspesifikke påvirkninger fra seismisk eksponering.

Artikkel **IV** undersøker effektene av seismiske luftkanoner på hoppekrepsen *Acartia tonsa*. Nauplietadier av *A. tonsa* ble eksponert for enten 2·40 tommer³ luftkanoner, båtkontroll eller stillekontroll i ~2.5 t. Direkte og forsinket dødelighet var betydelig høyere hos eksponerte nauplier sammenlignet med kontrollene, men med generelt lave dødelighetsrater. Studien avslørte også et forhold mellom behandling og tid, som indikerer lavere vekstrater hos naupliene etter eksponering av luftkanoner.

Artikkel **V** undersøker effektene av en seismisk undersøkelse (luftkanoner totalt 3060 tommer³) på dyreplankton. Til tross for et maksimalt lydeksponeringsnivå på 182.1 dB re 1 μPa^2 s, forble den vertikale fordelingen av dyreplankton stabil. Umiddelbar dødelighet hos *Calanus* spp. var <36%, og viste ingen betydelig økning med høyere lydnivåer. Kultiverte *Calanus finmarchicus* eksponert i poser viste lav umiddelbar dødelighet (<10%) med en gradvis økning opp til syv dager etter eksponering.

I konklusjon viser avhandlingen at påvirkningen av seismiske luftkanoner på dyreplankton er begrenset og varierer basert på faktorer som art, eksponeringsforhold og eksperimentell design. Effektene på ulike taksa av dyreplankton til seismisk eksponering er varierende, men generelt lav - noen grupper viser økte dødelighetsrater og endret atferd, mens andre viser ubetydelige effekter. Avhandlingen demonstrerer også at et raskt trykkfall i forbindelse med eksponering av luftkanoner kan skade dyreplankton, og understreker i hvilken grad forskjellig taksa kan bli påvirket av ulike faktorer. Resultatene understreker også den avgjørende rollen av å ta hensyn til andre miljøforhold og anerkjenne potensialet for påvirkningen på andre organismer når man evaluerer effektene av menneskeskapt undervannsstøy på marine økosystemer.

Summary

This thesis describes and explores the impact of seismic surveys on zooplankton. The thesis primarily focuses on the effects on mortality in zooplankton, but it also examines sublethal effects such as behavior and development. The thesis further investigates the characteristics of seismic airguns that may cause potential harm, highlighting the possibilities of species-specific effects. By addressing knowledge gaps from previous research through two literature reviews, the thesis integrates new findings from smaller laboratory experiments to extensive field studies. Through the use of various methods and examinations of different zooplankton taxa, the research provides new insights into how seismic airguns can affect zooplankton. Specifically, the thesis highlights species-specific effects from seismic airguns and identifies characteristics that have the potential to cause harm to zooplankton.

Paper **I** reviews previous studies examining the effects of anthropogenic underwater noise on zooplankton. The paper summarizes findings on lethal and sublethal effects, emphasizing variations in sound sources, experimental design, and endpoints. Among the included studies, the majority focus on meroplankton and endpoints related to development and mortality. The paper also highlights knowledge gaps from prior research and puts forth suggestions for further studies.

Paper **II** focuses on how scientific progress has influenced Norway's management and advisory of seismic surveys and their incorporation into new research projects. The paper reviews the literature on seismic surveys and their impact on marine life, primarily focusing on fish, mammals, and zooplankton. The paper also highlights Norway's evidence-based approach to management.

Paper **III** investigates the impact of a rapid pressure drop, a key characteristic of seismic airgun exposure, on two taxa of copepods, *Acartia* sp. and *Calanus* sp. A hydrostatic pressure drop was simulated (~2 bar), resulting in a higher mortality rate in pressure-exposed *Acartia* sp. compared to controls. The mortality rate in *Calanus* sp. increased only after 5 h. The study revealed that a rapid pressure drop can negatively impact mortality and behavior in zooplankton. Furthermore, it showed that *Acartia* sp. is more vulnerable than *Calanus* sp., suggesting potential taxon-specific effects from seismic exposure.

Paper **IV** investigates the effects of seismic airguns on the copepod *Acartia tonsa*. Naupliar stages of *A. tonsa* were exposed to either 2-40 inch³ airguns, boat control, or silent control for ~2.5 h. Both immediate and delayed mortality were significantly higher in the exposed nauplii compared to the controls, although overall mortality rates were generally low. The study also revealed an interaction between treatment and time, indicating lower growth rates in nauplii exposed to the airgun discharge.

Paper **V** investigates the effects of a full airgun array (3060 inch³) on zooplankton during an ongoing seismic survey. Despite reaching a maximum sound exposure level of 182 dB re 1 $\mu\text{Pa}^2 \text{ s}$, the vertical distribution of zooplankton remained stable. The immediate mortality in in situ *Calanus* spp. was <36%, showing no significant increase with higher sound levels. Cultured *Calanus finmarchicus* exposed in bags exhibited low immediate mortality (<10%) with a gradual increase up to seven days post-exposure.

In conclusion, the thesis demonstrates that the impact of seismic airguns on zooplankton is limited and varies based on factors such as species, exposure conditions, and study design. The effects on different taxa of zooplankton to seismic exposure vary but are generally low, with some groups showing increased mortality rates and altered behavior, while others exhibit negligible effects. The thesis also shows that a rapid pressure drop associated with airgun exposure can harm zooplankton, highlighting the extent to which different taxa can be affected by various factors. The results also emphasize the crucial role of considering other environmental conditions and recognizing the potential for impacts on other organisms when evaluating the effects of anthropogenic underwater noise on marine ecosystems.

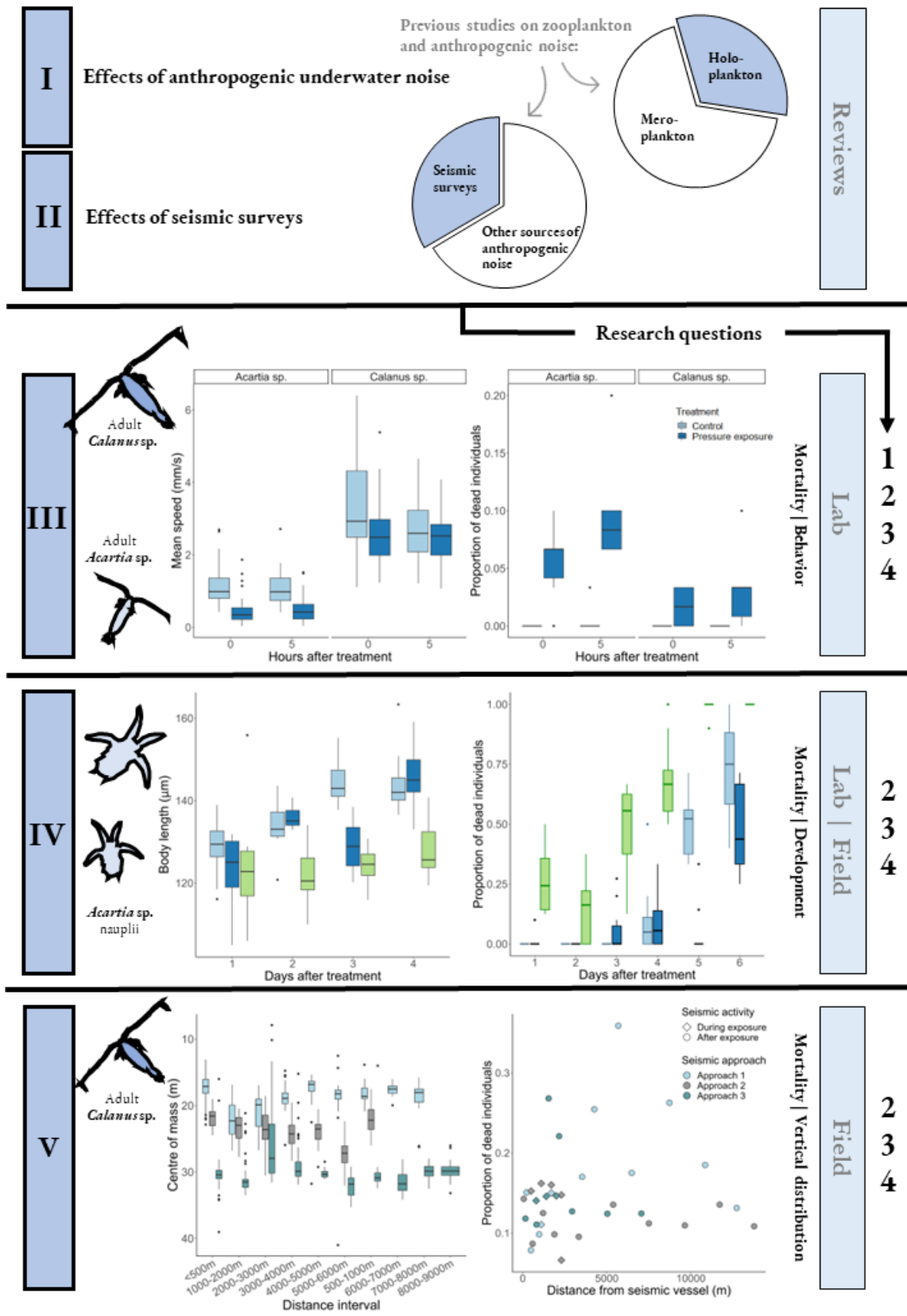


Fig. 1. Schematic overview of all papers (I-V). The figures in the upper panel are modified from paper I, and the figures below are modified from the respective papers (III-V).

1 Introduction

1.1 Anthropogenic underwater noise

Since the onset of the industrial revolution, human activities in the ocean have increased (McDonald et al. 2008, Hildebrand 2009, Duarte et al. 2021). Concurrently, there has been a decline in marine animal biomass and biodiversity (Worm et al. 2006, Pusceddo et al. 2014). These global changes have led to the recognition of new sources of pollution such as toxins, waste, atmospheric emissions, and anthropogenic underwater noise. Anthropogenic underwater noise, broadly classified as continuous or impulsive noise, originates from various sources such as pile driving, ship noise, or seismic surveys (reviewed in **I**; Fig. 2). These sources exhibit a broad spectrum of characteristics, including diverse source levels, bandwidths, amplitudes, and variations in time duration and directionality. Consequently, these sound sources have the potential to disturb and overlap with various natural sounds in the ocean, thereby posing potential threats to marine ecosystems (reviewed by Williams et al. 2015, **I, II**).

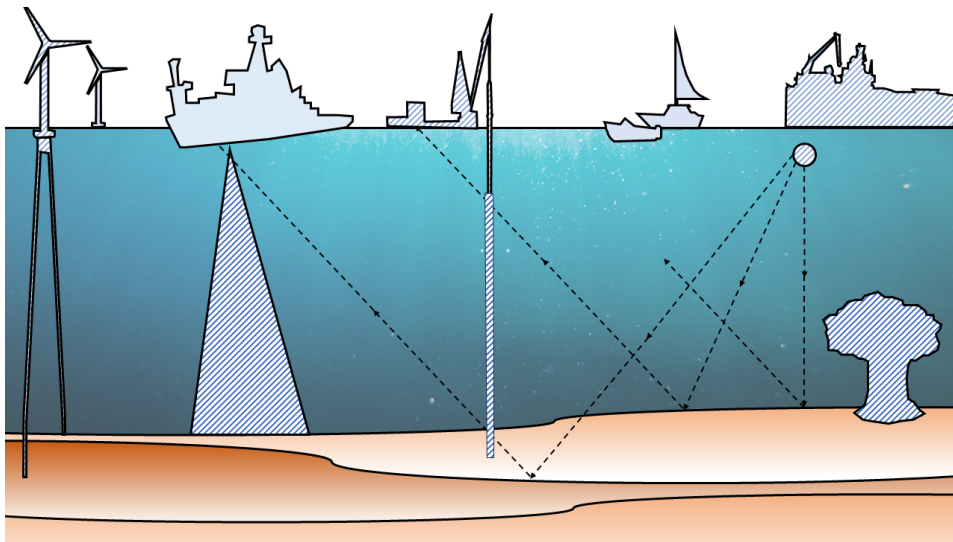


Fig. 2. Anthropogenic underwater noise sources are categorized as 1) continuous underwater noise (solid fill), defined as constant noise that continues or slowly fluctuates over a long time period, e.g., boat and ship traffic and operating wind turbines, or 2) impulsive underwater noise (stripes), with a short duration and rapid pulse rise time e.g., underwater explosions, pile driving, sonar, and seismic surveys.

1.2 Seismic surveys

Since the late 1960s, following the discovery of oil and gas reserves on the Norwegian Continental Shelf (NCS), seismic surveys have consistently been carried out in the Barents Sea, Norwegian Sea, and North Sea (Fig. 3). These surveys have utilized different sound sources to locate and estimate oil and gas reservoirs (reviewed in **II**). From the historical collection of seismic acquisition on the NCS, beginning in 1979, the total sum of square kilometers covered by seismic surveys peaked in 2014 (~80 000 km²; NDP 2021). In 2020, approximately 20 000 km² were covered. The decline in covered area is predominantly a result of more efficient data acquisition, and the number of boat kilometers has remained stable between 100 000 and 200 000 km in recent years (NDP 2021). On a global scale, there was a surge in seismic exploration activities in 2023, causing a growth in the seismic service sector. Seismic operations have become pivotal in the ongoing energy transition, and are implemented in activities such as the identification of suitable wind farm sites and Carbon Capture and Storage (CCS) initiatives. This trend is poised to continue over the upcoming years (Hurtado 2023).

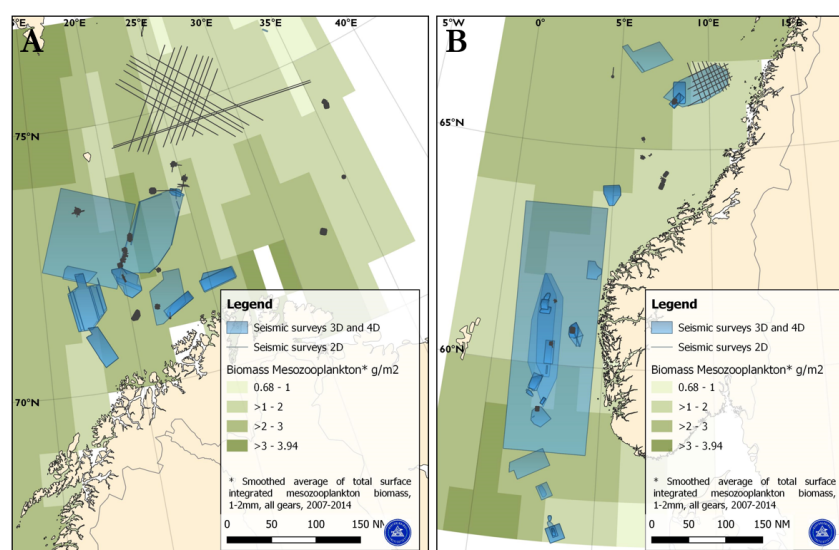


Fig. 3. Seismic surveys and zooplankton distribution in Norwegian waters (2016, 2017). The seismic surveys are only presented if they were carried out during periods when zooplankton are most abundant in the respective regions: May-October for the Barents Sea (A), March-August for the Norwegian Sea (B upper part), and March-June for the North Sea (B lower part). The figure is developed by Daniel Nyqvist, and modified from the ZoopSeis project description.

Airguns used in seismic surveys are the primary method used in the search for oil and gas and mapping of the seabed. An airgun discharges high-pressure compressed air, which then

generates sound waves. These sound waves travel to the seabed, where a part of the signal is reflected and detected by hydrophones, allowing for the examination of both the seabed and the underlying structure of the seafloor. The sound generated by airguns is characterized by high amplitude and primarily falls within the low-frequency range of 10-100 Hz (predominantly below 125 Hz; Goold & Fish 1998). However, it also includes higher frequencies. During a seismic survey, a set of airguns, typically between 18 and 48, is fired repeatedly over weeks and months, usually at 10 s intervals (Caldwell & Dragoset 2000, Slabbekoorn et al. 2019). The standard operating air pressure is approximately 2000 psi.

According to Dragoset (2000), the characteristic sound produced by airguns is called the airgun signature, encompassing 1) the direct arrival, 2) the surface reflection, and 3) the bubble pulses (Fig. 4). The direct arrival is the sound produced when the airgun fires, which is distinctive in characterizing an airgun exposure. The direct arrival is also characterized by a rapid rise time to maximum pressure followed by a rapid decrease (Dragoset 2000; Fig. 4). The direct arrival is followed by the surface reflection, also called the source ghost, the reflection of the direct arrival from the surface, and bubble pulses created by the expansion and collapse of the air bubble produced during firing (Fig. 4). Together, all the properties of the airgun signature are characterized by the strength (sound amplitude) and bubble period (time between consecutive bubbles) (Dragoset 2000). Dependent on factors such as the operating pressure, number of airguns, or amplitude, airgun exposure can impact marine life in various ways.

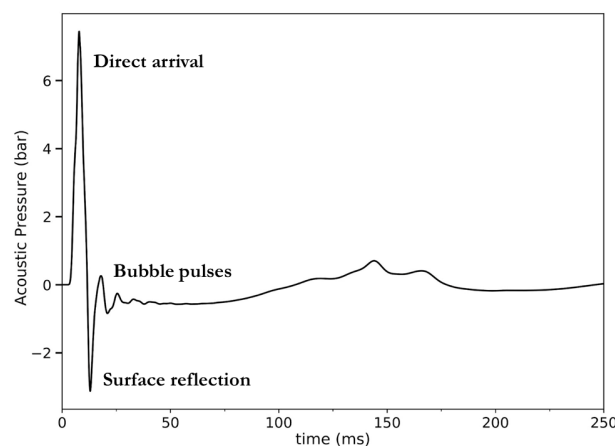


Fig. 4. An airgun signature modeled from an airgun array (2730 inch³) fired from 5 m below the surface. The simulated pressure measurements are positioned 8 m below the surface, directly beneath the airguns. The airgun signature consists of 1) the direct arrival, 2) the surface reflection, and 3) bubble pulses. The figure is modified from paper **III**.

1.3 Effects of seismic surveys on marine life

Several studies have reviewed and explored the impacts of seismic surveys on marine mammals (Affatati & Camerlenghi 2023, Guan & Brookens 2023), fish (Slabbekoorn et al. 2019, Pieniasek et al. 2023), and selected invertebrate species (Carroll et al. 2017, Solé et al. 2023; Box 1, Fig. 5). In Norway, the Institute of Marine Research (IMR) has integrated findings on observed and potential effects on biology and ecosystems into the guidance for both ongoing and planned seismic surveys, specifically incorporating insights related to fish and marine mammals (reviewed in **II**). However, it is important to highlight that, historically and as of 2024, invertebrates, including zooplankton, have never been incorporated into the advisory framework (Forland et al. 2024). This exclusion was mainly due to the scarcity of research that demonstrates negative impacts at far distances from the airguns (reviewed in **II**).

Seismic surveys can impact various marine mammal taxa (Box 1, Fig. 5). In general, the frequency of seismic sound often overlaps with common communication signals of baleen whales (10 Hz–1 kHz) and can be audible for toothed whales up to 100 km away from the source (Kavanagh et al. 2019). The impact on marine mammals stems from the sound pressure associated with seismic airgun activities (Southall et al. 2019). Similarly, studies have highlighted the impacts of seismic surveys on fish (reviewed by Pieniasek et al. 2023, **II**; Box 1, Fig. 5). Unlike marine mammals, the detection of sound in fish is primarily linked to the otolithic organs or the equivalent which sense particle motion (Popper & Hawkins, 2018, Popper et al. 2019) although some species also perceive sound pressure (Popper et al. 2019).

Box 1: Effects on marine life from seismic surveys

Seismic airgun exposure can cause diverse effects on various marine taxa. In the case of marine mammals, alterations in vocalization patterns (Di Iorio & Clark 2009, Thode et al. 2020), avoidance behaviors within survey zones (Kavanagh et al. 2019), and changes in overall behavior (Dunlop et al. 2015, van Beest et al. 2018) have been observed. Studies on fish have predominantly focused on behavioral impacts, but reports also indicate effects on physical damage, abundance, and catch rates. Paper II expands upon the effects of seismic surveys on fish, such as behavioral responses, instances of diminished fish stocks near seismic surveys, or physical damage leading to mortality in fish eggs and larvae. Note that for the latter, these instances were only in very close vicinity to the airguns. For invertebrates, research highlights organ damage and mortality in cephalopods exposed to airguns (reviewed by Guerra et al. 2004), stress responses in bivalves (La Bella et al. 1996), and tissue damage, behavioral alterations, and metabolic and stress responses in decapods (Christian et al. 2003, Day et al. 2019).

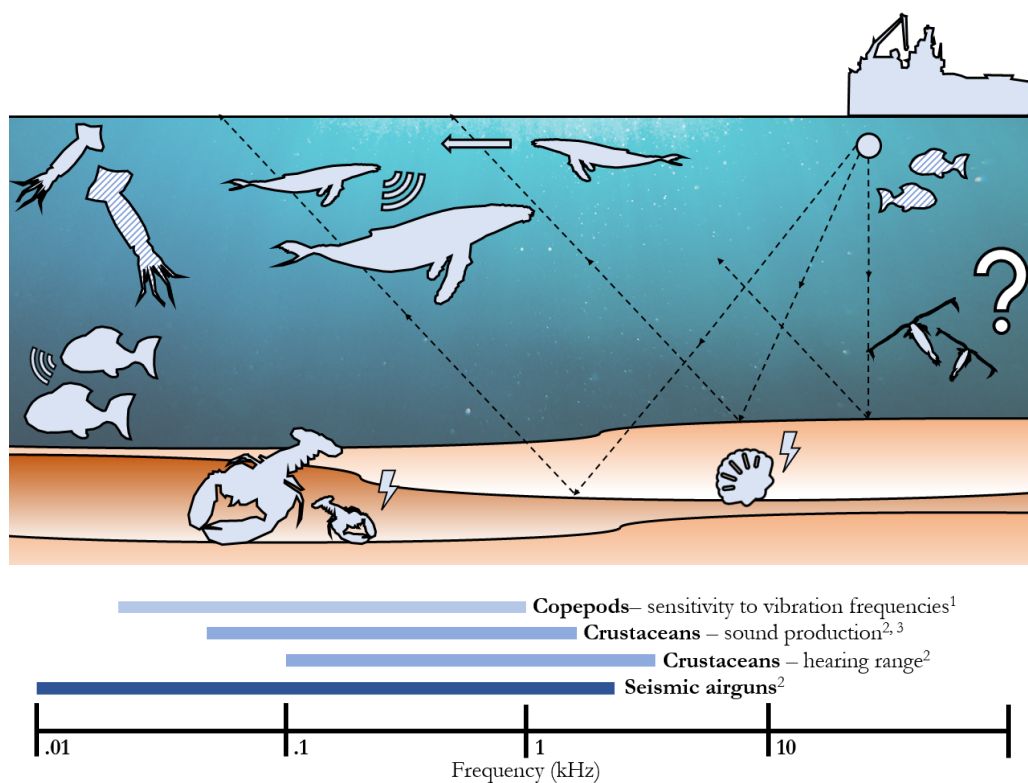


Fig. 5. Upper panel) Overview of reported lethal (diagonal stripes) and sublethal (solid fill) effects on marine life from seismic surveys. Marine mammals (changes in vocalization patterns, avoidance behavior, behavioral alterations), fish (behavioral responses, diminished fish stocks, physical damage leading to mortality in fish eggs and juvenile; only near the airguns), other invertebrates (cephalopods: organ damage, mortality; bivalves: stress responses; decapods: tissue damage, behavioral alterations, and metabolic and stress responses), and unknown effects in zooplankton. Lower panel) Frequency range of seismic airguns, sound production and hearing range in invertebrates, and the vibration sensitivity in copepods. ¹Yen et al. 1992, ²Duarte et al. 2021, references therein, ³Kühn et al. 2022.

A limited number of studies have also explored the effects of seismic surveys on invertebrates (reviewed in Carroll et al. 2017, **I**; Box 1, Fig. 5). The ability of invertebrates to perceive sound remains poorly understood, but some studies have shown neurological responses in cephalopods and decapods (Lovell et al. 2005, Mooney et al. 2010). Most marine invertebrates, including copepods, lack gas-filled cavities and specialized pressure-sensing organs (Solé et al. 2023). Therefore, it has traditionally been assumed that marine invertebrates primarily perceive particle motion over sound pressure (Nedelec et al. 2016, Solé et al. 2023). However, this view has evolved with recent findings indicating the potential significance of the pressure component (Solé et al. 2017). Despite these insights, the impacts on zooplankton from seismic surveys remain relatively underexplored, and the existing knowledge of the overall effects is limited (reviewed in **I**, **II**).

1.4 Zooplankton and seismic surveys

Zooplankton are widely defined as animals that inhabit the pelagic zone and lack the ability to swim against currents. They constitute an important component of marine ecosystems and are an essential link in marine food webs, facilitating energy transfer from primary producers to higher trophic levels (Pinti et al. 2023a). Zooplankton also play a vital role in the global carbon cycle by recycling and transforming particulate carbon into dissolved pools (Steinberg & Landry 2017, Pinti et al. 2023b). Furthermore, these organisms are important for numerous marine species that are essential to human livelihoods. In Norway alone, zooplankton, particularly larger copepods, serve as a critical food source for many commercially important fish such as herring (*Clupea harengus*), and mackerel (*Scomber scombrus*) (Tande 1991, Dalpadado et al. 2000, Prokopchuk & Sentyabov 2006; Fig. 6).

Despite their seemingly passive drift in ocean currents, zooplankton exhibit behavioral patterns driven by the necessity to survive and reproduce (Visser 2007). Sensing their environment is imperative for zooplankton as it aids in locating optimal feeding grounds, avoiding predators, and responding to environmental cues (Folt & Burns 1999). Zooplankton employ various sensory mechanisms, such as photoreception to detect changes in light (Hobbs et al. 2021), chemoreception to discern chemical gradients in water (Jackson & Kiørbo 2004, Heuschele & Selander 2014), and mechanoreception to perceive vibrations and currents (Buskey et al. 2002).

These sensory abilities allow zooplankton to navigate their surroundings, and detect prey, predators, and conspecifics, ensuring their survival in the dynamic but often unpredictable ocean environment. Zooplankton consist of 41 functional groups, encompassing various orders or phyla differing in size, morphology, life strategy, lipid content, behavior, and functional groups (Mackas & Beaugrand 2010, Litchman et al. 2013, Brandão et al. 2021). Consequently, the sensitivity and level of effects to outer stimuli or stressors, such as underwater sound, might differ between taxa.



Fig. 6. The large copepod *Calanus finmarchicus*; an essential contribution to the zooplankton community in Norwegian waters and one of the study species included in the thesis. © Dag Altin, BioTrix.

Our understanding of the sensitivity of zooplankton to underwater sound remains narrow. The mechanisms through which marine invertebrates detect underwater sound encompass three main pathways: The internal statocyst receptor system, the chordotonal organs, and the body superficial receptor systems (Budelmann 1992, reviewed in **I**). Similar features are also identified in planktonic invertebrates, with internal and/or superficial receptor systems. For example, cnidarians display sensitivity to sound through mechanoreceptive hair cells (Solé et al. 2017). Copepods also demonstrate sound detection capabilities through their superficial receptor system and sensory hairs (Yen et al. 1992, Gassie et al. 1993; Fig. 5), and perceive signals via vibrations, fluid disturbances (Yen et al. 1992, Kiørboe et al. 1999), or through strong pressure changes (Yen & Okubo 2002). Additionally, studies underscore their sound-producing ability, where crustacean zooplankton generate sounds within the hearing range of their fish predators (Giguère & Dill 1979, Kühn et al. 2022; Fig. 5). Despite this, the understanding of the overall effects and characteristics underlying potential damage from anthropogenic underwater sound, therein seismic airgun exposure, is still highly limited (reviewed in **I**).

This thesis investigates the influence of seismic surveys on zooplankton, with a particular focus on copepods, including *Acartia* sp., and *Calanus* spp., which are important and abundant taxa in the northern hemisphere (Beaugrand et al. 2002). The existing literature on this topic presents conflicting results, ranging from significant mortality to negligible effects on zooplankton (reviewed in **I**, **II**). We discuss the potential reasons for previous inconsistencies, such as sound sources and levels, exposure distances, and experimental designs in more detail in paper **I**. To account for these variations and the different impact levels across taxa, this thesis explores the effects of seismic surveys in various ways and across taxa. By examining the specific vulnerabilities of different zooplankton groups, this thesis aims to identify copepod species that may be more susceptible to the effects of seismic surveys. Understanding the varying degrees of vulnerability among zooplankton taxa will provide valuable insights into the ecological consequences of seismic exploration on marine ecosystems.

Similar to the limited and conflicting reported effects on zooplankton from seismic airguns, the underlying causes of potential damage remain largely unknown. McCauley et al. (2017) proposed that specific zooplankton species may experience increased mortality due to the mechanical stimulation of external hairs on their antennae, caused by hydrodynamic stimuli which occurs when an airgun is fired. Fields et al. (2019) suggested that elevated mortality in copepods could be linked to the acoustic pressure pulse, particle acceleration, and velocity associated with the acoustic pulse from the airgun. They also highlighted the role of fluid motion caused by the seismic pulse, which originates from bubble formation, as a potential factor affecting zooplankton. Consequently, various characteristics have been identified as potential causes of damage. However, this thesis focuses specifically on the rapid pressure drop associated with airgun exposure. This pressure peak and subsequent drop have been identified as potential airgun characteristics capable of harming marine fauna (McCauley & Duncan 2017, McCauley et al. 2021). The pressure drop has never before been tested specifically on zooplankton in relation to airguns, but effects on underwater explosions, which have comparable sound properties to airgun arrays have resulted in damages from spallation (Schardin 1950), oscillation of microbubbles in the tissue of marine animals (Goertner et al. 1994), and pressure gradients between different tissues (Wolf et al. 2009). Thus, we expect that a pressure drop, if strong enough, may damage zooplankton, which could lead to increased mortality or changes in behavior after exposure.

2 Aims and research questions

In this thesis, I present novel information on the impact of seismic airguns on zooplankton. To gain a comprehensive understanding of the effects of seismic surveys, I examined the rapid pressure drop associated with airgun blasts and its potential to cause harm. Additionally, to understand how and in what way the potential effects differ between taxa and traits, I examined both lethal and sublethal effects on two zooplankton taxa and different developmental stages. Furthermore, to gain knowledge on the extent of the effects, I explored how the effects vary with distance from the airguns and the sound level.

-
- 1 | Can a rapid pressure drop associated with airgun blasts harm zooplankton?
 - 2 | What are the lethal and sublethal effects of seismic airgun exposure on zooplankton?
 - 3 | Are zooplankton taxa and developmental stages affected differently by seismic airguns?
 - 4 | How do the effects of seismic airguns on zooplankton differ with distance from the airguns and sound level?
-

In paper **III**, we addressed research question 1 and investigated how and to what extent the pressure drop contributes to zooplankton damage. Papers **I** and **II** address research question 2 by reviewing previous studies and reported effects, where papers **III-V** assess both the lethal and sublethal effects of a rapid pressure drop (**III**) and seismic airgun exposure (**IV, V**). In papers **III-V**, we addressed research question 3 by using different copepod taxa and developmental stages. Papers **I** and **II** first address research question 4 by reviewing previous findings on the effects on zooplankton from different distances and sound levels, whereas papers **III-V** investigate the effects on zooplankton from various exposure levels or distances to the airguns, and discuss how effects can be upscaled.

3 Research methodology

To gain a deeper understanding of a field with limited and inconsistent findings (**I, II**), multiple approaches were explored to answer the research questions (**III-V**).

3.1 Sound and pressure exposures

To comprehensively investigate the impact of seismic surveys on zooplankton, papers **III-V** utilize various sound sources, sound levels, and duration of exposures.

Different sources of exposures were implemented in the studies; seismic sound sources (**IV-V**), as well as an experimental pressure tube (**III**). In papers **IV** and **V**, we exposed zooplankton to seismic sound, implementing seismic airguns. In the former, two small airguns were drawn after a vessel and exposed sound to the study animals at a set position. When assessing small field studies (e.g. paper **IV**), it is essential to underline that various factors, such as the frequency, direction, seabed formation, and environmental surroundings, have an impact on how and how quickly the sound waves attenuate (Erbe et al. 2022). For instance, signals can disappear after just a few kilometers in shallow water over a low-reflectivity seabed, while other signals, particularly those with low frequencies (<500 Hz), can travel thousands of kilometers down the continental slope (McCauley et al. 2008, Duncan et al. 2013). Coincidentally, these low-frequencies are also relevant to copepods, which often exhibit sensitivity to lower frequencies (Yen et al. 1992, Solé et al. 2021; Fig. 5). These variations are especially important when upscaling small-scale field and laboratory experiments to real-world scenarios. Therefore, it was imperative to further expose zooplankton around an actual airgun array during a seismic survey (**V**). In paper **III**, we examined the rapid pressure drop associated with airgun blasts (Khodabandeloo 2018), using an experimental tube built solely for this purpose.

Another important aspect relevant to underwater sound studies is the measurement and subsequent reporting and assessment of sound exposure. Paper **III** focuses on the associated hydrostatic pressure drop, not the general airgun exposure. Therefore, to compare with similar literature and report what we actually measured, this study describes the pressure drop in absolute pressure (bar). In difference, papers **IV** and **V** report the peak-to-peak sound pressure level (Pa), and sound exposure level (SEL) over time. These metrics are standard in studies of sound pressure

levels and can be found in related research (reviewed in **I**). In our previous analysis of sound in paper **IV**, an error was made in the calibration. The error has since been identified, and accurate sound levels have been included in this thesis. Furthermore, a correction has been submitted to the journal (which is included in the thesis after paper **IV**).

The lack of standard terminology and measurements is acknowledged as a key constraint in conducting comprehensive evaluations of underwater soundscapes and their impacts on marine life (Hawkins et al. 2015). Furthermore, the variation in ways of reporting sound exposures makes it challenging to compare studies and, therefore, also to establish precise threshold levels for various marine taxa (Ainslie et al. 2016). Several studies have remarked on this complexity and recommended a more commonly used and standardized assessment system (Popper et al. 2014, reviewed in **I**). Additionally, paper **I** highlights that interpreting the noise exposure in terms of particle motion is an important part of understanding the effects of anthropogenic sound on zooplankton. Notably, particle motion was not measured in papers **III-V**. Ideally, for a comprehensive understanding of the airgun characteristics underlying potential effects, we would have included measurements of particle motion (Hawkins et al. 2015). However, we prioritized other sound-related measures due to constraints in time, costs, and the unavailability of instruments that could easily be used in experimental set-ups. Furthermore, since we used real airguns (**IV, V**), there was no pressing need to test whether the particle motion field was similar to the one animals would encounter in the field.

3.2 Study animals

Papers **III-V** primarily focused on two copepod taxa: *Acartia* sp. and *Calanus* spp., both juvenile (**IV**) and adults (**III, V**; Fig. 1), both cultured (**IV, V**) and caught in situ (**III, V**).

Specific taxa were selected based on several criteria, including their crucial roles in marine ecosystems and characteristics (Table 1). The selection of taxa also aimed to address the knowledge gap in the impact of seismic surveys on holoplankton (reviewed in **I**).

Table 1. Zooplankton used in papers **III-V**.

Taxa	Paper	Length (mm)	Lipid status	Spawning strategy
<i>C. finmarchicus</i>	III, V	2-6	Rich	Free-spawner
<i>C. helgolandicus</i>	V	2-3	Rich	Free-spawner
<i>A. tonsa</i> , <i>Acartia</i> sp.	III, IV	0.9-1.5 (adult), 0.1-0.2 (NI-NIV)	Poor	Free-spawner
Full community	V	See Supp. in paper V	Rich and poor	Free-spawners and egg carriers

Acartia (Dana) is a genus of marine calanoid copepods, widely distributed worldwide, especially in coastal areas (Cervetto et al. 1995). *Acartia tonsa* feeds on phytoplankton, ciliates, and rotifers, acting as both a suspension and ambush feeder (Jonsson & Tiselius 1990). The species is also considered an important food source for several fish species.

Calanus (Leach) is another genus of marine calanoid copepods found across global seas, including the common species in Norwegian waters, *Calanus finmarchicus* (Fig. 6), and *Calanus helgolandicus* (Montero et al. 2021, Falkenhaug et al. 2022; Table 1). *C. finmarchicus* is the dominant mesopelagic species in the Norwegian Sea (Aarflot et al. 2017), acting as a key species and an important prey for many fish (Varpe & Fiksen 2010). These copepods are common in the Norwegian and North Seas, but their distribution extends from the Labrador Sea to the Arctic. Their diet primarily consists of microzooplankton and phytoplankton, and they employ both suspension and ambush feeding strategies, depending on the type of food available (Melle et al. 2014).

3.3 Experimental approach and study endpoints

By diversifying the experimental approaches, e.g., by using both field and laboratory experiments or focusing on several endpoints, both lethal and sublethal, we aimed to foster a more comprehensive and nuanced understanding of the objectives.

Laboratory and field experiments

When implementing laboratory (e.g., **III**) and field experiments (e.g., **V**) in underwater sound studies, weighing the advantages and disadvantages of each approach is essential. Field experiments closely approximate real-world conditions, providing authentic measurements of natural effects

under actual sound exposures (Slabbekoorn 2016, Nedelec et al. 2021, **V**). In comparison to previous research that did not utilize a full airgun array for zooplankton investigations (e.g., McCauley et al. 2017, Fields et al. 2019), paper **V** offers an understanding of the actual consequences following a seismic survey. This dataset provides new insights that can be used to compare with studies that employ alternative sound sources. However, field studies may have shortcomings related to the experimental design. For example, they may rely on controls before and after exposure in addition to control vs. impact comparisons, where the potential lack of controls can lead to misinterpretations (reviewed by Carroll et al. 2017). Factors challenging to control, such as mortality caused by boat-generated turbulence (Bickel et al. 2011), in situ conditions (e.g., disease or age), or background mortality (Tang et al. 2014, Tang & Elliot 2014) can also introduce confounding variables. Therefore, we aimed to examine the mortality in paper **V** in different ways, including using bags to control for other causes of mortality.

Laboratory experiments offer more access to controls and the ability to establish more controlled dose-dependent relationships. One can precisely manipulate parameters and enhance statistical robustness with more replicates. However, translating results to real-world scenarios may be challenging due to physical constraints, differences in sound measures, and the use of laboratory study animals, potentially introducing bias, as explored by Carroll et al. 2017. Balancing controlled laboratory studies (**III, IV**) and ecologically relevant field experiments (**IV, V**) is important for a complete assessment of the effects of underwater sound on aquatic organisms (reviewed by Wale et al. 2021, **I**)

Another essential consideration is the potential influence of background sound that zooplankton may experience. This background noise can arise from various sources, such as the climate room during experiments (**IV**), culturing facilities (**III**), or the temperature-controlled container (**V**). Despite our inability to control the background noise, I emphasize that we treated all animals in the studies similarly. In other words, the control animals experienced the same sources of background sound, and we included them to account for mortality or other potential effects originating from sources other than the exposure to seismic sound.

Study endpoints

In papers **III-V**, different study endpoints were included (Fig. 1). Paper **IV** explores mortality (immediate and delayed) and growth in copepod nauplii, while paper **III** focuses on mortality and behavior in copepods. Paper **V** focuses on mortality, both immediate and delayed, and vertical distribution during airgun array exposure.

Given the complexities of identifying subtle physical injuries caused by airgun exposure in small animals, mortality may give an effective indication of harm caused by airguns. Furthermore, mortality is also easy to compare with other studies (**I**) and for assessing the potential consequences of seismic surveys. In papers **III** and **IV**, we evaluated mortality through visual inspections under stereomicroscopes. In paper **V**, we evaluated the immediate mortality in cultured *C. finmarchicus* through visual inspection. Furthermore, we employed a Neutral Red Stain to assess mortality in in situ zooplankton samples (**V**).

In addition to immediate mortality, mortality over time was investigated in papers **III-V**; up to six (**IV**) and seven (**V**) days after treatment, or five hours post-treatment (**III**). In paper **IV**, mortality was evaluated in the same way as with immediate mortality. In paper **V**, we conducted daily visual inspections of the cultured *C. finmarchicus* in separate flasks, monitoring them up to seven days after treatment. Although we could not open the flasks or stimulate the animals with a plastic pipette, our observations enabled us to distinguish between live and dead animals. As reduced activity and a 'stunned' state were considered potential effects of exposure (McCauley et al. 2017), we also monitored the animals in paper **III** in Petri dishes for mortality assessment after a 5 h interval (**III**). The difference between delayed mortality occurring after days or hours naturally prompts the query of how delayed mortality is defined. One would ideally examine mortality over several days regarding physical damage from seismic exposure leading to potential mortality. This might be especially important when discussing potential population-level effects on a temporal scale. However, in considering the specific objective of paper **III**, which is to explore the airgun characteristic underlying zooplankton damage and variations between taxa, 5 h was a suitable choice.

Paper **III** explores the zooplankton behavior post-exposure. Paper **IV**, alongside mortality assessments, delves into the growth of *A. tonsa*. Daily measurements were conducted for up to six

days, capturing both live and dead animals through photography, with subsequent measurements. Paper **V** utilizes bottom-mounted echosounders (WBAT) to analyze zooplankton movement, Multinet for biomass assessment across various depth intervals, and additional environmental parameters.

4 Summary of results

In paper **I**, we conducted a comprehensive review of 21 studies that explored the impact of both continuous and impulsive underwater noise on marine holo- and meroplankton. The included studies were conducted in either laboratory or field settings and reported a range of responses, including positive, negative, or none. Most of the examined effects were related to development (28%), mortality (25%), and orientation and settlement (19%), and meroplankton (68%) was the most studied zooplankton group.

Paper **II** focuses on how scientific progress informs the management of seismic surveys in Norway. In this paper, we reviewed the literature on seismic surveys, marine mammals, fish, and zooplankton. It describes how Norway has managed seismic surveys based on their potential impact on fish stocks and fisheries since the late 1980s. Until 1996, spawning grounds and areas with drifting eggs and larvae were recommended as off-limits areas for seismic surveys. However, later findings showed that the effects of seismic surveys on early fish development stages were insignificant at a population level, which led to the reopening of areas with drifting eggs and larvae for seismic surveys. Additionally, this paper demonstrates how the Norwegian case serves as an example of evidence-based management. The information obtained in papers **I** and **II** was subsequently used to identify knowledge gaps and formulate the research questions addressed in papers **III-V** (Fig. 1).

In paper **III**, we focused on a key characteristic of seismic airgun signals that can lead to harmful effects on zooplankton: the rapid drop in hydrostatic pressure. We conducted an experiment in which we re-created a pressure drop (~2 bar) and observed the mortality rates and swimming activity of two zooplankton taxa, adult *Acartia* sp. and *Calanus* sp., both immediately and 5 h after treatment. The extent to which the pressure drop occurred was investigated by creating a model of the sound field surrounding a seismic airgun array. Additionally, we examined

whether the pressure drop caused cavitation. Our findings revealed that *Acartia* sp. experienced higher mortality rates than the control group both at 0 h (5.6%) and 5 h (10%) after treatment, whereas the mortality rates in *Calanus* sp. only increased after 5 h (3.3%; Fig. 1). Additionally, the swimming speed of pressure-exposed *Acartia* sp. (0 h: 0.49 mm s⁻¹, 5 h: 0.52 mm s⁻¹) was lower than that of the control group both at 0 h and 5 h after treatment, while the swimming speed of pressure-exposed *Calanus* sp. (0 h: 2.64 mm s⁻¹) only differed from the control group immediately after treatment (Fig. 1). These results demonstrate that rapid pressure drops can have negative effects on zooplankton mortality and behavior, particularly near airguns (Fig. 7), even without cavitation. Furthermore, this study indicates that *Acartia* sp. may be more sensitive to this pressure drop than *Calanus* sp., suggesting potential taxa- and/or trait-specific effects of seismic exposure.

In paper **IV**, we investigated the effects of airgun exposure on the early life stages of zooplankton. We conducted a field experiment to assess the mortality and naupliar body length of the calanoid copepod *A. tonsa* after exposure to two 40 inch³ airguns (Fig. 7). The nauplii were placed in plastic bags and attached to a line at a depth of 6 m. For each treatment, three bags of nauplii were exposed to one of three treatments for ~2.5 h: airgun array discharge, boat control, or silent control. After exposure, the nauplii were kept in filtered seawater in the laboratory, without food. The immediate mortality in the nauplii was approximately 14%, compared with less than 4% in the silent and boat controls. Similarly, there was higher mortality in the airgun-exposed nauplii up to six days after exposure than in the control treatments (Fig. 1). Nearly all of the airgun-exposed nauplii died after four days, while more than 50% of the nauplii in the control treatments were alive at six days post-exposure (Fig. 1). There was an interaction between treatment and time on naupliar body length, indicating lower growth in the nauplii exposed to the airgun discharge (growth rates after 4 days: 1.7, 5.4, and 6.1 $\mu\text{m d}^{-1}$ in the airgun exposed, silent control, and boat control, respectively; Fig. 1).

In paper **V**, we investigated the effects of a seismic survey on adult zooplankton. Using a seismic airgun array (3060 inch³) that emitted sound along three shooting lines, we collected samples from a research vessel positioned near the end of each line. Our study found that sound levels increased as the seismic vessel approached the research vessel, exceeding the ambient noise at around 6 km away. The broadband sound exposure level (SEL) reached a maximum of 182 dB re 1 $\mu\text{Pa}^2 \text{ s}$ over 10 s at the closest proximity of ~50 m (Fig. 7). The distribution of zooplankton

biomass, primarily *Calanus* spp., showed a consistent pattern before and after airgun exposure, which aligned with hydrographic data and chlorophyll distribution. Acoustic data from bottom-mounted echosounders (WBAT) at the end of each shooting line indicated stable vertical distribution of zooplankton during the seismic approach, with no significant changes with increasing sound levels (Fig. 1). The immediate mortality in *Calanus* spp. remained below 35.9%, similar to the background mortality, showing no significant increase with higher sound levels (Fig. 1). To exclude the impact of the vessel propeller, we exposed cultured *C. finmarchicus* to airgun exposure within submerged plastic bags. They displayed low immediate mortality (below 10%), with a gradually increasing trend (below 30%) up to 7 days post-exposure.

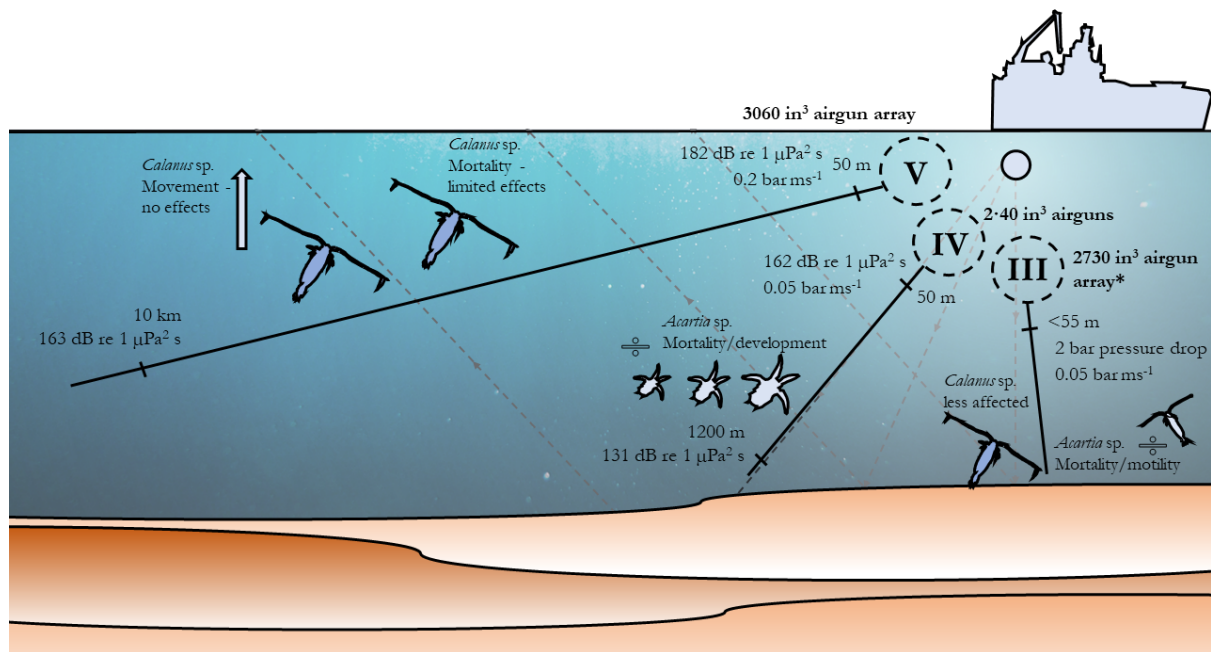


Fig. 7. Overview of observed effects on zooplankton from seismic surveys from paper III-V. For each paper, the seismic source, distance from the seismic source, sound level at the given distance, and calculated pressure drop rate are shown, together with the main findings from each study. Note that for paper III, the airgun array (*) was strictly used in the models calculating at what distance the examined pressure level (bar) would occur around a real seismic airgun array.

5 Discussion

5.1 Potential airgun characteristics causing damage

To gain a comprehensive understanding of the effects of seismic airguns, it is crucial to recognize specific airgun features that could potentially harm zooplankton. It is also necessary to establish the seismic sound level at which the damage occurs and how the intensity of these attributes varies depending on the distance from the airgun (McCauley et al. 2021). Some key attributes have previously been suggested as potential causes of zooplankton damage by seismic airguns: 1) particle motion (McCauley et al. 2017), 2) cavitation caused by pressure fluctuations near the airguns (Fields et al. 2019), and 3) rapid pressure drop associated with airgun blasts (McCauley & Duncan 2017, McCauley et al. 2021).

The movement of particles in response to the propagation of sound waves, known as particle motion, is an important factor in the impact of sound on marine invertebrates and zooplankton (Nedelec et al. 2016, Nedelec et al. 2021). Many marine invertebrates, such as decapods and bivalves, possess sensory setae that detect vibrations resulting from particle motion (Popper et al. 2001, André et al. 2016). Additionally, several zooplankton taxa have sensory hairs or setae that respond to particle motion (reviewed by Solé et al. 2023, **I**). McCauley et al. (2017) suggest that zooplankton can also be physically affected by ‘shaking’ in response to airgun signals, to the extent that their sensory hairs may be damaged. Day et al. (2019) found that exposure to airgun blasts damaged the statocysts of rock lobsters (*Jasus edwardsii*), specifically the chitinous sensory hairs. Although these hairs are not identical to the setae of copepods (Derby 2021), and the characteristics behind the damage were not investigated by Day et al. (2019), such responses suggest that airgun blasts and subsequent increased particle acceleration (McCauley et al. 2021) could harm zooplankton.

The collapse of cavitation bubbles due to a rapid pressure drop near airguns can lead to the phenomenon of cavitation (details in **III**). This has also been observed in snapping shrimp (*Alpheidae*), where the displacement of water caused by the collapse of cavitation bubbles produces loud snapping sounds (Versluis et al. 2000). In addition, the shock waves and high temperatures generated by collapsing bubbles can harm small prey animals by stunning or killing them (Versluis

et al. 2000). In paper **III**, I present novel data on the extent of cavitation in relation to copepods, as well as the connection between pressure and distance from the airgun for this phenomenon. Here, we report that while cavitation caused by the pressure drop from airguns can harm zooplankton, this is more likely to happen close to the airguns (**III**).

This thesis focuses on the rapid pressure drop associated with airgun blasts and its effects on zooplankton mortality and behavior. Through modeling, this characteristic was selected as the most plausible reason for zooplankton damage over other potential causes (Forland pers. comm.). For instance, in order for a small copepod to experience the maximum pressure gradient of a sound wave, the frequency should fall within the range of 500 to 1500 kHz, which only occurs very close to the airgun (Forland pers. comm., Hermannsen et al. 2015). It is important to note that this pressure gradient relates to particle motion, not the pressure drop. While particle motion has traditionally been considered a key factor affecting the auditory perception and sensitivity of anthropogenic underwater sound in invertebrates (Popper et al. 2001, Mooney et al. 2010), this thesis highlights the essential role that rapid pressure drops play in causing harm (**III**).

5.2 Rapid pressure drop associated with airgun blasts

The positive and negative pressure peaks occurring when an airgun is fired lead to a swift hydrostatic pressure drop (Dragoset 2000, Prior et al. 2021; Fig. 4). While the exact mechanisms behind potential damage from this pressure drop are not entirely known, I found in paper **III** that copepods can be affected solely by this pressure drop and that the effects vary among taxa.

Zooplankton are subject to natural pressure variations during their diel vertical and seasonal migration (Bandara et al. 2021). Nevertheless, pressure changes can affect zooplankton taxa in various ways. For example, the mortality in adult *Acartia* spp. increased following exposure to pressure changes related to the entrainment passage of a power station (Bamber & Seaby 2004), and changes in swimming behavior were observed in *C. finmarchicus* after changes in pressure (Lincoln 1971). The pressure drop rate associated with airgun blasts is substantially higher than during vertical migration and may therefore be more damaging. We discuss the pressure drop rate and potential reasons for damage from the rapid pressure drop in more detail in paper **III**.

Paper **III** reveals that variations in effects apply to the pressure drop associated with airguns, which for some taxa could have further implications for the buoyancy, orientation, or magnitude of their feeding current (Visser & Jónasdóttir 1999, Zarubin et al. 2016). It is also evident from previous studies that the effects of pressure changes on copepods are inconsistent between species. For example, exposure to changes in hydrostatic pressure negatively affected the grazing behavior of *C. helgolandicus* but not that of two other calanoid copepod species (Zarubin et al. 2016). However, the focus in paper **III** was the rate at which the pressure decreased, as it is more relevant to airgun blasts (see Fig. 4) than the pressure level alone.

In paper **III**, we exposed the animals to a pressure drop of ~2 bar, which would not likely extend beyond ~55 m from the airgun array (**III**). This range is substantially shorter than that reported in, e.g., McCauley et al. (2017), where increased mortality was observed 1 km from the airgun (McCauley et al. 2017), but more consistent with Fields et al. (2019), reporting effects <25 m from the airguns. Although we modeled the range of effects based on the pressure level (bar) in paper **III**, the pressure drop rate (bar ms^{-1}) is also an important indicator of potential impact. The drop rate during the closest blasts in papers **IV** and **V** was calculated based on the pressure peak (Pa) and subsequent drop (Figs. 7, 8). In the case of an airgun blast at the closest distance using two small airguns, a drop rate of 0.05 bar ms^{-1} occurred in paper **IV**, more or less similar to the one tested in paper **III** (Figs. 7, 8). During the exposure in paper **V**, the drop rate at the closest distance was 0.2 bar ms^{-1} (Figs. 7, 8), considerably higher than in papers **III** and **IV**. Therefore, as emphasized in paper **III**, the higher drop rate measured during exposure to a real airgun array indicates that effects might be observable within a larger range from the airgun.

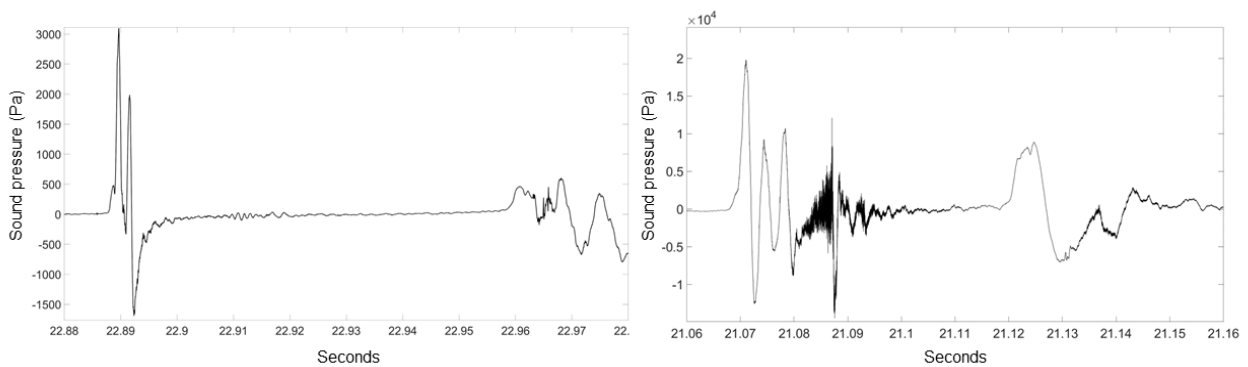


Fig. 8. The pressure (Pa) drop and subsequent variations, extracted from the received sound levels during airgun exposure in papers **IV** (left panel) and **V** (right panel). Both signals were the strongest from both studies, i. e., taken from the closest distance to the airguns (~50 m).

The drop rate during airgun blasts also depends on factors such as the directionality around the airgun (**III**), chamber setup, and type of airgun (Khodabandelo 2018). It is also imperative to consider additional factors when extrapolating findings from laboratory or field exposures, as results may vary between modeled and real shots. The isolated analysis of a pressure drop, followed by upscaling using data from a seismic survey (**III**), may not fully encompass subsequent phenomena, such as bottom reflections that occur during actual surveys, as seen in papers **IV** and **V** (Fig. 8).

In summary, the findings from paper **III** reveal that pressure drops from airgun blasts during seismic surveys can adversely affect zooplankton. While observed effects are confined within limited distances at tested levels, higher drop rates during full array blasts may suggest broader impacts. These findings highlight the importance of recognizing pressure drop as a factor influencing zooplankton vulnerability during seismic surveys.

5.3 Variations in zooplankton responses

The taxa used in papers **III-V** differ in certain traits, such as size and lipids (Table 1). The discrepancies in response between taxa (**III-V**) raise questions about why and how seismic airguns affect various zooplankton differently.

Zooplankton size is a characteristic common across taxonomy but also differs within the same taxon (Kjørboe & Hirst 2014), and one of the traits that differ between taxa that are affected differently by seismic airgun exposure. For example, Fields et al. (2019) found elevated but limited mortality and no effects on escape mechanisms in the large copepod *C. finmarchicus* after exposure to two airguns with a maximum sound level exposure of 182 dB re $\mu\text{Pa}^2 \text{ s}$ (Fig. 9). In contrast, McCauley et al. (2017) reported higher mortality in natural zooplankton communities dominated by krill larvae, cladocerans, and copepods, particularly smaller taxa (*Acartia tranterii*, *Oithona* spp.), after exposure to only one airgun with lower sound exposure levels (Fig. 9). Smaller copepods (e.g., *Oithona* spp.) also exhibited higher mortality rates than larger copepod taxa after exposure to two small airguns (Fields et al. unpub.). These differences align with the varying results found in this thesis (III-V). Paper III reports that *Acartia* sp. is more sensitive than *Calanus* sp., and the study animals in paper V, dominated by large copepods (*Calanus* spp.), showed lower mortality than those in McCauley et al. (2017), despite elevated sound exposure levels (Fig. 9). Studies examining both fish (Yelverton et al. 1975) and zooplankton (Metillo et al. 2016) have suggested an inverse relationship between sound wave effects and body size, indicating greater effects on smaller-sized organisms. Overall, the results obtained from papers III-V indicate that zooplankton size impacts their sensitivity to seismic airguns. This suggests that smaller species may be more vulnerable to the impact of seismic airguns than larger species.

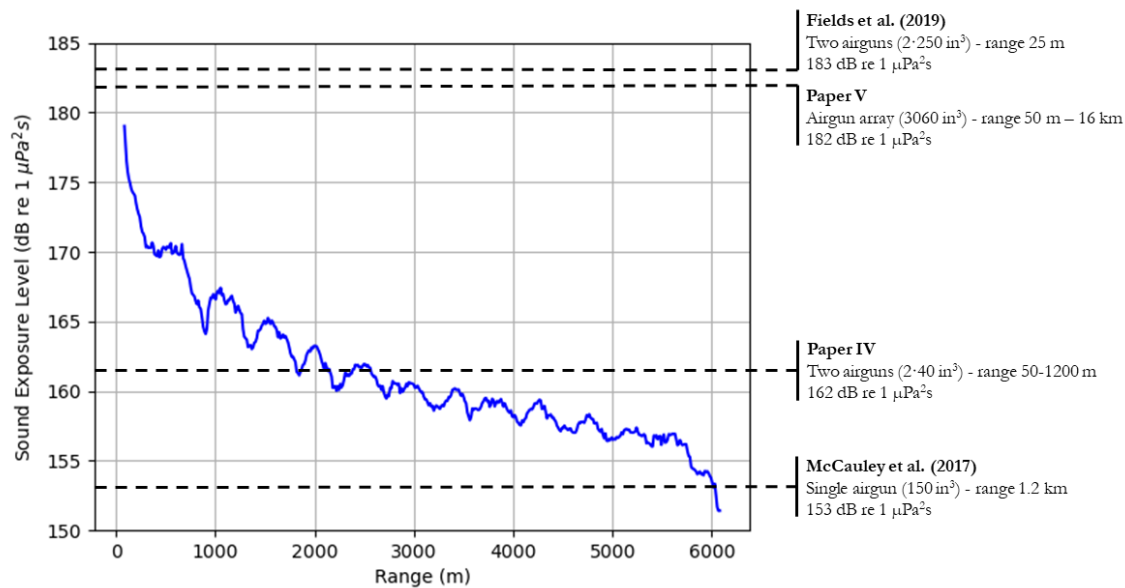


Fig. 9. Sound levels from current studies (IV, V) and two previous studies: Fields et al. (2019) and McCauley et al. (2017). The sound levels are the maximum during exposure and the closest distance to the seismic source for each study. The blue line is the measured sound exposure level (SEL) from a PGS (Petroleum Geo-Services) seismic survey using a full airgun array (3280 in³). The PGS sound levels and the figure are modified from the M.Sc. thesis of Arvid Lyngstad, NTNU.

Zooplankton, particularly copepods, exhibit variability in lipid content among taxa (Lee et al. 2006). Lipids play a crucial role as energy reserves and are essential for buoyancy regulation during vertical migration (Campbell & Dower 2003). Vertical migration exposes zooplankton and their lipid reserves to regular pressure changes, albeit not as rapid as those caused by airgun blasts. These rapid pressure variations may impact fluctuations in volume and the subsequent compression of the elastic shell, which is further discussed in paper III. Still, McCauley et al. (2017) documented elevated mortality in species with lower lipid content, and Fields et al. (2019) reported low mortality in lipid-rich *C. finmarchicus*. Therefore, the fewer adverse effects in *Calanus* sp. compared to *Acartia* sp. I found in paper III might imply that the effects linked to lipids might be more associated with buoyancy and orientation rather than mortality. Zarubin et al. (2016) suggest that disparities in behavioral responses to hydrostatic pressure changes could also be related to the ability of a species to regulate buoyancy through mechanisms unrelated to lipids, such as the accumulation of low-density ions. In other words, even though some animals contain lipids, their behavioral patterns might remain unaffected following pressure changes owing to alternative

regulatory mechanisms. This regulation is likely more applicable to behavioral aspects rather than potential physical damage. Moreover, the presence and composition of lipids can vary seasonally, between different habitats (Pond 2012), and across developmental stages (Zarubin et al. 2014), introducing the possibility of variation in effects within a single species.

Zooplankton sensory systems and responsiveness to external stimuli differ between taxa (Buskey et al. 2012), and stage (Titelman & Kiørboe 2003a, Titelman & Kiørboe 2003b), and their sensitivity to sound might also differ, as suggested by Radford et al. (2021) for decapod crustaceans. For example, Solé et al. (2021) found that exposing salmon lice (*Lepeophtheirus salmonis*) to noise for four hours resulted in setae fusion, occurring mostly when the organisms were exposed to a combination of 350 Hz and 500 Hz sounds. Moreover, exposure to boat noise significantly reduced the capture rates of phytoplankton in *A. tonsa* (Kühn et al. 2023), suggesting that sound may interfere with their normal feeding behavior or adversely affect their mechanoreceptive systems. In difference, Fields et al. (2019) found no impact on the escape response of *C. finmarchicus* after exposure to airgun noise. Such differences in behavioral responses might be caused by noise frequency ranges affecting various species (Radford et al. 2021), stages (Solé et al. 2021), or morphological differences in mechanoreceptive structures (Weatherby & Lenz 2000). Therefore, while the reduced naupliar growth in *A. tonsa* (IV) is most likely related to stage sensitivity, the difference between *Acartia* sp. and *Calanus* sp. in paper III might be linked to their mechanoreceptive structures or noise frequency ranges.

Zooplankton taxa exhibit distinct behavioral patterns, and feeding strategies (Paffenhöfer 1988, Almeda et al. 2017). The reduced motility of *Acartia* sp. I found in paper III could potentially disrupt its capacity for effective ambush feeding (Kiørboe et al. 1996) or affect the ability of the organism to switch between suspension and ambush feeding (Saiz & Kiørboe 1995). This could ultimately affect the rate of energy intake or prey selection (Almeda et al. 2018). While *Calanus* sp. exhibited less pronounced effects on swimming behavior following exposure to a pressure drop, there may still be an impact on the efficiency of its filter feeding (Zarubin et al. 2016). These impacts may not be immediately apparent in terms of motility or direct mortality but could have ecological implications, such as delayed mortality.

Generally, the larval stages of invertebrates are more susceptible to stressors than the adult stages (Gosselin & Qian 1997), especially in the transition from nauplius to copepodit stages

(Mauchline 1998), which may also apply to airgun blasts. Juvenile stages also have a higher natural mortality rate than adults (Aksnes & Magesen 1983). However, older copepod developmental stages have more efficient mechanoreception than younger ones (Fields & Yen 1997, Kiørboe et al. 1999). Therefore, the effects on juveniles and adults may differ depending on the type of harm from seismic surveys. The adverse effects on both mortality and growth of nauplii from airguns I found in paper **IV** highlight the need to also consider younger stages and differences in response within developmental stages.

In conclusion, the variations in the effects of seismic airguns on different zooplankton taxa and developmental stages highlight the complexity of these effects, and imply that zooplankton cannot be treated as one group that is uniformly affected. Rather than simply attributing these differences to specific taxa, variations can also be related to specific characteristics or traits, such as size, sensitivity to sound, behavior, or lipid content. Understanding the sensitivity across sizes, stages, as well as taxa, is crucial for comprehensively assessing the impacts of seismic airgun exposure on marine ecosystems. Future investigations should prioritize a more detailed examination of these factors to enhance our understanding of the vulnerability of zooplankton to airgun exposure.

5.4 Ecological relevance

The consequences of the effects of seismic surveys depend on the distribution, seasonality, and conditions of the survey. The ecological implications of increased zooplankton mortality following seismic surveys, as discussed by McCauley et al. (2017), warrant careful consideration. Regions with elevated zooplankton abundance often coincide with areas undergoing regular seismic survey activities (Fig. 3), implying consistent exposure and potential impact on zooplankton. Increased mortality may result in reduced food availability for predators or a shift in species composition and functional groups (reviewed by Daewel et al. 2013) given the varying vulnerability of taxa (**III**).

However, the reported mortality rates (**III-V**) suggest that seismic surveys will result in lethal effects on only a small proportion of zooplankton, at least on copepods, as examined in this thesis. Although mortality was documented in papers **III-V**, the mortality rates were low, indicating a relatively small-scale impact, which is further discussed in paper **IV**. These findings are

consistent with those of Fields et al. (2019), reinforcing the idea of low zooplankton mortality rates. The divergence in mortality between McCauley et al. (2017) and the results presented in my thesis underscores the importance of considering factors other than the endpoint itself. McCauley et al. (2017) used an individual airgun rather than an array, possessing differences in e. g., source signature or bubble oscillations (Dragoset 2000, Khodabandloo 2018), which might have an elevated impact even at lower sound levels (Fig. 9). These variations highlight the complexity of evaluating the impact of seismic surveys on zooplankton, and emphasize the need for a comprehensive consideration of multiple parameters in comparative studies. In summary, while concerns exist about the impact of seismic surveys on zooplankton mortality (e.g., in McCauley et al. 2017), our results suggest a relatively minor overall lethal effect when compared with background mortality in the field (reviewed by Tang et al. 2014). Nonetheless, it is essential to consider that the taxa included in this thesis are only a fraction of those in the community, and more substantial effects on mortality in other groups should not be dismissed.

Papers **III** and **IV**, along with prior research (reviewed in **I**, **II**), reveal that exposure to seismic airguns can induce sublethal effects on zooplankton growth, development, and behavior, which may have an impact beyond an individual level. For instance, the adverse effects on juvenile zooplankton resulting from seismic airgun exposure may lead to reduced growth or abnormalities (Christian et al. 2003, de Soto et al. 2013, **IV**). Such effects can subsequently lead to higher mortality rates during the larval stage, resulting in a decline in larval recruitment (Pine et al. 2012, de Soto et al. 2013). Decreased abundance of juvenile zooplankton, in turn, can affect predators like fish larvae, which heavily rely on nauplii and copepodites as their primary food source (Paradis et al. 2012).

Furthermore, the influence of seismic surveys on the behavior of zooplankton, as demonstrated by the observed reduced feeding rate in *A. tonsa* after exposure to boat noise (Kühn et al. 2023) or the decreased movement in *A. tonsa* after pressure exposure (**IV**), can lead to more detrimental consequences. For example, weakened predator avoidance due to reduced sensitivity or movement may elevate predation rates, making prey organisms more susceptible to predators (Chan et al. 2010). Studies have also indicated that larger crustaceans undergo changes in mating behavior and group dynamics when exposed to noise (Tidau & Briffa 2019, Ruiz-Ruiz et al. 2019), emphasizing the far-reaching consequences of noise-induced alterations in their behaviors.

Indirectly, offshore activities can also affect species distribution. For instance, the presence of echinoderm larvae within the zooplankton community (**V**) suggests that the introduction of new hard substrates through offshore activities has influenced its composition (Krone et al. 2013). This, in turn, may have led to an increase in meroplankton, potentially instigating alterations in the dynamics of the local food web (Abramic et al. 2022).

In a broader ecological context, activities such as seismic surveys can cause alterations that impact organisms ranging from small invertebrates to large marine mammals. These changes have the potential to disrupt essential ecosystem functions, despite their relatively limited impact on copepods observed in papers **III-V**. The potential of broader impact is manifested through the masking and alteration of morphology, physiology, and behavioral processes across a diverse range of taxa (Nichols et al. 2015, Erbe et al. 2019, Murchy et al. 2019, de Jong et al. 2020, Solé et al. 2021). The impact of anthropogenic noise extends widely, and may affect not only the directly affected species. For instance, marine mammals relocating due to seismic surveys (Kavanagh et al. 2019) can indirectly influence other groups, such as zooplankton, via trophic or behavioral cascades. In summary, while it is more difficult and extensive to analyze the long-term consequences of sublethal impacts of seismic surveys, they should not be dismissed on a larger scale.

6 Conclusions and future recommendations

This thesis provides novel insights into the effects of seismic surveys on marine life, revealing that these impacts are more nuanced and vary across different taxa and/or traits thus challenging previous assumptions (in e.g. McCauley et al. 2017).

The thesis offers new data on the airgun characteristics underlying damage to zooplankton, reporting that a rapid pressure drop associated with airgun blasts causes damage to zooplankton, although from a close distance from the airguns. The zooplankton included in this thesis (**III-V**) experienced significant negative, albeit small, lethal, and sublethal effects of seismic airguns or pressure drop associated with airgun blasts. Furthermore, the observed effects differed between taxa, from which I suggest that small copepods are more vulnerable to seismic blasts than larger copepods. However, I want to highlight that potential long-term consequences, such as delayed mortality or effects on feeding and predation, cannot be ruled out. The observed effects from these studies are limited to a close distance around seismic airguns. I find it crucial to recognize that the research covered in these papers only accounts for a small portion of the possible outcomes, especially considering that the thesis investigated only a restricted number of taxa. Given the ongoing prevalence of seismic surveys for purposes such as carbon capture and storage, introduction of new sources, and continuous rise in anthropogenic underwater noise, further research is needed to enhance our understanding of these dynamics across the field of ecosystem players - from small (**III-V**) to large.

7 Acknowledgements

I would like to thank Karen de Jong, Josefin Titelman, Anne Christine Utne Palm and Mette Dalgaard Agersted for their insightful comments and suggestions on this synthesis. I would also like to thank Tonje Nesse Forland, Babak Khodabandeloo and Arvid Lyngstad for help with figures.

References

- Abramic, A. , V. Cordero-Penin, and R. Haroun. 2022. "Environmental impact assessment framework for offshore wind energy developments based on the marine Good Environmental Status." *Environmental Impact Assessment Review* 97: 106862. <https://doi.org/https://doi.org/10.1016/j.eiar.2022.106862>.
- Affatati, Alice, and Angelo Camerlenghi. 2023. "Effects of marine seismic surveys on free-ranging fauna: a systematic literature review." *Frontiers in Marine Science*. <https://doi.org/https://doi.org/10.3389/fmars.2023.1222523>.
- Ainslie, Michael A., and Christ A. F. de Jong. 2016. "Sources of Underwater Sound and Their Characterization." *The Effects of Noise on Aquatic Life II*, New York, NY, 2016//.
- Aksnes, Dag, and Thorolf Magnesen. 1983. "Distribution, development, and production of *Calanus finmarchicus* (Gunnerus) in Lindåspollene, western Norway, 1979." *Sarsia* 68: 195-207. <https://doi.org/10.1080/00364827.1983.10420572>.
- Almeda, Rodrigo, Hans van Someren Gréve, and Thomas Kiørboe. 2017. "Behavior is a major determinant of predation risk in zooplankton." *Ecosphere* 8 (2): e01668. <https://doi.org/https://doi.org/10.1002/ecs2.1668>.
- . 2018. "Prey perception mechanism determines maximum clearance rates of planktonic copepods." *Limnology and Oceanography* 63 (6): 2695-2707. <https://doi.org/10.1002/lno.10969>.
- André, Michel, Kenzo Kaifu, Marta Solé, Mike van der Schaar, Tomonari Akamatsu, Andreu Balastegui, Antonio M Sánchez, and Joan V Castell. 2016. "Contribution to the understanding of particle motion perception in marine invertebrates." *The effects of noise on aquatic life II*.
- Bamber, R. N., and R. M. H. Seaby. 2004. "The effects of power station entrainment passage on three species of marine planktonic crustacean, *Acartia tonsa* (Copepoda), *Crangon crangon* (Decapoda) and *Homarus gammarus* (Decapoda)." *Marine Environmental Research* 57 (4): 281-294. <https://doi.org/10.1016/j.marenvres.2003.08.002>.
- Bandara, Kanchana, Øystein Varpe, Lishani Wijewardene, Vigdis Tverberg, and Ketil Eiane. 2021. "Two hundred years of zooplankton vertical migration research." *Biological Reviews* 96 (4): 1547-1589. <https://doi.org/https://doi.org/10.1111/brv.12715>.
- Beaugrand, Grégory, Philip C. Reid, Frédéric Ibañez, J. Alistair Lindley, and Martin Edwards. 2002. "Reorganization of North Atlantic Marine Copepod Biodiversity and Climate." *Science* 296 (5573): 1692-1694. <https://doi.org/10.1126/science.1071329>.

- Bickel, S. L., J. D. M. Hammond, and K. W. Tang. 2011. "Boat-generated turbulence as a potential source of mortality among copepods." *Journal of Experimental Marine Biology and Ecology* 401 (1-2): 105-109. <https://doi.org/10.1016/j.jembe.2011.02.038>.
- Brandão, Manoela C., Fabio Benedetti, Séverine Martini, Yawouvi Dodji Soviadan, Jean-Olivier Irisson, Jean-Baptiste Romagnan, Amanda Elineau, Corinne Desnos, Laëticia Jalabert, Andrea S. Freire, Marc Picheral, Lionel Guidi, Gabriel Gorsky, Chris Bowler, Lee Karp-Boss, Nicolas Henry, Colomban de Vargas, Matthew B. Sullivan, Silvia G. Acinas, Marcel Babin, Peer Bork, Emmanuel Boss, Chris Bowler, Guy Cochrane, Colomban de Vargas, Gabriel Gorsky, Lionel Guidi, Nigel Grimsley, Pascal Hingamp, Daniele Iudicone, Olivier Jaillon, Stefanie Kandels, Lee Karp-Boss, Eric Karsenti, Fabrice Not, Hiroyuki Ogata, Nicole Poulton, Stephane Pesant, Jeroen Raes, Christian Sardet, Sabrina Speich, Lars Stemmann, Matthew B. Sullivan, Shinichi Sunagawa, Patrick Wincker, Lars Stemmann, Fabien Lombard, and Coordinators Tara Oceans Consortium. 2021. "Macroscale patterns of oceanic zooplankton composition and size structure." *Scientific Reports* 11 (1): 15714. <https://doi.org/10.1038/s41598-021-94615-5>.
- Budelmann, Bernd U. 1992. "Hearing in Nonarthropod Invertebrates." In *The Evolutionary Biology of Hearing*, edited by Douglas B. Webster, Arthur N. Popper and Richard R. Fay, 141-155. New York, NY: Springer New York.
- Buskey, Edward, P. Len, and Daniel Hartline. 2002. "Escape behavior of planktonic copepods in response to hydrodynamic disturbances: High speed video analysis." *Marine Ecology Progress Series* 235. <https://doi.org/10.3354/meps235135>.
- Caldwell, Jack, and William Dragoset. 2000. "A brief overview of seismic air-gun arrays." *The Leading Edge* 19 (8): 898-902. <https://doi.org/10.1190/1.1438744>.
- Campbell, R. W., and J. F. Dower. 2003. "Role of lipids in the maintenance of neutral buoyancy by zooplankton." *Marine Ecology Progress Series* 263: 93-99.
- Carroll, A. G., R. Przeslawski, A. Duncan, M. Gunning, and B. Bruce. 2017. "A critical review of the potential impacts of marine seismic surveys on fish & invertebrates." *Marine Pollution Bulletin* 114 (1): 9-24. <https://doi.org/10.1016/j.marpolbul.2016.11.038>.
- Cervetto, G., M. Pagano, and R. Gaudy. 1995. "Feeding behaviour and migrations in a natural population of the copepod *Acartia tonsa*." *Hydrobiologia* 300 (1): 237-248. <https://doi.org/10.1007/BF00024464>.
- Chan, Alvin Aaden Yim-Hol, Paulina Giraldo-Perez, Sonja Smith, and Daniel T. Blumstein. 2010. "Anthropogenic noise affects risk assessment and attention: the distracted prey hypothesis." *Biology Letters* 6 (4): 458-461. <https://doi.org/doi:10.1098/rsbl.2009.1081>.
- Christian, John R., R. A. Buchanan, A. Mathieu, D. White, and D. H. Thomson. 2003. "Effect of seismic energy on snow crab (*Chionoecetes opilio*)." *Environmental Studies Research Fund*.

- Daewel, Ute, Solfrid Sætre Hjøllo, Martin Huret, Rubao Ji, Marie Maar, Susa Niiranen, Morgane Travers-Trolet, Myron A. Peck, and Karen E. van de Wolfshaar. 2013. "Predation control of zooplankton dynamics: a review of observations and models." *ICES Journal of Marine Science* 71 (2): 254-271. <https://doi.org/10.1093/icesjms/fst125>.
- Dalpadado, P., B. Ellertsen, W. Melle, and A. Dommasnes. 2000. "Food and feeding conditions of Norwegian spring-spawning herring (*Clupea harengus*) through its feeding migrations." *ICES Journal of Marine Science* 57 (4): 843-857. <https://doi.org/10.1006/jmsc.2000.0573>.
- Day, Ryan D, Robert D McCauley, Quinn P Fitzgibbon, Klaas Hartmann, and Jayson M Semmens. 2019. "Seismic air guns damage rock lobster mechanosensory organs and impair righting reflex." *Proceedings of the Royal Society B* 286 (1907): 20191424.
- de Jong, Karen, Tonje Nesse Forland, Maria Clara P. Amorim, Guillaume Rieucou, Hans Slabbekoorn, and Lise Doksæter Sivle. 2020. "Predicting the effects of anthropogenic noise on fish reproduction." *Reviews in Fish Biology and Fisheries* 30 (2): 245-268. <https://doi.org/10.1007/s11160-020-09598-9>.
- de Soto, N. A., N. Delorme, J. Atkins, S. Howard, J. Williams, and M. Johnson. 2013. "Anthropogenic noise causes body malformations and delays development in marine larvae." *Science Reports* 3: 2831. <https://doi.org/10.1038/srep02831>.
- Derby, Charles D. 2021. "The Crustacean Antennule: A Complex Organ Adapted for Lifelong Function in Diverse Environments and Lifestyles." *The Biological Bulletin* 240 (2): 67-81. <https://doi.org/10.1086/713537>.
- Di Iorio, Lucia, and Christopher W. Clark. 2010. "Exposure to seismic survey alters blue whale acoustic communication." *Biology Letters* 6 (1): 51-54. <https://doi.org/doi:10.1098/rsbl.2009.0651>.
- Dragoset, Bill. 2000. "Introduction to air guns and air-gun arrays." *Geophysics* 19. <https://doi.org/10.1190/1.1438741>.
- Duarte, Carlos M., Lucille Chapuis, Shaun P. Collin, Daniel P. Costa, Reny P. Devassy, Victor M. Eguiluz, Christine Erbe, Timothy A. C. Gordon, Benjamin S. Halpern, Harry R. Harding, Michelle N. Havlik, Mark Meekan, Nathan D. Merchant, Jennifer L. Miksis-Olds, Miles Parsons, Milica Predragovic, Andrew N. Radford, Craig A. Radford, Stephen D. Simpson, Hans Slabbekoorn, Erica Staaterman, Ilse C. Van Opzeeland, Jana Winderen, Xiangliang Zhang, and Francis Juanes. 2021. "The soundscape of the Anthropocene ocean." *Science* 371 (6529): eaba4658. <https://doi.org/doi:10.1126/science.aba4658>.
- Duncan, Alec J., Alexander N. Gavrilov, Robert D. McCauley, Iain M. Parnum, and Jon M. Collis. 2013. "Characteristics of sound propagation in shallow water over an elastic seabed with a thin cap-rock layer." *The Journal of the Acoustical Society of America* 134 (1): 207-215. <https://doi.org/10.1121/1.4809723>.

- Dunlop, Rebecca A., Michael J. Noad, Robert D. McCauley, Eric Kniest, David Paton, and Douglas H. Cato. 2015. "The behavioural response of humpback whales (*Megaptera novaeangliae*) to a 20 cubic inch air gun." *Aquatic Mammals* 41 (4): 412.
- Erbe, Christine, Alec Duncan, and Kathleen J. Vigness-Raposa. 2022. "Introduction to Sound Propagation Under Water." In *Exploring Animal Behavior Through Sound: Volume 1: Methods*, edited by Christine Erbe and Jeanette A. Thomas, 185-216. Cham: Springer International Publishing.
- Erbe, Christine, Sarah A. Marley, Renée P. Schoeman, Joshua N. Smith, Leah E. Trigg, and Clare Beth Embling. 2019. "The Effects of Ship Noise on Marine Mammals—A Review." *Frontiers in Marine Science* 6. <https://doi.org/10.3389/fmars.2019.00606>.
- Falkenhaus, Tone, Cecilie Broms, Espen Bagøien, and Nikolaos Nikolioudakis. 2022. "Temporal Variability of Co-Occurring *Calanus finmarchicus* and *C. helgolandicus* in Skagerrak." *Frontiers in Marine Science* 9. <https://doi.org/10.3389/fmars.2022.779335>.
- Fields, D. M., M. Niemisto, S. D. Shema, K. de Jong, E. H. Vereide, M. Mihaljevic, T. N. Forland, A. B. Skiftesvik, and H. I. Browman. Unpublished. "Airgun blasts used in marine seismic surveys have limited effects on mortality of natural zooplankton populations"
- Fields, David M., Nils Olav Handegard, John Dalen, Christiane Eichner, Ketil Malde, Ørjan Karlsen, Anne Berit Skiftesvik, Caroline M. F. Durif, Howard I. Browman, and Purnima Ratilal. 2019. "Airgun blasts used in marine seismic surveys have limited effects on mortality, and no sublethal effects on behaviour or gene expression, in the copepod *Calanus finmarchicus*." *ICES Journal of Marine Science* 76 (7): 2033-2044. <https://doi.org/10.1093/icesjms/fsz126>.
- Fields, David M., and Jeanette Yen. 1997. "The escape behavior of marine copepods in response to a quantifiable fluid mechanical disturbance." *Journal of Plankton Research* 19 (9): 1289-1304. <https://doi.org/10.1093/plankt/19.9.1289>.
- Folt, Carol L., and Carolyn W. Burns. 1999. "Biological drivers of zooplankton patchiness." *Trends in Ecology & Evolution* 14 (8): 300-305. [https://doi.org/https://doi.org/10.1016/S0169-5347\(99\)01616-X](https://doi.org/https://doi.org/10.1016/S0169-5347(99)01616-X).
- Forland, Tonje Nesse, Lise Doksæter Sivle, Karen de Jong, Geir Pedersen, Marte Louise Strømme, Tina Kutti, Caroline Durif, Endre Grimsbø, Kate McQueen, and Henning Wehde. 2024. *Advice from the Institute of Marine Research on anthropogenic noise in the sea*. Institute of Marine Research.
- Gassie, Donald V., Petra H. Lenz, Jeannette Yen, and Daniel K. Hartline. 1993. "Mechanoreception in Zooplankton First Antennae: Electrophysiological Techniques." *Bulletin of Marine Science* 53 (1): 96-105. <https://www.ingentaconnect.com/content/umrsmas/bullmar/1993/00000053/00000001/art00008>.

- Giguère, Louis A, and Lawrence M Dill. 1979. "The predatory response of *Chaoborus* larvae to acoustic stimuli, and the acoustic characteristics of their prey." *Zeitschrift für Tierpsychologie* 50 (2): 113-123.
- Goertner, John F., Martin L. Wiley, George A. Young, and William W. McDonald. 1994. "Effects of Underwater Explosions on Fish Without Swimbladders."
- Goold, John C., and Peter J. Fish. 1998. "Broadband spectra of seismic survey air-gun emissions, with reference to dolphin auditory thresholds." *The Journal of the Acoustical Society of America* 103 (4): 2177-2184.
- Gosselin, Louis, and Pei-Yuan Qian. 1997. "Juvenile mortality in benthic marine invertebrates." *Marine Ecology Progress Series* 146: 265-282. <https://doi.org/10.3354/meps146265>.
- Guan, Shane, and Tiffini Brookens. 2023. "An overview of research efforts to understand the effects of underwater sound on cetaceans." *Water Biology and Security* 2 (2): 100141. <https://doi.org/https://doi.org/10.1016/j.watbs.2023.100141>.
- Guerra, A., González. Á., and F. Rocha. 2004. "A review of the records of giant squid in the north-eastern Atlantic and severe injuries in *Architeuthis dux* stranded after acoustic explorations." ICES Annual Science Conference.
- Hawkins, Anthony D., Ann E. Pembroke, and Arthur N. Popper. 2015. "Information gaps in understanding the effects of noise on fishes and invertebrates." *Reviews in Fish Biology and Fisheries* 25 (1): 39-64. <https://doi.org/10.1007/s11160-014-9369-3>.
- Hermanssen, L., J. Tougaard, K. Beedholm, J. Nabe-Nielsen, and P. T. Madsen. 2015. "Characteristics and Propagation of Airgun Pulses in Shallow Water with Implications for Effects on Small Marine Mammals." *PLoS One* 10 (7): e0133436. <https://doi.org/10.1371/journal.pone.0133436>.
- Heuschele, Jan, and Erik Selander. 2014. "The chemical ecology of copepods." *Journal of Plankton Research* 36 (4): 895-913. <https://doi.org/10.1093/plankt/fbu025>.
- Hildebrand, J. A. 2009. "Anthropogenic and natural sources of ambient noise in the ocean." *Marine Ecology Progress Series* 395: 5-20. <https://doi.org/10.3354/meps08353>.
- Hobbs, Laura, Neil S. Banas, Jonathan H. Cohen, Finlo R. Cottier, Jørgen Berge, and Øystein Varpe. 2021. "A marine zooplankton community vertically structured by light across diel to interannual timescales." *Biology Letters* 17 (2): 20200810. <https://doi.org/doi:10.1098/rsbl.2020.0810>.
- Hurtado, Ariana. 2023. "Seismic survey market finally recovering." *Offshore Magazine*.
- Jackson, George, A. , and Thomas Kiørbo. 2004. "Zooplankton use of chemodetection to find and eat particles." *Marine Ecology Progress Series* 269: 153-162. <https://www.int-res.com/abstracts/meps/v269/p153-162/>.

- Jonsson, P., and P. Tiselius. 1990. "Feeding behavior, prey detection and capture efficiency of the copepod *Acartia tonsa* feeding on planktonic ciliates." *Marine Ecology Progress Series* 60. <https://doi.org/10.3354/meps060035>.
- Kavanagh, A. S., M. Nykänen, W. Hunt, N. Richardson, and M. J. Jessopp. 2019. "Seismic surveys reduce cetacean sightings across a large marine ecosystem." *Scientific Reports* 9 (1): 19164. <https://doi.org/10.1038/s41598-019-55500-4>.
- Khodabandeloo, Babak. 2018. "Modeling and characterizing acoustic signals from cavity clouds generated by marine seismic air-gun arrays: Implications for marine mammals." Ph.D. Ph.D. dissertation, NTNU, Trondheim, Norway.
- Kjørboe, Thomas, and Andrew G. Hirst. 2014. "Shifts in Mass Scaling of Respiration, Feeding, and Growth Rates across Life-Form Transitions in Marine Pelagic Organisms." *The American Naturalist* 183 (4): E118-E130. <https://doi.org/10.1086/675241>.
- Kjørboe, Thomas, Enric Saiz, and Markku Viitasalo. 1996. "Prey switching behaviour in the planktonic copepod *Acartia tonsa*." *Marine Ecology Progress Series* 143: 65-75.
- Kjørboe, Thomas, Enric Saiz, and Andy Visser. 1999. "Hydrodynamic signal perception in the copepod *Acartia tonsa*." *Marine Ecology Progress Series* 179: 97-111. <https://doi.org/10.3354/meps179097>.
- Krone, R., L. Gutow, T. J. Joschko, and A. Schröder. 2013. "Epifauna dynamics at an offshore foundation-implications of future wind power farming in the North Sea." *Mar Environ Res* 85: 1-12. <https://doi.org/10.1016/j.marenvres.2012.12.004>.
- Kühn, Saskia, Franziska King, and Katja Heubel. 2023. "Decreased feeding rates of the copepod *Acartia tonsa* when exposed to playback harbor traffic noise." *Frontiers in Marine Science* 10. <https://doi.org/10.3389/fmars.2023.1134792>.
- Kühn, Saskia, Anne Christine Utne-Palm, and Karen de Jong. 2022. "Two of the most common crustacean zooplankton *Meganycitiphanes norvegica* and *Calanus* spp. produce sounds within the hearing range of their fish predators." *Bioacoustics* 32 (1): 73-89. <https://doi.org/10.1080/09524622.2022.2070542>.
- La Bella, G., S. Cannata, C. Frogli, A. Modica, S. Ratti, and G. Rivas. 1996. "First Assessment of Effects of Air-Gun Seismic Shooting on Marine Resources in the Central Adriatic Sea." SPE Health, Safety and Environment in Oil and Gas Exploration and Production Conference. <https://doi.org/10.2118/35782-MS>.
- Lee, Richard, W. Hagen, and G. Kattner. 2006. "Lipid storage in marine zooplankton." *Marine Ecology Progress Series* 307: 273-306. <https://doi.org/10.3354/meps307273>.
- Lincoln, R. J. 1971. "Observations of the effects of changes in hydrostatic pressure and illumination on the behaviour of some planktonic crustaceans." *Journal of Experimental Biology* 54 (3): 677-688.

- Litchman, Elena, Mark D. Ohman, and Thomas Kiørboe. 2013. "Trait-based approaches to zooplankton communities." *Journal of Plankton Research* 35 (3): 473-484.
<https://doi.org/10.1093/plankt/fbt019>.
- Lovell, J. M., M. M. Findlay, R. M. Moate, and H. Y. Yan. 2005. "The hearing abilities of the prawn *Palaemon serratus*." *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology* 140 (1): 89-100.
<https://doi.org/https://doi.org/10.1016/j.cbpb.2004.11.003>.
- Mackas, David, L. , and Gregory Beaugrand. 2010. "Comparisons of zooplankton time series." *Journal of Marine Systems* 79 (3): 286-304.
<https://doi.org/https://doi.org/10.1016/j.jmarsys.2008.11.030>.
- Mauchline, J. 1998. "9. Growth." In *Advances in Marine Biology*, edited by J. Mauchline, 296-346. Academic Press.
- McCauley, R. D., R. D. Day, K. M. Swadling, Q. P. Fitzgibbon, R. A. Watson, and J. M. Semmens. 2017. "Widely used marine seismic survey air gun operations negatively impact zooplankton." *Nature Ecology and Evolution* 1 (7): 195.
<https://doi.org/10.1038/s41559-017-0195>.
- McCauley, R. D., S. R. Rennie, J. R. Hughes, and A. J. Duncan. 2008. "Transmission of marine seismic signals in Australian waters." *Bioacoustics* 17 (1-3): 130-132.
<https://doi.org/10.1080/09524622.2008.9753790>.
- McCauley, Robert D., and Alec J. Duncan. 2017. "How do impulsive marine seismic surveys impact marine fauna and how can we reduce such impacts?".
- McCauley, Robert D., Mark G. Meekan, and Miles J. G. Parsons. 2021. "Acoustic Pressure, Particle Motion, and Induced Ground Motion Signals from a Commercial Seismic Survey Array and Potential Implications for Environmental Monitoring." *Journal of Marine Science and Engineering* 9 (6): 571. <https://www.mdpi.com/2077-1312/9/6/571>.
- McDonald, Mark, John Hildebrand, Sean Wiggins, and Donald Ross. 2008. "A 50 Year comparison of ambient ocean noise near San Clemente Island: A bathymetrically complex coastal region off Southern California." *The Journal of the Acoustical Society of America* 124: 1985-92. <https://doi.org/10.1121/1.2967889>.
- Melle, Webjørn, Jeffrey Runge, Erica Head, Stéphane Plourde, Claudia Castellani, Priscilla Licandro, James Pierson, Sigrun Jonasdottir, Catherine Johnson, Cecilie Broms, Høgni Debes, Tone Falkenhaus, Eilif Gaard, Astthor Gislason, Michael Heath, Barbara Niehoff, Torkel Gissel Nielsen, Pierre Pepin, Erling Kaare Stenevik, and Guillem Chust. 2014. "The North Atlantic Ocean as habitat for *Calanus finmarchicus*: Environmental factors and life history traits." *Progress in Oceanography* 129: 244-284.
<https://doi.org/https://doi.org/10.1016/j.pocean.2014.04.026>.

- Metillo, Ephrime, Mac Euan Malugao, and Sheldon Boco. 2016. "Effects of in situ firecrackers explosion on copepods (Crustacea, Copepoda) and *Siganus guttatus* (Pisces, *Siganidae*) larvae." *Asian Journal of Biological and Life Sciences* 5: 135-140.
- Montero, José T., Mauricio Lima, Sergio A. Estay, and Enrico L. Rezende. 2021. "Spatial and temporal shift in the factors affecting the population dynamics of *Calanus* copepods in the North Sea." *Global Change Biology* 27 (3): 576-586.
<https://doi.org/https://doi.org/10.1111/gcb.15394>.
- Mooney, T. Aran, Roger T. Hanlon, Jakob Christensen-Dalsgaard, Peter T. Madsen, Darlene R. Ketten, and Paul E. Nachtigall. 2010. "Sound detection by the longfin squid (*Loligo pealeii*) studied with auditory evoked potentials: sensitivity to low-frequency particle motion and not pressure." *Journal of Experimental Biology* 213 (21): 3748-3759.
<https://doi.org/10.1242/jeb.048348>.
- Murchy, Kelsie A., Hailey Davies, and Hailey Shafer. 2019. "Impacts of noise on the behavior and physiology of marine invertebrates: A meta-analysis." *Proceedings of Meetings on Acoustics* 37: 40002-40002. <https://doi.org/10.1121/2.0001217>.
- NDP. 2021. "Seismic." Norwegian Petroleum Directory. Accessed 27 December.
<https://www.npd.no/en/facts/seismic/>.
- Nedelec, Sophie, Michael Ainslie, Mathias Andersson, Cheong Sei-Him, Michele Halvorsen, Markus Linné, Bruce Martin, Andreas Nöjd, Stephen Robinson, Stephen Simpson, Lian Wang, and Jake Ward. 2021. *Best Practice Guide for Underwater Particle Motion Measurement for Biological Applications*.
- Nedelec, Sophie L., James Campbell, Andrew N. Radford, Stephen D. Simpson, and Nathan D. Merchant. 2016. "Particle motion: the missing link in underwater acoustic ecology." *Methods in Ecology and Evolution* 7 (7): 836-842.
<https://doi.org/https://doi.org/10.1111/2041-210X.12544>.
- Nichols, Tye A., Todd W. Anderson, and Ana Širović. 2015. "Intermittent Noise Induces Physiological Stress in a Coastal Marine Fish." *PLOS ONE* 10 (9): e0139157.
<https://doi.org/10.1371/journal.pone.0139157>.
- Paffenhöfer, Gustav-Adolf. 1988. "Feeding Rates and Behavior of Zooplankton." *Bulletin of Marine Science* 43 (3): 430-445.
<https://www.ingentaconnect.com/content/umrsmas/bullmar/1988/00000043/00000003/art00009>.
- Paradis, Vanessa, Pascal Sirois, Martin Castonguay, and Stéphane Plourde. 2012. "Spatial variability in zooplankton and feeding of larval Atlantic mackerel (*Scomber scombrus*) in the southern Gulf of St. Lawrence." *Journal of Plankton Research* 34 (12): 1064-1077.
<https://doi.org/10.1093/plankt/fbs063>.

- Pieniasek, R. H., R. K. Beach, G. M. Dycha, M. F. Mickle, and D. M. Higgs. 2023. "Navigating noisy waters: A review of field studies examining anthropogenic noise effects on wild fish." *The Journal of the Acoustical Society of America* 154 (5): 2828-2842.
<https://doi.org/10.1121/10.0022254>, <https://doi.org/10.1121/10.0022254>.
- Pine, Matthew, K., Andrew G. Jeffs, and Craig A. Radford. 2012. "Turbine Sound May Influence the Metamorphosis Behaviour of Estuarine Crab Megalopae." *PLOS ONE* 7 (12): 1-8.
<https://doi.org/10.1371/journal.pone.0051790>.
- Pinti, J., T. DeVries, T. Norin, C. Serra-Pompei, R. Proud, D. A. Siegel, T. Kiørboe, C. M. Petrik, K. H. Andersen, A. S. Brierley, and A. W. Visser. 2023. "Model estimates of metazoans' contributions to the biological carbon pump." *Biogeosciences* 20 (5): 997-1009.
<https://doi.org/10.5194/bg-20-997-2023>.
- Pinti, Jérôme, Sigrún H. Jónasdóttir, Nicholas R. Record, and André W. Visser. 2023. "The global contribution of seasonally migrating copepods to the biological carbon pump." *Limnology and Oceanography* n/a (n/a). <https://doi.org/https://doi.org/10.1002/lno.12335>.
- Pond, David W. 2012. "The physical properties of lipids and their role in controlling the distribution of zooplankton in the oceans." *Journal of Plankton Research* 34 (6): 443-453.
- Popper, A. N., A. D. Hawkins, O. Sand, and J. A. Sisneros. 2019. "Examining the hearing abilities of fishes." *Journal of the Acoustical Society of America* 146 (2): 948.
<https://doi.org/10.1121/1.5120185>.
- Popper, Arthur N. , and Anthony D. Hawkins. 2018. "The importance of particle motion to fishes and invertebrates." *The Journal of the Acoustical Society of America* 143 (1): 470-488.
<https://doi.org/10.1121/1.5021594>.
- Popper, Arthur N., Anthony D. Hawkins, Richard R. Fay, David A. Mann, Soraya Bartol, Thomas J. Carlson, Sheryl Coombs, William T. Ellison, Roger L. Gentry, Michele B. Halvorsen, Svein Løkkeborg, Peter H. Rogers, Brandon L. Southall, David G. Zeddies, and William N. Tavolga. 2014. "Sound Exposure Guidelines." In *ASA S3/SC1.4 TR-2014 Sound Exposure Guidelines for Fishes and Sea Turtles: A Technical Report prepared by ANSI-Accredited Standards Committee S3/SC1 and registered with ANSI*, edited by Arthur N. Popper, Anthony D. Hawkins, Richard R. Fay, David A. Mann, Soraya Bartol, Thomas J. Carlson, Sheryl Coombs, William T. Ellison, Roger L. Gentry, Michele B. Halvorsen, Svein Løkkeborg, Peter H. Rogers, Brandon L. Southall, David G. Zeddies and William N. Tavolga, 33-51. Cham: Springer International Publishing.
- Popper, Arthur N., Michael Salmon, and Kenneth W. Horch. 2001. "Acoustic detection and communication by decapod crustaceans." *Journal of Comparative Physiology A* 187: 83-89.
- Prior, Mark K., Michael A. Ainslie, Michele B. Halvorsen, Iris Hartstra, Robert M. Laws, Alexander MacGillivray, Roel Müller, Stephen Robinson, and Liansheng Wang. 2021. "Characterization of the acoustic output of single marine-seismic airguns and clusters: The

- Svein Vaage dataset." *The Journal of the Acoustical Society of America* 150 (5): 3675-3692. <https://doi.org/10.1121/10.0006751>.
- Prokopchuk, Irina, and Evgeny Sentyabov. 2006. "Diets of herring, mackerel, and blue whiting in the Norwegian Sea in relation to *Calanus finmarchicus* distribution and temperature conditions." *Ices Journal of Marine Science* 63: 117-127. <https://doi.org/10.1016/j.icesjms.2005.08.005>.
- Puseddu, Antonio, Silvia Bianchelli, Jacobo Martín, Pere Puig, Albert Palanques, Pere Masqué, and Roberto Danovaro. 2014. "Chronic and intensive bottom trawling impairs deep-sea biodiversity and ecosystem functioning." *Proceedings of the National Academy of Sciences* 111 (24): 8861-8866. <https://doi.org/doi:10.1073/pnas.1405454111>.
- Radford, C. A., K. Tay, and M. L. Goeritz. 2021. "Comparative sound detection abilities of four decapod crustaceans." *Journal of Experimental Biology*: jeb.243314. <https://doi.org/10.1242/jeb.243314>.
- Ruiz-Ruiz, Paula A., Iván A. Hinojosa, Angel Urzua, and Mauricio A. Urbina. 2019. "Anthropogenic noise disrupts mating behavior and metabolic rate in a marine invertebrate." *Proceedings of Meetings on Acoustics*.
- Saiz, Enric, and Thomas Kiørboe. 1995. "Predatory and suspension feeding of the copepod *Acartia tonsa* in turbulent environments." *Marine Ecology Progress Series* 122: 147-158. <https://doi.org/10.3354/meps122147>.
- Schardin, Hubert. 1950. "The physical principles of the effects of a detonation." *German Aviation Medicine, World War II* 2: 1207-1224.
- Slabbekoorn, Hans. 2016. "Aiming for Progress in Understanding Underwater Noise Impact on Fish: Complementary Need for Indoor and Outdoor Studies." *The Effects of Noise on Aquatic Life II*, New York, NY, 2016//.
- Slabbekoorn, Hans, John Dalen, Dick Haan, Hendrik V. Winter, Craig Radford, Michael A. Ainslie, Kevin D. Heaney, Tobias Kooten, Len Thomas, and John Harwood. 2019. "Population-level consequences of seismic surveys on fishes: An interdisciplinary challenge." *Fish and Fisheries* 20 (4): 653-685. <https://doi.org/10.1111/faf.12367>.
- Solé, Marta, Kenzo Kaifu, T. Aran Mooney, Sophie L. Nedelec, Frédéric Olivier, Andrew N. Radford, Mirella Vazzana, Matthew A. Wale, Jayson M. Semmens, Stephen D. Simpson, Giuseppa Buscaino, Anthony Hawkins, Natacha Aguilar de Soto, Tomoari Akamatsu, Laurent Chauvaud, Ryan D. Day, Quinn Fitzgibbon, Robert D. McCauley, and Michel André. 2023. "Marine invertebrates and noise." *Frontiers in Marine Science* 10. <https://doi.org/10.3389/fmars.2023.1129057>.

- Solé, Marta, Marc Lenoir, José Alos, Steffen De Vreese, Mike Schaar, and Michel André. 2021. "Sea Lice Are Sensitive to Low Frequency Sounds." *Journal of Marine Science and Engineering* 9: 765-765. <https://doi.org/10.3390/jmse9070765>.
- Solé, Marta, Peter Sigray, Marc Lenoir, Mike van der Schaar, Emilia Lalander, and Michel André. 2017. "Offshore exposure experiments on cuttlefish indicate received sound pressure and particle motion levels associated with acoustic trauma." *Scientific Reports* 7 (1): 45899. <https://doi.org/10.1038/srep45899>.
- Southall, Brandon L., James J. Finneran, Colleen Reichmuth, Paul E. Nachtigall, Darlene R. Ketten, Ann E. Bowles, William T. Ellison, Douglas P. Nowacek, and Peter L. Tyack. 2019. "Marine mammal noise exposure criteria: Updated scientific recommendations for residual hearing effects." *Aquatic Mammals* 45 (2): 125-232.
- Steinberg, Deborah K., and Michael R. Landry. 2017. "Zooplankton and the Ocean Carbon Cycle." *Annual Review of Marine Science* 9 (1): 413-444. <https://doi.org/10.1146/annurev-marine-010814-015924>.
- Tande, Kurt S. 1991. "*Calanus* in North Norwegian fjords and in the Barents Sea." *Polar Research* 10 (2): 389-408. <https://doi.org/10.3402/polar.v10i2.6754>.
- Tang, Kam, and David Elliott. 2014. "Copepod carcasses: Occurrence, fate and ecological importance (authors' final version)."
- Tang, Kam W., Michail I. Gladyshev, Olgo P. Dubovskaya, Georgiy Kirillin, and Hans-Peter Grossart. 2014. "Zooplankton carcasses and non-predatory mortality in freshwater and inland sea environments." *Journal of Plankton Research* 36 (3): 597-612. <https://doi.org/10.1093/plankt/fbu014>.
- Thode, A. M., S. B. Blackwell, A. S. Conrad, K. H. Kim, T. Marques, L. Thomas, C. S. Oedekoven, D. Harris, and K. Bröker. 2020. "Roaring and repetition: How bowhead whales adjust their call density and source level (Lombard effect) in the presence of natural and seismic airgun survey noise." *J Acoust Soc Am* 147 (3): 2061. <https://doi.org/10.1121/10.0000935>.
- Tidau, Svenja, and Mark Briffa. 2019. "Anthropogenic noise pollution reverses grouping behaviour in hermit crabs." *Animal Behaviour* 151: 113-120.
- Titelman, Josefin, and Thomas Kiørboe. 2003a. "Motility of copepod nauplii and implications for food encounter." *Marine Ecology Progress Series* 247: 123-135. <https://doi.org/10.3354/meps247123>.
- . 2003b. "Predator avoidance by nauplii." *Marine Ecology Progress Series* 247: 137-149. <https://doi.org/10.3354/meps247137>.
- van Beest, Floris M., Jonas Teilmann, Line Hermannsen, Anders Galatius, Lonnie Mikkelsen, Signe Sveegaard, Jeppe Dalgaard Balle, Rune Dietz, and Jacob Nabe-Nielsen. 2018. "Fine-scale movement responses of free-ranging harbour porpoises to capture, tagging and

- short-term noise pulses from a single airgun." *Royal Society Open Science* 5 (1): 170110.
<https://doi.org/doi:10.1098/rsos.170110>.
- Varpe, Øystein, and Øyvind Fiksen. 2010. "Seasonal plankton–fish interactions: light regime, prey phenology, and herring foraging." *Ecology* 91 (2): 311-318.
<https://doi.org/https://doi.org/10.1890/08-1817.1>.
- Versluis, Michel, Barbara Schmitz, Anna von der Heydt, and Detlef Lohse. 2000. "How Snapping Shrimp Snap: Through Cavitating Bubbles." *Science* 289 (5487): 2114-2117.
<https://doi.org/doi:10.1126/science.289.5487.2114>.
- Visser, A. W., and S. H. Jónasdóttir. 1999. "Lipids, buoyancy and the seasonal vertical migration of *Calanus finmarchicus*." *Fisheries Oceanography* 8 (s1): 100-106.
<https://doi.org/https://doi.org/10.1046/j.1365-2419.1999.00001.x>.
- Visser, André W. 2007. "Motility of zooplankton: fitness, foraging and predation." *Journal of Plankton Research* 29 (5): 447-461. <https://doi.org/10.1093/plankt/fbm029>.
- Wale, Matthew, Robert Briers, and K. Diele. 2021. "Marine invertebrate anthropogenic noise research – Trends in methods and future directions." *Marine Pollution Bulletin* 173: 112958. <https://doi.org/10.1016/j.marpolbul.2021.112958>.
- Weatherby, Tina, and Petra Lenz. 2000. "Mechanoreceptors in calanoid copepods: Designed for high sensitivity." *Arthropod structure & development* 29: 275-88.
[https://doi.org/10.1016/S1467-8039\(01\)00011-1](https://doi.org/10.1016/S1467-8039(01)00011-1).
- Williams, R. , A. J. Wright, E. Ashe, L. K. Blight, R. Brintjes, R. Canessa, C. W. Clark, S. Cullis-Suzuki, D. T. Dakin, C. Erbe, P. S. Hammond, N. D. Merchant, P. D. O' Hara, J. Purser, A. N. Radford, S. D. Simpson, L. Thomas, and M. A. Wale. 2015. "Impacts of anthropogenic noise on marine life: Publication patterns, new discoveries, and future directions in research and management." *Ocean & Coastal Management* 115: 17-24.
<https://doi.org/https://doi.org/10.1016/j.ocecoaman.2015.05.021>.
- Wolf, S. J., V. S. Bebarta, C. J. Bonnett, P. T. Pons, and S. V. Cantrill. 2009. "Blast injuries." *Lancet* 374 (9687): 405-15. [https://doi.org/10.1016/s0140-6736\(09\)60257-9](https://doi.org/10.1016/s0140-6736(09)60257-9).
- Worm, Boris, Edward B. Barbier, Nicola Beaumont, J. Emmett Duffy, Carl Folke, Benjamin S. Halpern, Jeremy B. C. Jackson, Heike K. Lotze, Fiorenza Micheli, Stephen R. Palumbi, Enric Sala, Kimberley A. Selkoe, John J. Stachowicz, and Reg Watson. 2006. "Impacts of Biodiversity Loss on Ocean Ecosystem Services." *Science* 314 (5800): 787-790.
<https://doi.org/10.1126/science.1132294>.
- Yelverton, John T., Donald R. Richmond, William Hicks, H C Saunders, and E. Royce Fletcher. 1975. "The Relationship between Fish Size and Their Response to Underwater Blast."

- Yen, Jeannette, Petra H. Lenz, Donald V. Gassie, and Daniel K. Hartline. 1992. "Mechanoreception in marine copepods: electrophysiological studies on the first antennae." *Journal of Plankton Research* 14 (4): 495-512. <https://doi.org/10.1093/plankt/14.4.495>.
- Yen, Jeannette, and Akira Okubo. 2002. "Particle and prey detection by mechanoreceptive copepods: a mathematical analysis." *Hydrobiologia* 480 (1): 165-173. <https://doi.org/10.1023/A:1021249521259>.
- Zarubin, Margarita, Viviana Farstey, Anette Wold, Stig Falk-Petersen, and Amatzia Genin. 2014. "Intraspecific differences in lipid content of calanoid copepods across fine-scale depth ranges within the photic layer." *PloS one* 9 (3): e92935.
- Zarubin, Margarita, Yoav Lindemann, Otis Brunner, David M. Fields, Howard I. Browman, and Amatzia Genin. 2016. "The effect of hydrostatic pressure on grazing in three calanoid copepods." *Journal of Plankton Research* 38 (1): 131-138. <https://doi.org/10.1093/plankt/fbv110>.
- Aarflot, Johanna Myrseth, Hein Rune Skjoldal, Padmini Dalpadado, and Mette Skern-Mauritzen. 2017. "Contribution of *Calanus* species to the mesozooplankton biomass in the Barents Sea." *ICES Journal of Marine Science* 75 (7): 2342-2354. <https://doi.org/10.1093/icesjms/fsx221>.

I



Effects of Anthropogenic Noise on Marine Zooplankton

Emilie Hernes Vereide and Saskia Kühn

Contents

Introduction	2
Methods	3
Sound Exposure	5
Continuous Underwater Noise	7
Impulsive Underwater Noise	10
Study Animals and Developmental Stages	10
Continuous Underwater Noise	10
Impulsive Underwater Noise	13
Study Designs and Outcomes	14
Continuous Underwater Noise	14
Impulsive Underwater Noise	14
Discussion	14
Sound Exposures	14
Study Animals and Developmental Stages	16
Study Designs and Outcomes	18
Potential Population and Ecosystem Effects	19
Conclusions	20
References	20

Abstract

Anthropogenic underwater noise is increasing in the oceans, making the establishment of sound exposure criteria for marine taxa imperative for protecting and managing a good environmental status of the seas. Zooplankton play a key role in the marine carbon cycle and act as linkage between phytoplankton and higher trophic levels. Still, studies of the effects of underwater noise on zooplankton are

E. H. Vereide (✉)

Ecosystem Acoustics, Institute of Marine Research, Bergen, Norway
e-mail: emilie.hernes.veraide@hi.no

S. Kühn

Coastal Ecology, Research and Technology Centre West Coast, Kiel University, Kiel, Germany
e-mail: kuehn@ftz-west.uni-kiel.de

limited. This chapter reviewed 21 studies that found positive, negative, and no responses of marine holo- and meroplankton to continuous and impulsive underwater noise from experiments conducted in the laboratory, field, or both. The majority of the examined effects were related to development (28%), mortality (25%), and orientation and settlement (19%). Meroplankton (68%) were the most investigated zooplankton group. These studies indicated that both lethal and sublethal effects are stage- and species-specific. Variations were found in the implemented sound exposures, and a standardized manner in reporting sound levels is needed. Further studies combining laboratory and field experiments are required to establish sound exposure criteria for marine ecosystems, which can be used as international directives for underwater noise.

Keywords

Zooplankton · Noise pollution · Anthropogenic noise · Mortality · Behavior · Development · Impulsive noise · Continuous noise

Introduction

Anthropogenic underwater noise is an increasing source of environmental stress (Fritschi et al. 2011; Duarte et al. 2021). The goal of directives, such as the EU Marine Strategy Framework Directive (Directive 2008/56/EC 2008), is to monitor underwater noise and establish threshold values that do not adversely affect the marine environment. Typically, noise is divided into continuous and impulsive underwater noise, for which no threshold value has yet been integrated (Dekeling et al. 2020; Vasilakopoulos et al. 2022). Throughout the chapter, the term “sound exposure criteria” is used instead of “threshold values,” which is defined as “sound levels, based on acoustic response thresholds, above which sound levels may have adverse effects on specified animals” (Hawkins et al. 2020).

Continuous underwater noise can be described as a constant or slowly fluctuating sound pressure over a long time interval, which neither is instantaneous nor involves (typically) pulsed characteristics. Continuous underwater noise is a broad term for several different sound sources, such as boat traffic or turbine sound from offshore wind parks (Kinneging and Tougaard 2021), that increases ambient sound levels, particularly at low frequencies. The sound levels are determined by the number and size of the boats and turbines, whereas boat noise levels are further controlled by the speed of the vessel (Kaplan and Solomon 2016; Tougaard et al. 2020). In contrast, impulsive underwater noise is defined as an instantaneous change in sound pressure, often of high amplitude, e.g., from air guns used in seismic surveys and from pile driving. During seismic surveys, air guns emit impulsive sound primarily at low frequencies by rapidly releasing compressed air (Hovem and Tronstad 2012). Pile driving emits intense broadband impulsive sound that can propagate far through the water and ocean floor (Stenton et al. 2022). Much of what is known about the effects

of anthropogenic underwater noise, such as altered or disrupted communication, orientation, feeding, and antipredator behavior, comes from studies investigating marine mammals and fish (Popper and Hawkins 2016, 2018; Duarte et al. 2021). Less is known about marine invertebrates (Hawkins and Popper 2017; Murchy et al. 2019), such as zooplankton.

Zooplankton are an essential link between primary producers and higher trophic levels; hence their fitness and mortality directly affect the path and storage of organic carbon in the food web (Steinberg and Landry 2017). They comprise a large group of animals that drift in the pelagic zone, either entirely (holoplankton) or partly (meroplankton), throughout their life cycle. Zooplankton differ in morphological and functional traits, e.g., size (Lindeque et al. 2013; Deagle et al. 2018; Evans et al. 2020), energy content (Chen et al. 2019), and behavior (Kiørboe et al. 2010; Almeda et al. 2017). Therefore, various groups or species may be affected by external stressors, such as underwater sound, in different ways and degrees.

By interpreting the results and methods of previous studies investigating the effects of anthropogenic noise on zooplankton, this chapter summarizes the previous findings and highlights the knowledge gaps for future studies.

Methods

All studies included in this chapter were systematically selected by first creating an overview of marine zooplankton groups (Table 1). Note that ichthyoplankton, meroplankton consisting of fish eggs and larvae, were not included. This group contributes a relatively small proportion of plankton, and it is challenging to implement a systematic definition for different species at the transition stage of nekton. The second criterion used in the literature search was sound source. For continuous underwater noise, all low-frequency sound sources (independent of the sound exposure duration used in the studies) that were not impulsive by definition (see [Introduction](#)) were included in this chapter. Noise that did not originate from a real-life anthropogenic sound source found in the ocean was categorized as artificial low-frequency noise. For impulsive underwater noise, only two sound sources have been investigated for their effects on zooplankton: seismic air guns and pile driving.

Potential studies were searched using the phrase *noise effects on zooplankton*. The following terms were used for sources of noise: *underwater noise*, *low-frequency noise*, *continuous noise*, *boat/vessel/traffic noise*, *turbine noise*, *wind farm noise*, *air guns*, *seismic exploration*, *seismic surveys*, and *pile driving*. The groups listed in Table 1 were used to search for zooplankton species and (sub) phyla.

Three main types of information were extracted from the collected studies: (1) sound exposure, in which the sound sources and sound characteristics of various studies were presented, (2) study animals and developmental stages, and (3) study design and outcomes. For the latter, the outcomes of each study were categorized into lethal (mortality) and sublethal effects. The sublethal effects were further

Table 1 Overview of marine zooplankton groups (Animalia)

Kingdom	Holo-meroplankton	(Sub) phylum	Class or order
Animalia	Holoplankton	Cnidaria	Hydrozoa (also part of meroplankton)
			Myxozoa
			Cubozoa
			Scyphozoa*
		Ctenophora	Ctenophora
		Rotifera	Rotifera
		Platyhelminthes	Platyhelminthes
		Nematomorpha	Nectonema
		Mollusca	Heteropoda
			Pteropoda
		Crustacea	Cladocera
			Ostracoda
			Isopoda
			Copepoda*
			Mysidacea
			Amphipoda
			Euphausiacea
		Chaetognatha	Chaetognatha
		Chordata	Appendicularia
	Pyrosoma		
	Doliolida		
	Salpida		
	Meroplankton	Mollusca	Bivalvia*
			Gastropoda*
			Nudibranchia
			Cephalopoda
		Cnidaria	Anthozoa*
		Chordata	Ascidians*
		Crustacea	Thecostraca*
Malacostraca*			
Annelida		Polychaeta	
Nemertea		Nemertinea	
Bryozoa	Gymnolaemata*		
Echinozoa	Echinoidea*		

The zooplankton groups reported in the chapter are marked in bold and with an asterisk (*). The table is adapted from the *Census of Marine Zooplankton*. Retrieved 10.11.2022: http://www.cmarz.org/species_pages/phyla/phyla.htm

divided into physiology (including oxidative stress and gene expression), morphology (including injuries to cells), development, orientation or settlement, and behavior (including swimming, feeding, and antipredator behavior). The responses for each outcome were then categorized as either negative (e.g., increased mortality),

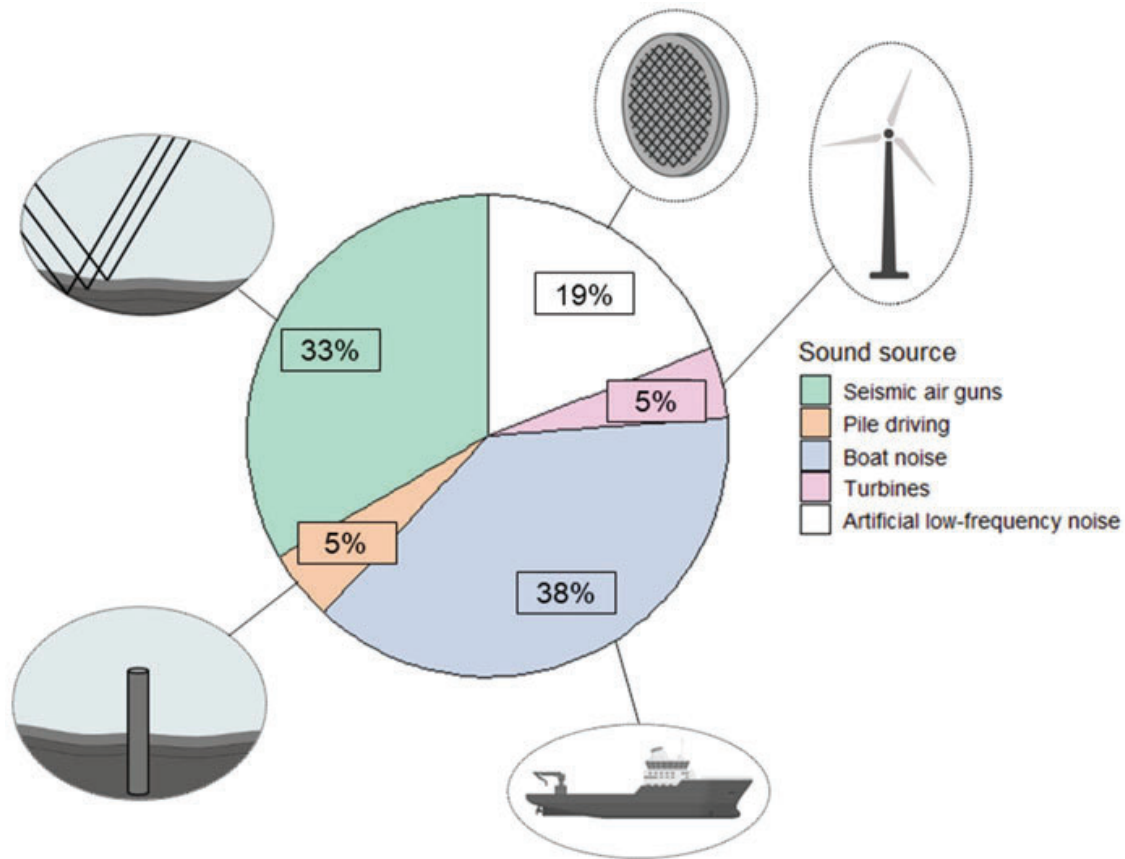


Fig. 1 Schematic overview of the proportion of studies covering the five main sources of sound exposure ($n_{\text{all studies}} = 21$): seismic air guns, pile driving, boat noise, turbines, and artificial low-frequency noise. The legend is read counterclockwise through the pie chart. (Icons by biorender.com)

other (e.g., different patterns in the settlement but not clearly negative), or none (no response observed). Note that potential positive effects were categorized as “other,” as it is with the present information not possible to determine whether, for example, increased settlement positively affects an individual or populations. All study animals were individually considered as either meroplankton or holoplankton. In addition, if a study presented several degrees of effects, for example, negative effects on mortality, but no effect on settlement, both outcomes were included. Therefore, the number (n) of each parameter differed among the graphical overviews (Figs. 1, 2 and 3).

Sound Exposure

Of all the studies ($n = 21$), 13 (62%) investigated the effects of continuous underwater noise, and 8 investigated (38%) the effects of impulsive underwater noise on zooplankton (Fig. 1, Table 2).

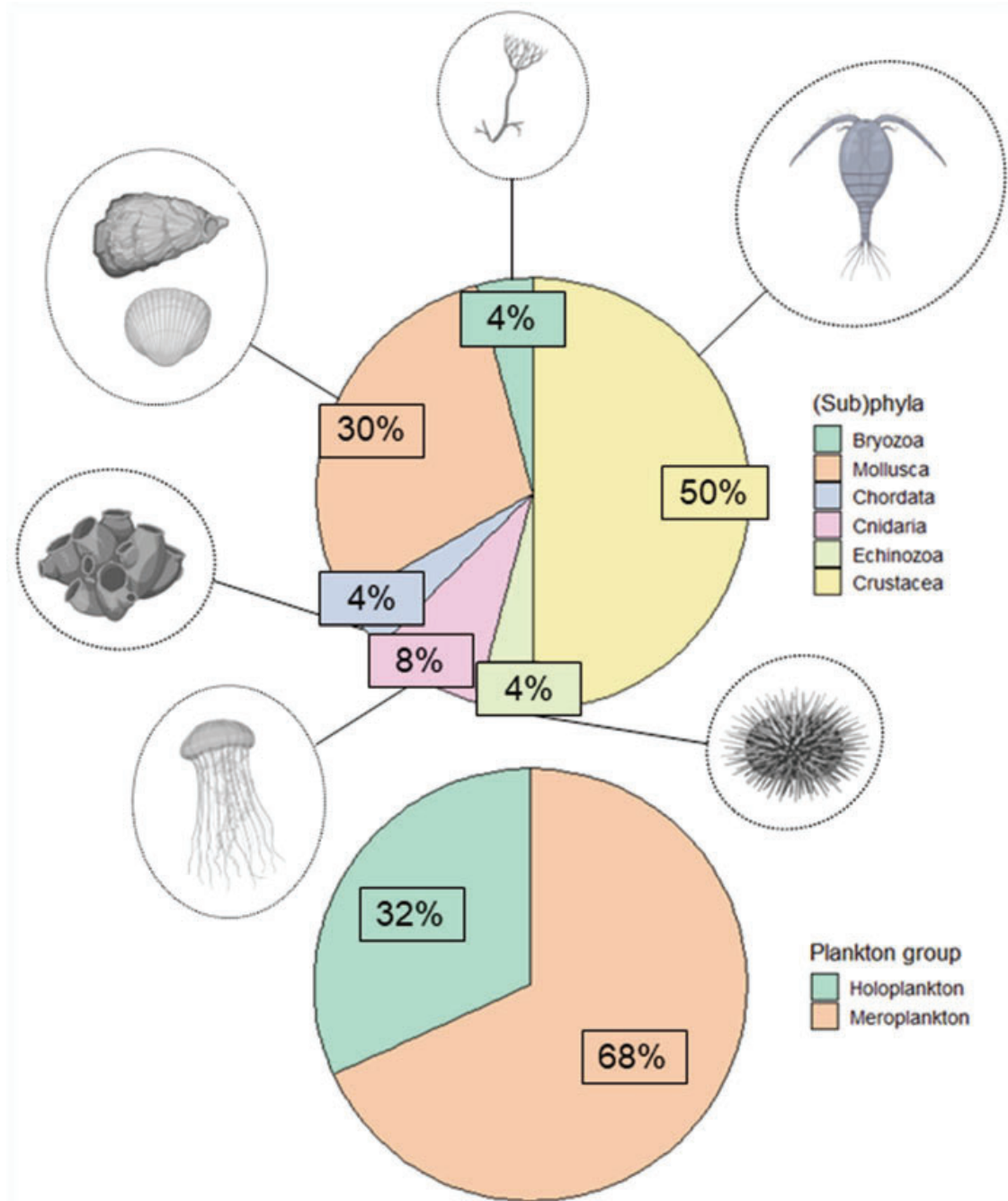


Fig. 2 Schematic overview of the proportion of different zooplankton groups. Upper panel, groups of subphylum or phylum covered in the studies ($n_{\text{total reported (sub)phylum}} = 24$): Bryozoa, Mollusca, Chordata, Cnidaria, Echinozoa, and Crustacea*; and lower panel, plankton group ($n_{\text{total reported plankton groups}} = 22$): holoplankton and meroplankton. Note that one study could include several sub(phyla) or plankton groups. The legends are read counterclockwise through the pie chart. *In McCauley et al. (2017), in situ zooplankton samples were investigated. However, as the majority consisted of copepods, the study animals are categorized as Crustacea. (Icons by [biorender.com](https://www.biorender.com))

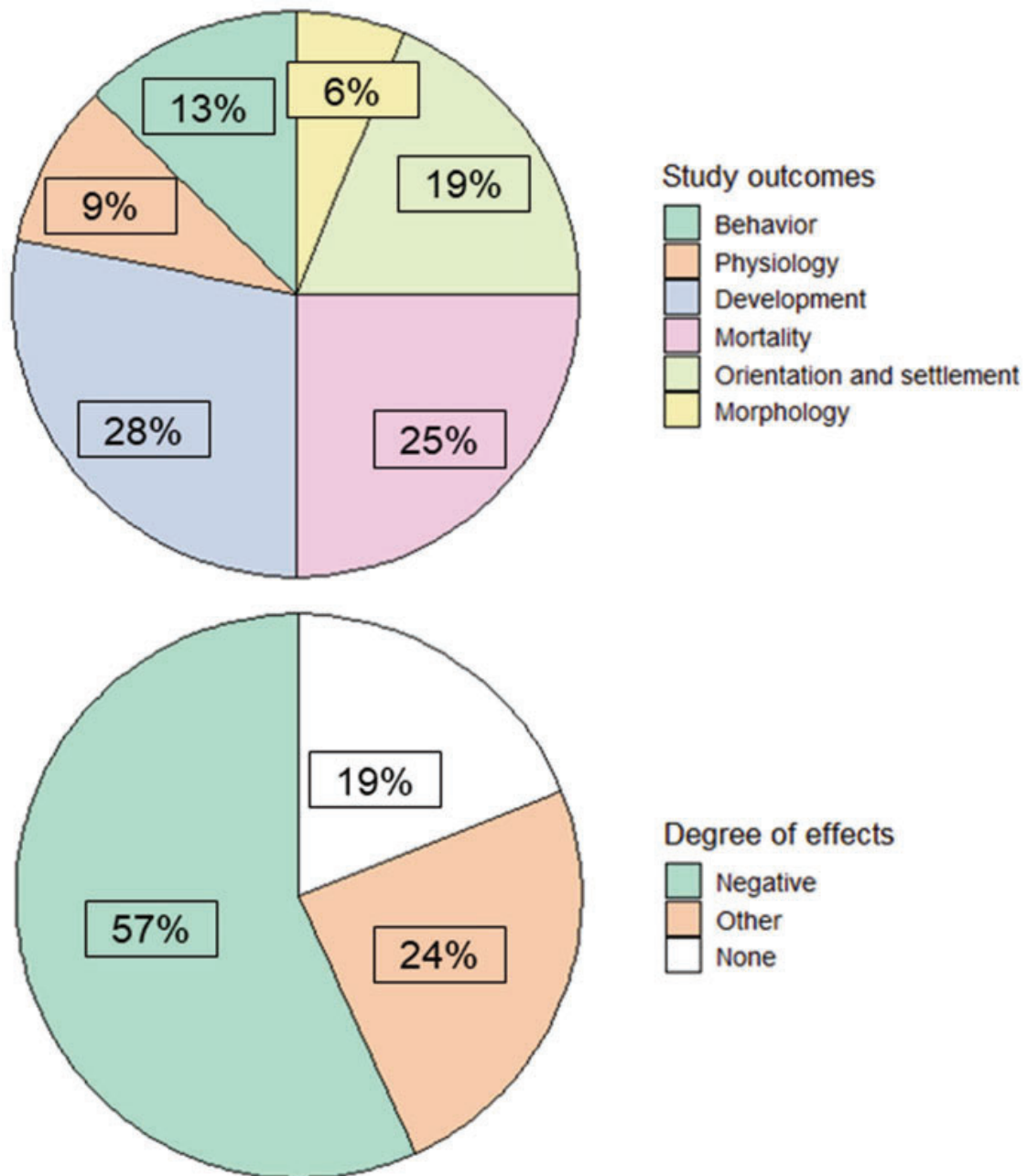


Fig. 3 Schematic overview of the proportion of different outcomes and the degree of effects observed in the studies. Upper panel, categories of study outcomes covered in the studies ($n_{\text{total reported study outcomes}} = 32$): behavior, physiology, development, mortality, orientation and settlement, and morphology; and lower panel, the degree of effect ($n_{\text{total reported effects}} = 37$): negative, other, and none. Note that one study could include study outcomes or report different effects. The legends are read counterclockwise through the pie chart

Continuous Underwater Noise

The effects of boat noise on zooplankton were examined using playback sound exposure in a laboratory tank or field (Table 3), whereas only McDonald et al. (2014) used real-life observations to confirm the results of the playback exposure.

Table 2 Overview of the sound exposures from reviewed studies. Information is given on the sound sources, sound levels, and exposure durations

Study	Sound source	Sound levels	Duration
Tremblay et al. (2019)	Artificial: Noise Egg (method, de Jong et al. 2017)	< 5000 Hz up to 20 dB (PSD) ↑ than ambient	9 days
Solé et al. (2021)	Artificial: Playbacks of discrete frequencies of 100–1000 Hz and discrete and combined frequencies of 350 and 500 Hz	160–195 dB (SEL) re 1 μPa^2	Few hours up to 2 weeks
Nedelec et al. (2014)	Boat noise: playback	110 dB (PSD) re 1 $\mu\text{Pa}^2 \text{Hz}^{-1}$; 80 dB re 1($\mu\text{m s}^{-2}$) ² Hz^{-1} at around 100 Hz 20 dB ↑ than ambient	12-h cycle for 5 days
Branscomb and Rittschof (1984)	Artificial: Discrete frequency playback at 15, 25, 30, 37, and 45 Hz	No information	20 h
McDonald et al. (2014)	Boat noise: playback	30–100 Hz 110–120 dB (RMS) re 1 $\mu\text{Pa Hz}^{-1}$; 128–141 dB re 1 μPa	Loop of 2-min sequences: up to 26 h
Stocks et al. (2012)	Boat noise: playback	100–300 Hz –30 dB re 1 $\mu\text{Pa}^2 \text{Hz}^{-1}$; 30–50 dB ↑ than control	5 min
Pine et al. (2012)	Wind turbine: playback Tidal turbine: playback	145 dB re 1 μPa ; 20 dB ↑ than mudflat sounds	Every 6 h checked, up more than 200 h
Jolivet et al. (2016)	Boat noise: playback	127 ± 3 dB re 1 μPa 100–1000 Hz; 20 dB ↑ than ambient	67 h
Wilkins et al. (2012)	Boat noise: playback	126 and 100 dB (RMS) re 1 μPa ; 60 dB and 40 dB ↑ than ambient	8–16 h
Sal Moyano et al. (2021)	Boat noise: playback	129.5 dB (SPL RMS) re 1 μPa ; 9 dB ↑ than ambient	5 min
Solé et al. (2016)	Artificial: playback of 50–400 Hz sinusoidal wave sweeps	157 ± 5 dB (not clear) re 1 μPa ; peak 175 dB (SPL) re 1 μPa	2 h
Lecchini et al. (2018)	Boat noise: playback	At 400 Hz and 900 Hz 90 dB (SPL) re 1 μPa ; >10 dB ↑ than controls	4-h playback track
Kühn et al. (2023)	Boat noise: playback	Peak at 130 Hz 150 dB (PSD) re 1 $\mu\text{Pa}^2 \text{Hz}^{-1}$; 174 dB PSD (RMS) re 1 $\mu\text{Pa}^2 \text{Hz}^{-1}$ one boat passing	24-h loop of a 20-min recording
McCauley et al. (2017)	Seismic air guns: 1 air gun (150 inches ³) (13.8 MPa)	SEL 156 (509–658 m) – 153 (1.1–1.2 km) dB re 1 $\mu\text{Pa}^2\text{s}$	App. 110 shots

(continued)

Table 2 (continued)

Study	Sound source	Sound levels	Duration
Fields et al. (2019)	Seismic air guns: 2 air guns*260 inches ³ (13–14.4 MPa)	SEL 221 dB re 1 $\mu\text{Pa}^2\text{s}$ (0 m), 183 dB re 1 $\mu\text{Pa}^2\text{s}$ (25 m)	Not given
Vereide et al. (2023)	Seismic air guns: 2 air guns*40 inches ³ (11 MPa)	SEL 180 (50 m), 166 (1100 m) dB re 1 $\mu\text{Pa}^2\text{s}$	2.5 h
Parry et al. (2002)	Seismic air guns: Air gun array (24) (total volume 3542 inches ³)	Max. source strength 211 dB/rel to 1 μPa at 1 m at frequency 50 Hz	Not given (but 2 km transect)
de Soto et al. (2013)	Seismic air guns: playbacks of an air gun array (6920 inches ³)	SEL from 161 to 165 dB re 1 $\mu\text{Pa}^2\text{s}$	24–90 h, 3 s intervals
Pearson et al. (1994)	Seismic air guns: Air gun array (7), total volume 840 inches ³	Max. (1 m) 230 dB re 1 μPa	10 s intervals
Day et al. (2016)	Seismic air guns: 1 air gun (3 setups): 45 inches ³ (2000 psi), 150 inches ³ (1300 psi), 150 inches ³ (2000 psi)	Max. SEL 186, 189, 190 dB re 1 $\mu\text{Pa}^2\text{s}$ (3 setups)	17.2–24.3 min, 11.6 s intervals
Stenton et al. (2022)	Pile driving: playback	170 dB _{pk-pk} re 1 μPa ; 82.7 \pm 3.4 – 84.6 \pm 2.6 dB _{pk} re 1 $\mu\text{m s}^{-2}$	5 days

Furthermore, all studies, except for Nedelec et al. (2014), conducted playback experiments in laboratory tank setups without additionally measuring particle motion. Note that Nedelec et al. (2014) conducted playback experiments in the field. These studies also differed in their control exposures, using silent or aquarium ambient sound controls (Stocks et al. 2012; Wilkens et al. 2012; McDonald et al. 2014; Jolivet et al. 2016; Kühn et al. 2023) or playback recordings from natural ambient soundscapes (Nedelec et al. 2014; Lecchini et al. 2018; Sal Moyano et al. 2021). The duration of the sound exposure ranged from 5 min to several days (Table 2). Lastly, the studies reporting spectral information on the original recordings measured similar sound pressure and particle motion levels for the playback exposures. However, sound levels varied between the studies due to different boat noise recording approaches and playback setups (Table 2).

Only one study examined the effect of turbine noise (Pine et al. 2012). Laboratory experiments were conducted to test the effects of tidal turbine noise (digital analog based on published spectra) and coastal wind turbine noise (playback) (Table 2). The maximum output sound exposure levels used in their experiments were 30 dB and 9 dB less than the published in situ sound levels from tidal and wind turbines, respectively.

Four studies used different approaches to generate artificial low-frequency noise: broadband noise, discrete frequencies, or specific combinations of frequencies (Table 2). Overall, the exposure sound levels, especially at low frequencies, were

well above the ambient sound levels in studies that provided information on the measured sound spectra.

Impulsive Underwater Noise

In seven studies that investigated the effects of air guns used in seismic surveys on zooplankton, variations were found in the number of air guns used, distance to the air guns, and exposure duration (Table 2). Therefore, the measured sound levels showed considerable differences between studies (Table 2). Furthermore, the studies differed in terms of exposing the animals to one or a series of shots (Table 2). One study used playback exposure from air guns (de Soto et al. 2013), while the rest conducted field experiments. Only one of these studies provided data on particle motion (de Soto et al. 2013).

Stenton et al. (2022) conducted two playback pile driving exposure experiments and reported the sound pressure and particle motion levels (Table 2). The measured playback sound levels resulted in a smaller proportion of sound at lower frequencies but increased at higher frequencies compared to the in situ pile driving recordings. The control playback consisted of ambient recordings made in the field, without anthropogenic sounds.

Study Animals and Developmental Stages

Of all the included studies, 7 investigated the effects on holoplankton, and 15 investigated the effects on meroplankton. Furthermore, 50% of all study species were crustaceans (Fig. 2 and Table 3). Additionally, the reported effects on zooplankton varied between negative (57%), other (24%), and none (19%) (Fig. 3 and Table 3).

Continuous Underwater Noise

Of the studies investigating the effects of continuous noise on zooplankton, 4 of the 21 species were holoplankton and the rest were meroplankton (Table 3).

Zooplankton Groups

Studies that focused on holoplankton ($n = 4$) examined the potential effects of noise on copepods and jellyfish. The physiology, morphology, and behavior of all copepods were negatively affected by noise (Table 3). Jellyfish were negatively affected by noise in their morphological structure (Table 3). Nine studies examined meroplankton (Table 3). In crustaceans, continuous noise had either negative or no effect on settlement or development (Table 3). Likewise, Cnidaria and Bryozoa were negatively affected by noise in settlement and swimming behavior, whereas Echinozoa species showed no behavioral response (Table 3). Other types of effects not categorized as negative were only found in studies that looked into sublethal

Table 3 Overview of the study animals and outcomes from reviewed studies

Study	Lab/ field	Holo/mero (plankton)	(Sub) phylum	Species	Stage	Outcomes	Effect
Tremblay et al. (2019)	L	Holo	Crustacea	<i>Acartia tonsa</i>	Preadult	Physiology Behavior	Increased stress None
Solé et al. (2021)	L, F	Holo	Crustacea	<i>Lepeophtheirus salmonis</i>	(pre-)Adult	Morphology	Injuries
Nedelec et al. (2014)	F	Mero	Mollusca	<i>Stylocheilus striatus</i>	Larvae Egg, embryo	Mortality Development	Increased Inhibited
Branscomb and Rittschof (1984)	L	Mero	Crustacea	<i>Balanus amphitrite</i>	Larvae	Orientation/settlement Development	Decreased Decreased
McDonald et al. (2014)	L, F	Mero	Chordata	<i>Ciona intestinalis</i>	Larvae	Orientation/settlement Development Mortality	Increased Increased Decreased
Stocks et al. (2012)	L	Mero	Mollusca Bryozoa Echinozoa	<i>Bembicium nanum</i> <i>Bugula neritina</i> <i>Helicoidaris erythrogramma</i>	Larvae	Behavior	Increased Decreased None
Pine et al. (2012)	L	Mero	Mollusca Crustacea	<i>Crassostrea gigas</i> <i>Austrohelice crassa</i> <i>Hemigrapsus crenulatus</i>	Larvae	Development	Increased Delayed Delayed
Jolivet et al. (2016)	L	Mero	Mollusca	<i>Mytilus edulis</i>	Larvae	Orientation/settlement	Increased
Wilkins et al. (2012)	L	Mero	Mollusca	<i>Perna canaliculus</i>	Larvae	Orientation/settlement	Increased
Sal Moyano et al. (2021)	L	Mero	Crustacea	<i>Cyrtograpsus angulatus</i> <i>Cyrtograpsus altimanus</i> <i>Neohelice granulata</i> <i>Leptuca uruguayensis</i>	Larvae	Orientation/settlement	None

(continued)

Table 3 (continued)

Study	Lab/ field	Holo/mero (plankton)	(Sub) phylum	Species	Stage	Outcomes	Effect
Solé et al. (2016)	L	Holo	Cnidaria	<i>Cotylorhiza tuberculata</i> <i>Rhizostoma pulmo</i>	Adult	Morphology	Injuries
Lecchini et al. (2018)	L	Mero	Cnidaria	<i>Pocillopora damicornis</i> <i>Acropora cytherea</i>	Larvae	Orientation/settlement	Disruption settlement
Kühn et al. (2023)	L	Holo	Crustacea	<i>Acartia tonsa</i>	(pre-)Adult	Behavior	Decreased
McCauley et al. (2017)	F	Holo Mero	Crustacea	Various, including Copepoda	Adult, larvae	Mortality	Increased
Fields et al. (2019)	F	Holo	Crustacea	<i>Calanus finmarchicus</i>	Adult	Mortality Behavior Physiology	Increased None None
Vereide et al. (2023)	F	Holo	Crustacea	<i>Acartia tonsa</i>	Larvae	Mortality Development	Increased Decreased
Parry et al. (2002)	F	Mero	Mollusca	Not given	Larvae	Mortality	None
de Soto et al. (2013)	L	Mero	Mollusca	<i>Pecten novaezelandiae</i>	Larvae	Development	Decreased
Pearson et al. (1994)	F	Mero	Crustacea	<i>Cancer magister</i>	Larvae	Mortality Development	None None
Day et al. (2016) ^a	F	Mero	Crustacea	<i>Jasus edwardsii</i>	Larvae	Development	None
Stenton et al. (2022)	L	Mero	Crustacea	<i>Nephrops norvegicus</i>	Larvae	Mortality Development Physiology	Increased Delayed Increased stress

Information is given on whether the experiments were conducted in the laboratory or the field, plankton group (holoplankton or meroplankton), (sub)phyla, study species, development stages, study outcomes, and the degree of effects

^aThe adult females were exposed, but the effects were measured in hatched larvae

outcomes in bivalves, chordates, and gastropods (Table 3). However, Nedelec et al. (2014) also found adverse effects of sound on the mortality and development of gastropods.

Development Stages

For the holoplankton groups, copepodite and adult copepod stages and the medusa stage in jellyfish (Scyphozoa) were used in the experiments (Table 3). Most meroplankton studies looked into the developmental stages before metamorphosis and larvae settlement. For example, two studies investigated the effects of continuous noise on Malacostraca species (Pine et al. 2012; Sal Moyano et al. 2021) and looked into the last larval stage before settlement, megalopa, considered as an intermediate stage between planktonic and benthic. Nedelec et al. (2014) investigated the mortality of veliger stages after hatching and the development of eggs or embryos of sea hares when exposed to boat noise. Lecchini et al. (2018) looked into the coral larval stage, planulae.

Impulsive Underwater Noise

Of the studies examining the effects of impulsive underwater noise, three out of eight looked at holoplankton, whereas more than half looked at the effects on meroplankton (Table 3).

Zooplankton Groups

Studies on holoplankton have focused primarily on copepods. Two studies solely investigated copepods, reporting adverse but limited effects on mortality after air gun exposure (Table 3). McCauley et al. (2017) looked at the effects of air guns on copepods but as a proportion of a natural zooplankton community from in situ samples. The authors reported severe effects on mortality after exposure.

All included meroplankton species (Table 3) were crustaceans or bivalves, but none of them investigated the same species. Furthermore, only two studies have reported adverse effects, one from air gun noise on scallop larvae and the second from pile driving on lobster larvae. Interestingly, both studies reporting negative effects exposed the animals to sound in the laboratory, whereas the other six exposed the animals to impulsive underwater sounds in the field.

Developmental Stages

Of the two studies examining the effects on copepods, one focused on adult stages and the other on naupliar stages (Table 3). In contrast, McCauley et al. (2017) tested the effects on in situ zooplankton samples and reported several species and stages in the same study. Regarding meroplankton, only the younger stages prior to the settlement of bivalves and crustaceans have been investigated.

Study Designs and Outcomes

The majority of studies examined sublethal effects: behavior (13%), physiology (9%), development (28%), orientation and settlement (19%), and morphology (6%) (Fig. 3). A number of the studies investigated several outcomes, e.g., combining development and settlement (Fig. 3, Table 3).

Continuous Underwater Noise

The exposure duration ranged from instant (5 min) to long time intervals (up to 8 days) when investigating sublethal outcomes. For meroplankton species, the focus was on orientation and settlement, development, and changes in swimming behavior (Tables 2 and 3). Two studies (McDonald et al. 2014; Nedelec et al. 2014) found additional lethal effects of long-term sound exposure (Table 3). For holoplankton, feeding behavior and physiological and morphological aspects, such as oxidative stress and cell injury, were investigated (Table 3). All outcomes were measured either during or directly after the end of the experimental sound exposure.

Impulsive Underwater Noise

Studies have covered different outcomes, from mortality to sublethal effects, such as behavior, gene expression, and development (Table 3). In addition, studies have focused on both short- and long-term effects, from immediate and long-term mortality to direct and long-term effects on physiology and development. For example, McCauley et al. (2017) examined the effects on mortality directly after air gun exposure, whereas Fields et al. (2019) investigated mortality additionally 1 week after exposure. Similarly, Vereide et al. (2023) measured mortality every day for 6 days after air gun exposure in copepod nauplii.

Discussion

Similarities, variations, and inconsistencies were found among existing studies on the effects of underwater noise on zooplankton, which are discussed in the following section. Additionally, general predictions are made regarding the potential effects of noise pollution on individual zooplankton and their subsequent effects on marine ecosystems.

Sound Exposures

All the presented studies on continuous underwater noise were conducted in a laboratory or field setup, where no studies used real-life in situ sound sources (except

for the additional field observations by McDonald et al. 2014). In general, responses in zooplankton were found during sound exposure from 10 dB above ambient sound levels, which is concerning because continuous noise through shipping led to more than 30 dB elevated sound levels, especially in coastal areas (Kinneking and Tougaard 2021; Farcas et al. 2020). In addition, Pine et al. (2012) observed adverse responses to sound levels well below the in situ measurements of offshore turbines. Thus, the reported effects of boat noise, wind, and tidal turbines can be observed in high traffic, fairways, and operational areas (Kinneking and Tougaard 2021). Furthermore, the use of artificial low-frequency noise (Table 2) may provide information on the general frequency and sound-level characteristics that affect marine organisms.

The comparability among studies is complicated for impulsive underwater noise owing to the different setups and difficulty of simulating impulsive sound in experimental tanks. Several studies have reported varying effects despite implementing similar sound levels but often with different exposure durations and distances from the study animals (Tables 2 and 3). The sound pressure level from air guns depends on the number of air guns (often consisting of 18–48 air guns distributed in subarrays), operating pressure, and total gun volume (NDP 2021). The volume of air guns used in real seismic surveys ranges from 20 to 800 inches³, which is within the range of air guns used in the included studies. On the other hand, yielding source levels have been calculated up to 260 dB rms re 1 μ Pa at 1 m output pressure, which is substantially higher than those reported in the included studies. In addition, the peak spectral levels for industry arrays are often in the 5–300 Hz range (Hildebrand 2009). Another important aspect of transferring reported results to a real-life setting is the natural movement and location of the zooplankton. Zooplankton move along with water currents and undergo diel vertical migration, which may affect the timing and duration of impulsive noise exposure. Therefore, although a real-life survey may cover 1000–3000 km² (Hovem and Tronstad 2012) and continuously shoot over weeks or months (Weilgart 2013), the animals will not be constantly exposed throughout that period. The duration of exposure in the reviewed studies lasted for a maximum of 3–4 days, which may even be considered too long to be transferred into a real-life setting, considering advection and migration. To transfer the results from field or laboratory studies to a natural environment, other potential factors that may alter the strength of noise exposure must be considered.

General Anthropogenic Underwater Noise

Anthropogenic noise from, e.g., boat traffic and seismic surveys potentially overlap as low frequencies can travel several thousand kilometers in deep waters. Boat noise is predominant in coastal areas, in shallow waters where low-frequency noise propagation is limited (Kinneking and Tougaard 2021; Farcas et al. 2020). An overall increase in commercial shipping can be expected in the future, in combination with larger ships and increased shipping distances across the oceans (Kaplan and Solomon 2016). As wind turbines are a constant noise source, the increased construction of wind parks (often several 100 turbines) will lead to locally increased ambient sound levels (Tougaard et al. 2020). A model by Siebert et al. (2014)

indicated that noise from air guns would be impulsive to intermittent up to 1000 km but may change beyond continuous underwater noise. The model shows that ambient sound levels can increase by 45 dB between 500 and 2000 km from the source, particularly at low frequencies. Hence, the long-distance effects of air gun shots on zooplankton could be comparable to those presented here for continuous underwater noise (see [Sound Exposure](#)). Furthermore, seismic surveys may occur for several months over large distances; therefore, the spectrum of impacts on zooplankton based on near-field experiments may underestimate the full range of effects.

An overall challenge when investigating the literature on continuous and impulsive anthropogenic underwater noise is that many studies present the received sound and exposure levels in different and limited formats. Reporting the information in a standard manner would facilitate the interpretation of the relationship between sound levels and the degree of effects in the study animals, which is urgently needed for the integration of sound exposure criteria.

Future studies would benefit from reporting (1) sound levels in standard formats, such as PSD for continuous underwater noise for comparisons among calibrated hydrophones and SEL for impulsive underwater noise. The amplitude of the PSD is normalized over the spectral resolution, which makes it independent of hydrophone sampling rates. Further, studies should report (2) distances, (3) durations, (4) ambient or controlled sound levels, and (5), if possible, particle motion. Particle motion can injure animals, mask sound cues, induce stress, or alter the behavior of marine organisms (Nedelec et al. 2021). In addition, particle motion levels in noise-related laboratory tank experiments are higher than those in in situ recordings or playback experiments in the field (see data by Nedelec et al. 2014, 2015). Hence, the true exposure perceived by zooplankton cannot be predicted from the measured sound pressure levels.

Study Animals and Developmental Stages

The degree to which marine animals are affected by anthropogenic noise is often species- and stage-specific. Furthermore, impacts may be linked to their perception of sound, physiology, and type of sound source used in the exposure.

Perception of Underwater Sound

Despite the increasing use and knowledge of anthropogenic sound in the oceans, understanding how invertebrates affect and detect sound is limited. In particular, sound perception in zooplankton needs to be fully understood (Hawkins and Popper 2017). In contrast to marine mammals and certain fish species, zooplankton are incapable of “hearing” and may be affected in other ways by underwater sound, e.g., through mechanoreception or cell injuries.

Crustaceans, such as copepods, use mechanoreceptive setae to detect predators, prey, and potential mates. Mechanoreception requires relative physical movement, which can be produced by the hydroacoustic motion of a receptor-activating structure involving a stretch-sensitive ion-channel molecule (Yen et al. 1992; Lenz and

Hartline 2014). By detecting hydrodynamic stimuli, several copepod species, such as *Lepeophtheirus salmonis* (Heuch and Karlsen 1997) or *Calanus finmarchicus* (Weatherby and Lenz 2000), detect and avoid prey and obstacles. Thus, anthropogenic noise can disrupt the fitness-relevant processes in crustaceans. For example, anthropogenic noise may mask the acoustical cues from a soundscape that could alter the settlement choice for suitable habitats (Branscomb and Rittschof 1984) or potentially mask the hydromechanical cues from a prey (Kühn et al. 2023). Noise can also distract the animals and alter physiological processes, such as increased stress (Tremblay et al. 2019, Stenton et al. 2022), or lead to cell injury (Solé et al. 2021). For example, fusion of sensory cells was found in the parasitic copepod species *L. salmonis* (Solé et al. 2021). Solé et al. (2021) hypothesized that such changes in an animal's sensory organs may impair the detection of a potential host.

Bivalves may also detect and react to sound (Stocks et al. 2012; Wilkens et al. 2012; Jolivet et al. 2016). However, the underlying mechanisms are not yet well understood. For example, Eggleston et al. (2015) found an increased settlement rate in oyster larvae (*Crassostrea virginica*) during sound exposure compared to silent conditions, whereas clam (*Mercenaria mercenaria*) larvae showed no differences. Because bivalves lack gas-filled spaces, they are most likely unaffected by pressure changes (de Soto et al. 2013). However, studies have suggested specialized organs and statocysts as mechanisms that make them perceptible to sound particle motion (Hubert et al. 2022).

Other mollusks, such as gastropods, may also be capable of detecting sound via their statocysts. For example, Nedelec et al. (2014) hypothesized three mechanisms by which noise affects the development and survival of sea hares. First, the development might have been affected by tissue damage owing to strong molecular vibrations from boat noise, where a potentially similar mechanism was found by Solé et al. (2016, 2021). Second, the survival of sea hare veligers may have decreased due to barotrauma. Finally, they suggested that sea hares might suffer from stress when exposed to noise.

Jellyfish possess hair cell structures that respond to mechanical displacements (mechanoreceptors) from, e.g., vibrations and sound pressure waves (Solé et al. 2016). How noise causes cell damage in the two Cnidaria species is unknown. Solé et al. (2016) hypothesized that noise propagation vibrations could directly trigger the mechanical displacement of external sensory cells. Like jellyfish, other Cnidaria species, such as coral planulae, can detect sounds through cilia. Therefore, coral planulae can distinguish between soundscape habitats and boat noise, which may lead to the avoidance or masking of the signal needed from a suitable habitat (Lecchini et al. 2018).

In summary, the effects of anthropogenic noise may be either detection-dependent (mechanoreception) or detection-independent. First, if zooplankton detect noise with their sensory organs, it could increase stress, distract the animal, or mask acoustic signals from their surroundings. Second, strong vibrations from noise can cause morphological damage independent of their detection. However, knowledge still needs to be completed, and for many invertebrates, it remains to be seen if and how they detect sound (Stocks et al. 2012).

Differences in Morphological Characteristics and Developmental Stages

The morphological differences between zooplankton groups may indicate that certain species are affected by one component of underwater sound, such as particle motion (Nedelec et al. 2016; Popper and Hawkins 2018), whereas others may be more affected by other components. For example, adult copepods, with a robust external layer and internal lipid sack of different densities than the surrounding water, may be affected by pressure changes from air guns. Similarly, de Soto et al. (2013) suggested that damage observed in scallop larvae after air gun exposure, because of their small size and absence of strong tissue density gradients, is more related to particle motion rather than pressure changes. These morphological differences may also explain the variation in the results of studies examining different zooplankton groups. For continuous underwater noise, contradictory results, namely, no response versus adverse effects, have been found in behavioral experiments in copepods (Tremblay et al. 2019, Kühn et al. 2023), whereas physiology and morphology were negatively affected in all investigated holoplankton groups (Solé et al. 2016, 2021; Tremblay et al. 2019). Contradicting results were also found in studies investigating the effects of impulsive noise (Table 3), although only two studies found negative effects on meroplankton, in contrast to the holoplankton studies that observed adverse effects in all studies (Table 3). Overall, the responses to the sound exposures were highly species-specific for holo- and meroplankton, but crustaceans seemed to be most often negatively affected. The sensitivity of crustaceans to sound may be due to their highly sensitive mechanoreception, as described above, and the reaction thresholds are stage-dependent (Fields and Yen 1997). In addition, only one study focused solely on the juvenile stages of holoplankton (Table 3). Regarding the importance of nauplii and their role in ecosystems, more knowledge is needed regarding earlier plankton stages. In general, the majority of studies focused on meroplankton in order to study benthic organisms (Table 3). Regarding the importance of zooplankton as a functional group, more studies focusing on holoplankton and their different developmental stages are needed.

Study Designs and Outcomes

Continuous underwater noise can alter the sublethal processes and mortality after only a few hours of exposure (Tables 2 and 3). Note that the reported swimming activity and orientation effects were seen after 5 min of sound exposure (Stocks et al. 2012, Sal Moyano et al. 2021). Hence, continuous underwater noise alters behavioral responses to short-term exposure; however, there is no information about long-term behavioral responses in relation to physiological responses. More than half of the impulsive underwater noise studies either focused primarily on or included mortality but also on development and physiology. In general, there is an increasing trend in the combination of areas of biology and outcomes (Wale et al. 2021). This was also reflected in Wale et al. (2021), who examined the trends in methods and future directions of studies investigating the effects of anthropogenic noise on

marine invertebrates and reported that 39% of the studies in the same period covered a combination of biological outcomes. Combining investigations into physiological, morphological, and behavioral outcomes in noise research will facilitate unraveling the underlying mechanisms of noise impacts in different species.

Another important aspect to investigate is the effect of the experimental arena by comparing anthropogenic underwater noise studies done in the laboratory with studies done in the field. Several studies (e.g., Day et al. 2016) have previously highlighted this issue, which is highly relevant when translating possible effects into real-life effects. First, the studies included in this chapter presented and discussed contrasting laboratory and field results. For example, de Soto et al. (2013) conducted experiments in small tanks in the laboratory using air gun playbacks and reported negative effects on development in lobster larvae. However, Day et al. (2016) suggest that the long wavelengths produced by accurate sound sources, such as an air gun, cannot be emulated in a small tank. Also, the sound reflected from the surfaces in small tanks might result in an unrealistic picture and relationship between the sound pressure and particle motion of the sound (Parvulescu 1964, 1967; Rogers et al. 2015, Nedelec et al. 2016). Second, laboratory and field studies provide different possibilities regarding study design and outcomes. For example, when using a laboratory approach, the mechanisms behind potential damage to zooplankton can be easier isolated than out in the field. Furthermore, one can potentially exclude other impacts by keeping the study animals in a controlled environment. For example, when conducting field experiments, one needs to consider background mortality from, e.g., boat propellers or other physical disturbances, which are easier to control in the laboratory. In addition, a controlled environment is relevant when looking into long-term vs. immediate effects, as long-term effects may be challenging to detect in the field in a natural environment – but are highly relevant. For example, short-time experiments may miss the impact of potential habituation, as found in blue mussels' reduced responsiveness over several sound exposures (Hubert et al. 2022), and possible population effects.

Potential Population and Ecosystem Effects

Based on the results of this chapter, any response of zooplankton to underwater noise can affect ecosystem functioning. For example, when zooplankton species are affected by noise, any positive or negative outcomes on mortality, physiology, or fitness-relevant behavior could lead to increased or decreased species abundance. In turn, these changes in abundance could lead to modifications in grazing and predation pressure on phytoplankton and other zooplankton groups (Lynam et al. 2017). As noise can alter fitness-relevant behavior at the individual level, it may also affect the strength and direction of intra- and interspecies interactions (Lagardère 1982; Schwarz and Greer 1984; McCauley et al. 2003). Therefore, a potential outcome in a system with low resilience may shift the phytoplankton and zooplankton abundance and community structure. Furthermore, higher trophic levels may be affected by an increase or decrease in energy transfer from lower levels. On the other hand,

zooplankton, especially copepods, are important for deep-sea carbon storage by fast-sinking fecal pellets (Shatova et al. 2012; Turner 2015). Hence, a change in abundance may increase or decrease the rate of this process.

Conclusions

Underwater noise affects zooplankton, which is either detection-independent or detection-dependent. For the latter, interpreting the noise exposure in terms of particle motion is important, and a standardized manner of reporting sound levels is needed. However, several studies have reported no effects of underwater noise, indicating that the effects vary among sound sources, strength, and zooplankton groups. In order to understand how noise affects zooplankton and potentially establish sound exposure criteria, the interplay of the effects of noise on physiology, morphology, and behavior must be investigated simultaneously in different developmental stages. Information on the differences between short- and long-term exposure effects and potential habituation to various sound sources is largely missing. Further studies combining laboratory and field experiments are needed to predict future outcomes in the real world and, hence, the effect of noise on ecosystem functioning.

Acknowledgments This work was supported by the Research and Technology Centre West Coast, Kiel University (DE), and the project ZoopSeis (#302675), funded by the Research Council of Norway. The authors would like to thank the Aquatic Noise Committee 2022 for a successful, insightful, and social conference, where early career researchers were not just able but encouraged to take the stage. We would also like to thank Karen de Jong, Katja Heubel, and Anne Christine Utne Palm for their resourceful advice and support.

References

- Almeda R, van Someren Gréve H, Kjørboe T (2017) Behavior is a major determinant of predation risk in zooplankton. *Ecosphere* 8(2):e01668. <https://doi.org/10.1002/ecs2.1668>
- Branscomb ES, Rittschof D (1984) An investigation of low frequency sound waves as a means of inhibiting barnacle settlement. *J Exp Mar Biol Ecol* 79(2):149–154. [https://doi.org/10.1016/0022-0981\(84\)90215-6](https://doi.org/10.1016/0022-0981(84)90215-6)
- Chen C-T, Bănarău D, Carlotti F, Faucheux M, Harmelin-Vivien M (2019) Seasonal variation in biochemical and energy content of size-fractionated zooplankton in the bay of Marseille (North-Western Mediterranean Sea). *J Mar Syst* 199:103223. <https://doi.org/10.1016/j.jmarsys.2019.103223>
- Day RD, McCauley RD, Fitzgibbon QP, Semmens JM (2016) Seismic air gun exposure during early-stage embryonic development does not negatively affect spiny lobster *Jasus edwardsii* larvae (Decapoda: Palinuridae). *Sci Rep* 6:22723. <https://doi.org/10.1038/srep22723>
- de Jong K, Schulte G, Heubel KU (2017) The noise egg: a cheap and simple device to produce low-frequency underwater noise for laboratory and field experiments. *Methods Ecol Evol* 8(2): 268–274. <https://doi.org/10.1111/2041-210x.12653>

- de Soto NA, Delorme N, Atkins J, Howard S, Williams J, Johnson M (2013) Anthropogenic noise causes body malformations and delays development in marine larvae. *Sci Rep* 3:2831. <https://doi.org/10.1038/srep02831>
- Deagle BE, Clarke LJ, Kitchener JA, Polanowski AM, Davidson AT (2018) Genetic monitoring of open ocean biodiversity: an evaluation of DNA metabarcoding for processing continuous plankton recorder samples. *Mol Ecol Resour* 18(3):391–406
- Dekeling RPA, Ainslie MA, Anderson M, Borsani JF, Le Courtois F, Hedgeland D, Kinneking NA, Leaper R, Liebschner A, Merchant ND, Prospathopoulos A, Sanchez M, Sigray P, Taroudakis M, Tasker ML, Tougaard J, Weilgart L, Ferreira M (2020) Towards threshold values for underwater noise-Common methodology for assessment of impulsive noise. *TG Noise Technical Advice report DL.1*, pp 47–47
- Directive 2008/56/EC (2008) Establishing a framework for community action in the field of marine environmental policy (Marine strategy framework directive). Official Journal of the European Union
- Duarte CM, Chapuis L, Collin SP, Costa DP, Devassy RP, Eguiluz VM, Erbe C, Gordon TAC, Halpern BS, Harding HR, Havlik MN, Meekan M, Merchant ND, Miksis-Olds JL, Parsons M, Predragovic M, Radford AN, Radford CA, Simpson SD, Slabbekoorn H, Staaterman E, Opzeeland ICV, Winderen J, Zhang X, Juanes F (2021) The soundscape of the Anthropocene Ocean. *Science* 371(6529):eaba4658. <https://doi.org/10.1126/science.aba4658>
- Eggleston D, Lillis A, Bohnenstiehl D (2015) Soundscapes and larval settlement: larval bivalve responses to habitat-associated underwater sounds. *Adv Exp Med Biol* 875:255–263. https://doi.org/10.1007/978-1-4939-2981-8_30
- Evans LE, Hirst AG, Kratina P, Beaugrand G (2020) Temperature-mediated changes in zooplankton body size: large scale temporal and spatial analysis. *Ecography* 43(4):581–590. <https://doi.org/10.1111/ecog.04631>
- Farcas A, Powell CF, Brookes KL, Merchant ND (2020) Validated shipping noise maps of the Northeast Atlantic. *Sci Total Environ* 735:139509–139509. <https://doi.org/10.1016/j.scitotenv.2020.139509>
- Fields DM, Yen J (1997) The escape behavior of marine copepods in response to a quantifiable fluid mechanical disturbance. *J Plankton Res* 19(9):1289–1304. <https://doi.org/10.1093/plankt/19.9.1289>
- Fields DM, Handegard NO, Dalen J, Eichner C, Malde K, Karlsen Ø, Skiftesvik AB, Durif CMF, Browman HI, Ratilal P (2019) Airgun blasts used in marine seismic surveys have limited effects on mortality, and no sublethal effects on behaviour or gene expression, in the copepod *Calanus finmarchicus*. *ICES J Mar Sci* 76(7):2033–2044. <https://doi.org/10.1093/icesjms/fsz126>
- Fritschi L, Brown A, Kim R, Schwela D, Kephelopoulos S, and (eds) (2011) Burden of disease from environmental noise: quantification of healthy life years lost in Europe. WHO Regional Office for Europe, Copenhagen
- Hawkins AD, Popper AN (2017) A sound approach to assessing the impact of underwater noise on marine fishes and invertebrates. *ICES J Mar Sci* 74(3):635–651. <https://doi.org/10.1093/ICESJMS/FSW205>
- Hawkins AD, Johnson C, Popper AN (2020) How to set sound exposure criteria for fishes. *J Acoust Soc Am* 147(3):1762–1762. <https://doi.org/10.1121/10.0000907>
- Heuch PA, Karlsen E (1997) Detection of infrasonic water oscillations by copepodids of *Lepeophtheirus salmonis* (Copepoda Caligida). *J Plankton Res* 19(6):735–747. <https://doi.org/10.1093/plankt/19.6.735>
- Hildebrand JA (2009) Anthropogenic and natural sources of ambient noise in the ocean. *Mar Ecol Prog Ser* 395:5–20. <https://doi.org/10.3354/meps08353>
- Hovem JM, Tronstad TV (2012) Propagation of anthropogenic noise in the ocean. In: 35th Scandinavian symposium on physical acoustics. Geilo, Norway
- Hubert J, Booms E, Witbaard R, Slabbekoorn H (2022) Responsiveness and habituation to repeated sound exposures and pulse trains in blue mussels. *J Exp Mar Biol Ecol* 547:151668. <https://doi.org/10.1016/j.jembe.2021.151668>

- Jolivet A, Tremblay R, Olivier F, Gervaise C, Sonier R, Genard B, Chauvaud L (2016) Validation of trophic and anthropic underwater noise as settlement trigger in blue mussels. *Sci Rep* 6(1): 33829–33829. <https://doi.org/10.1038/srep33829>
- Kaplan MB, Solomon S (2016) A coming boom in commercial shipping? The potential for rapid growth of noise from commercial ships by 2030. *Mar Policy* 73:119–121. <https://doi.org/10.1016/j.marpol.2016.07.024>
- Kinneging NA, Tougaard J (2021) “Assessment North Sea”, report of the EU INTERREG joint monitoring programme for ambient noise North Sea (Jomopans), February 2021
- Kjørboe T, Jiang H, Colin SP (2010) Danger of zooplankton feeding: the fluid signal generated by ambush-feeding copepods. *Proc R Soc B Biol Sci* 277(1698):3229–3237
- Kühn S, King F, Heubel K (2023) Decreased feeding rates of the copepod *Acartia tonsa* when exposed to playback harbor traffic noise. *Front Mar Sci* 10:624. <https://doi.org/10.3389/fmars.2023.1134792>
- Lagardère JP (1982) Effects of noise on growth and reproduction of *Crangon crangon* in rearing tanks. *Mar Biol* 71(2):177–185
- Lecchini D, Bertucci F, Gache C, Khalife A, Besson M, Roux N, Berthe C, Singh S, Parmentier E, Nugues MM, Brooker RM, Dixon DL, Hédouin L (2018) Boat noise prevents soundscape-based habitat selection by coral planulae. *Sci Rep* 8(1):9283–9283. <https://doi.org/10.1038/s41598-018-27674-w>
- Lenz PH, Hartline DK (2014) Mechanoreception in crustaceans of the pelagic realm. In: Derby C, Thiel M (eds) *Nervous systems and control of behavior*. Oxford University Press, pp 293–320
- Lindeque PK, Parry HE, Harmer RA, Somerfield PJ, Atkinson A (2013) Next generation sequencing reveals the hidden diversity of zooplankton assemblages. *PLoS One* 8(11):e81327. <https://doi.org/10.1371/journal.pone.0081327>
- Lynam CP, Llope M, Möllmann C, Helaouët P, Bayliss-Brown GA, Stenseth NC (2017) Interaction between top-down and bottom-up control in marine food webs. *Proc Natl Acad Sci* 114(8): 1952–1957. <https://doi.org/10.1073/pnas.1621037114>
- McCauley RD, Fewtrell J, Popper AN (2003) High intensity anthropogenic sound damages fish ears. *J Acoust Soc Am* 113(1):638–642. <https://doi.org/10.1121/1.1527962>
- McCauley RD, Day RD, Swadlow KM, Fitzgibbon QP, Watson RA, Semmens JM (2017) Widely used marine seismic survey air gun operations negatively impact zooplankton. *Nat Ecol Evol* 1(7):195. <https://doi.org/10.1038/s41559-017-0195>
- McDonald JI, Wilkens SL, Stanley JA, Jeffs AG (2014) Vessel generator noise as a settlement cue for marine biofouling species. *Biofouling* 30(6):741–749. <https://doi.org/10.1080/08927014.2014.919630>
- Murphy KA, Davies H, Shafer H (2019) Impacts of noise on the behavior and physiology of marine invertebrates: a meta-analysis. *Proc Meet Acoust* 37:40002. <https://doi.org/10.1121/2.0001217>
- NDP (2021) In: Norwegian Petroleum Directorate (ed) *Seismic*. Norwegian Petroleum Directory
- Nedelec SL, Radford AN, Simpson SD, Nedelec B, Lecchini D, Mills SC (2014) Anthropogenic noise playback impairs embryonic development and increases mortality in a marine invertebrate. *Sci Rep* 4(1):5891–5891. <https://doi.org/10.1038/srep05891>
- Nedelec SL, Simpson SD, Morley EL, Nedelec B, Radford AN (2015) Impacts of regular and random noise on the behaviour, growth and development of larval Atlantic cod (*Gadus morhua*). *Proc Biol Sci* 282(1817):20151943. <https://doi.org/10.1098/rspb.2015.1943>
- Nedelec SL, Campbell J, Radford AN, Simpson SD, Merchant ND (2016) Particle motion: the missing link in underwater acoustic ecology. *Methods Ecol Evol* 7(7):836–842. <https://doi.org/10.1111/2041-210X.12544>
- Nedelec SL, Ainslie MA, Andersson MH, Cheong SH, Halvorsen MB, Linné M, Martin B, Nöjd A, Robinson S, Simpson SD, Wang L, Ward J (2021) Best practice guide for underwater particle motion measurement for biological applications. Technical report by the University of Exeter for the IOGP Marine Sound and Life Joint Industry Programme

- Parry GD, Heislens S, Werner GF, Asplin MD, Gason A (2002) Assessment of environmental effects of seismic testing on scallop fisheries in Bass Strait. Marine and Freshwater Resources Institute
- Parvulescu A (1964) Problems of propagation and processing. In: Tavalga WN (ed) *Marine bio-acoustics*. Pergamon Press, Oxford, pp 87–100
- Parvulescu A (1967) The acoustics of small tanks. In: Tavalga WN (ed) *Marine bio-acoustics*, 2nd edn. Pergamon Press, Oxford, pp 7–13
- Pearson WH, Skalski JR, Sulkin SD, Malme CI (1994) Effects of seismic energy releases on the survival and development of Zoeal-larvae of Dungeness-crab (*Cancer-Magister*). Mar Environ Res 38(2):93–113. [https://doi.org/10.1016/0141-1136\(94\)90003-5](https://doi.org/10.1016/0141-1136(94)90003-5)
- Pine MK, Jeffs AG, Radford CA (2012) Turbine sound may influence the metamorphosis behaviour of estuarine crab Megalopae. PLoS One 7(12):1–8. <https://doi.org/10.1371/journal.pone.0051790>
- Popper AN, Hawkins A (2016) *The effects of noise on aquatic life II*. Springer, New York
- Popper AN, Hawkins AD (2018) The importance of particle motion to fishes and invertebrates. J Acoust Soc Am 143(1):470–488. <https://doi.org/10.1121/1.5021594>
- Rogers P, Hawkins A, Popper A, Fay R, Gray M (2015) Parvulescu revisited: small tank acoustics for bioacousticians. Adv Exp Med Biol 875:933–941. https://doi.org/10.1007/978-1-4939-2981-8_115
- Sal Moyano M, Ceraulo M, Hidalgo F, Luppi T, Nuñez J, Radford CA, Mazzola S, Gavio M, Buscaino G (2021) Effect of biological and anthropogenic sound on the orientation behavior of four species of brachyuran crabs. Mar Ecol Prog Ser 669. <https://doi.org/10.3354/meps13739>
- Schwarz AL, Greer GL (1984) Responses of Pacific herring, *Clupea harengus pallasi*, to some underwater sounds. Can J Fish Aquat Sci 41(8):1183–1192
- Shatova O, Koweeck D, Conte MH, Weber JC (2012) Contribution of zooplankton fecal pellets to deep ocean particle flux in the Sargasso Sea assessed using quantitative image analysis. J Plankton Res 34(10):905–921. <https://doi.org/10.1093/plankt/fbs053>
- Siebert U, Dähne M, Danehl S, Meyer-Klaeden O, Van Neer A (2014) Assessment of potential for masking in marine mammals of the Antarctic exposed to underwater sound from airguns. Umweltbundesamt, Texte | 16/2014
- Solé M, Lenoir M, Fontuño JM, Durfort M, van der Schaar M, André M (2016) Evidence of cnidarians sensitivity to sound after exposure to low frequency noise underwater sources. Sci Rep 6(1):37979–37979. <https://doi.org/10.1038/srep37979>
- Solé M, Lenoir M, Alos J, De Vreese S, Schaar M, André M (2021) Sea lice are sensitive to low frequency sounds. J Mar Sci Eng 9:765–765. <https://doi.org/10.3390/jmse9070765>
- Steinberg DK, Landry MR (2017) Zooplankton and the ocean carbon cycle. Annu Rev Mar Sci 9(1):413–444. <https://doi.org/10.1146/annurev-marine-010814-015924>
- Stenton CA, Bolger EL, Michenot M, Dodd JA, Wale MA, Briers RA, Hartl MGJ, Diele K (2022) Effects of pile driving sound playbacks and cadmium co-exposure on the early life stage development of the Norway lobster, *Nephrops norvegicus*. Mar Pollut Bull 179: 113667–113667. <https://doi.org/10.1016/j.marpolbul.2022.113667>
- Stocks J, Broad A, Radford C, Minchinton TE, Davis A (2012) Response of marine invertebrate larvae to natural and anthropogenic sound: a pilot study. Open Mar Biol J 6:57–61. <https://doi.org/10.2174/1874450801206010057>
- Tougaard J, Hermannsen L, Madsen PT (2020) How loud is the underwater noise from operating offshore wind turbines? J Acoust Soc Am 148(5):2885–2885. <https://doi.org/10.1121/10.0002453>
- Tremblay N, Leiva L, Beermann J, Meunier C, Boersma M (2019) Effects of low-frequency noise and temperature on copepod and amphipod performance. Proc Meet Acoust 37(1):040005. <https://doi.org/10.1121/2.0001275>
- Turner JT (2015) Zooplankton fecal pellets, marine snow, phytodetritus and the ocean's biological pump. Prog Oceanogr 130:205–248. <https://doi.org/10.1016/j.pocan.2014.08.005>

- Vasilakopoulos P, Palialexis A, Boschetti ST, Cardoso A, Druon J-N, Konrad C, Kotta M, Magliozzi C, Palma M, Piroddi C, Ruiz-Orejón L, Salas Herrero F, Stips A, Tornero V, Hanke G (2022) Marine strategy framework directive. In: Thresholds for MSFD criteria: state of play and next steps. Technical report by the Joint Research Centre (JRC)
- Vereide EH, Mihaljevic M, Browman HI, Fields DM, Agersted MD, Titelman J, de Jong K (2023) Effects of airgun discharges used in seismic surveys on development and mortality in nauplii of the copepod *Acartia tonsa*. *Environ Pollut* 327:121469. <https://doi.org/10.1016/j.envpol.2023.121469>
- Wale M, Briers R, Diele K (2021) Marine invertebrate anthropogenic noise research – trends in methods and future directions. *Mar Pollut Bull* 173:112958. <https://doi.org/10.1016/j.marpolbul.2021.112958>
- Weatherby T, Lenz P (2000) Mechanoreceptors in calanoid copepods: designed for high sensitivity. *Arthropod Struct Dev* 29:275–288. [https://doi.org/10.1016/s1467-8039\(01\)00011-1](https://doi.org/10.1016/s1467-8039(01)00011-1)
- Weilgart L (2013) A review of the impacts of seismic Airgun surveys on marine life. In: CBD expert workshop on underwater noise and its impacts on marine and coastal biodiversity, 25–27 February 2014, London, UK
- Wilkens S, Stanley J, Jeffs A (2012) Induction of settlement in mussel *Perna canaliculus* larvae by vessel noise. *Biofouling* 28:65–72. <https://doi.org/10.1080/08927014.2011.651717>
- Yen J, Lenz PH, Gassie DV, Hartline DK (1992) Mechanoreception in marine copepods: electrophysiological studies on the first antennae. *J Plankton Res* 14(4):495–512. <https://doi.org/10.1093/plankt/14.4.495>

II

Article

Effects of Sound from Seismic Surveys on Fish Reproduction, the Management Case from Norway

Lise Doksæter Sivle ^{1,*}, Emilie Hernes Vereide ¹, Karen de Jong ¹ , Tonje Nesse Forland ¹, John Dalen ² and Henning Wehde ¹

- ¹ Ecosystem Acoustics Department, Institute of Marine Research, Postboks 1870 Nordnes, NO-5817 Bergen, Norway; emilie.hernes.vereide@hi.no (E.H.V.); karen.de.jong@hi.no (K.d.J.); tonje.nesse.forland@hi.no (T.N.F.); henningsw@hi.no (H.W.)
² SoundMare, Helleveien 243, NO-5039 Bergen, Norway; johndal@broadpark.no
* Correspondence: lisedo@hi.no

Abstract: Anthropogenic noise has been recognized as a source of concern since the beginning of the 1940s and is receiving increasingly more attention. While international focus has been on the effects of noise on marine mammals, Norway has managed seismic surveys based on the potential impact on fish stocks and fisheries since the late 1980s. Norway is, therefore, one of very few countries that took fish into account at this early stage. Until 1996, spawning grounds and spawning migration, as well as areas with drifting eggs and larvae were recommended as closed for seismic surveys. Later results showed that the effects of seismic surveys on early fish development stages were negligible at the population level, resulting in the opening of areas with drifting eggs and larvae for seismic surveys. Spawning grounds, as well as concentrated migration towards these, are still closed to seismic surveys, but the refinement of areas and periods have improved over the years. Since 2018, marine mammals have been included in the advice to management. The Norwegian case provides a clear example of evidence-based management. Here, we examine how scientific advancements informed the development of Norwegian management and how management questions were incorporated into new research projects in Norway.

Keywords: management; fish; anthropogenic sound; seismic surveys; electromagnetic surveys



Citation: Sivle, L.D.; Vereide, E.H.; de Jong, K.; Forland, T.N.; Dalen, J.; Wehde, H. Effects of Sound from Seismic Surveys on Fish Reproduction, the Management Case from Norway. *J. Mar. Sci. Eng.* **2021**, *9*, 436. <https://doi.org/10.3390/jmse9040436>

Academic Editor: Giuseppa Buscaino

Received: 26 March 2021

Accepted: 14 April 2021

Published: 17 April 2021

Publisher's Note: MDPI stays neutral with regard to jurisdictional claims in published maps and institutional affiliations.



Copyright: © 2021 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (<https://creativecommons.org/licenses/by/4.0/>).

1. Introduction

Anthropogenic noise pollution is considered an important pollutant of terrestrial and aquatic ecosystems [1–3]. There are few records of systematic underwater anthropogenic noise measurements prior to 1990, but they show that ambient noise levels have increased by as much as 12 dB in 30 years in some parts of the ocean [4–6]. Impulsive anthropogenic sound is currently the subject of monitoring within the frame of the regional agreements such as OSPAR. Maximum sound exposure levels have been proposed for marine mammals and fish based on physical damage [7]. However, the masking of acoustic information from the environment may affect animals at a much lower sound level, and, thus, further away from the source. Most of the energy of anthropogenic caused sound lies in the lower frequency ranges [8]. This may affect a wide range of animals. For example, all fish can hear low-frequency sounds (<500 Hz) and can, consequently, be disturbed by man-made sound activities [7,9].

Noise disturbance can affect the physical integrity (at very high levels), the physiology, and the behavior of aquatic animals. This may affect individual fitness and could, ultimately, lead to population and ecosystem-level consequences [10–12]. The effects of noise on aquatic life have been reviewed extensively (e.g., [7,8,11–19]). These reviews highlight the absence of observational evidence of population-level impacts. Experimental data often show short-term damage or behavioral changes in individual animals only, while

numerical models are needed to provide information on whether such changes can lead to population-level effects.

In Norway, the first research on the effects of sound generated by seismic sources has been developed in response to concerns from fishermen that fish may be scared away from fishing grounds. Fishing, a key industry in Norway, has been influenced by oil and gas exploration activities as the two industries operate in much of the same areas. Thus, there have been demands for balanced coexistence between fisheries and the oil industry since the start of the oil era in the 1970s, to ensure the acceptable development of both industries [20]. Therefore, protecting core habitats and fishing grounds of commercially important fish stocks with reproductive success from exposure to seismic surveys is an important element within this balance and is of major importance for the management of seismic surveys in Norway.

Reproduction is vital to population sustainability but can be very sensitive to stress and changes in environmental conditions [21]. Even if yearly variations in spawning stocks are not necessarily correlated to recruitment, long-term reduction in egg production is expected to lead to a mean decrease in the population [22]. In addition, spawning is the most clearly quantifiable investment in a specific mating and, as such, directly related to fitness. Moreover, for many fish species, the spawning period may be highly sensitive to impacts from noise, if individuals gather in dense, localized spawning aggregations [23]. Disturbances in the spawning period may thus affect a larger fraction of the population than disturbances during other periods. Additionally, fish may be vulnerable to external stressors during spawning [24], because fish are often in their poorest body condition in this period [25,26].

In this study, we review how management advice has been given through a period of about 30 years and how improved scientific knowledge has transferred into scientific advice. There was an additional focus on how external drivers have induced scientific questions and how weakly documented knowledge-based advice has exposed the need for more research to obtain better and more scientifically based advice. This process is shown in Figure 1.

Year	Outer factor	Scientific question	Investigation	Advice	Reasoning
1985	Sci. exp. indicate sound to scare fish. ^{27,28,29}			Plankton: Protect areas of egg/larvae Adult fish: Protect spawning areas Marine mammals: No restrictions	Precaution. Protect areas with sensitive life stages for commercial fish species.
1990	Incident with dead cod in fish farm after refraction seismic. Public worry.	Do seismic shooting cause death/injury on egg/larvae?	Exposure exp. document death. Different ranges. ^{30,31,32}	Protect areas of egg/larvae Protect spawning areas No restrictions	Prevent damage/mortality to avoid affecting recruitment of commercial fish species
		Do seismic shooting cause death/injury on adult fish?	Exposure exp. document no mortality, some injury close to air gun. ^{33,34,35}		
1995	Claims that fishery reduced during/after seismic	Can fish/larva move away before injured?	Model show adult fish can swim away, larvae cannot. ³⁶	No restrictions Protect spawning areas No restrictions	No need to protect egg/larvae concentrations when naturally mortality is higher. Spawning protected as precautionary.
		Can injuries from seismic survey affect recruitment?	Model show mortality from seismic survey is neglectable. ³⁷		
		Does seismic change behaviour of fish?	Lowered catches and fish move away from shooting area. ^{38,39,40}		
2010	Should electromagnetic surveys (EMU) be managed similar as seismic?	Where and when do fish spawn?	Back calculating from eggs to spawning date inform models estimating more precise spawning area/periods. ^{41,42}	No restrictions Protect important spawning areas, migration + bufferzone No restrictions	Prevent fish to move away from concentrated spawning areas/periods.
		How do EMU affect fish behaviour?	Literature review indicate EMU may disturb migration patterns. ⁴³		
2015	Why no regulations on whales?	Can seismic give hearing injury or change behaviour for whales?	Literature review indicate hearing damage at close range and potentially disturb feeding behaviour for baleen whales. ⁴⁴	No restrictions Protect important spawning areas, migration + bufferzone Protect baleen whale feeding areas.	Prevent fish to move away from spawning areas. Prevent feeding disturbance for baleen whales.
2020	Contradicting results on how and at what zooplankton are affected by seismic. ^{45,46}	Does spawning fish really avoid seismic sound?	Exposure exp. in field and net pens to investigate effects on spawning. Results pending.	Need for restrictions for zooplankton? Loosen or keep the spawning restrictions? Protect baleen whale feeding areas.	Planktonic and adult fish advice should be based on updated scientific knowledge.
		Does seismic kill zooplankton?	Exposure exp. in lab, field and through modelling to understand the mechanisms of physical injuries.		

Figure 1. Overview of how management advice has changed since the beginning of the advisory practice in the late 1980s. The “Outer factor” column covers drivers from outside the scientific community that may induce new scientific questions and lead to research activity. The “Scientific question” column lists the research questions being raised to improve management advice, which may arise from outer factors or from existing research that raises new questions. The “Scientific investigation” column briefly describes the main findings from research projects. The “Advice” column summarizes the management advice from IMR to the Norwegian Petroleum Directorate and is divided into different advice given for three specific groups of animals; plankton (small organisms with very little or no self-movement, including egg, fry, larvae, and zooplankton), adult fish, and marine mammals. The “Reasoning” column describes the rationale for the particular advice given. Timeline is indicative and not to scale. The numbers in the bottom corner refer to publications given in the reference list; [27–46].

2. The Norwegian Story—A Journey through the History of Management Advice

Since the beginning of oil exploration in the 1960s, seismic surveys applying different sound sources have been carried out within the Norwegian Exclusive Economic Zone (NEZ) to locate and estimate oil and gas resources. To reach an optimal basis for development it has been a goal for the Norwegian Government to have a good coexistence between the traditionally existing fishing industry and the newly established oil industry. The Norwegian Petroleum Directorate (NPD) issues licenses for seismic surveys in Norwegian waters, but several stakeholders within governmental organizations have been asked for advice since 1983. The Institute of Marine Research (IMR) is asked for advice on the potential impact on biology and ecosystems, while the Directorate of Fisheries is asked for advice on the likely impact and potential conflicts with ongoing fishery activities. In the beginning, the advice from IMR was mainly based on a precautionary approach; preventing potential impact on presumed sensitive habitats. Therefore, spawning areas and areas with spawning migration, as well as areas with drifting eggs and larvae in the periods of the respective migration, spawning, and drifting, were recommended to be closed for seismic surveys to avoid impact on these volatile ecosystem compounds.

Recommendations from IMR on the regulation of seismic activity have always been given in the form of geographical and temporal restrictions to avoid seismic exposure of sensitive habitats, i.e., specifically to protect fish engaged in susceptible activities such as

spawning and concentrated spawning migrations. The NPD and the seismic operator are not obliged to follow the advice given, and, until the late 1990s, the NPD oversaw these recommendations to some extent, but due to frequent contact and communication over the years, the advice given today is almost always followed.

In July 1989, one particular incident brought attention to how sound from seismic surveys could potentially affect fish; in a fish farm in Northern Norway, high mortality of cod was observed after explosives for refractational seismic investigations were detonated nearby [47]. This raised the question of how seismic exposures could potentially cause damage in wild fish. In order to clarify these issues, several research projects were initiated in the early 1990s. The main concern was that seismic blasting could cause injury and even death in fish.

2.1. The Early 1990s: Physical Injuries and Death

Knutsen and Dalen [30] previously analyzed mortality and damage to fish eggs, larvae, and small juveniles of cod (*Gadus morhua*) after exposure to seismic airguns, describing that some of the larger larvae developed problems with their balance, but returned to normal swimming after few minutes and, overall, there were no significant differences in injuries and death between the control and exposed groups. A larger project was initiated that investigated the effects of airguns on fish eggs, larvae, and juveniles of cod, saithe (*Pollachius virens*), turbot (*Scophthalmus maximus*), plaice (*Pleuronectes platessa*), and herring (*Clupea harengus*) [32]. Despite some differences between species, results showed significantly increased mortality rates in exposed groups, but only rather close to the air guns; up to 1.35 m for eggs, 0.9–3 m yolk sac larval stage, 2–5 m for larval stage, up to 1.5 m for post-larval stages, and up to 1.3 m for the fry stages. Different sublethal effects, e.g., injuries to neuromats and swimbladder, and changes in behavior due to buoyancy were observed for some species and life stages. The studies concluded that the highest mortality rate was observed about 1.4 m from the airgun, with potential minor damages up to 5 m away from the airgun [32]. These Norwegian studies were in line with similar international studies at the time, documenting lethal and sublethal effects at distances equal or closer than 3 m from the airguns on fish egg and larvae [48,49].

These results thus showed that fish at early life stages could experience both indirect and direct mortality, but only at rather close range within a few meters of the air guns. To propose realistic scenarios for impacts from a seismic survey, results from these experiments, together with fish biology and physiology knowledge, the vertical distributions of larvae, and the sound intensity output from the seismic source were included in a modeling study. The results from this study demonstrated that adult fish would be able to swim away from the spatial zone of potential injuries, while the smallest larvae and fry would not, as they would suffer from total exhaustion, and, therefore, would not be able to escape from the zone of injury [36,50].

In summary, these studies show that some injuries, including lethal ones, may occur, but at ranges less than 5 m from the air gun. However, in a management context, the most interesting issue is whether these effects can translate into the negative development of the stock or stock recruitment. Sætre and Ona [37], therefore, used these results to assess the potential total mortality rate on fish larvae from a regular 3D seismic survey. Assuming a lethal radius of 2 m from the air guns, the mortality rate for cod larvae was 0.45%—in a worst-case scenario, and 0.3‰ in a more realistic scenario, compared to a natural daily mortality rate of 5–15%. Therefore, they concluded that the mortality due to 3D seismic surveying is negligible compared to the natural mortality in the larval stage.

The conclusion was, therefore, that mortality can occur at the earliest life stages of fish, but only at very close range, and that the risk that such mortality negatively affects recruitment to the fishable stock is close to non-existent. Therefore, the recommendations were updated to allow seismic surveys in areas and periods with drifting eggs and larvae [47]. This meant that larger areas of the NEZ became available for seismic surveys for a larger

part of the year. The restrictions for spawning areas and areas with spawning migration, however, were kept as before.

2.2. The Later 1990s: Reduced Catches and Behavioral Response

Based on the above documentation, it seemed clear that physical injuries occurred only in the nearest few meters of the air gun and mostly affected early-stage larvae. However, fishermen claimed reduced catches at much further distances from operating seismic vessels than could be explained by the injured fish close to the air guns. This could only be explained if the fish heard and responded to the sound of the seismic shooting.

Fish hearing was intensively studied in the 1960s, showing that fish hear well, with the highest sensitivity below 1 kHz (e.g., [51–53]). Fish were also shown to be able to discriminate the direction of sounds (e.g., [54–57]). Fish can, therefore, hear seismic noise and determine the direction of its source [28,58,59]. In 1969, Chapman and Hawkins reported that shoals of whiting (*Merlangius merlangus*) dive deeper and form more compact schools in response to seismic air gun shots. Later in the 1980s, Dalen and Raknes (1985) found fish distribution, mainly saithe (*Gadus virens* L.), cod, and haddock (*Melanorammus aeglefinus* L.) recorded by echosounder and echo integrator to be reduced by 36%, and for blue whiting (*Micromesistius poutassou*) by 54% after the previously compared seismic blasting. Similar results were demonstrated for rockfish [58].

Reduced catches in areas of seismic investigations were, therefore, assumed to be associated with the fish either avoiding the shooting area, or descending closer to the bottom and thus becoming less catchable. Several research projects were initiated in the early 1990s, with the purpose of documenting whether catches were actually reduced, as well as trying to understand the underlying mechanisms. Holand et al. [38] conducted a controlled experiment with cod swimming freely in a bay, and cod enclosed in a net pen. They observed startle responses at the onset of the air gun, as well as that the largest fish stopped feeding during exposures. While free-swimming fish did not react with an increased heartbeat frequency, the enclosed fish increased their heartbeat after repeated exposure. Løkkeborg and Soldal [39] analyzed catch records from logbooks of longliners and trawlers operating in areas of ongoing seismic surveys, documenting that the lowest catch rates were closest to the seismic survey area and then that the catch rates increased with increasing distance from the seismic survey. These findings were, together with [31], used to design a full-scale fishery experiment in the Barents Sea, using trawl, longline, and acoustic quantity determination within and outside set distances from a seismic shooting area of 3×10 nautical miles. Both trawl and longline catches of cod and haddock were considerably reduced up to at least 18 nautical miles from the seismic blasting area [40]. The reduction was largest in the center of the area, with gradually decreased impact towards the outer edges of the area. Acoustic quantity determination showed that the decline in catch rates was caused by a reduction in spatial fish density in the area. These studies all point in the same direction; seismic exposure appears to disturb the fish, and responses may be in the form of avoidance of the exposed area and/or cessation of foraging. Repeated exposure of enclosed fish, which are thus unavailable to avoid exposure, can cause increased heartbeat frequency, indicative of an increase in stress level.

These results have had great importance for management advice. Before this, spawning areas of commercial fish were recommended to be closed to seismic surveys mainly on a precautionary basis. Now, scientific results support this advice. Many of the offshore fish populations are distributed over a large area most of the year, but gather within specific, smaller defined areas during spawning. These areas are not random, but may have specific characteristics, such as bottom type for the bottom spawners (e.g., herring and capelin (*Mallotus villosus*)), and are localized so that the spawned eggs will drift with current to favorable areas with the available food supply of specific zooplankton. The same holds for the temporal component; the spawning period usually occurs so that the fish eggs will hatch during the zooplankton spring bloom, ensuring food abundance. The scientific studies as described above show that seismic may cause fish to swim away from an area of

seismic exposure, and that such avoidance may be in the order of more than 18 nmi [40]. If similar avoidance occurs when fish are at the spawning grounds, they may move too far away from these optimal geographical and oceanographical conditions, or if they delay or even stop their spawning, the spawning may be less successful with regards to time and physical conditions. From 1996, therefore, scientifically based advice was given that seismic surveys should avoid spawning areas during the spawning period. Additionally, based on the result that several fish species moved away for a distance of at least 18 nmi from the blasting area, an additional 20 nmi buffer zone around spawning grounds was recommended to be closed for 3D seismic surveys [40,60,61].

2.3. Into a New Millennium with New Studies Drawing a More Complex Picture

Into the new millennium, behavioral responses continued to be the main topic of interest and scientific focus. Until now, scientific results had shown a clear trend that fish avoided areas of seismic exposure. However, as we shall exemplify here, more research does not always draw a clearer picture.

Sometimes seismic surveys are conducted in areas and periods of potentially large ecosystem consequences. This was the case for a survey in the Norwegian Sea in April 1999 overlapping with an area of a high density of migrating pelagic fish, mainly post-spawned herring migrating out from the spawning areas at the coast. Therefore, the advice from IMR was to postpone the survey. When this was not possible, IMR agreed to monitor the fish density in the shooting area to make sure the density did not exceed a predetermined limit, otherwise, the seismic survey had to be stopped. This monitoring created the opportunity to study the abundance and vertical movement of pelagic fish before, during and after a seismic survey. Results showed that schools of blue whiting (*Micromesistius poutassou*) move deeper during exposure but found no horizontal or vertical response of herring [62]. Furthermore, in 2009, NPD planned a 3D seismic exploration in Vesterålen, an area normally closed to commercial seismic activity due to its status as a highly important ecosystem. In order to evaluate the potential negative impact on fish and fisheries, several studies were initiated. Løkkeborg et al. [63] summarize the findings from acoustic mapping with echo sounders and gillnet and longline catches before, during, and after the seismic survey, documenting that most fish species did not leave the area, but rather changed their onsite behavior; increased catches in gillnets are likely caused by increased swimming behavior, while reduced longline catches indicate less feeding motivation. Another study showed that schools of young herring in the area did not respond to the seismic blasting with changes in swimming direction, speed, or vertical position in the water column [64].

Conflicts between seismic activity and fishing have occurred now and then and have at times become quite harsh. This has also occasionally initiated research to clarify whether there is any scientific basis for such claims. In Norway, a sandeel (*Ammodytes marinus*) fishery in the North Sea, close to several oil and gas fields, is such an example. Fishermen claimed to have reduced catches and explained this with the sound from seismic surveys causing sandeel to migrate away, or to bury themselves in the sand during seismic exposure. Video of caged sandeel during seismic exposure did reveal some alarm responses to the sound, but no burrowing into the sand [65]. Similar claims have also been posed for mackerel (*Scomber scombrus*), initiating a study where mackerel were kept in net pens and exposed to a small, approaching air gun, with gradually increasing sound exposure. Neither of these studies showed any particular reaction in terms of diving, startling, or increased swimming speed in mackerel [66]. Similar conflicts have been reported elsewhere in the world; scientific studies on seismic exposure in a redfish (*Sebastes* sp.) fishery in California revealed that fish elicit alarm responses [59] and reduced longline catches [67]. However, it should be noted that studies were conducted with caged fish, which may influence the observed behavior, as well as inhibit larger-scale movements such as flight or avoidance, although this depends on the size and design of the enclosure [18,68].

These studies, as well as other studies conducted in other countries (e.g., [69–71]), show that a behavioral response is not always present, and, by nature, will vary in characteristic and strength. Some studies showed that the fish did not move away, while other studies showed that the fish left the area of exposure. Hence, responses may depend both on the species and the context. Throughout the first 10–15 years of the millennium, new knowledge was evaluated as it emerged to improve management recommendations. Despite the variable nature of how fish respond behaviorally during exposure to sound from seismic surveys, there was still a core knowledge-based conviction that fish could abandon their spawning sites if exposed to seismic blasting, so the advice to protect these areas and periods was not changed.

2.4. The 2010s: Towards Better Basis for Exclusion Zones (Refining Spawning Maps)

To effectively protect spawning areas, good knowledge of the actual spawning areas and periods of those species is crucial. An extensive report describing the spawning habitats and periods with drifting eggs and larvae from historic and recent data acquisition was published in 1991 [72]. These data were used to pinpoint areas and periods where seismic surveys should be avoided. Spawning areas are, however, dynamic habitats and change over time with changes in environmental variables, such as temperature (e.g., [73]). To better ensure that the recommendations reflect the actual spawning habitats, as well as to give more precise estimates of the relative importance of different spawning areas and periods, two projects were initiated to improve existing information on spawning areas and periods for the Norwegian and Barents Sea [41] and the North Sea [42]. These reports also took into account both historic and new knowledge from spawning surveys, as well as data from scientific surveys. Furthermore, data from fisheries on sampled egg and fish larvae were back-calculated to their spawning position using drift models. The results of these studies produced updated spawning maps, and, importantly, pinpointed those areas where the most significant and concentrated spawning occurred in time and space. For many species, restriction areas could be narrowed down to those most concentrated areas, without jeopardizing the links to recruitment. In addition to the species of greatest commercial importance that until now had been included in the advice, these projects also provided data to map spawning areas of other fish species. New questions, therefore, arose concerning which species to include in the advice in addition to those already included. Based on the evaluation of ecological importance, stock condition, and data basis, several species of less commercial importance, such as Greenland halibut (*Reinhardtius hippoglossoides*) and golden redfish (*Sebastes norvegicus*) were also included in the recommendations given from around 2015.

2.5. 2015 Onwards; New Technical Achievements Require New Advice

Another emerging trend since the 2000s was the use of electromagnetic (EM) surveys to more precisely locate and verify oil and gas deposits in the seabed. With this technique, electric and magnetic fields are generated within the water column. Several species of marine animals use electric and/or magnetic fields for orientation, migration, and prey or predator detection [74–76] thus with the potential of disturbing that behavior. During the first years of EM surveys, the recommendations from IMR for such surveys were the same as for a seismic survey, and the same areas were restricted, only without a buffer zone. This was, however, a highly questionable practice, as was pointed out by both the industry and the scientific community. A literature study was initiated and the results indicated that the main EM disturbances to fish species are likely to occur during their navigation during migration [43]. In accordance with the general goal of the recommendations: to prevent recruitment failure, the migration towards spawning grounds was considered to be most important to protect. From 2019, recommendations for EM surveys were to avoid known spawning migration routes during the migration periods.

Further studies on how the EM field induced by these surveys affect orientation and behavior of early-stage fish are currently (spring 2021) ongoing and the results thereof will be implemented within the advice as they emerge.

2.6. The Late 2010s: Inclusion of Marine Mammals

While Norway may have been very early to include fish in management advice, recommendations with respect to marine mammals have largely been lacking, and in contrast to most other countries, no restrictions were made to protect this group from potential effects from seismic blasting. The question of whether to include marine mammals in management advice has been regularly raised, e.g., by environmental organizations, the scientific community, and the general public. A challenge with including marine mammals in management advice is that Norwegian waters have many species, which are distributed over large areas, and that data on distribution, and, in particular, data on the relative importance of different habitats, is largely lacking. In response to the increasing amount of seismic activity in the Barents Sea, the demand for better management of seismic activity in these important mammal habitats increased [77]. From 2018, a new regulation made ramp-up procedures prior to seismic blasting mandatory by law to protect marine mammals from hearing injuries. In this respect, IMR also saw the need for marine mammals to be included in their recommendations. In the absence of specific studies on the impact of seismic exposure on mammals in Norway, the evaluation of seismic exposure studies elsewhere, as well as an extensive amount of scientific publications on exposure experiments of low-frequency naval sonar, another high intensive sound source, in Norwegian waters with different mammal species were considered as the basis for giving advice. Exposure to such low-frequency sonar has been documented to reduce foraging in several common species in Norwegian waters for humpback whales (*Megaptera novaeangliae*) [78], blue whales (*Balaenoptera musculus*) [79], bottlenose whales (*Hyperoodon ampullatus*) [80], sperm whales (*Physeter catodon*) [81], and killer whales (*Orcinus orca*) [82]. In particular, species that feed intensively within a season and depend on dense prey concentrations can experience severe consequences [79,83]. Baleen whales migrate to the Barents Sea to feed intensively during summer and early autumn to feed on the large concentrations of zooplankton and small fish [84]. Based on this knowledge, from 2019, areas and periods with intensive feeding of baleen whales were included in the recommendations of where to restrict seismic activity.

2.7. Into the 2020s: Increasing Scientific Effort

Since the first advice was given, spawning habitats for fish have been recommended to be avoided. As described above, the rationale for this recommendation is that if the sound from seismic airguns causes fish to avoid these habitats, this can lead to failure of reproduction and stock recruitment. However, the question of whether spawning behavior is actually hampered by the sound from seismic surveys has been raised repeatedly. Some argue that the “drive” to reproduce is so strong that other behaviors, such as avoidance, are depressed, and that they thus may likely ignore the seismic disturbance. If so, the need for strong protection of spawning habitats may not be the most efficient advice to prevent potential negative impacts on fish stocks. Therefore, a large project investigating the effects of seismic on spawning behavior and spawning performance as well as avoidance was initiated in 2018; “Effects of sound on spawning behavior and reproductive success of cod” (SpawnSeis) (<https://prosjektbanken.forskingsradet.no/project/FORISS/280367?Kilde=FORISS&distribution=Ar&chart=bar&calcType=funding&Sprak=no&sortBy=score&sortOrder=desc&resultCount=30&offset=0&Fritekst=SpawnSeis>, accessed on 17 April 2021) From this project, there are indications that continuous noise may be more hazardous for fish reproduction than intermittent blasts [18]. However, loud impulsive noise has been shown to produce stress, which could affect the spawning output. While the general literature on fish reproduction shows that stress should be avoided during spawning, the buffer zones, particularly, could be adjusted if the sound from seismic air guns does not seem to affect spawning behavior at the levels of exposure in SpawnSeis. Results from three years of

experimental work in net pens and in the field are currently being analyzed and will be used to update advice.

Areas with drifting planktonic organisms have been excluded from the protection zones since the mid-1990s. Despite some documented effects on increased mortality and damage to zooplankton and other invertebrates, a large number of studies demonstrate the lack of effects unless in the very vicinity of the air gun [30–33]. However, in 2017, McCauley et al. [45] presented some noticeably contradictory results from Australian waters. Here, the abundance of zooplankton exposed to experimental airgun signals decreased by more than 50% in comparison with the control groups, and effects were observed up to 1.2 km from the airgun source. They concluded that seismic surveys have a highly negative impact on zooplankton, particularly, small copepods [45,85]. Thus, attention was created, as these organisms constitute the basis of the food web and support many of the most important fish stocks worldwide [86]. In contrast, a Norwegian study published in 2019 [46] found such effects to occur only at distances of five meters or closer to the air gun on larger copepods, and the increase in mortality did not exceed more than 30% at any distances from the airgun. In addition, no effects on escape response nor important changes in genes were detected. Together with previous similar results, these contradictions lead to the initiation of a research project on understanding the mechanisms of potential impact from the pressure and particle motion associated with seismic shooting (ZoopSeis). The project started in 2020 and will continue until 2023 and the results will inform recommendations as they emerge.

3. Advisory Tools

As described above, the recommendations from IMR on the regulation of seismic activity have always been provided in the form of geographical and seasonal restrictions to avoid sound exposure of sensitive habitats and periods. Such management rules are easily expressed in a map, and maps of sensitive habitats have always been used as tools.

In parallel to the scientific investigations described in the previous sections, advisory tools have been improved from relatively static maps in paper format to digital maps, so-called restriction maps, showing the exact area to avoid in two-week periods throughout the year (Figure 2). These maps include all the recommendations (spawning grounds, spawning migration areas, and feeding areas for marine mammals as well as buffer zones) in one map, and the operator can choose the type of survey (2D/3D seismic surveys, site survey, or EM survey) and obtain a full overview of when and where advice not to conduct seismic activity will be given. This approach simplifies planning for commercial seismic companies, and may have increased the acceptance of the recommendations. The areas and periods that are included in the restriction maps are evaluated once a year by experts on the different species of fish and marine mammals. The latest ongoing development is that these restriction maps are included in the online application process for seismic surveys. If the planned surveys overlap with a restriction area, an automatic warning will be given when either the area or the time period must be changed for the survey to be approved. Since 2018, IMR has published an annual report describing the restriction maps for that year and the scientific background behind the recommendations. The newest report can be found at <https://www.hi.no/hi/nettrapporater/rappport-fra-havforskningen-2021-4> (accessed on 17 April 2021).

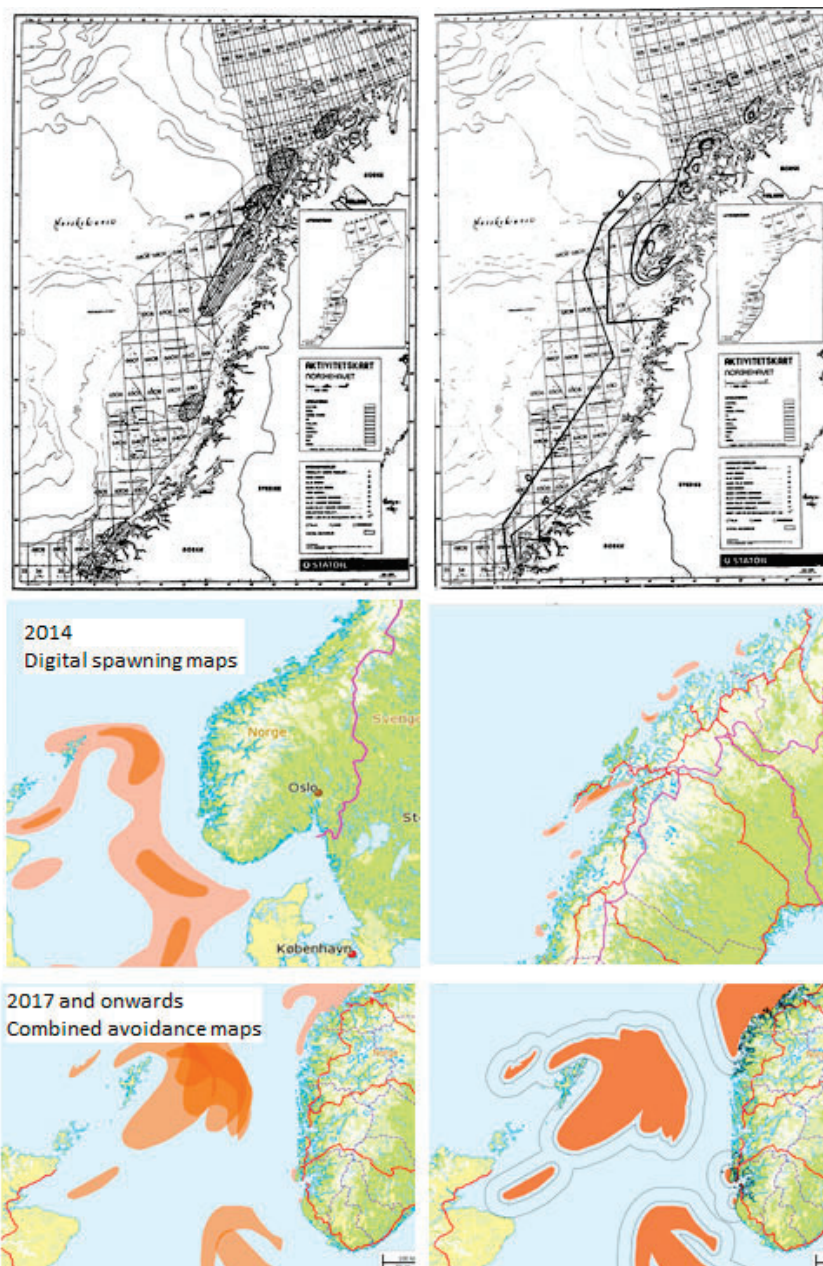


Figure 2. Upper panel: Examples of maps of spawning areas of and of areas of drifting eggs and larvae, as used to give advice in the period 1991 to 2014 [72]. These maps only existed in paper format. **Left:** Spawning areas for cod, with restriction periods between 15 March and 15 May. **Right:** Drifting cod eggs. Restriction periods between 1 April and 30 April. The restriction on drifting eggs and larvae ended in 1996, while the restrictions on the spawning areas still hold, but the exact area and period have been updated. **Middle panel:** Digital spawning maps available from 2014. Areas divided into important and less important spawning areas. This example is for cod, with darker areas being the most important ones. The important restrictions are applied in (dark) areas. **Right:** North Sea cod. **Left:** Northeast Arctic cod. **Lower panel:** Spawning maps for each 2 week period of the year merged into maps with restriction areas. **Left:** Important spawning maps for different North Sea fish species (cod, Norway pout, saithe, herring). **Right:** Avoidance map for period 1 to 15 March. These are made by combining all the maps for important spawning areas for those fish that spawn in this period (which are those shown on the map to the left), as well as two buffer zones (dotted lines) of 5 and 20 nmi, and the advised restrictions for site surveys and regular seismic surveys, respectively.

In parallel to advice from IMR on biological implications, the Norwegian Directorate of Fisheries gives advice to all seismic surveys on potential conflicts with ongoing fishery activity. In areas with traditional seasonal fishing grounds, such as those for herring and mackerel, it is advised that seismic surveys are conducted either before or after the fishing season. Additionally, their advice includes a requirement to always have a fishery liaison officer on board the seismic vessel, to handle all communication between the seismic vessel and fishing vessels in the area to ensure cooperation. The fishery liaison officer will inform the captain on the seismic vessel, e.g., about the specifics of the fishing tools used in the area and how to best avoid them, as well as talking to the fishers and telling them about the seismic production and how they can best conduct their activity without being in the way of the seismic vessel.

4. The Way Forward—The Science Needed to Make Good Management Decisions

The above example from Norway shows that scientific input can be routinely used in management decisions by including scientific institutions in the management process. To ensure that scientific research in the field is applicable to management, Prewlaski et al. [87] highlight some important issues, including identifying useful metrics and species, and the ability to generalize results to a certain degree among species and regions. Further, to ensure that regulations are applicable, recommendations should be balanced between highly restrictive regulations and the loss of resource benefits. Effective research-based management, therefore, requires close collaboration between scientists, industry, and regulators to frame scientific results into applicable regulations. For example, in theory, there may always be one or more species spawning, mating, or feeding in an area that can be argued as a reason for avoiding disturbance, and, hence, closing the area year-round. However, such a strict regulation will never be applied by managers. Therefore, instead of the manager taking a potentially arbitrary decision on where and when to allow seismic survey, the scientist should help identify those areas and time periods that are most important to protect.

During the past 20 years, several guidelines have proposed certain sound threshold levels that should not be exceeded both for marine mammals [88,89] and fish [7,90]. Such criteria are useful and relatively easy to apply. Such thresholds are effective to prevent physical injury, as these are likely to arise when the animal is exposed to sound levels exceeding a certain level. Behavioral responses, however, are far more complex and a response may also depend on factors such as time of day [91], season [92,93], context [94,95], and previous exposure (e.g., [96,97]). Hawkins et al. [98] highlight the need for research on how fish respond to sounds at different levels and changes during the course of sound presentation while the sound characteristics (pressure and particle motion) are carefully measured. Further, Duarte et al. [19] emphasized that a new, globally binding agreement on the regulation of anthropogenic sound in the sea is needed, e.g., by inclusion into the UN Law of the Sea.

Some issues of high importance for better management decisions that remain unsolved include the extent and duration of displacement, as well as the thresholds of received sound levels or distances from the source that lead to avoidance of essential habitats, such as spawning, mating, or foraging sites for various species and animal groups. Additionally, studies should preferably enable an evaluation of how the measured effects could disturb the population, stock, or habitat as a whole, as this is usually the main unit that is managed.

In Norway, management has focused on commercially important fish stocks. This was related to a focus on sustainable management of fish stocks at IMR and a focus on coexistence between oil exploration and fisheries at a government level. Currently, an ecosystem-based approach is called for, as a more productive approach for the management of sustainable harvest [99–101]. To reach this goal, a wider range of species should be included in future management advice, including key species for the ecosystem and threatened species. Because data availability is a limiting factor for many such species, this

requires a continued effort to collect data on the reproductive behavior of such species in relation to noise.

Furthermore, noise is not the only stressor that affects reproduction, and multi-stressor approaches could provide more insight into anthropogenic effects on underwater life. Thus, future management should also focus more on the overall effects of human impact on the ecosystem, by integrating different types of pressures instead of managing them one by one.

Author Contributions: Conceptualization, L.D.S., K.d.J.; Original draft preparation, L.D.S., E.H.V., K.d.J., T.N.F.; Writing—Review & Editing, L.D.S., E.H.V., K.d.J., T.N.F., J.D.; Visualization, L.D.S.; Project administration, L.D.S., H.W.; Funding acquisition, L.D.S., H.W. All authors have read and agreed to the published version of the manuscript.

Funding: This research was funded by internal funding from the Institute of Marine Research for authors L.D.S., K.d.J., T.N.F. and H.W. Funding for E.H.V. was given by the Norwegian Research Council, grant number 302675. Author J.D. was funded by Soundmare.

Institutional Review Board Statement: Not applicable.

Informed Consent Statement: Not applicable.

Data Availability Statement: Data sharing not applicable. No new data were created or analyzed in this study. Data sharing is not applicable to this article.

Acknowledgments: Egil Ona and Svein Løkkeborg are acknowledged for their background information on the research conducted in the early 1990s.

Conflicts of Interest: The authors declare no conflict of interest.

References

- Francis, C.D.; Barber, J.R. A framework for understanding noise impacts on wildlife: An urgent conservation priority. *Front. Ecol. Environ.* **2013**, *11*. [[CrossRef](#)]
- Shannon, G.; McKenna, M.F.; Angeloni, L.A.; Crooks, K.R.; Fristrup, K.M.; Brown, E.; Warner, K.A.; Nelson, M.D.; White, C.; Briggs, J.; et al. A synthesis of two decades of research documenting the effects of noise on wildlife. *Biol. Rev.* **2016**, *91*, 982–1005. [[CrossRef](#)]
- Slabbekoorn, H.; Dooling, J.D.; Popper, A.N.; Fay, R.R. *Effects of Anthropogenic Noise on Animals*; Springer: New York, NY, USA, 2018. [[CrossRef](#)]
- Andrew, R.K.; Howe, B.M.; Mercer, J.A.; Dzieciuch, M.A. Ocean ambient sound: Comparing the 1960s with the 1990s for a receiver off the California coast. *Acoust. Res. Lett. Online* **2002**, *3*, 65. [[CrossRef](#)]
- McDonald, M.A.; Hildebrand, J.A.; Wiggins, S.A. Increases in deep ocean ambient noise in the Northeast Pacific west of San Nicolas Island, California. *J. Acoust. Soc. Am.* **2006**, *120*, 711. [[CrossRef](#)]
- Hildebrand, J.A. Anthropogenic and natural sources of ambient noise in the ocean. *Mar. Ecol. Prog. Ser.* **2009**, *5*, 20. [[CrossRef](#)]
- Popper, A.N.; Hawkins, A.D.; Fay, R.R.; Mann, D.A.; Bartol, S.; Carlson, T.J.; Coombs, S.; Ellison, W.T.; Gentry, R.L.; Halvorsen, M.B.; 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; ASA S3/SC1.4 TR-2014*; Springer: New York, NY, USA, 2014.
- Slabbekoorn, H.; Bouton, N.; van Opzeeland, I.; Coers, A.; ten Cate, C.; Popper, A.N. A noisy spring: The impact of globally rising underwater sound levels on fish. *Trends Ecol. Evol.* **2010**, *25*, 419–427. [[CrossRef](#)] [[PubMed](#)]
- Popper, A.N.; Fewtrell, J.; Smith, M.E.; McCauley, R.D. Anthropogenic sound: Effects on the behaviour and physiology of fishes. *Mar. Technol. Sci. J.* **2004**, *37*, 35–40. [[CrossRef](#)]
- New, L.F.; Clark, J.S.; Costa, D.P.; Fleishman, E.; Hindell, M.A.; Klanjšček, T.; Lusseau, D.; Kraus, S.; McMahon, C.R.; Robinson, P.W. Using short-term measures of behaviour to estimate long-term fitness of southern elephant seals. *Mar. Ecol. Prog. Ser.* **2014**, *496*, 99–108. [[CrossRef](#)]
- Kunc, H.P.; McLaughlin, K.E.; Schmidt, R. Aquatic noise pollution: Implications for individuals, populations, and ecosystems. *Proc. R. Soc. B* **2016**, *283*, 20160839. [[CrossRef](#)] [[PubMed](#)]
- Slabbekoorn, H. Noise Pollution. *Curr. Biol.* **2019**, *29*, R942–R995. [[CrossRef](#)]
- Radford, A.N.; Kerridge, E.; Simpson, S.D. Acoustic communication in a noise world: Can fish compete with anthropogenic noise? *Behav. Ecol.* **2014**, *25*, 1022–1030. [[CrossRef](#)]
- Williams, R.; Wright, A.J.; Ashe, E.; Blight, L.K.; Bruinjes, R.; Canessa, R.; Clark, C.W.; Cullis-Suzuki, S.; Dakin, D.T.; Erbe, C. Impacts of anthropogenic noise on marine life: Publication patterns, new discoveries, and future directions in research and management. *Ocean. Coast. Manag.* **2015**, *115*, 17–24. [[CrossRef](#)]

15. Carroll, A.G.; Przeslawski, R.; Duncan, A.; Gunning, M.; Bruce, B. A critical review of the potential impacts of marine seismic surveys on fish & invertebrates. *Mar. Pollut. Bull.* **2017**, *114*, 9–24.
16. Hawkins, A.D.; Popper, A.N. A sound approach to assessing the impact of underwater noise on marine fishes and invertebrates. *ICES J. Mar. Sci.* **2017**, *74*, 635–651. [[CrossRef](#)]
17. Cox, K.; Brennan, L.P.; Gerwing, T.G.; Dudas, S.E.; Juanes, F. Sound the alarm: A meta-analysis on the effect of aquatic noise on fish behavior and physiology. *Glob. Chang. Biol.* **2018**, *24*, 3105–3116. [[CrossRef](#)]
18. de Jong, K.; Forland, T.N.; Amorim, M.C.P.; Rieucou, G.; Slabbekoorn, H.; Sivle, L.D. Predicting the effects of anthropogenic noise on fish reproduction. *Rev. Fish. Biol. Fish.* **2020**, *30*, 245–268. [[CrossRef](#)]
19. Duarte, C.M.; Chapuis, L.; Collin, S.P.; Costa, D.P.; Devassy, R.P.; Eguiluz, V.M.; Erbe, C.; Gordon, T.A.C.; Halpern, B.S.; Harding, H.R.; et al. The soundscape of the Anthropocene ocean. *Science* **2021**, *371*, eaba4658. [[CrossRef](#)] [[PubMed](#)]
20. Anonymous. *Veileder: Gjennomføring av Seismiske Undersøkelser på Norsk Kontinentalsokkel*; (Guide: Implementation of seismic investigations on the Norwegian Continental Shelf. Norwegian Ministry of Fisheries and Coastal Affairs and the Norwegian Ministry of Oil and Energy, Oslo, Norway); Fiskeri- og Kystdepartement og Olje- og Energidepartement: Oslo, Norway, 2013; 28p. (In Norwegian)
21. Bonga, S.E.W. The stress response in fish. *Physiol. Rev.* **1997**, *77*, 591–625. [[CrossRef](#)] [[PubMed](#)]
22. Szuwalski, C.S.; Vert-Pre, K.A.; Punt, A.E.; Branch, T.A.; Hilborn, R. Examining common assumptions about recruitment: A meta-analysis of recruitment dynamics of worldwide marine fisheries. *Fish Fish.* **2014**, *16*, 633–648. [[CrossRef](#)]
23. Colin, P.L.; Sadovy, Y.J.; Domeier, M.L. *Manual for the Study and Conservation of Reef Fish Aggregations*; Society for the Conservation of Reef Fish Aggregations: Fallbrook, CA, USA, 2003.
24. Portner, H.O.; Farrel, A.P. Physiologu and climate change. *Science* **2008**, *322*, 690–692. [[CrossRef](#)] [[PubMed](#)]
25. Holst, J.C. The herring. In *The Norwegian Sea Ecosystem*; Skjoldal, H., Ed.; Fagbokforlaget: Bergen, Norway, 2004.
26. Rose, G.A.; Bradbury, I.R.; de Young, B. Rebuilding Atlantic cod: Lessons from a spawning ground in coastal Newfoundland. In *Resiliency of Gadid Stocks to Fishing and Climate Change*; Kruse, G.H., Drinkwater, K., Ianelli, J.N., Link, J.S., Stram, D.L., Wespestad, V., Woodby, D., Eds.; Alaska Sea Grant College Program: Fairbanks, AK, USA, 2008; pp. 197–218.
27. Dalen, J.; Raknes, A. *Skremmeeffekter på Fisk frå 3-Dimensjonale Seismiske Undersøkingar. (Scaring Effects in Fish from 3-Dimensional Seismic Explorations)*; Report No FO 8504; Institute of Marine Research: Bergen, Norway, 1985; 22p. (In Norwegian with English Abstract)
28. Dalen, J. *Stimulering av Sildestimer. Forsøk i Hopavågen og Imsterfjorden-Verraffjorden 1973. (Stimulating Herring Shoals. Experiments in Hopavågen and Imsterfjorden-Verraffjorden)*; Report to the Royal Norwegian Council for Scientific and Industrial Research (NTNF); No. 73-143-T; The Norwegian Institute of Technology (NTH): Trondheim, Norway, 1973; 36p. (In Norwegian)
29. Chapman, C.J.; Hawkins, A.J. *The Importance of Sound in Fish Behavior in Relation to Capture by Trawls*; FAO Fisheries Reports; FAO: Rome, Italy, 1969; Volume 621, pp. 717–729.
30. Knutsen, G.M.; Dalen, J. *Skadeeffekter på egg, Larver og Yngel Fra Seismiske Undersøkelser (Harmful Effects on Eggs, Larvae and Fry from Seismic Explorations)*; Report No FO 8505; Institute of Marine Research: Bergen, Norway, 1985; 26p. (In Norwegian with English Abstract)
31. Dalen, J.; Knutsen, G.M. Scaring effects in fish and harmful effects on eggs, larvae and fry by offshore seismic explorations. In *Progress in Underwater Acoustics*; Merklinger, H.M., Ed.; Plenum Publishing Corporation: New York, NY, USA, 1987; pp. 93–102.
32. Booman, C.; Dalen, J.; Leivestad, H.; Levsen, A.; van der Meeren, T.; Toklum, K. *Effekter av Luftkanonskyting på Egg, Larver og Yngel. Undersøkelser ved Havforskningsinstituttet og Zoologisk Laboratorium, UiB. (Effects from Air Gun Shooting on Eggs, Larvae, and Fry. Experiment at the Institute of Marine Research and Zoological Laboratory, Univ. of Bergen)*; Fisker og Havet, No 3-1996; Institute of Marine Research: Bergen, Norway, 1996; 83p. (In Norwegian with English Summary, Figure and Table Legends)
33. Kosheleva, V. The impact of air guns used in marine seismic explorations on organisms living in the Barents Sea. In *Proceedings of the Control Petro PISCIS II '92 Conference F-5*, Bergen, Norway, 6–8 April 1992.
34. Soldal, A.V.; Engås, A.; Løkkeborg, S. *Refraksjonsseismiske Spregninger i Øygarden. Effekten på Vill- og Oppdrettsfisk. (Refraction Seismic Blasting in Øygarden. The Effect in Wild and Farmed Fish)*; Report. Research Number 06-90; Institute of Fishery Tehcnology: Bergen, Norway, 1990; 20p. (In Norwegian)
35. Engås, A.; Olsen, S.; Soldal, A.V. *Undersøkelser av Effekten på Torsk i Mær av Refraksjonsseismiske Spregninger i Øygarden. (Investigations in Penned Cod from Refraction Seismic Blasting in Øygarden)*; Report; Institute of Fishery Tehcnology: Bergen, Norway, 1989; 21p. (In Norwegian)
36. Holmstrøm, S. *Effekter av Luftkanonseismikk på Larver og Yngel—Modellering og Simulering (Effects from Airgun Seismic in Larvae and Fry—Modelling and Simulating)*; SINTEF Report No STF48 A93007; SINTEF: Trondheim, Norway, 1993; 70p. (In Norwegian)
37. Sætre, R.; Ona, E. *Seismiske Undersøkelser og Skader på Fiskeegg og -Larver; en Vurdering av Mulige Effekter på Bestandsnivå. (Seismic Investigations and Injuries in Fish Eggs and Larvae; an Assessment of Potential Effects on Stock Level)*; Fisker og Havet, No 8-1996; Institute of Marine Research: Bergen, Norway, 1996; 25p. (In Norwegian with English Summary)
38. Holand, B.; Walsø, Ø.; Berg, T. *Seismiske Eksperimenter i Våg (Seismic Experiments in a Bay)*; SINTEF Report No STF23 A93005; SINTEF: Trondheim, Norway, 1993; 45p. (In Norwegian)
39. Løkkeborg, S.; Soldal, A.V. The influence of seismic exploration with air guns on cod (*Gadus morhua*) behaviour and catch rates. In *Proceedings of the ICES Marine Science Symposium 201*, Bergen, Norway, 21–23 June 1993; Volume 196, pp. 62–67.

40. Engås, A.; Løkkeborg, S.; Ona, E.; Soldal, A.V. Effects of seismic shooting on local abundance and catch rates of cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*). *Can. J. Fish. Aquat. Sci.* **1996**, *53*, 2238–2249. [[CrossRef](#)]
41. Sundby, S.; Fossum, P.; Sandvik, A.; Vikebø, F.B.; Aglen, A.; Buhl-Mortensen, L.; Folkvord, A.; Bakkeplass, K.; Buhl-Mortensen, P.; Johannessen, M.; et al. *Kunnskapsinnhentning Barentshavet—Lofoten—Vesterålen. KILO. Rapport fra KILO-Prosjektet (Knowledge Acquisition the Barents Sea—Lofoten—Vesterålen. KILO. Report of the KILO Project)*; Fisker og Havet No 3-2013; The Institute of Marine Research: Bergen, Norway, 2013; 186p. (In Norwegian)
42. Sundby, S.; Kristiansen, T.; Nash, R.; Johannessen, T.; Bakkeplass, K.; Höffle, H.; Opstad, I. *Dynamic Mapping of North Sea Spawning. Report of the KINO Project*; Fisker og Havet 2-2017; The Institute of Marine Research: Bergen, Norway, 2017; 195p, ISSN 0071–5638.
43. Nyqvist, D.; Durif, C.; Johnsen, M.G.; de Jong, K.; Forland, T.N.; Sivle, L.D. Electric and magnetic senses in marine animals, and potential behavioral effects of electromagnetic surveys. *Mar. Environ. Res.* **2020**, *155*, 104888. [[CrossRef](#)]
44. Sivle, L.D.; Forland, T.N.; de Jong, K.; Nyqvist, D.; Grimsbø, E. *Havforskningsinstituttets Rådgivning for Menneskeskapt lyd i Havet: Seismikk, Elektromagnetiske Undersøkelser og Undersjøiske Sprengninger—Kunnskapsgrunnlag, Vurderinger og Råd*; (Advice from the Institute of Marine Research of anthropocentric noise in the sea: Seismic, electromagnetic surveys and underwater explosions); No 2019-10; Institute of Marine Research: Bergen, Norway, 2019; 75p, ISSN 1893-4536. (In Norwegian with English Summary)
45. McCauley, R.D.; Day, R.D.; Swadlow, K.M.; Fitzgibbon, Q.; Watson, R.A.; Semmens, J.M. Widely used marine seismic survey air gun operations negatively impact zooplankton. *Nat. Ecol. Evol.* **2017**, *1*. [[CrossRef](#)] [[PubMed](#)]
46. Fields, D.M.; Handegard, N.O.; Dalen, J.; Eichner, C.; Malde, K.; Karlsen, Ø.; Skiftesvik, A.B.; Durif, C.M.F.; Browman, H.I. Airgun blasts used in marine seismic surveys have limited effects on mortality, and no sublethal effects on behaviour or gene expression, in the copepod *Calanus finmarchicus*. *ICES J. Mar. Sci.* **2019**, *76*, 2033–2044. [[CrossRef](#)]
47. Dalen, J.; Ona, E.; Vold, A.S.; Sætre, R. *Seismiske Undersøkelser til Havs: En Vurdering av Konsekvenser for Fisk og Fiskerier. (Offshore Seismic Investigations: An Evaluation of Consequences for Fish and Fisheries)*; Fisker og havet, No 9-1996; Institute of Marine Research: Bergen, Norway, 1996; 26p. (In Norwegian with English Summary)
48. Holliday, D.V.; Pieper, R.E.; Clarke, M.E.; Greenlaw, C.F. *Effects of Airgun Energy Releases on the Northern Anchovy*; API Publ. No 4453; American Petroleum Institute, Health and Environmental Sciences Department: Washington, DC, USA, 1987; 108p.
49. Matishov, G.G. The reaction of bottom-fish larvae to airgun pulses in the context of the vulnerable Barents Sea ecosystem. In Proceedings of the Control Petro PISCIS II '92 F-5, Bergen, Norway, 6–8 April 1992.
50. Dalen, J. *Effektar av Luftkanonseismikk på Larvar og Yngel til Havs. NFFR Sluttrapport 1701-701.354. (Effects from Airgun Seismic on Offshore Larvae and Fry. NFFR Final Report 1701-701.354)*; Report No 9-1993; Institute of Marine Research: Bergen, Norway, 1993; 18p, ISSN 0804-2128. (In Norwegian)
51. Enger, P.S.; Anderson, R. An electrophysical field study of hearing in fish. *Comp. Biochem. Physiol.* **1967**, *22*, 517–525. [[CrossRef](#)]
52. Chapman, C.J.; Johnstone, A.D.F. Some auditory discrimination experiments on marine fish. *J. Exp. Biol.* **1974**, *61*, 521–528.
53. Chapman, C.J.; Hawkins, A.J. A field study of hearing in the cod. *J. Comp. Physiol.* **1973**, *85*, 147–167. [[CrossRef](#)]
54. Olsen, K. *Directional Responses in Herring to Sound and Noise Stimuli*; Conference and meeting documents; ICES Annual Science Conference 1969; ICES: Burnaby, BC, Canada, 1969; 8p.
55. Olsen, K. *Directional hearing in cod (Gadus morhua)*; International Working Group for Fishing Technology: Rome, Italy, 1969; pp. 77–88.
56. Hawkins, A.J.; Sand, O. Directional hearing in the median vertical plane by the cod. *J. Comp. Biol. Physiol. A* **1977**, *122*, 1–8. [[CrossRef](#)]
57. Schuijff, A. Directional hearing of cod (*Gadus morhua*) under approximate free field conditions. *J. Comp. Physiol.* **1975**, *98*, 307–332. [[CrossRef](#)]
58. Pearson, W.H.; Skalski, J.R.; Malme, C.I. *Effects of Sounds from a Geophysical Survey Device on Fishing Success*; OCS Study MMS-86-0032; BBN Laboratories Inc.: Cambridge, MA, USA; Battelle, Marine Research Laboratory: Washington, DC, USA, 1987; 293p.
59. Pearson, W.H.; Skalski, J.R.; Malme, C.I. Effects of sounds from a geophysical survey device on behavior of captive rockfish (*Sebastes* spp). *Can. J. Fish. Aquat. Sci.* **1992**, *49*, 1343–1356. [[CrossRef](#)]
60. Kramer, F.S.; Peterson, R.A.; Walter, W.C. *Seismic Energy Sources 1968. Handbook*. Prep: Staff Members of United Geophysical Corporation. In Proceedings of the 38th Annual Meeting of the SEG, Denver, CO, USA, 18–19 October 1968.
61. Malme, C.I.; Smith, P.W., Jr.; Miles, P.R. *Characterization of Geophysical Acoustic Survey Sounds*; OCS Study MMS-86-0032; BBN Laboratories Inc.: Cambridge, MA, USA, 1986.
62. Slotte, A.; Hansen, K.; Dalen, J.; Ona, E. Acoustic mapping of pelagic fish distribution and abundance in relation to a seismic shooting area off the Norwegian west coast. *Fish. Res.* **2004**, *67*, 143–150. [[CrossRef](#)]
63. Løkkeborg, S.; Ona, E.; Vold, A.; Salthaug, A. Sounds from seismic air guns: Gear- and species specific effects on catch rates and fish distribution. *Can. J. Fish. Aquat. Sci.* **2012**, *69*, 1278–1291. [[CrossRef](#)]
64. Peña, H.; Handegard, N.O.; Ona, E. Feeding herring schools do not react to seismic air gun surveys. *ICES J. Mar. Sci.* **2013**, *70*, 1174–1180. [[CrossRef](#)]
65. Hassel, A.; Knutsen, T.; Dalen, J.; Skaar, K.; Løkkeborg, S.; Misund, O.A.; Østensen, Ø.; Fonn, M.; Haugland, E.K. Influence of seismic shooting on the lesser sandeel (*Ammodytes marinus*). *ICES J. Mar. Sci.* **2004**, *61*, 1165–1173. [[CrossRef](#)]

66. Sivle, L.D.; Forland, T.N.; Hansen, R.R.; Andersson, M.; Grimsbø, E.; Linne, M.; Karlsen, H.E. *Behavioural Effects of Seismic Dose Escalation Exposure on Captive Mackerel (Scomber scombrus)*. Rapport fra Havforskningen; Report No 34-2017; Institute of Marine Research: Bergen, Norway, 2017; ISSN 1893-453.
67. Skalski, J.R.; Pearson, W.H.; Malme, C.I. Effects of sounds from a geophysical survey device on catch-per-unit-effort in a hook-and-line fishery for rockfish (*Sebastes* spp.). *Can. J. Fish. Aquat. Sci.* **1992**, *49*, 1357–1365. [[CrossRef](#)]
68. Slabbekoorn, H. Aiming for progress in understanding underwater noise impact on fish: Complementary need for indoor and outdoor studies. In *The Effects of Noise on Aquatic Life II, Advances in Experimental Medicine and Biology 875*; Popper, A.N., Hawkins, A., Eds.; Springer: Berlin, Germany, 2016; pp. 1057–1065.
69. Hirst, A.G.; Rodhouse, P.G. Impacts of geophysical seismic surveying on fishing success. *Rev. Fish. Biol. Fish.* **2000**, *10*, 113–118. [[CrossRef](#)]
70. Wardle, C.S.; Carter, T.J.; Urquhart, G.G.; Johnstone, A.D.F.; Ziolkowski, A.M.; Hampson, D.; Mackie, D. Effects of seismic air guns on marine Fish. *Cont. Shelf Res.* **2001**, *21*, 1005–1027. [[CrossRef](#)]
71. Fewtrell, J.L.; McCauley, R.D. Impact of air gun noise on the behaviour of marine fish and squid. *Mar. Pollut. Bull.* **2012**, *64*, 984–993. [[CrossRef](#)]
72. Bjørke, H.; Dalen, J.; Bakkeplass, K.; Hansen, K.; Rey, L. *Tilgjengelighet av Seismiske Aktiviteter i Forhold til Sårbare Fiskeresurser (Seismic Explorations' Accessibility in Relation to Vulnerable Fish Resources)*; HELP-Report No 38; Institute of Marine Research: Bergen, Norway, 1991; 119p. (In Norwegian with English Summary and Figure and Table Legends).
73. Sundby, S.; Nakken, O. Spatial shifts in spawning habitats of Arcto-Norwegian cod related to multidecadal climate oscillations and climate change. *ICES J. Mar. Sci.* **2008**, *65*, 953–962. [[CrossRef](#)]
74. Collin, S.; Whitehead, D. The functional roles of passive electroreception in non-electric fishes. *Anim. Biol.* **2004**, *54*, 1–25.
75. Kalmijn, A.J. Electric and magnetic detection in elasmobranch fishes. *Science* **1982**, *218*, 916–918. [[CrossRef](#)] [[PubMed](#)]
76. Kullnick, U. Influences of Electric and Magnetic Fields on Aquatic Ecosystems. In Proceedings of the International Seminar on Effects of Electromagnetic Fields on the Living Environment, Ismaning, Germany, 4–5 October 1999; pp. 113–132.
77. Kvalsheim, P.; Sivle, L.D.; Hansen, R.R.; Karlsen, H.E. *Effekter av Menneskeskapt Støy på Havmiljø. Rapport til Miljødirektoratet om Kunnskapsstatus (Effects from Man-Made Noise on Ocean Environment. Report to the Norwegian Environment Agency of Status of Knowledge)*; FFI Report No 17/00075; Norwegian Defence Research Establishment (FFI): Horten, Norway, 2017; 75p. (In Norwegian with English Summary)
78. Sivle, L.D.; Wensveen, P.J.; Kvalsheim, P.H.; Lam, F.P.A.; Visser, F.; Curé, C.; Harris, C.M.; Tyack, P.L.; Miller, P.J.O. Naval sonar disrupts foraging in humpback whales. *Mar. Ecol. Prog. Ser.* **2016**, *562*, 211–220. [[CrossRef](#)]
79. Goldbogen, J.A.; Southall, B.L.; DeRuiter, S.L.; Calambokidis, J.; Friedlaender, A.S.; Hazen, E.L.; Falcone, E.A.; Schorr, G.S.; Douglas, A.; Moretti, D.J. Blue whales respond to simulated mid-frequency military sonar. *Proc. R. Soc. B Biol. Sci.* **2013**, *280*, 20130657. [[CrossRef](#)] [[PubMed](#)]
80. Miller, P.J.O.; Kvalsheim, P.H.; Lam, F.P.A.; Tyack, P.L.; Cure, C.; DeRuiter, S.L.; Hooker, S.K. First indications that northern bottlenose whales are sensitive to behavioural disturbance from anthropogenic noise. *R. Soc. Open Sci.* **2015**, *2*. [[CrossRef](#)]
81. Isojunno, S.; Curé, C.; Kvalsheim, P.H.; Lam, F.P.; Tyack, P.L.; Wensveen, P.; Miller, P.J.O. Sperm whales reduce foraging effort during exposure to 1–2 kHz sonar and killer whale sounds. *Ecol. Appl.* **2016**, *26*, 77–93. [[CrossRef](#)]
82. Miller, P.J.O.; Kvalsheim, P.H.; Lam, F.P.A.; Wensveen, P.J.; Antunes, R.; Alves, A.C.; Visser, F.; Kleivane, L.; Tyack, P.L.; Sivle, L.D. The Severity of Behavioral Changes Observed During Experimental Exposures of Killer (*Orcinus orca*), Long-Finned Pilot (*Globicephala melas*), and Sperm (*Physeter macrocephalus*) Whales to Naval Sonar. *Aquat. Mamm.* **2012**, *38*, 362–401. [[CrossRef](#)]
83. Farmer, N.A.; Baker, K.; Zeddies, D.G.; Denes, S.L.; Noren, D.P.; Garrison, L.P.; Zykov, M. Population consequences of disturbance by offshore oil and gas activity for endangered sperm whales (*Physeter macrocephalus*). *Biol. Conserv.* **2018**, *227*, 189–204. [[CrossRef](#)]
84. Mauritzen, M.; Johannesen, E.; Bjørge, A.; Øien, N. Baleen whale distributions and prey associations in the Barents Sea. *Mar. Ecol. Prog. Ser.* **2011**, *426*, 289–301. [[CrossRef](#)]
85. Richardson, A.J.; Matear, R.J.; Lenton, A. *Potential Impacts on Zooplankton of Seismic Surveys*; CSIRO: Canberra, Australia, 2017; 34p.
86. Kaiser, M.J.; Attrill, M.J.; Jennings, S.; Thomas, D.N.; Barnes, D.K.A.; Brierley, A.S.; Graham, N.A.J.; Hiddink, J.G.; Howell, K.L.; Kaartokallio, H. *Marine Ecology: Processes, Systems, and Impacts*, 3rd ed.; Oxford University Press: New York, NY, USA, 2020.
87. Przeslawski, R.; Brooke, B.; Carroll, A.G.; Fellows, M. An integrated approach to assessing marine seismic impacts: Lessons learnt from the Gippsland Marine Environmental Monitoring project. *Ocean. Coast. Manag.* **2019**, *160*, 117–123. [[CrossRef](#)]
88. Southall, B.; Bowles, A.; Ellison, W.; Finneran, J.; Gentry, R.; Greene, C., Jr.; Kastak, D.; Ketten, D.; Miller, J.; Nachtigall, P.; et al. Marine mammal noise exposure criteria: Initial scientific recommendations. *Aquat. Mamm.* **2007**, *33*, 411–521. [[CrossRef](#)]
89. Southall, B.L.; Finneran, J.J.; Reichmuth, C.; Nachtigall, P.E.; Ketten, D.R.; Bowles, A.E.; Ellison, W.T.; Nowacek, D.P.; Tyack, P.L. Marine mammal noise exposure criteria: Updated scientific recommendations for residual hearing effects. *Aquat. Mamm.* **2019**, *45*, 125–232. [[CrossRef](#)]
90. Andersson, M.H.; Andersson, S.; Ahlsen, J.; Andersson, B.L.; Hammar, J.; Persson, L.K.; Pihl, J.; Sigray, P.; Wisstrom, A. *A Framework for Regulating Underwater Noise during Pile Driving*; A Technical Vindal Report; Environmental Protection Agency: Stockholm, Sweden, 2017.
91. Hawkins, A.D.; Roberts, L.; Cheesman, S. Responses of freelifving coastal pelagic fish to impulsive sounds. *J. Acoust. Soc. Am.* **2014**, *135*, 3101–3116. [[CrossRef](#)]

92. Skaret, G.; Slotte, A.; Handegard, N.O.; Axelsen, B.E.; Jørgensen, R. Pre-spawning herring in a protected area showed only moderate reaction to a surveying vessel. *Fish. Res.* **2006**, *78*, 359–367. [[CrossRef](#)]
93. Vabø, R.; Olsen, K.; Huse, I. The effect of vessel avoidance of wintering Norwegian spring spawning herring. *Fish. Res.* **2002**, *58*, 59–77. [[CrossRef](#)]
94. Ellison, W.T.; Southall, B.L.; Clark, C.W.; Frankel, A.S. A New context-based approach to assess marine mammals behavioral responses to anthropogenic sounds. *Conserv. Biol.* **2011**, *26*, 21–28. [[CrossRef](#)] [[PubMed](#)]
95. Harris, C.M.; Thomas, L.; Falcone, E.A.; Hildebrand, J.; Houser, D.; Kvadsheim, P.H.; Lam, F.-P.A.; Miller, P.J.O.; Moretti, D.J.; Read, A.J.; et al. Marine mammals and sonar: Dose-response studies, the risk-disturbance hypothesis and the role of exposure context. *J. Appl. Ecol.* **2017**, 1–9. [[CrossRef](#)]
96. Neo, Y.Y.; Hubert, J.; Bolle, L.J.; Winter, H.V.; Slabbekoorn, H. European seabass respond more strongly to noise exposure at night and habituate over repeated trials of sound exposure. *Environ. Pollut.* **2018**, *239*, 367–374. [[CrossRef](#)]
97. Goetz, T.; Janik, V.M. Aversiveness of sounds in phocid seals: Psycho-physiological factors, learning processes and motivation. *J. Exp. Biol.* **2010**, *213*, 1536–1548. [[CrossRef](#)]
98. Hawkins, A.D.; Johnson, C.; Popper, A.N. How to set sound exposure criteria for fishes. *J. Acoust. Soc. Am.* **2020**, *147*. [[CrossRef](#)]
99. FAO Fisheries Department. *The Ecosystem Approach to Fisheries*; FAO Technical Guidelines for Responsible Fisheries 4, (Suppl. 2); FAO: Rome, Italy, 2008; 112p.
100. Garcia, S.M.; Cochrane, K.L. Ecosystem approach to fisheries: A review of implementation guidelines. *ICES J. Mar. Sci.* **2005**, *62*, 311–318. [[CrossRef](#)]
101. Link, J.S.; Browman, H.I. Integrating what? Levels of marine ecosystem-based assessment and management. *ICES J. Mar. Sci.* **2005**, *71*, 1170–1173. [[CrossRef](#)]

III



The copepod *Acartia* sp. is more sensitive to a rapid pressure drop associated with seismic airguns than *Calanus* sp.

Emilie Hernes Vereide*, Babak Khodabandeloo, Karen de Jong

Institute of Marine Research, Nykirkekaaien 1, 5004 Bergen, Norway

ABSTRACT: Airguns used in seismic surveys release high-pressure air, generating sound waves that may have adverse effects on marine life. However, knowledge of how seismic exposure impacts zooplankton is limited. One key characteristic of seismic signals that could potentially cause damage is a rapid pressure drop. In this study, the rapid pressure drop (~2 bar) was re-created in the laboratory using a pressure tube. To determine the range at which this drop occurs, the sound field around a seismic airgun array was modeled. The effects of this pressure drop on mortality and swimming behavior were tested in 2 common copepods, *Acartia* sp. and *Calanus* sp., both immediately and 5 h after treatment. Pressure-exposed *Acartia* sp. showed higher mortality rates (0 h: 5.6%; 5 h: 10%) compared to the controls, while mortality in *Calanus* sp. only increased after 5 h (3.3%). The swimming speed of pressure-exposed *Acartia* sp. (0 h: 0.49 mm s⁻¹; 5 h: 0.52 mm s⁻¹) was lower than in the control treatment, whereas the swimming speed in pressure-exposed *Calanus* sp. (2.64 mm s⁻¹) only differed immediately after treatment. This study demonstrates that a rapid pressure drop can negatively affect zooplankton mortality and behavior at close range. The results also show that *Acartia* sp. is more sensitive to this pressure drop than *Calanus* sp., suggesting potential species-specific impacts from seismic exposure. Identifying the sound characteristics that can be harmful to zooplankton allows for a more accurate assessment of the most affected species and the range at which impacts can occur.

KEY WORDS: Seismic surveys · Anthropogenic noise · Impulsive underwater noise · Zooplankton · Mortality · Mobility · Hydrostatic pressure

1. INTRODUCTION

An increase in human activities in marine environments, including ship traffic, pile driving, dredging, and seismic surveys, has resulted in the recognition of noise pollution in the oceans (Williams et al. 2015, Duarte et al. 2021). Anthropogenic underwater noise, both impulsive and continuous, may have adverse effects on marine life (Williams et al. 2015, Merchant et al. 2022). However, limited information is available regarding the impact of seismic surveys on marine organisms occupying lower trophic levels, such as zooplankton and other invertebrates (Carroll et al.

2017, Solé et al. 2023, Vereide & Kühn 2023). Airguns are the most common and efficient type of marine seismic source in the search for oil and gas deposits. They transmit loud low-frequency (< 100 Hz) sound waves that propagate thousands of meters down in the sediments under the seabed. A single seismic survey may cover an area of more than 2000 km², shooting approximately every 10 s over weeks or months (Weilgart 2013, Slabbekoorn et al. 2019). Seismic exposure can affect marine fauna and cause direct and indirect damage, such as changes in predator–prey interactions or species composition (Todd et al. 2015, Kavanagh et al. 2019, Slabbekoorn et al. 2019).

*Corresponding author: emilie.hernes.vereide@hi.no

© The authors 2024. Open Access under Creative Commons by Attribution Licence. Use, distribution and reproduction are unrestricted. Authors and original publication must be credited.

Publisher: Inter-Research · www.int-res.com

Furthermore, seismic airguns impact animals in different ways, e.g. by overlapping the frequencies used in the communication of whales (Kavanagh et al. 2019) or by affecting the behavior of fish through the detection of particle motion or sound pressure (Slabbekoorn et al. 2019). Most of what is known about the effects of seismic exposure on marine life comes from studies on mammals and fish (Gordon et al. 2003, Popper & Hawkins 2016, 2019).

Only a few studies have investigated the effects of seismic activities on zooplankton (Solé et al. 2023), despite their crucial role in marine ecosystems (Pinti et al. 2023a). These studies have reported a range of impacts, including severe physical damage and mortality as well as no significant effects (Carroll et al. 2017, Vereide & Kühn 2023). For example, Fields et al. (2019) reported low immediate mortality (~10% in the exposed vs. ~2% in the control) in *Calanus finmarchicus* after exposure to 2 small airguns at a short distance (<5 m). Similarly, Vereide et al. (2023) showed a small increase in immediate mortality (~14% in the exposed vs. ~4% in the control) in *Acartia tonsa* nauplii when exposed to 2.5 h of seismic blasting at different distances (50 m to 1.2 km). Pearson et al. (1994) observed no effects on mortality or development in crab larvae (*Cancer magister*) after seismic exposure. The low levels of mortality in these 3 studies contrast with those of McCauley et al. (2017), who reported a substantial increase in mortality (~45% in the exposed vs. ~20% in the control) in natural zooplankton communities after seismic exposure up to a maximum sampling distance of >1 km from an airgun source. These variations may be caused by species-specific differences in sensitivity or by differences in sound exposures, such as sound levels, sound sources, or exposure time. In this study, we tested the effect of the same exposure in 2 different zooplankton species.

Zooplankton exhibit diversity in both their physical characteristics and functions (Lindeque et al. 2013, Deagle et al. 2018). They vary in size (Evans et al. 2020, Brandão et al. 2021) and display distinct behaviors (Kiørboe et al. 2010a, Almeda et al. 2017). Consequently, the impact of exposure may differ among zooplankton species and taxa, depending on factors such as their size, physiology, or behavior. Among the studies investigating the effects of seismic exposure on copepods (McCauley et al. 2017, Fields et al. 2019, Vereide et al. 2023), the mortality and growth of copepods are negatively affected, albeit to varying degrees. However, these studies have investigated the effects in different species. For example, large copepods have shown no behavioral responses and experienced lim-

ited but adverse effects on mortality (Fields et al. 2019), whereas zooplankton communities dominated by small copepods have been reported to be more affected (McCauley et al. 2017). These variations may be caused by species-specific differences in sensitivity. Therefore, to test the differences between copepod species, we used 2 genera of zooplankton that are common in both coastal and open-ocean marine environments: *Acartia* and *Calanus*.

Aside from mortality, our understanding of the impact of seismic surveys on zooplankton behavior is even more limited. Sound exposure can cause physical harm to marine animals, including zooplankton, which may result in decreased sensitivity or ability to move (Solé et al. 2021). Fields et al. (2019) found no changes in the escape behavior of *C. finmarchicus* following airgun exposure. However, they only examined escape behavior and not overall activity. Copepods are dependent on mechanoreceptive setae for sensing and reacting to external stimuli (Fields et al. 2002, Solé et al. 2021). Therefore, alterations in the behavior of copepods, such as changes in swimming activity, could potentially indicate sub-lethal physical damage. The swimming behavior of zooplankton can be affected by external factors like turbulence, which may hinder their ability to evade predators (Visser et al. 2008). Consequently, changes in mobility, in addition to being an indication of sub-lethal damage, could suggest reduced survival ability in the field (Buskey et al. 2002). Therefore, our study tested the effects of exposure on swimming activity in zooplankton to assess any potential adverse effects on their condition.

When an airgun is fired, high-pressure compressed air (typically 137 bar) is released (Caldwell & Dragoset 2000) into the surrounding water, forming a rapidly expanding bubble. The resulting sound wave, or acoustic signal, consists of an initial high-amplitude pressure pulse, followed by decaying pulses formed by oscillations of the resulting air bubble (Dragoset 2000). To increase the source energy and focus more energy downward, several individual airguns (typically 18–48) are arranged in an airgun array. Airguns are usually deployed at depths of 5–15 m (Prior et al. 2021), and the surface reflection of the signal is added to the transmitted pulse with a short delay. The reflected surface signal has an opposite phase, causing the positive pressure peak to be reflected as a negative pressure peak. Therefore, positive pressure is followed by negative pressure, resulting in a fast hydrostatic pressure drop (McCauley et al. 2021). This pressure drop is typical for impulsive signals and much larger and steeper than the pressure

fluctuations observed in continuous sounds like boat noise. For both seismic exposures and detonations, this phenomenon can be fatal for marine animals near the source, particularly if they have air inclusions. Even fish without swim bladders have been observed to die near detonations, likely due to the oscillations of microbubbles in their tissues (Goertner et al. 1994). Sound waves generated by airguns can propagate over 1000 km from the source (Thode et al. 2010), but their amplitude decreases rapidly in close proximity to the source and less rapidly as the distance from the source increases (Caldwell & Dragoset 2000). Thus, to assess at what distances potential effects may occur, we modeled at what range from an airgun array this pressure drop will occur.

Copepods are regularly exposed to hydrostatic pressure changes as they undergo diel and seasonal vertical migration, since pressure changes at 0.1 bar per meter depth (Hays et al. 1994, Bandara et al. 2021, Pinti et al. 2023b). For example, *C. finmarchicus* can migrate to depths between several hundred and >2000 m, which would result in a pressure change of up to 200 bar (Kvile et al. 2022). The magnitude of the pressure drop caused by commonly used marine seismic sources (Caldwell & Dragoset 2000) is not nearly as intense. For example, a seismic airgun array with 2730 in³ (~44 737 cm³) volume and 137 bar firing pressure would result in an approximate 9 bar drop in the hydrostatic pressure immediately adjacent to the source, which decreases rapidly with distance (Khodabandloo et al. 2017). However, with a common ascent swimming speed of <6 mm s⁻¹ (Berge et al. 2014), these natural changes occur relatively slowly (6 × 10⁻⁷ bar ms⁻¹) compared to the pressure drop that animals are exposed to close to a seismic airgun (~0.4 bar ms⁻¹). Therefore, the rapid pressure drop that occurs close to seismic airguns may cause damage and is likely one of the characteristics underlying the negative effects of an exposure to sound from seismic airguns reported in the literature. Here we simulated this hydrostatic pressure drop in isolation, excluding other aspects of sound exposure, such as particle motion.

In this study, we tested the effects of a rapid pressure drop associated with seismic airguns on the mortality and swimming behavior of 2 genera of copepods, *Acartia* and *Calanus*. Based on the previously observed differences, we hypothesized that the negative effects would be stronger in *Acartia* sp. than in *Calanus* sp. In addition, to assess whether damage from seismic surveys could lead to population-level effects, we modeled at what range this pressure drop can occur in the sound field around a seismic airgun array.

2. MATERIALS AND METHODS

All experiments were conducted at the Institute of Marine Research, Austevoll Research Station (60° 5' 9.02'' N, 5° 15' 41.94'' E), between 23 August and 9 September 2022 (Table 1). During the experiments, *Acartia* sp. and *Calanus* sp. were sampled in the field (60° 5' 9.51'' N, 5° 15' 22.49'' E; 60° 5' 18.09'' N, 5° 16' 0.91'' E) and exposed to either a pressure drop or a control treatment, following measurements of swimming behavior and mortality immediately and 5 h after treatment (see Section 2.5).

2.1. Experimental animals

The study focuses on *Calanus finmarchicus* (Gunnerus, 1770) and *Acartia tonsa* Dana, 1849, as they constituted the majority of the genera *Calanus* and *Acartia*, respectively, which were sampled at the time of the study in Austevoll.

C. finmarchicus is a calanoid epipelagic copepod that is most commonly found in the Norwegian Sea and North Sea. In these areas, *C. finmarchicus* may account for more than 80% of mesozooplankton biomass (Aarflot et al. 2018). The species is considered a large copepod (2–4 mm) that accumulates large lipid stores (up to 31% of the total dry weight) (Lee et al. 2006), converting carbon from phyto- and microzooplankton to accessible energy (Skottene et al. 2020).

A. tonsa is also a calanoid epipelagic copepod distributed throughout the oceans of the world but is commonly found in coastal and estuarine areas (Cervetto et al. 1995). In Norwegian coastal waters, *A. tonsa* is often one of the dominant species of smaller copepods throughout summer and spring and serves as an important food source for many fish species (Sullivan et al. 2007). The body length of adult *A. tonsa* ranges from 0.5 to 1.5 mm, and the species contains low lipid reservoirs compared with *C. finmarchicus* (Lee et al. 2006).

2.2. Sampling of animals

Acartia sp. was sampled using a WP2 plankton net (mesh size 180 µm) (Table 1). The plankton net was towed behind a small boat at approximately 1 m s⁻¹ at a depth of 10 m. Two net hauls were collected on each sampling day (Table 1). *Calanus* sp. was sampled using a light trap at a depth of 20 m. The light trap was deployed at night and returned the following morning (Table 1). All sampling and treatment times can

Table 1. Overview of species, sampling, environmental conditions, and treatments. Each set consisted of a pressure exposure and a control. Dates are given as d/mo/yr

Species	Sampling gear	Sampling depth (m)	Sampling date	<i>In situ</i> temp. (°C)	<i>In situ</i> salinity (psu)	Treatment date	Sets (pressure exposure + control)
<i>Acartia</i> sp.	WP2 plankton net (180 µm)	10	23/08/22	17.2	31.1	24/08/22	1 and 2
			25/08/22	17.0	31.1	25/08/22	3 and 4
			26/08/22	17.0	31.1	26/08/22	5 and 6
<i>Calanus</i> sp.	Light trap (200 µm)	20	06/09/22	16.0	31.7	07/09/22	1 and 2
			08/09/22	16.0	31.7	08/09/22	3 and 4
			08/09/22	16.0	31.7	09/09/22	5 and 6

be found in Table 1. Both of the sampling locations were in close proximity to the laboratory. After sampling, the nets and cod ends were rinsed, and all animals were transferred to large buckets filled with seawater. Subsequently, the buckets were carried to the laboratory, where they were immediately placed in a climate-controlled room at a constant temperature, adjusted to the *in situ* temperature at the current sampling times (Table 1). Slow aeration was then applied to the buckets. The light:dark cycle was 12:12 h, and no food was provided.

2.3. Pressure tube and pressure measurements

The pressure tube consisted of a polyvinyl chloride (PVC) tube (external diameter: 38 mm; length: 260 mm). Valves (25 mm; FIP Easyfit PVC-U Ball) were attached to both ends (Fig. 1). One of these valves was used to introduce and retrieve the water and animals, the other was used to release the pressure.

A 4.8 kHz digital dynamic pressure sensor (Applied Measurements Limited, USB Pa-USB-FQ) was attached to the tube wall to measure the pressure inside

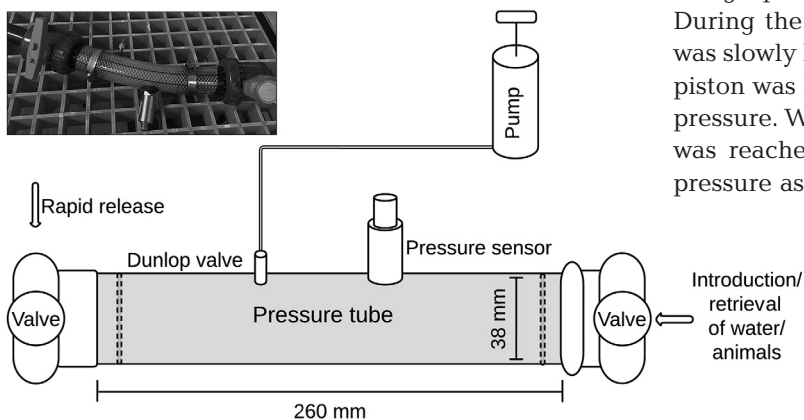


Fig. 1. Setup of the pressure tube with notations and placements of its components. Inset: pressure tube

the chamber (Fig. 1). The pressure sensor was connected to a PC via a USB cable, from where the pressure was observed, using the FSU Toolkit software (Mantracourt, version 01.03). A Dunlop valve was also attached to the tube, to which a pump with a hand-operated piston was connected (maximum pressure 160 psi/11 bar, height 67 cm).

2.4. Experimental setup

Six sets of each treatment (control, pressure exposure) were conducted for both species (Fig. 2; Table 1). For each treatment, 30 individuals were counted and picked using a Leica stereomicroscope (Leica Microsystems, Stereozoom S9i) and then transferred to an evaporating glass dish filled with filtered seawater. The same stereomicroscope was used for all measurements. Second, the pressure tube and pump were filled with filtered seawater at the *in situ* temperature, and all animals were carefully poured from the glass dish into the tube while avoiding the introduction of air bubbles. Any remaining air bubbles were removed by carefully sweeping the inner walls of the tube using a plastic strip. Thereafter, the valve was closed. During the pressure exposure treatment, the piston was slowly launched to push water into the tube. The piston was launched only once to reach the targeted pressure. When the target absolute pressure of ~3 bar was reached, the valve was opened to release the pressure as quickly as possible, resulting in a ~2 bar pressure drop. The absolute pressure indicates a measure using absolute zero as a reference point. Therefore, when the pressure is released by ~2 bar, the pressure returns to the atmospheric pressure (~1 bar, 1 atm = 1.01325 bar). After each treatment, the animals were carefully poured from the tube into a container for further measurements.

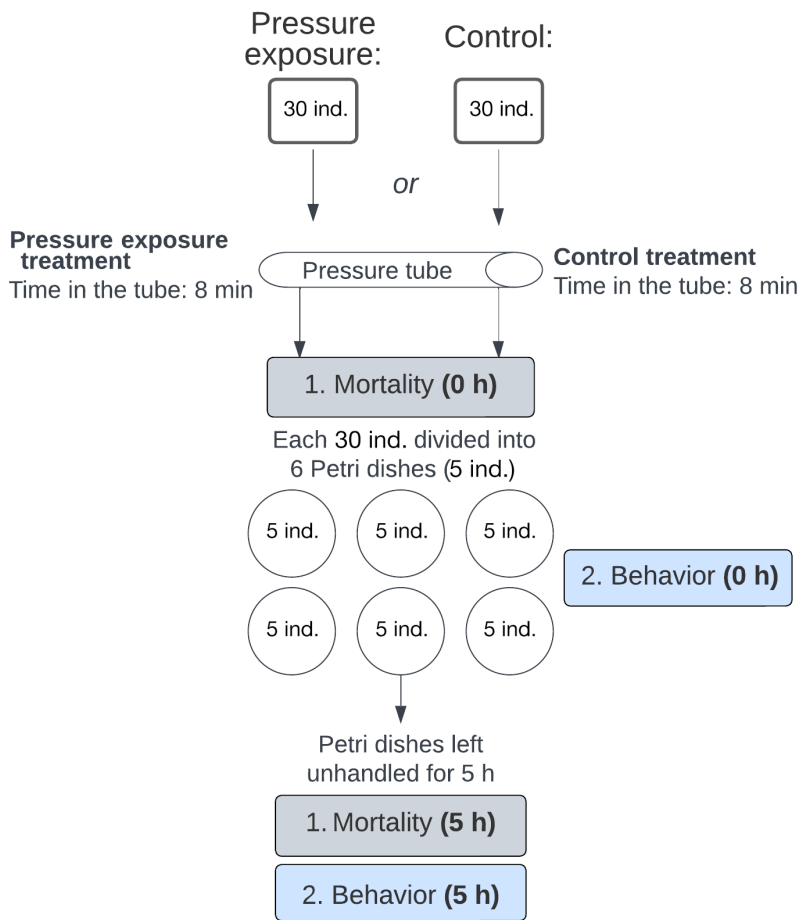


Fig. 2. Experimental setup. The setup was identical for *Acartia* sp. and *Calanus* sp. (1) Mortality of the copepods of each treatment (pressure exposure and control) was measured immediately after treatment, with a total of 6 sets (6× pressure exposure, 6× control). After dividing 30 individuals into 6 Petri dishes, the animals were recorded, and (2) the swimming behavior was measured. The same measurements were conducted after 5 h

The tube was rinsed several times to ensure that all individuals had been removed. The full exposure treatment lasted 8 min from introduction to removal of the animals. Therefore, the animals were kept in the tube for 8 min during the control treatment, and treated identically, although without changing the pressure. The order of the control and the corresponding exposure treatment were randomized.

2.5. Mortality and activity measurements

Immediate mortality was investigated within 10 min of treatment using a stereoscope by carefully stimulating the animals using a plastic pipette. Animals that did not exhibit any response within 10 s of stimulation were considered dead. After measurements, the 30 in-

dividuals from each treatment were haphazardly divided into 6 plastic Petri dishes (diameter 95 mm, height 15 mm) filled with filtered seawater at *in situ* temperature. Both dead and live animals were included in the recordings to confirm that the animals were dead and not stunned by the pressure exposure. Thus, there were 5 individuals per dish (Fig. 2). To record activity, these 6 Petri dishes were placed beneath 3 cameras (SONY HDR-GW55VE, HDR-CX280E). After an acclimatization period of 30 s, the dishes were recorded for 4 min (van Duren & Videler 1995). The Petri dishes were then left unhandled for 5 h in the same climate room. After 5 h, mortality was measured again in the same manner as previously described, followed by the same recording procedure for activity. Finally, after all measurements were taken, pictures of all individuals were taken using an AirLab 2.0 Leica Microsystems equipped with a Leica CLS150 LED light. From the pictures, the prosome length of all individuals was measured using the software ImageJ (version 1.53e) (Schneider et al. 2012).

All video recordings of copepod swimming activity were analyzed using the annotation tool software Kinovea 0.9.5 (Charmant 2021). The path of each copepod was tracked during the 4 min of recording, from which parameters such as distance, speed, and coordinates could be exported. In addition, for each dish, it was noted whether the individual was alive or dead; the latter was excluded from behavioral analyses. Furthermore, as it was not realistically possible to identify and track the same individual within each dish immediately and after 5 h, we used the mean speed of the live individuals in each Petri dish.

2.6. Modeling approach: hydrostatic pressure variations around a seismic airgun array

To understand how a seismic airgun array impacts the hydrostatic pressure in its vicinity, the pressure field at time t and location (x, y, z) was modeled using notional source signatures (Ziolkowski et al. 1982, Khodabandloo 2018) as:

$$p(t, x, y, z) = 10^5 + \rho z g + \sum_{i=1}^N \frac{1}{r_i} p_{ni} \left(t - \frac{r_i}{c} \right) + \sum_{i=1}^N \frac{R}{r_{gi}} p_{ni} \left(t - \frac{r_{gi}}{c} \right) \quad (1)$$

where N is the number of airguns in the array, p_{ni} is the notional source signature of the i^{th} airgun in the array. The distances between the point (x, y, z) and the i^{th} airgun, as well as its reflected acoustic wave from the sea surface (referred to as ghost), are shown by r_i and r_{gi} , respectively. Depth is shown by z . The speed of sound is represented by c , its density by ρ , and $R = -1$ is the reflection coefficient from the sea surface. The notional source signatures were modeled using the seismic air gun modeling package NUCLEUS™, a product of Petroleum Geo-Services. The airgun array consisted of 30 airguns (total 2730 in³) arranged in 3 sub-arrays (see Khodabandeloo et al. 2017). The hydrostatic pres-

sure changes (maximum minus minimum) at different locations around the array caused by the acoustic pressure propagation from the airgun were modeled using Eq. (1) and are plotted in Fig. 3.

2.7. Theoretical modeling of cavitation and bubble-dynamics

Acoustic waves generated by seismic airguns have the potential to cause cavitation by reducing the pressure below the vapor pressure of water (Mellen 1954, Plesset 1970). Cavitation can occur at these locations, which causes extreme expansion and sudden collapse at cavitation nuclei sites (e.g. microbubbles) (Mellen 1954, Ceccio & Brennen 1991). Seawater microbubbles, which act as nucleation sites, have

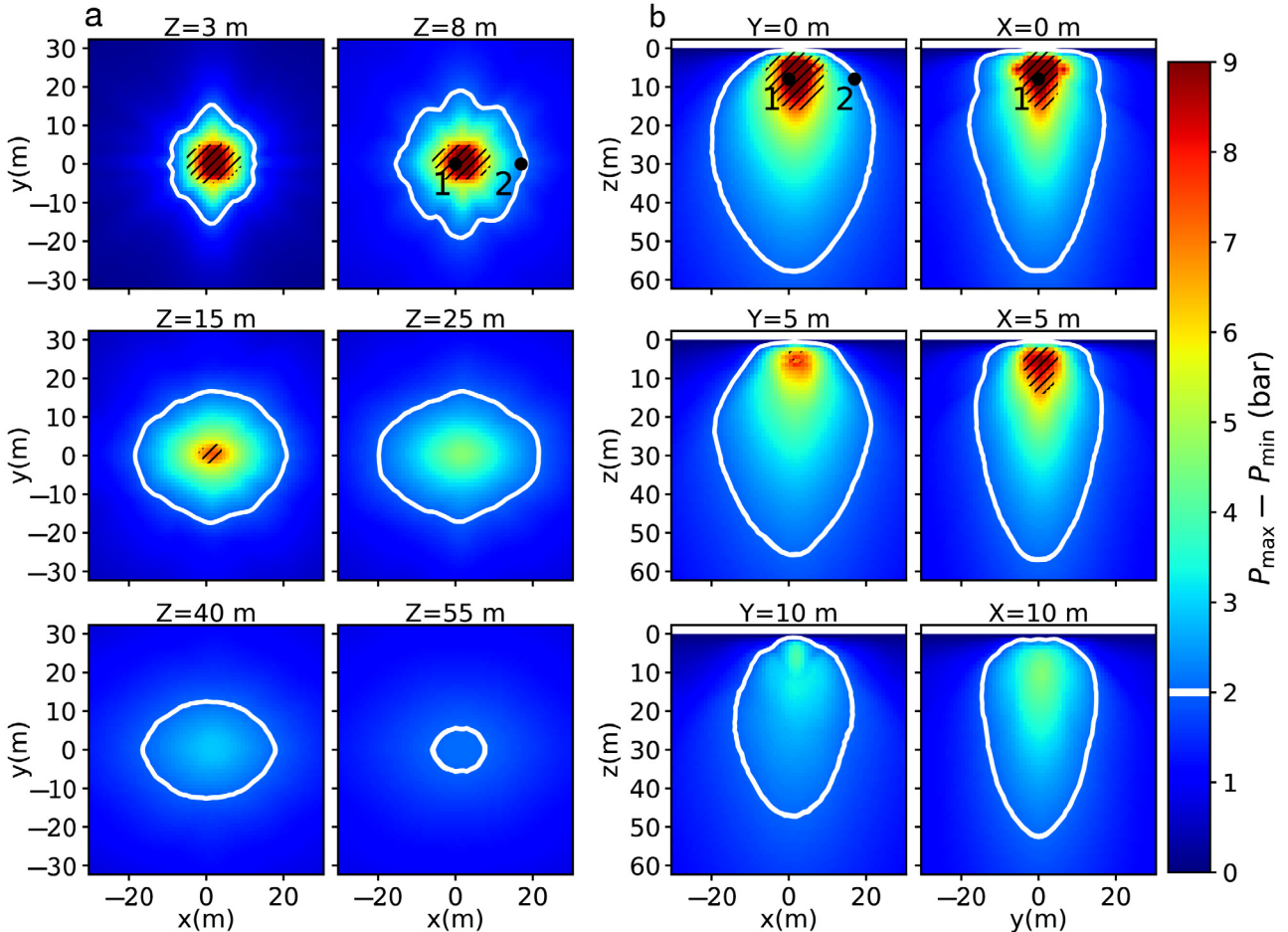


Fig. 3. Pressure drop (difference between the maximum and minimum pressures) at different distances from an airgun array. The modeled airgun was a 2730 in³ (~44 737 cm³) array located at a depth of 5 m. x is the direction the airgun travels (positive x points towards the bow), positive y is the starboard direction, and positive z is the water depth measured from the water surface. (a) Top view of the pressure drop at different depths. (b) Side view of the pressure drop at different x,z and y,z planes with offsets (0, 5, and 10 m). The white solid line indicates 2 bar, which is equivalent to the pressure drop in the pressure tube experiment. The hatched area refers to the area in which the absolute pressure drops below the water vapor pressure and cavitation could occur. The response of a microbubble at locations '1' and '2' (marked by black dots) is plotted in Fig. 4

radii between 1 and 100 μm (Ceccio & Brennen 1991). Cavitation can cause severe harm to nearby organisms, and snapping shrimp utilize this phenomenon to stun or kill their prey (Versluis et al. 2000). When cavitation occurs, a 20 μm bubble can grow up to approximately 11 mm (Fig. 4a), and its subsequent collapse generates an intense acoustic wave (Versluis et al. 2000, Khodabandello et al. 2017). To test whether cavitation could have occurred in our setup, we modeled the response of a microbubble subjected to pressure variations around the seismic airgun and pressure tube using equations that govern bubble dynamics (Fig. 4) (Prosperetti & Lezzi 1986, Khodabandello et al. 2017).

2.8. Data analyses

All data analyses were implemented using R (version 4.2.2) (R Core Team 2022). For all analyses, a significance threshold of 5% was used. First, to test whether the pressure drop the animals were exposed to differed between species, the pressure measurements from the pressure exposure sets for each species were tested using a paired *t*-test. Here, the difference in the mean pressure drop between *Acartia* sp. and *Calanus* sp. was tested (Table 2), i.e. if the pressure drop rate was different between copepod groups. The effect of treatment on mortality was tested separately for *Acartia* sp. and *Calanus* sp. immediately and 5 h after treatment. Because there was a total absence of dead individuals in the control treatment group for *Acar-*

tia sp. immediately after treatment, and for *Calanus* sp. both immediately after and after 5 h, and thus a lack of variation within those treatments, it was not possible to apply binomial models to compare mortality between different treatments. Consequently, the impact of treatment on mortality was assessed by conducting Kruskal-Wallis tests separately for each time point after treatment for both groups ($n_{\text{replicate}} = 12$; 6 per treatment) (Table 2).

The effect of treatment on behavior (swimming speed) was first tested in a global model using a generalized linear mixed-effect model (GLMM). In this model, we used the mean speed in each dish as a dependent variable. We included treatment, time after treatment (0 and 5 h), and species as fixed factors, and replicate as random factor. We also included the interactions between time after treatment and species, treatment (pressure exposure vs. control) and species, and treatment and time after treatment as fixed effects. To account for a potential effect of the time the animals spent in the laboratory between sampling and the start of the experiment (Table 1), we added days between sampling and experiment as a covariate (Table 2). Secondly, to test the effect of treatment separately for each time point (0 and 5 h), we used 4 separate models (GLMMs) with the mean speed within each dish as a dependent variable, with treatment (pressure exposure vs. control) as a fixed effect and replicate as a random factor (Table 2; $n_{\text{dish}} = 72$; 36 per treatment; $n_{\text{replicate}} = 12$; 6 per treatment). Because a difference in copepod size could result in a difference in speed unrelated to treatment (Svetlichny et al.

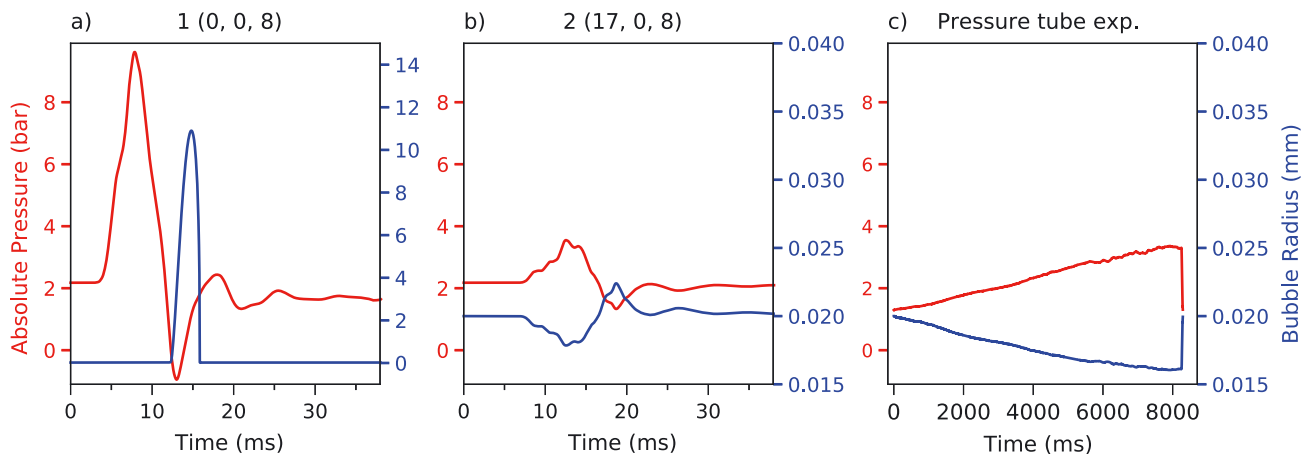


Fig. 4. Modeled response of a microbubble (blue line) to the pressure variations (red line) using bubble dynamics equations. (a,b) A microbubble with radius 20 μm in response to the pressure variations at 2 different locations (marked '1' and '2' in Fig. 3). (c) Response of a 20 μm microbubble to the pressure variations in the pressure tube experiment. The titles illustrate the coordinates of the locations where the pressure is modeled (*x* [m], the direction the airgun travels; *y* [m], starboard direction; and *z* [m], the water depth measured from the water surface)

Table 2. Overview of statistical tests. (a) Paired *t*-test on the effect of species on pressure drop rate. (b) Kruskal-Wallis test on the effect of treatment on the proportion of dead individuals for *Acartia* sp. and *Calanus* sp. after 0 h and 5 h, separately. (c) Generalized linear mixed-effect model (GLMM) (global model) on the effect of treatment, species, time after treatment, as well as the interactions, and days between sampling and experiment (Days) on mean swimming speed for each Petri dish. (d) GLMM (separate models) on the effect of treatment (control, pressure exposure) on mean swimming speed for each Petri dish. Significant values are displayed in **bold**

(a) Pressure drop rate		Effects	95% CI (min./max.)	<i>t</i>	p	
		Pressure drop rate	−0.012/0.009	−0.303	0.774	
(b) Mortality	Group	Effects	df	χ^2	p	
	<i>Acartia</i> 0 h	Pressure	1	7.301	7.0×10^{-3}	
	<i>Acartia</i> 5 h	Pressure	1	9.103	3.0×10^{-3}	
	<i>Calanus</i> 0 h	Pressure	1	3.667	0.056	
	<i>Calanus</i> 5 h	Pressure	1	5.333	0.021	
(c) Swimming activity						
Global model		Effects	Estimate	SE	<i>t</i>	p
		(Intercept)	1.172	0.391	2.996	3.0×10^{-3}
		Pressure	1.304	0.319	4.083	< 0.0001
		<i>Calanus</i>	−0.648	0.328	−1.974	0.048
		Time (0 and 5 h)	6.0×10^{-3}	0.083	0.07	0.944
		Days	−0.144	0.244	−0.591	0.555
		Pressure: <i>Calanus</i>	−1.223	0.468	−2.610	0.01
		Time: <i>Calanus</i>	0.063	0.088	0.712	0.476
		Pressure:Time	−0.046	0.052	−0.879	0.379
Separate models	Model	Effects	Estimate	SE	<i>t</i>	p
	<i>Acartia</i> 0 h	(Intercept)	1065.7	115.8	9.202	< 0.0001
		Pressure	1505.4	115.4	13.045	< 0.0001
	<i>Acartia</i> 5 h	(Intercept)	1006.3	154.4	6.519	< 0.0001
		Pressure	1139.7	243.3	4.684	< 0.0001
	<i>Calanus</i> 0 h	(Intercept)	303.14	23.92	12.675	< 0.0001
		Pressure	80.53	34.66	2.323	0.02
	<i>Calanus</i> 5 h	(Intercept)	373.48	27.77	13.448	< 0.0001
		Pressure	41.11	38.36	1.071	0.28

2020), we tested for differences in copepod prosome length between treatments using a *t*-test.

3. RESULTS

3.1. Pressure measurements

The mean \pm SD of the maximum absolute pressure in an exposure was 2.97 ± 0.05 bar for *Calanus* sp. ($n = 6$) and 2.93 ± 0.08 bar for *Acartia* sp. ($n = 6$) (Fig. A1 in the Appendix). The pressure drop of ~ 2 bar had a mean \pm SD drop rate of 0.06 ± 0.01 bar ms^{-1} during the pressure exposure sets of *Calanus* sp. and 0.05 ± 0.01 bar ms^{-1} in *Acartia* sp. There was no significant difference in either the maximum pressure or mean drop rate in pressure between the exposures of the 2 species (Table 2).

3.2. Pressure drop in the experiment vs. that around a seismic airgun array

The hydrostatic pressure drop around a seismic airgun array due to its acoustic wave was modeled using Eq. (1) and is represented spatially in Fig. 3. The airgun array used in the modeling consisted of 3 sub-arrays with a total volume of 2730 in^3 (see Khodabandloo et al. 2017). The rapid pressure drop in the experimental setup was ~ 2 bar.

A hydrostatic pressure drop of 2 bar or more occurred within a horizontal radius of 5 m around the airgun array at a depth of 55 m and 20 m around the airgun array at a depth of 8 m (Fig. 3). Vertically, this area extended to a maximum of 60 m directly below the airgun array (Fig. 3). For the given airgun array, the area in which cavitation may occur, e.g. where the absolute hydrostatic pressure dropped below the

water vapor pressure of 0 bar, extended to a maximum of ~ 10 m horizontally and ~ 15 m vertically (Fig. 3). However, it should be noted that the pressure drop in the seismic survey in this area occurred more rapidly than the pressure drop we re-created in the pressure tube (Fig. A1).

To illustrate where cavitation occurs, the response of a microbubble with an equilibrium radius of $20\ \mu\text{m}$ subjected to pressure variations at 2 specific points (labeled '1' and '2' in Fig. 3) was modeled using the bubble dynamics equations (Fig. 4). The pressure tube simulated the hydrostatic pressure drop in the area around the airgun array where cavitation was not expected (Fig. 4b,c). In addition, the modeled response of a similar-sized microbubble subjected to pressure variations within the pressure tube did not indicate cavitation (Fig. 4c).

3.3. Mortality

In *Acartia* sp., the proportion of dead individuals in the pressure exposure treatment was significantly higher than that in the control treatment, both immediately and 5 h after treatment (Table 2). The mean \pm SD mortality in the pressure-exposed *Acartia* sp. was $5.6 \pm 3.4\%$ immediately after exposure and $10.0 \pm 5.1\%$ 5 h after exposure (Fig. 5), while in the control treatment, only 1 individual died ($0.6 \pm 1.4\%$) (after 5 h). In *Calanus* sp., mortality was significantly higher in the pressure-exposed copepods compared to the control 5 h after treatment ($3.3 \pm 3.6\%$ vs. no mortality). Immediately after treatment, there was a tendency for higher mortality after pressure exposure, but no significant difference between treatments (pressure-exposed: $1.6 \pm 1.8\%$ vs. no mortality; Fig. 5; Table 2).

3.4. Behavior: swimming speed

The mean swimming speed was significantly lower after the pressure exposure treatment compared to the control treatment (Table 2). The mean swimming speed was higher in *Calanus* sp. than in *Acartia* sp. (Table 2; Fig. 6). In *Acartia* sp., the mean swimming speed of the pressure-exposed animals (0 h: $0.49 \pm 0.68\ \text{mm s}^{-1}$; 5 h: $0.52 \pm 0.71\ \text{mm s}^{-1}$ [mean \pm SD]) was significantly lower than in the control groups both immediately and 5 h after treatment (0 h: $1.12 \pm 0.77\ \text{mm s}^{-1}$; 5 h: $1.10 \pm 0.73\ \text{mm s}^{-1}$) (Fig. 6; Table 2). In *Calanus* sp., the swimming speed was lower in the pressure-exposed copepods ($2.64 \pm 1.28\ \text{mm s}^{-1}$) than

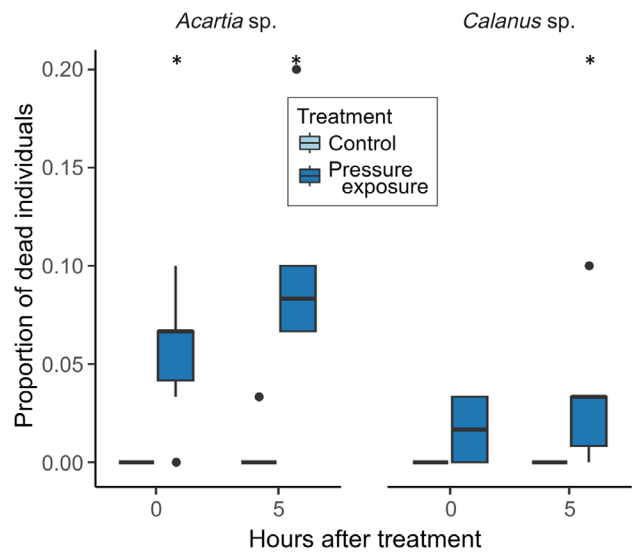


Fig. 5. Proportion of dead individuals of *Acartia* sp. and *Calanus* sp. after exposure to a control treatment or a pressure exposure treatment, measured 0 h and 5 h after treatment. The proportion is calculated from replicates ($n = 6$) with 30 individuals each. Significance is demonstrated with an asterisk (*) at the top of the graph. The horizontal middle line shows the median (25th and 75th percentile), and the whiskers display the minimum and maximum values within 1.5 times the interquartile range above/below the 75th/25th percentile. Potential outliers are shown as black dots

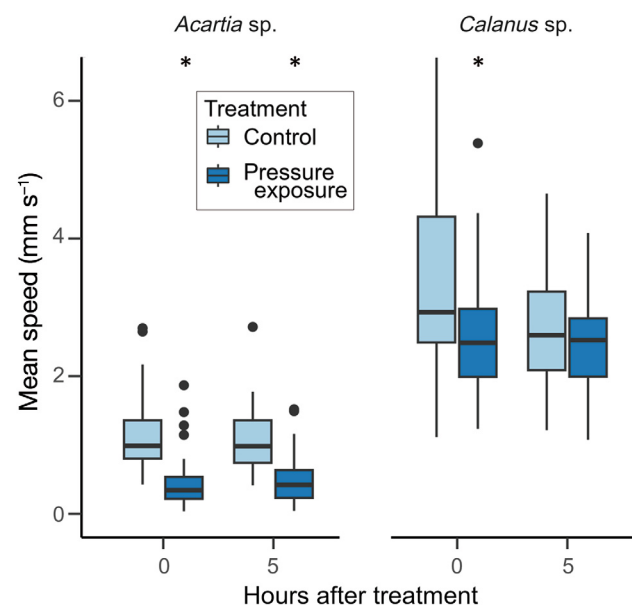


Fig. 6. Measured mean swimming speed (mm s^{-1}) of *Acartia* sp. and *Calanus* sp. after exposure to a control treatment or a pressure exposure treatment, measured 0 h and 5 h after treatment. The mean swimming speed was calculated from each dish (6 from each replicate, $n = 6$). Significance is demonstrated with an asterisk (*) at the top of the graph. Box plot description as in Fig. 5

in the control group ($3.32 \pm 1.68 \text{ mm s}^{-1}$) immediately after treatment. After 5 h, the mean swimming speed showed no differences (pressure exposure: $2.6 \pm 1.27 \text{ mm s}^{-1}$, control treatment: $2.71 \pm 1.16 \text{ mm s}^{-1}$). There was no significant difference in copepod prosome length between treatments for either species (*t*-test, *Acartia* sp., $p = 0.89$; *Calanus* sp., $p = 0.30$). During the 4 min of recording, the mean speed per minute remained stable for both species and time points after treatment (0 and 5 h).

4. DISCUSSION

This study demonstrates a method for re-creating a rapid pressure drop associated with seismic airguns in the laboratory. Although the size of the pressure drop was similar to the pressure drop of 20–60 m from a modeled airgun array, the speed of the drop was approximately 6 times slower (airgun array: 0.37 bar ms^{-1} ; Khodabandloo 2018). Even so, the mortality rate of the pressure-exposed *Acartia* sp. was significantly affected by the re-created pressure drop. In contrast, the mortality rate of pressure-exposed *Calanus* sp. was only significantly affected after 5 h. Pressure-exposed *Acartia* sp. was also significantly less active than the control group up to 5 h after treatment, whereas behavior in *Calanus* sp. significantly differed between treatments only immediately after treatment. The potential expansion of microbubbles in animals was excluded as a potential cause of damage. Thus, a pressure drop alone can cause damage to zooplankton. The results of this study could help interpret those of previous studies that have investigated the effects of seismic exposure on mortality and behavior in zooplankton (McCauley et al. 2017, Fields et al. 2019, Vereide et al. 2023) by adding novel data on the characteristics of the sound field that could cause damage to zooplankton, and which taxa may be most vulnerable.

4.1. Effects on mortality and behavior in copepods

4.1.1. Mortality

Higher mortality was detected in pressure-exposed *Acartia* sp. compared to control groups both immediately and 5 h after treatment. In *Calanus* sp., there was a difference between pressure-exposed copepods and control only after 5 h, although a tendency for a similar effect was also observed immediately after treatment. The impact of seismic exposure on mortality

has previously been investigated in both *Calanus* sp. and *Acartia* sp. Fields et al. (2019) reported an immediate maximum mortality rate of 15% in airgun-exposed adult *C. finmarchicus*, which was distinctly higher than that of *Calanus* sp. in this study. The animals were exposed to a single shot from 2 small airguns (520 in^3 [$\sim 8521 \text{ cm}^3$] in total), but significant effects on mortality were detected only 5 m from the source (Fields et al. 2019). Investigating *A. tonsa*, Vereide et al. (2023) found an immediate mortality of $\sim 14\%$ in the naupliar stages of the copepod, also higher than that observed in our current study. Vereide et al. (2023) exposed the nauplii to the airguns for ~ 2.5 h, which was significantly longer than the exposure time in this study, where only a single pressure drop was applied. In contrast to both of these studies, McCauley et al. (2017) noted increased immediate mortality in natural zooplankton communities by up to 2.5-fold after exposure to a seismic transect compared to the control transects (~ 45 vs. $\sim 20\%$). The re-created pressure drop of ~ 2 bar would occur in a sound wave with a peak pressure level of 226 dB re $1 \mu\text{Pa}$ (200 kPa) (ISO 2017). This is lower than the measured peak pressure of 1369 kPa (closest to the airguns) in Fields et al. (2019) but higher than that reported by Vereide et al. (2023) (48.9 kPa, 50 m from the source) and McCauley et al. (2017) (1.4 kPa, 509–658 m). Our results indicate that only lower levels of mortality may be expected even for the more sensitive *Acartia* sp. However, the duration of the exposure was short, and longer exposure may lead to increased mortality (Kok et al. 2023).

The mortality rate in pressure-exposed *Calanus* sp. increased from 0 h to 5 h, whereas it was already elevated in *Acartia* sp. immediately after treatment. This observation suggests that mortality may become apparent after a longer duration, similar to the delayed mortality observed in *Acartia* nauplii following seismic exposure (Vereide et al. 2023). Hence, it is important to exercise caution and avoid underestimating the potential mortality over time, despite the initially low mortality rates reported in this and other studies (Pearson et al. 1994, Parry et al. 2002, Fields et al. 2019).

4.1.2. Swimming behavior

The swimming activity in pressure-exposed *Acartia* sp. was lower both 0 h and 5 h after treatment, whereas decreased activity was only detected in *Calanus* sp. immediately after treatment. The effects of seismic exposure on zooplankton behavior are widely unknown, both individually and at a popula-

tion level, and although some studies have looked into behavioral impact in zooplanktonic species from anthropogenic underwater noise (Aspirault et al. 2023), few studies have examined behavioral effects in copepods (Vereide & Kühn 2023). For example, Fields et al. (2019) found no effects on the escape responses in *C. finmarchicus*. They measured escape performance and changes in the sensory threshold needed to initiate an escape but reported no difference for any distance to the airgun. To our knowledge, no studies have examined the effects of seismic exposure on the behavior of *Acartia* sp. However, Kühn et al. (2023) reported that the feeding rate of *A. tonsa* decreased when exposed to boat noise, a continuous sound source. Thus, different species might react differently to exposure of seismic airguns or anthropogenic sound. The few studies conducted also highlight the need for more knowledge on behavioral effects after noise exposure.

On a larger scale, McCauley et al. (2017) observed a 'hole' in the zooplankton layer after exposure to a seismic airgun. Using a 120 kHz sonar frequency, they were unable to observe individual zooplankton, but they could detect larger aggregations. They suggested that the 'hole' is due to changes in zooplankton orientation or a spread in the zooplankton mass. Furthermore, zooplankton may be disabled in their sensory capacity, resulting in behavioral changes and sinking of the animals (McCauley et al. 2017). Although our study did not measure sinking, it demonstrated overall less swimming activity in *Acartia* sp. than in *Calanus* sp. Therefore, the differences observed in the results of previous studies might indicate that smaller copepods or species similar to *Acartia* sp. may exhibit less movement after seismic exposure compared to larger copepods like *Calanus* sp. Furthermore, the absence of significant differences in activity between the pressure-exposed and control group after 5 h, as opposed to immediately after exposure, in *Calanus* sp., could indicate a recovery process. This suggests that the animals may experience effects only in the short term following exposure but manage to recover within a few hours.

It is noteworthy that the swimming activity was measured in a 2-dimensional setup, and it may not directly reflect real-life scenarios. However, the primary focus of this study was to compare the differences between exposure and control groups, as well as variations between different species. Consequently, the study highlights the significance of investigating potential airgun characteristics and species-specific responses, rather than providing data on natural swimming speeds.

4.2. Differences between species

Both species used in this study are commonly used in laboratory and field experiments (Jonsson & Tiselius 1990, Hygum et al. 2000, Aarflot et al. 2018, Rotolo et al. 2021). The species differ in their physiological and functional traits despite being visually similar. First, *Calanus* sp. is a more lipid-rich species, containing proportionally more lipids per unit body area than *Acartia* sp. (Lee et al. 2006). Studies have suggested that changes in pressure may harm animals that have areas of different densities in their bodies, e.g. lipid storage vacuoles (Bamber & Seaby 2004). Zarubin et al. (2016) also detected a pattern of greater effects of pressure change on the grazing rate of lipid-rich copepods. However, this contrasts with the results of this study, in which *Calanus* sp. experienced fewer effects on mortality and fewer changes in swimming activity after a pressure drop than *Acartia* sp. Second, the species differ in their behavioral patterns, such as swimming and escape strategies. For example, *Calanus* sp. has a higher velocity and beat cycle (leg stroke duration and pause) than *Acartia* sp. (Kjørboe et al. 2010b). While this distinction may not directly influence long-term mortality or behavioral alterations, it could potentially help explain why the behaviors of different species are affected in distinct ways. These findings suggest that *Acartia* sp. experience a greater impact on the swimming activity compared to *Calanus* sp., raising the possibility that *Acartia* sp. may be more sensitive to exposure or that the effects on swimming activity are more pronounced following exposure.

Furthermore, copepods possess external sensory hair and mechanoreceptive setae (Gassie et al. 1993), and respond to hydrodynamic stimuli, with which behavioral responses can be altered (Lenz & Hartline 2015). Behavioral responses, the ability to modify behavioral patterns, and sensitivity to external signals can vary among species (Kjørboe et al. 2018). The observed differences could indicate that *Calanus* sp. have a wider sensory system and can potentially use other mechanisms if exposed to pressure changes. Furthermore, low-frequency sound can cause damage in the sensory setae of copepods (Solé et al. 2021), which can differ between species (Fields 2014). Lastly, as previously mentioned, McCauley et al. (2017) detected a substantial increase in mortality after airgun exposure. Interestingly, they reported that the group of dead copepods was dominated by smaller species (*A. tranteri*, *Oithona* spp.), similar in size to *Acartia* sp. used in this study. Overall, the variations observed in the effects on swimming activity

suggest that different species may be influenced in distinct ways, potentially due to their varying morphologies or behavioral patterns. To determine which morphological characteristics are most susceptible and the underlying reasons, further specialized investigations are required.

4.3. Pressure drop as a potential cause of damage

The study demonstrated that the pressure drop around a seismic airgun array can trigger cavitation only in a small area around the source. The majority of the water surrounding the source experiences pressure increase and decrease without cavitation, even in the region where a 2 bar pressure drop is observed. Thus, this experiment reflects the region between 20 and 55 m around a typical airgun array. The pressure drop we re-created was between 3 and 1 bar absolute pressure. It has previously been speculated that the high positive peak followed by a high negative peak (peak pressure gradient), similar to the pressure drop in this study, may cause physical damage to some marine taxa (McCauley & Duncan 2017, McCauley et al. 2021). Ideally, negative pressure should therefore have been used; however, achieving this in a laboratory setting is very challenging. Consequently, the pressure was slowly increased and then rapidly released to create a pressure drop.

Liquids, known for their high incompressibility, maintain a relatively constant volume under compression. The bulk modulus of a liquid, which measures its compressibility, can be defined as:

$$K = -dp/(dV/V_0) \quad (2)$$

where K (N m^{-2}) represents the bulk modulus, dp is the applied pressure changes on the liquid, dV is the change in volume, and V_0 denotes its initial volume (Munson et al. 2002). The bulk modulus is a characteristic of a liquid and varies with temperature. At 15°C , the bulk modulus of seawater is approximately 2.34 GPa, while that of paraffin oil is around 1.66 GPa. Paraffin oil can serve as an analog for lipids found in copepods. It is worth mentioning that although these liquids exhibit substantial resistance to pressure, their volume experiences slight fluctuations under high-pressure conditions. Therefore, when a liquid organism with an elastic shell experiences an increase in hydrostatic pressure, the elastic shell undergoes compression to counteract the volume reduction of the organism. On the other hand, liquids typically have negligible tensile strength. That is, when the pressure drops and the

volume of the organism returns to its initial value, there is minimal resistance from the liquid inside the organism, and only the elastic shell experiences tensile stress. This way, a pressure drop could harm the elastic shell, which could potentially lead to physical damage, or even mortality. It is important to note that the pressure drop occurred independently of any generation of acoustic waves within the pressure tube, resulting in the absence of particle velocity that would normally be associated with the acoustic waves. This absence of particle motion is a considerable advantage in the experimental setup. It facilitates the isolation of the effects of the rapid pressure drop on zooplankton. Many studies on the effects of underwater sound on invertebrates emphasize particle motion (Nedelec et al. 2016). In this study, we show that a pressure drop itself can impact zooplankton. Future studies could focus on gaining a better understanding of the mechanisms behind this damage.

Similar methods of exposing zooplankton to pressure changes have previously been adopted for hydrostatic pressure changes over a longer time and with lower pressure (e.g. in relation to diel vertical migration) (Zarubin et al. 2016). Investigating effects of real seismic surveys are often expensive and logistically difficult. Furthermore, it is close to impossible to isolate certain characteristics underlying potential damage when conducting field experiments. Therefore, the pressure tube offers a unique method of testing how zooplankton may be damaged from seismic surveys.

4.4. Transferrable to real-life settings?

This study isolated and re-created a rapid pressure drop similar to those observed close to airguns. From the measured and modeled pressure variations, we can estimate at which range from a real-life airgun array such pressure drops occur.

The comparison between the re-created pressure drop and that of an airgun array (2730 in^3) demonstrates that the hydrostatic pressure drop of ~ 2 bar would not occur at distances further away than ~ 55 m from the airgun (vertically, below the airgun). This suggests that the mortality found in this study corresponds to the studies reporting effects in relatively close distance from an airgun array. However, because the pressure drop in the laboratory was slower than the pressure drop that occurs in the sound field around a real airgun array, the range at which damage occurs may be larger in the field.

Although we modeled a typical airgun array, seismic surveys may operate with arrays of total chamber volume up to 5300 in³ (~86 851 cm³) (Hovem & Tronstad 2012, Slabbekoorn et al. 2019). In that case, the pressure drop of ~2 bar may in other cases extend beyond the distances modeled in this study. However, even a tenfold increase in range compared to the range modeled here would only amount to a 600 m range around the airgun array. Thus, our results corroborate findings from studies that find low levels of mortality close to airgun arrays (Pearson et al. 1994, Fields et al. 2019, Vereide et al. 2023), but they cannot explain mortality at larger distances of up to 1 km from the source as found in McCauley et al. (2017).

4.5. Conclusions

This study demonstrated a novel setup to expose zooplankton to a rapid pressure drop associated with seismic airgun arrays at close range, and showed that such a rapid pressure drop can negatively affect zooplankton mortality and behavior. Moreover, our results indicate that the pressure drop itself can cause damage, independently from cavitation and particle motion. The results also show that *Acartia* sp. is more sensitive to this pressure drop than *Calanus* sp. This targeted focus solely on the pressure drop enables us to precisely identify its effects on zooplankton, eliminating potential confounding variables associated with particle motion. All in all, this study shows how a single characteristic of the sound field around an airgun array may cause damage to zooplankton, at what distance this is likely to happen, and that such effects can be species-specific. These data can be used to design future studies on the effects of anthropogenic noise on zooplankton, and shed light on the mechanisms behind how damage can occur.

Acknowledgements. We thank Tonje Nesse Forland for her valuable advice and input on the experiment setup and previous versions of this manuscript, as well as David M. Fields for his help designing the setup. We also thank the employees at Austevoll Research Station, especially Annhild Engevik, Marina Mihaljevic, Glenn Sandtorv, Andreas Habbestad Andersen, Jorunn Sanden, and Nils Ingmar Gokstad. E.H.V., B.K., and K.d.J. were funded through the ZoopSeis project (the Research Council of Norway, #302675), and the JPI OCEANS Project ORCHESTRA funded through the Research Council of Norway (#339519).

LITERATURE CITED

- plankton biomass in the Barents Sea. *ICES J Mar Sci* 75: 2342–2354
- ✦ Almeda R, van Someren Gréve H, Kiørboe T (2017) Behavior is a major determinant of predation risk in zooplankton. *Ecosphere* 8:e01668
 - ✦ Aspirault A, Winkler G, Jolivet A, Audet C and others (2023) Impact of vessel noise on feeding behavior and growth of zooplanktonic species. *Front Mar Sci* 10:111466
 - ✦ Bamber RN, Seaby RMH (2004) The effects of power station entrainment passage on three species of marine planktonic crustacean, *Acartia tonsa* (Copepoda), *Crangon crangon* (Decapoda) and *Homarus gammarus* (Decapoda). *Mar Environ Res* 57:281–294
 - ✦ Bandara K, Varpe Ø, Wijewardene L, Tverberg V, Eiane K (2021) Two hundred years of zooplankton vertical migration research. *Biol Rev Camb Philos Soc* 96: 1547–1589
 - ✦ Berge J, Cottier F, Varpe Ø, Renaud PE and others (2014) Arctic complexity: a case study on diel vertical migration of zooplankton. *J Plankton Res* 36:1279–1297
 - ✦ Brandão MC, Benedetti F, Martini S, Soviadan YD and others (2021) Macroscale patterns of oceanic zooplankton composition and size structure. *Sci Rep* 11:15714
 - ✦ Buskey EJ, Lenz PH, Hartline DK (2002) Escape behavior of planktonic copepods in response to hydrodynamic disturbances: high speed video analysis. *Mar Ecol Prog Ser* 235:135–146
 - ✦ Caldwell J, Dragoset W (2000) A brief overview of seismic air-gun arrays. *Leading Edge* 19:898–902
 - ✦ Carroll AG, Przeslawski R, Duncan A, Gunning M, Bruce B (2017) A critical review of the potential impacts of marine seismic surveys on fish & invertebrates. *Mar Pollut Bull* 114:9–24
 - ✦ Ceccio SL, Brennen CE (1991) Observations of the dynamics and acoustics of travelling bubble cavitation. *J Fluid Mech* 233:633–660
 - ✦ Cervetto G, Pagano M, Gaudy R (1995) Feeding behaviour and migrations in a natural population of the copepod *Acartia tonsa*. *Hydrobiologia* 300:237–248
 - ✦ Charmant J (2021) Kinovea (0.9.5). <https://www.kinovea.org/>
 - ✦ Deagle BE, Clarke LJ, Kitchener JA, Polanowski AM, Davidson AT (2018) Genetic monitoring of open ocean biodiversity: an evaluation of DNA metabarcoding for processing continuous plankton recorder samples. *Mol Ecol Resour* 18:391–406
 - ✦ Dragoset B (2000) Introduction to air guns and air-gun arrays. *Leading Edge* 19:892–897
 - ✦ Duarte CM, Chapuis L, Collin SP, Costa DP and others (2021) The soundscape of the Anthropocene ocean. *Science* 371:eaba4658
 - ✦ Evans LE, Hirst AG, Kratina P, Beaugrand G (2020) Temperature-mediated changes in zooplankton body size: large scale temporal and spatial analysis. *Ecography* 43: 581–590
 - ✦ Fields DM (2014) The sensory horizon of marine copepods. In: Seuront L (ed) *Copepods: diversity, habitat and behavior*. Nova Science Publishers, Hauppauge, NY, p 157–179
 - ✦ Fields DM, Shaeffer DS, Weissburg MJ (2002) Mechanical and neural responses from the mechanosensory hairs on the antennule of *Gaussia princeps*. *Mar Ecol Prog Ser* 227:173–186
 - ✦ Fields DM, Handegard NO, Dalen J, Eichner C and others (2019) Airgun blasts used in marine seismic surveys have
 - ✦ Aarflot JM, Skjoldal HR, Dalpadado P, Skern-Mauritzen M (2018) Contribution of *Calanus* species to the mesozoo-

- limited effects on mortality, and no sublethal effects on behaviour or gene expression, in the copepod *Calanus finmarchicus*. ICES J Mar Sci 76:2033–2044
- ✦ Gassie DV, Lenz PH, Yen J, Hartline DK (1993) Mechanoreception in zooplankton first antennae: electrophysiological techniques. Bull Mar Sci 53:96–105
- ✦ Goertner JF, Wiley ML, Young GA, McDonald WW (1994) Effects of underwater explosions on fish without swimbladders. Report No. NSWC TR 88-114. Naval Surface Warfare Center Dahlgren Division, White Oak Detachment, Silver Spring, MD
- ✦ Gordon J, Gillespie D, Potter J, Frantzis A, Simmonds M, Swift R, Thompson D (2003) A review of the effects of seismic surveys on marine mammals. Mar Technol Soc J 37:16–34
- ✦ Hays GC, Proctor CA, John AWG, Warner AJ (1994) Interspecific differences in the diel vertical migration of marine copepods: the implications of size, color, and morphology. Limnol Oceanogr 39:1621–1629
- ✦ Hovem JM, Tronstad TV (2012) Propagation of anthropogenic noise in the ocean. 35th Scandinavian Symposium on Physical Acoustics, Geilo, 29 January–1 February 2012. Norwegian Physical Society, Oslo
- ✦ Hygum B, Rey-Rassat C, Hansen B (2000) Growth and development rates of *Calanus finmarchicus* nauplii during a diatom spring bloom. Mar Biol 136:1075–1085
- ✦ ISO (International Organization for Standardization) (2017) ISO 18405:2017 Underwater acoustics – terminology. International Organization for Standardization, Vernier. <https://www.iso.org/standard/62406.html>
- ✦ Jonsson PR, Tiselius P (1990) Feeding behaviour, prey detection and capture efficiency of the copepod *Acartia tonsa* feeding on planktonic ciliates. Mar Ecol Prog Ser 60:35–44
- ✦ Kavanagh AS, Nykänen M, Hunt W, Richardson N, Jessopp MJ (2019) Seismic surveys reduce cetacean sightings across a large marine ecosystem. Sci Rep 9:19164
- ✦ Khodabandeloo B (2018) Modeling and characterizing acoustic signals from cavity clouds generated by marine seismic air-gun arrays: implications for marine mammals. PhD dissertation, Norwegian University of Science and Technology, Trondheim
- ✦ Khodabandeloo B, Landrø M, Hanssen A (2017) Acoustic generation of underwater cavities—Comparing modeled and measured acoustic signals generated by seismic air gun arrays. J Acoust Soc Am 141:2661–2672
- ✦ Kjørboe T, Andersen A, Langlois VJ, Jakobsen HH (2010a) Unsteady motion: escape jumps in planktonic copepods, their kinematics and energetics. J R Soc Interface 7: 1591–1602
- ✦ Kjørboe T, Jiang H, Colin SP (2010b) Danger of zooplankton feeding: the fluid signal generated by ambush-feeding copepods. Proc R Soc B 277:3229–3237
- ✦ Kjørboe T, Saiz E, Tiselius P, Andersen KH (2018) Adaptive feeding behavior and functional responses in zooplankton. Limnol Oceanogr 63:308–321
- ✦ Kok ACM, Berkhout BW, Carlson NV, Evans NP and others (2023) How chronic anthropogenic noise can affect wildlife communities. Front Ecol Evol 11:1130075
- ✦ Kühn S, King F, Heubel K (2023) Decreased feeding rates of the copepod *Acartia tonsa* when exposed to playback harbor traffic noise. Front Mar Sci 10:1134792
- ✦ Kvile KØ, Prokopchuk IP, Stige LC (2022) Environmental effects on *Calanus finmarchicus* abundance and depth distribution in the Barents Sea. ICES J Mar Sci 79: 815–828
- ✦ Lee RF, Hagen W, Kattner G (2006) Lipid storage in marine zooplankton. Mar Ecol Prog Ser 307:273–306
- ✦ Lenz PH, Hartline DK (2015) Mechanoreception in crustaceans of the pelagic realm. In: Derby C, Thiel M (eds) Nervous systems and control of behavior. The natural history of the crustacea, Vol 3. Oxford University Press, New York, NY, p 293–320
- ✦ Lindeque PK, Parry HE, Harmer RA, Somerfield PJ, Atkinson A (2013) Next generation sequencing reveals the hidden diversity of zooplankton assemblages. PLOS ONE 8: e81327
- ✦ McCauley RD, Duncan AJ (2017) How do impulsive marine seismic surveys impact marine fauna and how can we reduce such impacts? In: ACOUSTICS 2017—sound, science and society. Proc Annu Conf Acoust Aust, Perth, 19–22 November 2017. The Australian Acoustical Society, Perth
- ✦ McCauley RD, Day RD, Swadling KM, Fitzgibbon QP, Watson RA, Semmens JM (2017) Widely used marine seismic survey air gun operations negatively impact zooplankton. Nat Ecol Evol 1:195
- ✦ McCauley RD, Meekan MG, Parsons MJG (2021) Acoustic pressure, particle motion, and induced ground motion signals from a commercial seismic survey array and potential implications for environmental monitoring. J Mar Sci Eng 9:571
- ✦ Mellen RH (1954) Ultrasonic spectrum of cavitation noise in water. J Acoust Soc Am 26:356–360
- ✦ Merchant ND, Putland RL, André M, Baudin E, Felli M, Slabekoom H, Dekeling R (2022) A decade of underwater noise research in support of the European Marine Strategy Framework Directive. Ocean Coast Manag 228: 106299
- ✦ Munson BR, Young DF, Okiishi TH (2002) Fundamentals of fluid mechanics, 4th edn. John Wiley & Sons,
- ✦ Nedelec SL, Campbell J, Radford AN, Simpson SD, Merchant ND (2016) Particle motion: the missing link in underwater acoustic ecology. Methods Ecol Evol 7: 836–842
- ✦ Parry GD, Heislors S, Werner GF, Asplin MD, Gason A (2002) Assessment of environmental effects of seismic testing on scallop fisheries in Bass Strait. MFRI Rep 50. Marine and Freshwater Resources Institute, Queenscliff
- ✦ Pearson WH, Skalski JR, Sulkin SD, Malme CI (1994) Effects of seismic energy releases on the survival and development of zoeal larvae of Dungeness crab (*Cancer magister*). Mar Environ Res 38:93–113
- ✦ Pinti J, DeVries T, Norin T, Serra-Pompei C and others (2023a) Model estimates of metazoans' contributions to the biological carbon pump. Biogeosciences 20: 997–1009
- ✦ Pinti J, Jónasdóttir SH, Record NR, Visser AW (2023b) The global contribution of seasonally migrating copepods to the biological carbon pump. Limnol Oceanogr 68: 1147–1160
- ✦ Plesset MS (1970) Effect of dissolved gases on cavitation in liquids. Rep 85-55. Division of Engineering and Applied Science, California Institute of Technology, Pasadena, CA
- ✦ Popper AN, Hawkins A (eds) (2016) The effects of noise on aquatic life II. Springer, New York, NY
- ✦ Popper AN, Hawkins AD (2019) An overview of fish bioacoustics and the impacts of anthropogenic sounds on fishes. J Fish Biol 94:692–713

- ✦ Prior MK, Ainslie MA, Halvorsen MB, Hartstra I and others (2021) Characterization of the acoustic output of single marine-seismic airguns and clusters: the Svein Vaage dataset. *J Acoust Soc Am* 150:3675–3692
- ✦ Prosperetti A, Lezzi A (1986) Bubble dynamics in a compressible liquid. Part 1. First-order theory. *J Fluid Mech* 168:457–478
- R Core Team (2022) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- ✦ Rotolo F, Vitiello V, Pellegrini D, Carotenuto Y, Buttino I (2021) Historical control data in ecotoxicology: eight years of tests with the copepod *Acartia tonsa*. *Environ Pollut* 284:117468
- ✦ Schneider CA, Rasband WS, Eliceiri KW (2012) NIH Image to ImageJ: 25 years of image analysis. *Nat Methods* 9: 671–675
- ✦ Skottene E, Tarrant AM, Altin D, Olsen RE, Choquet M, Kvile KØ (2020) Lipid metabolism in *Calanus finmarchicus* is sensitive to variations in predation risk and food availability. *Sci Rep* 10:22322
- ✦ Slabbekoorn H, Dalen J, de Haan D, Winter HV and others (2019) Population-level consequences of seismic surveys on fishes: an interdisciplinary challenge. *Fish Fish* 20: 653–685
- ✦ Solé M, Lenoir M, Fortuño JM, De Vreese S, van der Schaar M, André M (2021) Sea lice are sensitive to low frequency sounds. *J Mar Sci Eng* 9:765
- ✦ Solé M, Kaifu K, Mooney TA, Nedelec SL and others (2023) Marine invertebrates and noise. *Front Mar Sci* 10:1129 057
- ✦ Sullivan BK, Costello JH, Van Keuren D (2007) Seasonality of the copepods *Acartia hudsonica* and *Acartia tonsa* in Narragansett Bay, RI, USA during a period of climate change. *Estuar Coast Shelf Sci* 73:259–267
- ✦ Svetlichny L, Larsen PS, Kiørboe T (2020) Kinematic and dynamic scaling of copepod swimming. *Fluids* 5:68
- ✦ Thode A, Kim KH, Greene CR Jr, Roth E (2010) Long range transmission loss of broadband seismic pulses in the Arctic under ice-free conditions. *J Acoust Soc Am* 128: EL181–EL187
- ✦ Todd VLG, Todd IB, Gardiner JC, Morrin ECN, MacPherson NA, DiMarzio NA, Thomsen F (2015) A review of impacts of marine dredging activities on marine mammals. *ICES J Mar Sci* 72:328–340
- ✦ van Duren LA, Videler JJ (1995) Swimming behaviour of developmental stages of the calanoid copepod *Temora longicornis* at different food concentrations. *Mar Ecol Prog Ser* 126:153–161
- Vereide EH, Kühn S (2023) Effects of anthropogenic noise on marine zooplankton. In: Popper AN, Sisneros J, Hawkins AD, Thomsen F (eds) *The effects of noise on aquatic life: principles and practical considerations*. Springer, Cham, p 1–24
- ✦ Vereide EH, Mihaljevic M, Browman HI, Fields DM, Agersted MD, Titelman J, de Jong K (2023) Effects of airgun discharges used in seismic surveys on development and mortality in nauplii of the copepod *Acartia tonsa*. *Environ Pollut* 327:121469
- ✦ Versluis M, Schmitz B, von der Heydt A, Lohse D (2000) How snapping shrimp snap: through cavitating bubbles. *Science* 289:2114–2117
- ✦ Visser AW, Mariani P, Pigolotti S (2008) Swimming in turbulence: zooplankton fitness in terms of foraging efficiency and predation risk. *J Plankton Res* 31:121–133
- ✦ Weilgart L (2013) A review of the impacts of seismic airgun surveys on marine life. CBD Expert Workshop on Underwater Noise and its Impacts on Marine and Coastal Biodiversity, London, 25–27 February 2014. Secretariat of the Convention on Biological Diversity, Montreal
- ✦ Williams R, Wright AJ, Ashe E, Blight LK and others (2015) Impacts of anthropogenic noise on marine life: publication patterns, new discoveries, and future directions in research and management. *Ocean Coast Manag* 115: 17–24
- ✦ Zarubin M, Lindemann Y, Brunner O, Fields DM, Browman HI, Genin A (2016) The effect of hydrostatic pressure on grazing in three calanoid copepods. *J Plankton Res* 38: 131–138
- ✦ Ziolkowski A, Parkes G, Hatton L, Haugland T (1982) The signature of an air gun array: computation from near-field measurements including interactions. *Geophysics* 47:1413–1421

Appendix.

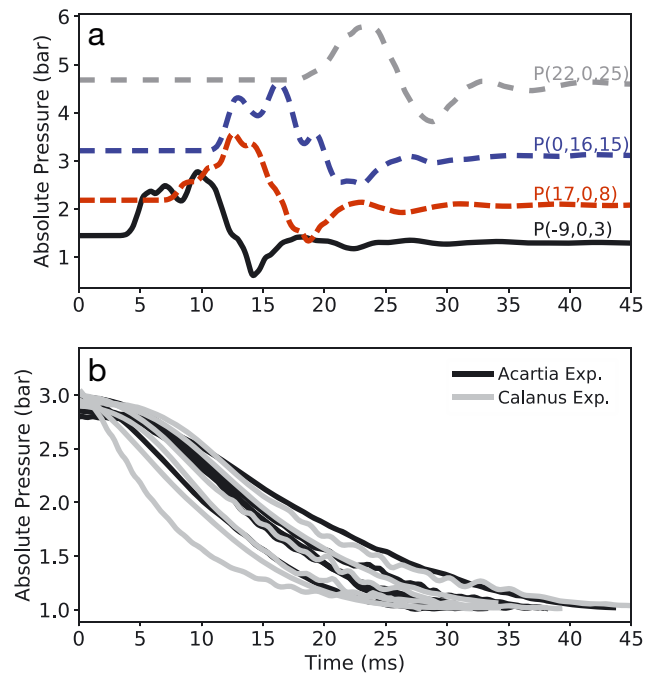
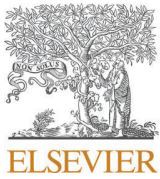


Fig. A1. (a) Modeled absolute pressure variation (bar) at 4 different points located at (x, y, z) around the 2730 in^3 ($\sim 44737 \text{ cm}^3$) airgun array (x [m], the direction the airgun travels; y [m], starboard direction; and z [m], the water depth measured from the water surface). (b) Maximum absolute pressure following the rapid release in the pressure exposure treatments in *Acartia* sp. and *Calanus* sp.

Editorial responsibility: Shin-ichi Uye,
Higashi-Hiroshima, Japan
Reviewed by: L. Prosnier and 2 anonymous referees

Submitted: June 30, 2023
Accepted: December 20, 2023
Proofs received from author(s): March 3, 2024

IV



Effects of airgun discharges used in seismic surveys on development and mortality in nauplii of the copepod *Acartia tonsa*[☆]

Emilie Hernes Vereide^{a,*}, Marina Mihaljevic^b, Howard I. Browman^c, David M. Fields^d,
Mette Dalgaard Agersted^e, Josefin Titelman^f, Karen de Jong^a

^a Institute of Marine Research, Ecosystem Acoustics Group, Nykirkekaien 1, NO-5004 Bergen, Norway

^b Institute of Marine Research, Austevoll Research Station, Sauganeset 16, NO-5392 Storebø, Norway

^c Institute of Marine Research, Ecosystem Acoustics Group, Austevoll Research Station, Sauganeset 16, NO-5392 Storebø, Norway

^d Bigelow Laboratory for Ocean Sciences, 60 Bigelow Drive, P.O. Box 380 East Boothbay, ME, 04544, USA

^e Aarhus University, Department of Ecoscience, Frederiksborgvej 399, 4000 Roskilde, Denmark

^f University of Oslo, Department of Biosciences, PO BOX 1066 Blindern, NO-0316 Oslo, Norway

ARTICLE INFO

Keywords:

Anthropogenic noise
Noise pollution
Seismic surveys
Zooplankton
Copepods
Acartia

ABSTRACT

Seismic surveys are conducted worldwide to explore for oil and gas deposits and to map subsea formations. The airguns used in these surveys emit low-frequency sound waves. Studies on zooplankton responses to airguns report a range of effects, from none to substantial mortality. A field experiment was conducted to assess mortality and naupliar body length of the calanoid copepod *Acartia tonsa* when exposed to the discharge of two 40-inch airguns. Nauplii were placed in plastic bags and attached to a line at a depth of 6 m. For each treatment, three bags of nauplii were exposed to one of three treatments for 2.5 h: Airgun array discharge, a boat control, or a silent control. After exposure, nauplii were kept in filtered seawater in the laboratory without food. Immediate mortality in the nauplii was approximately 14% compared to less than 4% in the silent and boat control. Similarly, there was higher mortality in the airgun exposed nauplii up to six days after exposure compared to the control treatments. Nearly all of the airgun exposed nauplii were dead after four days, while >50% of the nauplii in the control treatments were alive at six days post-exposure. There was an interaction between treatment and time on naupliar body length, indicating lower growth in the nauplii exposed to the airgun discharge (growth rates after 4 days: 1.7, 5.4, and 6.1 $\mu\text{m d}^{-1}$ in the airgun exposed, silent control, and boat control, respectively). These experiments indicate that the output of two small airguns affected mortality and growth of the naupliar stages of *Acartia tonsa* in close vicinity to the array.

1. Introduction

Anthropogenic underwater noise, such as that generated by boat traffic or seismic surveys, is an increasingly important source of environmental stress for marine organisms (Hildebrand, 2009; Fritschi et al., 2011; Swaddle et al., 2015; Cox et al., 2018; Duarte et al., 2021). In the Norwegian Exclusive Economic Zone alone, more than 18000 vessel $\text{km}^2 \text{yr}^{-1}$ are covered by seismic surveys (NDP, 2021). Seismic airguns rapidly release high-pressure air (airgun discharge) to generate an acoustic signal dominated by frequencies lower than 200 Hz, and their output has been recorded over 4000 km away from the source (Kavanagh et al., 2019).

Most studies on the possible impacts of seismic surveys on marine organisms have focused on fish and mammals (Gordon et al., 2003; Slabbekoorn et al., 2019). Seismic surveys interfere with the social interactions, behavior, and orientation of marine mammals and fish with well-developed auditory systems (Engås et al., 1996; Gordon et al., 2003; Cox et al., 2018; Popper and Hawkins, 2019). Some studies have also demonstrated increased mortality and damage in fish (Carroll et al., 2017) and fish larvae (Kostyuchenko, 1973; Booman et al., 1996) exposed to airgun discharges.

Few studies have investigated the effects of seismic survey activity on zooplankton (Solé et al., 2023). The results are contradictory and suggest species- and stage-specific responses and the need for standardized

[☆] This paper has been recommended for acceptance by Sarah Harmon.

* Corresponding author.

E-mail address: emilie.hernes.vereide@hi.no (E.H. Vereide).

<https://doi.org/10.1016/j.envpol.2023.121469>

Received 13 September 2022; Received in revised form 12 March 2023; Accepted 19 March 2023

Available online 22 March 2023

0269-7491/© 2023 The Authors. Published by Elsevier Ltd. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

Table 1
Summary of previous studies on the effects of seismic surveys on zooplankton.

Study	Zooplankton group	Measured parameters	Level of effects	Sound type	Received sound level (MD/MS) ^a		Distance from the source (m)	Size and number of airgun (s) (vol/pressure)
					Sound pressure (kPa) (ptp/ztp) ^b	SEL (dB re 1 μPa^2 s)		
Copepods:								
McCauley et al., 2017	Various, <i>in situ</i> samples	Mortality	High	Live	1.4 (509–658 m), 0.8 (1.1–1.2 km) (MS) (ptp)	156 (509–658 m), 153 (1.1–1.2 km) (MS)	71–1300	1*150 inch ³ /13.8 MPa
Fields et al., 2019	Large copepods (<i>Calanus finmarchicus</i>)	Mortality, behavior, gene expression	Little to no effect	Live	1363 (0 m) (MS) (ztp)	221 (0 m), 183 (25 m) (MS)	0–25	2*260 inch ³ /13–14.4 MPa
This study	Small copepods (<i>Acartia tonsa</i>)	Mortality, growth	Little	Live	48.9 (50 m) (MS) (ptp)	180 (50 m), 166 (1100 m) (MS)	50–1200	2*40 inch ³ /11 MPa
Bivalve larvae:								
Parry et al., 2002	Scallop larvae (and adult)	Mortality, population/catch rates	No effect	Live	Not given	Not given	~11–600	Airgun (24) array of total 3542 inch ³ /not given
de Soto et al., 2013	Scallop larvae	Development, abnormalities	High	Recorded	Not given	161 to 165 (MD)	0.05–0.1	Airgun array of total 6920 inch ³ /not given
Other crustacean larvae:								
Pearson et al., 1994	Crab larvae (zoea)	Mortality and development	No effect	Live	316.2 (max, 1 m) (MS) (ptp)	Not given	1–10	7 airguns, total volume 840 inch ³ /not given
Day et al., 2016 ^c	Lobster larvae	Fecundity, morphology, competency	No effect	Live	141.3 to 223.9 (MS) (ptp)	186 to 190 (max) (MS)	~0–1000	1*45–150 inch ³ /13.8 MPa (max)

^a MD: Modeled, or MS: Measured.

^b The sound pressure levels (kPa) were given as either peak-to-peak (ptp), or zero-to-peak (ztp). From the studies demonstrating sound pressure levels in dB, the calculation to Pa was made using the following equation.

$$p(\text{Pa}) = p_0 \cdot 10^{\frac{L_p(\text{dBSPL})}{20}}$$

^c The adult females were exposed, whereas the effects were measured in hatched larvae.

methodological approaches (Table 1). Fields et al. (2019) reported a small, localized impact from the discharge of a two airgun array on the copepod *Calanus finmarchicus*, a key species in North Atlantic waters (Fields et al., 2019). The immediate mortality increased by less than 10% in animals close to the airguns (<5 m), followed by a nominal

increase in mortality 7 days after exposure, but again, only at close range (<5 m). The zoea of Dungeness crab (*Metacarcinus magister*) experienced only 0–2% immediate mortality and no longer-term effects of exposure to airgun discharges (Pearson et al., 1994). In contrast, McCauley et al. (2017) reported a two-to three-fold increase in dead zooplankton, both

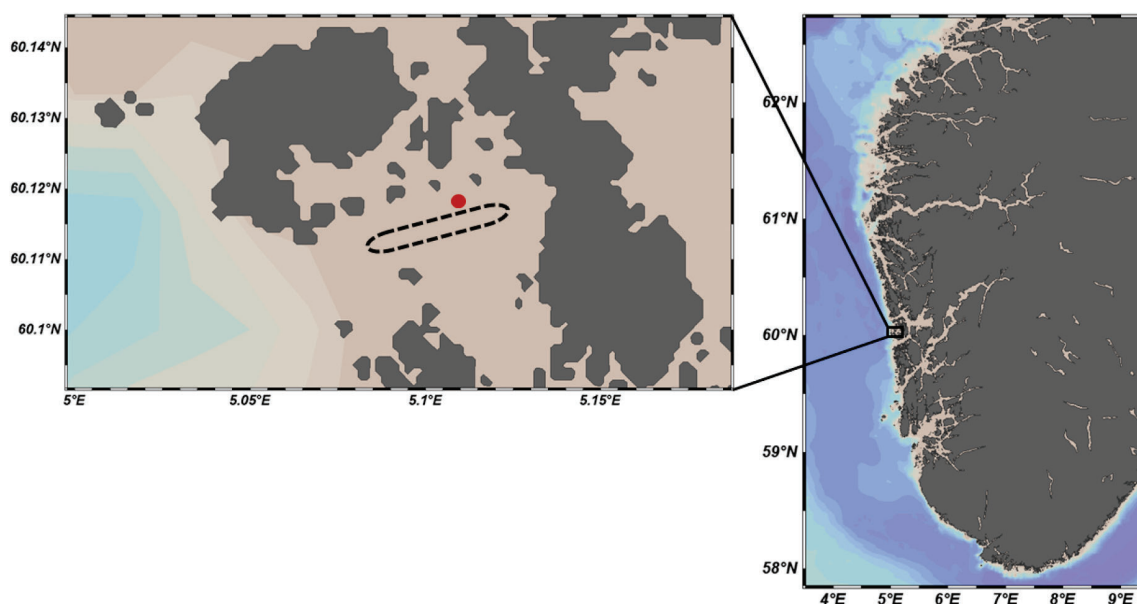


Fig. 1. Study area. On the left, the location where the zooplankton were exposed is indicated with a red circle. A dotted black line denotes the transect of the vessel towing the airgun array. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Table 2

Environmental conditions during the field experiment to expose *Acartia tonsa* nauplii to a silent control, a boat control, or an airgun array discharge. The temperature and light at 6 m depth are the averages during the exposure time. *The bags in the airgun array treatment were deployed in the water at 16:00, but the airgun array shooting did not start until 17:00.

Date	Treatment	Nauplii/bag (mean \pm SD)	Bags exposure time	Secchi depth (m)	Temp. surface ($^{\circ}$ C)	Temp. 6 m ($^{\circ}$ C)	Light 6 m (lux, lm/m ²)
15.2.21	Airgun array	1500 \pm 156	17:00*-19:35	11.0	2.5	3.1	76
16.2.21	Boat control	2014 \pm 253	14:01-16:45	13.0	2.4	3.3	379
19.2.21	Silent control	331 \pm 130	10:16-13:00	11.0	2.4	3.2	1066

larvae and adults, after exposure to one airgun in the field. These negative impacts were observed up to the maximum sampling range of 1200 m (McCauley et al., 2017).

In addition to the direct effects of the airgun discharge on mortality, sublethal effects include altered developmental rates and morphological deformities. For example, snow crab (*Chionoecetes opilio*) eggs (Christian et al., 2003), lobster juveniles (*Jasus edwardsii*) (Day et al., 2022), and larval scallops (*Pecten novaezelandiae*) (de Soto et al., 2013) developed slower than the control groups after exposure to seismic airguns and exhibited morphological abnormalities. These effects are species- and stage-specific, as is also the case for mortality (Pearson et al., 1994; Day et al., 2016).

Given the limited number of studies on the effects of airgun exposure on zooplankton, particularly on the juvenile stages, and the contradictory results of the few published reports, more knowledge is needed to understand potential impacts. This study aimed to test the effects of airgun discharge on immediate and delayed mortality and growth in the nauplii of a marine copepod (*Acartia tonsa* Dana).

2. Materials and methods

The effects of airgun array discharges used in seismic surveys were investigated by exposing *Acartia tonsa* nauplii to the discharge of an airgun array in a controlled experiment with three treatments (silent control, boat control, and airgun array). After exposure, immediate and delayed mortality (1–6 days after exposure) and naupliar growth were investigated. The experiments were conducted during winter 2021 at Austevoll Research Station (Institute of Marine Research, Norway), and copepods were exposed to the discharge of a seismic airgun array in Bakkasund, Austevoll (60.116667°N, 5.11°E) (Fig. 1, Table 2).

2.1. Experimental animals

Acartia tonsa is an epipelagic calanoid copepod that is commonly

found in Norwegian waters and is widely distributed worldwide, especially in near-shore and estuarine areas (Cervetto et al., 1999). This species has a high tolerance to salinity and temperature changes (Sunar and Kir, 2021). In the North Atlantic coastal waters, *Acartia* sp. is frequently among the common zooplankton in spring and summer and serves as an important food source for many commercial fish species (Sullivan et al., 2007).

2.2. Egg hatching

Several cultures of *Acartia tonsa* were established from resting eggs (sourced from C-Feed AS; Trondheim, Norway). To produce nauplii for the experiments, a portion of the eggs was incubated in 80 L tanks with 0.2 μ m filtered seawater (FSW) at 21 $^{\circ}$ C under heavy aeration until hatching (according to the manufacturer's instructions). After 24 h, nauplii were transferred to gently aerated 5 L tanks, in which the temperature was slowly adjusted (-0.3 $^{\circ}$ C h⁻¹) to 6 $^{\circ}$ C (i.e., the temperature in the sea at the exposure site) over the next 48 h (Table 2).

2.3. Experimental setup

2.3.1. Before exposure

On each treatment day (Table 2), newly hatched nauplii were transferred from the culture to three experimental bags (50 \times 18 cm). Because of the short hatching time it was necessary to use different batches of eggs each day (i.e., for each treatment). These batches varied in the number of nauplii produced. Therefore, the number of nauplii differed between treatments (Table 2). Bags (~1 L) were filled with 0.2 μ m FSW with no head space. The bags were sealed, attached at 0.5 m intervals to an 8-m long line, and transported in a soundproof box to the experimental site (Figs. 1 and 2). A temperature/light data logger (HOBO Pendant® MX) was attached to this line. The line was suspended at a depth of 6 m between two buoys at a distance of 50 m from one edge of the transect of the vessel towing the seismic airgun array (Figs. 1 and

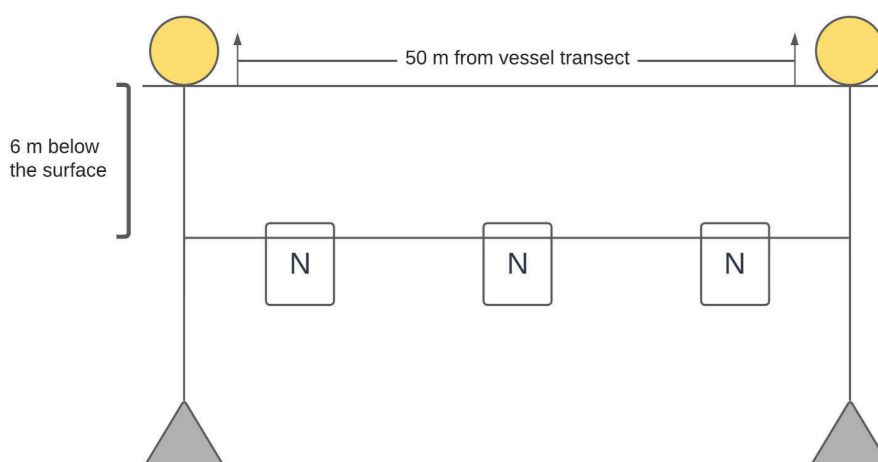


Fig. 2. A schematic diagram showing the field setup used to expose *Acartia tonsa* nauplii to either a silent control, a boat control, or an airgun array discharge. Buoys (circles) with attached weights (triangles) were located at a 50 m distance at the closest, parallel to the ship transect. The line with the bags was attached at 6 m depth. The bags were attached to the line every 0.5 m.

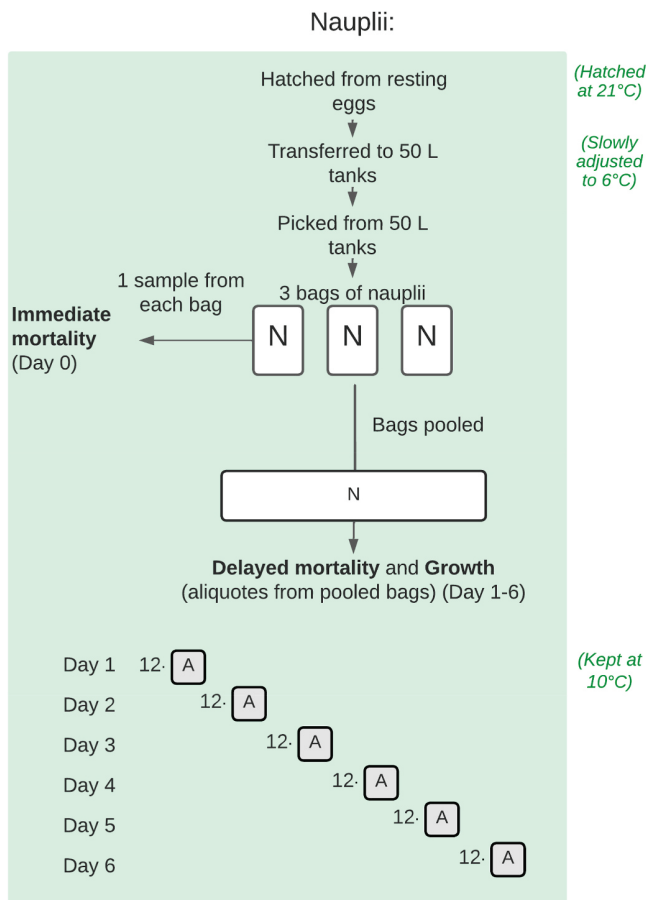


Fig. 3. Overview of the number of bags, samples, and endpoints of nauplii of *Acartia tonsa* for each treatment (silent control, boat control, airgun array). Immediate mortality was measured from 3 replicates (one from each bag) immediately after exposure. Delayed mortality and growth were measured from 12 aliquots from the pooled bags for each treatment and each day after exposure (1–6 days).

Table 3

Overview of statistical tests. a) Binomial GLM on the effect of treatment (silent control, boat control, airgun array) on immediate mortality in *Acartia tonsa* nauplii ($n = 9$), and b) Kruskal-Wallis on the effect of treatment on the proportion of dead nauplii for each day separately, up to 6 days after exposure (delayed mortality) ($n_{\text{aliquots per day}} = 29\text{--}36$). c) LMM on the effect of treatment (silent control, boat control, airgun array) on individual *Acartia tonsa* body length (μm) ($n_{\text{individual}} = 356$ (silent control), 392 (boat control), 167 (airgun array), and d) Pearson's Correlation Coefficient test on the correlation between body length and developmental stages in nauplii ($n_{\text{individual}} = 915$).

	Effects	Estimate	SE	z	P
a) Immediate mortality	(Intercept)	3.34	0.18	18.82	<2e-16
	Treatment: Boat	0.22	0.20	1.11	0.27
	Treatment: Airgun array	-1.60	0.19	-8.53	<2e-16
b) Delayed mortality	Days after treatment	-	-	χ^2	P
	Day 1	-	-	27.87	8.90e-07
	Day 2	-	-	16.43	2.70e-04
	Day 3	-	-	22.44	1.34e-05
	Day 4	-	-	23.04	9.95e-06
	Day 5	-	-	32.56	8.51e-08
	Day 6	-	-	22.53	1.28e-05
c) Body length	Effects	Estimate	SE	95% CI (min/max)	
	(Intercept)	124.028	2.47	119.27/128.80	
	Treatment: Boat	-5.57	3.43	-12.20/1.05	
	Treatment: Airgun array	-4.61	3.88	-12.13/2.89	
	Day	5.40	0.90	3.66/7.14	
	Interaction of Boat with Day	0.70	1.27	-1.75/3.16	
Interaction of Airgun array with Day	-3.69	1.47	-6.53/-0.84		
d) Body length and stage	Correlation coefficient			Df	P
	0.91			903	<2.2e-16

2).

2.3.2. Treatments

The experiment consisted of three treatments: Exposure to multiple discharges from two airguns (the "airgun array"), a boat control, and a silent control. The airgun array treatment consisted of two small airguns (40 inch³, HGS Sleeve Guns) fired at a pressure of 110 bar every 10 s for 3 h. The airgun array was towed at 2 knots at a depth of 3–4 m along an oval transect (3 nmi in total) by the research vessel "H. U. Sverdrup II", for another study (McQueen et al., 2022). The vessel sailed between 50 m and 1220 m from the line holding the bags (Fig. 1). During the boat control treatment, H.U. Sverdrup followed the same transect without discharging the airguns. The boat control treatment was included to control for the sound generated by the vessel itself. During the silent control treatment, H.U. Sverdrup was outside the area. Exposure lasted for approximately 2.5 h (see Table 2 for details). After each exposure (Table 2), bags for each treatment were recovered and transported to the laboratory in a sound-absorbing box. During all treatments, the weather was partly cloudy, wind speed was 6–7 m/s, and wave height was 0.5–1 m. The air temperature ranged from 7 to 12 °C during all three days.

2.4. Analysis of animals exposed to the different treatments

Copepods were counted and sorted using a Leica stereomicroscope (Leica Microsystems, Switzerland, Stereozoom S9i). Morphometrics were measured from photos taken with an AirLab 2.0 Leica Microsystems equipped with a Leica CLS150 LED light.

2.4.1. Naupliar mortality

Immediate mortality of the nauplii was measured within 2 h of returning to the laboratory (<4 h after exposure). Samples (50–100 ml) from each nauplii bag were removed and the number of live and dead individuals was quantified under a stereomicroscope (Olympus SZX10), carefully stimulating the animals with water movements to check for signs of life. To investigate delayed mortality for each treatment, 72 aliquots of 8 nauplii each (7.5 ± 2.2) were transferred to individual 15 ml-wells (6 wells/plate, Nunc A/S Denmark) with 0.2 μm FSW. The well plates were incubated at 10 °C to limit the increase in temperature after exposure under a 12:12 h light-dark cycle for 1–6 d after exposure. No food was added during this experiment to avoid confounding effects of

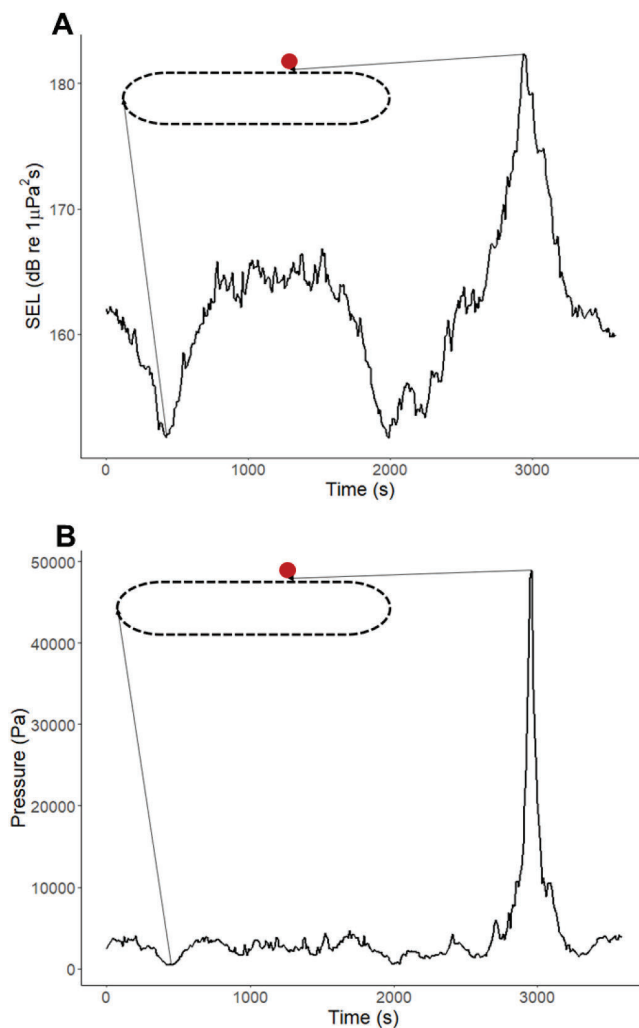


Fig. 4. Sound pressure levels during the airgun array exposure. A) The sound exposure level (SEL) and B) the peak-to-peak sound pressure level (Pa) as a function of time (s) during the airgun array exposure. The dotted line indicates the trajectory of the vessel, and the red dot indicates the location of the nauplii, from where the arrows demonstrate the sound pressure level and sound exposure level at selected distances from the vessel. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

variation in feeding between individuals and/or aliquots. Within the experimental time of six days, some individuals would most likely develop into stage III (at which *Acartia tonsa* nauplii begin to feed) and, therefore, these nauplii would eventually die of starvation. However, since the study's objective was to test the effect of treatment on the first naupliar stages, and not on later development, this did not impact the evaluation. Dead and live nauplii were counted on each consecutive day in 12 of the 72 wells: 12 new wells each day (Fig. 3). After counting, the developmental stage of the nauplii was scored, the nauplii were photographed, and body length was measured from the photos.

2.4.2. Body length and development

The naupliar developmental stage of both dead and live individuals was scored according to Murphy and Cohen (1978), and body length (μm) was measured from the micrographs using ImageJ (ImageJ 1.53e) (Schneider et al., 2012). Body length and developmental stage were measured for all individuals from days 1–6 after exposure. However, as all airgun-exposed individuals had died by day 5 and only live animals

were included in this analysis, differences in growth and development between the treatments could only be tested for days 1 to day 4. Growth rates were calculated from model estimates (described below). Because different individuals were measured at each time point, growth rates represent the average body weight/length differences over time.

2.5. Data analysis

All data analyses were conducted using the R statistical software (R Core Team, 2022). Before conducting statistical tests, all data were graphically assessed for normality. The effect of treatment on immediate mortality was tested using the proportion of live nauplii versus the proportion of dead nauplii (Fig. 3) as a dependent variable and treatment (silent control, boat control, airgun array) as a fixed effect in a binomial GLM ($n = 9$, one subsample obtained from each of the three bags for each treatment) (Fig. 5) (Table 3). It was not possible to test the effect of treatment on delayed mortality using a binomial GLM because of overdispersion. Therefore, we tested the effect of treatment on the proportion of dead individuals using a Kruskal-Wallis test for each day separately (1–6 days after exposure; 29–36; aliquots per day) (Fig. 5) (Table 3). The number of nauplii within each aliquot (individual wells) was $7.5 (\pm 2.2)$. Aliquots with <5 individuals (9.5% of the samples) were excluded from the analyses, therefore, the total number of aliquots per treatment varied ($n_{\text{aliquot}} = 64$ (silent control), 66 (boat control), 61 (airgun array)). The effect of treatment on naupliar body length (μm) was tested using a Linear Mixed-Effects Model (LMM). In this model the body length for each individual is a dependent variable, with aliquot as a random factor, and the treatment (silent control, boat control, airgun array), the number of days after exposure (days 1–4), and the interaction between these two variables, as fixed effects (Table 3) ($n_{\text{individual}} = 356$ (silent control), 392 (boat control), 167 (airgun array); $n_{\text{aliquot}} = 48$ (silent control), 48 (boat control), 45 (airgun array)) (Fig. 6, Table 3). The relationship between body length and developmental stage (NI–NIV) was tested using Pearson's Correlation Coefficient Test on all individuals. ($n_{\text{individual}} = 915$). For all analyses, the model assumptions were verified by a visual assessment of the fitted values versus the residuals.

3. Results

3.1. Sound measurements

The sound pressure level (kPa) ranged from 0.420 kPa at the furthest distance from the nauplii (~ 1200 m) to a maximum of 48.90 kPa at the closest distance (50 m) (Fig. 4A). The sound exposure level (SEL) was 152 dB re $1 \mu\text{Pa}^2 \text{s}$ furthest away and 183 dB re $1 \mu\text{Pa}^2 \text{s}$ at the closest distance (Fig. 4B). The sound exposure levels were reported for each second, the seconds without airgun blasts corresponded to the sound level in the boat control. Ambient sound levels during the experiment were between approximately 40 and 100 dB re $1 \mu\text{Pa}^2 \text{s/Hz}$ (McQueen et al., 2022).

3.2. Mortality

3.2.1. Immediate mortality of nauplii

The immediate mortality was significantly higher in the airgun array treatment than in the silent and boat control treatments (Fig. 5A, Table 3). On average, $13.5 \pm 3.8\%$ of the nauplii in the airgun array exposed treatment died immediately after exposure, compared to $3.4 \pm 1.3\%$ in the silent control and $2.6 \pm 1.7\%$ (mean \pm SD) in the boat control.

3.2.2. Delayed mortality of nauplii

There was a significant difference in delayed mortality between the treatments (Fig. 5B, Table 3). On days 1 and 2 after exposure, nearly all of the nauplii from the control groups were alive, while $27.0 \pm 14.2\%$

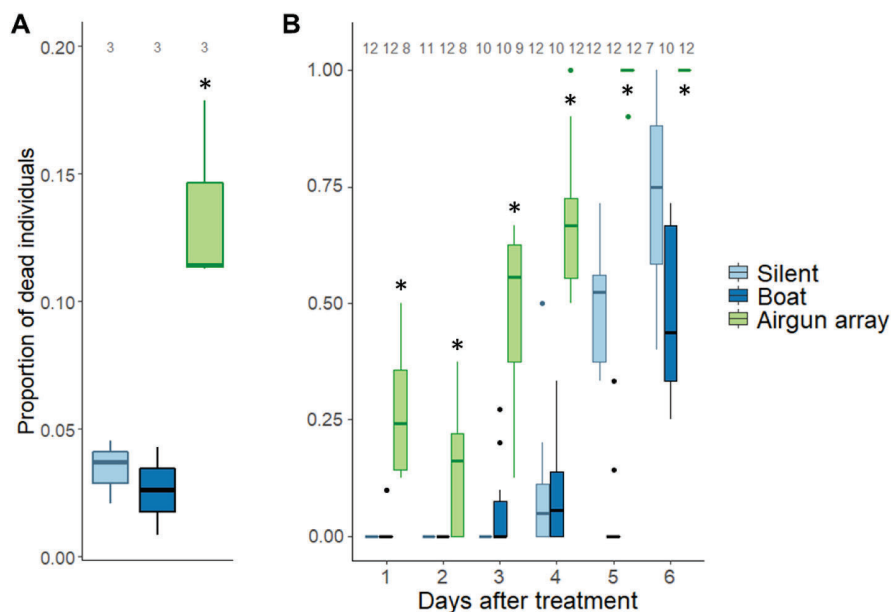


Fig. 5. The mortality of *Acartia tonsa* nauplii after experimental exposure to a silent control, a boat control, or an airgun array. A) Immediate mortality within 4 h of exposure, and B) delayed mortality from days 1–6 after exposure. Significance between treatments is noted with black asterisks. The total number of aliquots counted for each treatment per day is noted at the top of the figure. The horizontal lines indicate the median, and boxes indicate the 25th percentile (lower quartile), and the 75th percentile (upper quartile).

and $14.8 \pm 14.2\%$ of the airgun array exposed nauplii had died in the aliquots from day 1 and day 2, respectively. Mortality started occurring from day 3 ($5.7 \pm 10.1\%$, boat control) and 4 ($9.4 \pm 14.4\%$, silent control) in the control treatments but with lower mortality than in the airgun array exposed treatment (day 3, $47.5 \pm 19.2\%$ dead nauplii). In the aliquots from days 5 and 6 after the treatments, almost all of the airgun array exposed nauplii were dead, in contrast to the control groups, in which the proportion of dead nauplii was $49.2 \pm 12.0\%$ on day 5, and $72.6 \pm 21.8\%$ day 6 in the silent control and $4.0 \pm 10.1\%$ on day 5 and $48.4 \pm 17.9\%$ on day 6 in the boat control.

3.3. Growth and development

There was a significant interaction between treatment and time (days) on the body length (μm) of the nauplii, with lower growth from day 1–4 in the airgun array exposed treatment than in the control treatments (Fig. 6, Table 3). On day 1 after treatment, the average body length was $125 \pm 10 \mu\text{m}$. After 4 days, the average body length in the airgun array exposed nauplii was $128 \pm 7 \mu\text{m}$, which differed from the silent control ($144 \pm 8 \mu\text{m}$) and the boat control ($146 \pm 7 \mu\text{m}$). Over the first 4 days after exposure, the growth rates were 1.7 (4.1% in total), 5.4 (12.5%), and $6.1 \mu\text{m d}^{-1}$ (18.7%) in the airgun array exposed, silent control, and boat control, respectively.

Naupliar development stages (NI–NIV) were positively correlated with body length (μm) (Table 3). In all treatments, $>50\%$ of the nauplii reached stage NII one day after exposure. By day 4, $43 \pm 26.9\%$ of the airgun array exposed nauplii were still in NI, compared with $11 \pm 12.7\%$ in the silent control and $1 \pm 3.6\%$ in the boat control. Only four individuals reached stage NIV: 3 in the silent control and 1 in the boat control (Fig. 6).

4. Discussion

4.1. Effects on mortality and development

There were statistically significant effects of airgun discharges on mortality and development of *Acartia* nauplii. This is consistent with previous studies reporting that zooplankton in close proximity to an airgun discharge incurred higher immediate and delayed mortality than unexposed groups (Table 1, references therein). Although we did not test the effects of distance from the airgun, previous studies suggest that the

impact may be limited to relatively close proximity (Fields et al., 2019).

The results observed here are consistent with many previous studies that show small effects of airgun discharges on zooplankton mortality (Table 1). For example, no effects were detected in bivalve larvae sampled 2 km away from the source after exposure to airgun discharges (Parry et al., 2002) or in adult scallops (*Pecten fumatus*) sampled up to 1 km from the source shortly after exposure (Harrington et al., 2010). Similarly, Fields et al. (2019) reported that the mortality of *C. finmarchicus* adults to a two airgun array discharge increased ($<5\%$) compared to that of the control groups, but only at < 10 m from the airguns and no effects at distances from 10 to 50 m (Fields et al., 2019). There are also notable differences in these results from previous studies. For example, in contrast to Fields et al. (2019), this study found significantly higher mortality in the exposed animals compared to the controls at distances of 50–1200 m. Although the sound exposure levels were higher in Fields et al. (2019) than those in this study, the animals in this study were exposed to multiple airgun discharges that resulted in a cumulative exposure that lasted much longer (Table 2). The cumulative exposure of multiple blasts coupled with the younger stage used in this study may help to explain the higher mortality. Despite the higher mortality, the immediate mortality observed in this study is much lower than the 50% mortality in zooplankton at > 1 km from the source (McCauley et al., 2017). Even though the absolute immediate mortality was lower than that reported by McCauley et al. (2017), the relative increase in mortality compared to the controls was somewhat greater in this study ($>$ threefold increase) than in McCauley et al. (2017) (two- to threefold increase). However, in McCauley et al. (2017), the mortality in the controls was $\sim 20\%$ compared to less than 4% in this study. In this study, the mortality rate in nauplii directly after exposure was lower than the natural mortality rates observed in *Acartia* nauplii (up to 0.35 d^{-1}), although this is dependent on temperature, season, and region (Elliott and Tang, 2011). This indicates that the population-level effect of airgun exposure might not be detectable from the background mortality.

Studies on delayed mortality in zooplankton after airgun discharges are scarce. Day et al. (2017) reported increased mortality in scallops 14 days after exposure to airgun discharges, but the effect vanished after 4 months. No effects were reported in scallops up to 10 months after a seismic survey (Przeslawski et al., 2018), rock lobsters (*Jasus edwardsii*) the following weeks to years after exposure (Parry and Gason, 2006), American lobsters (*Homarus americanus*) several months after exposure

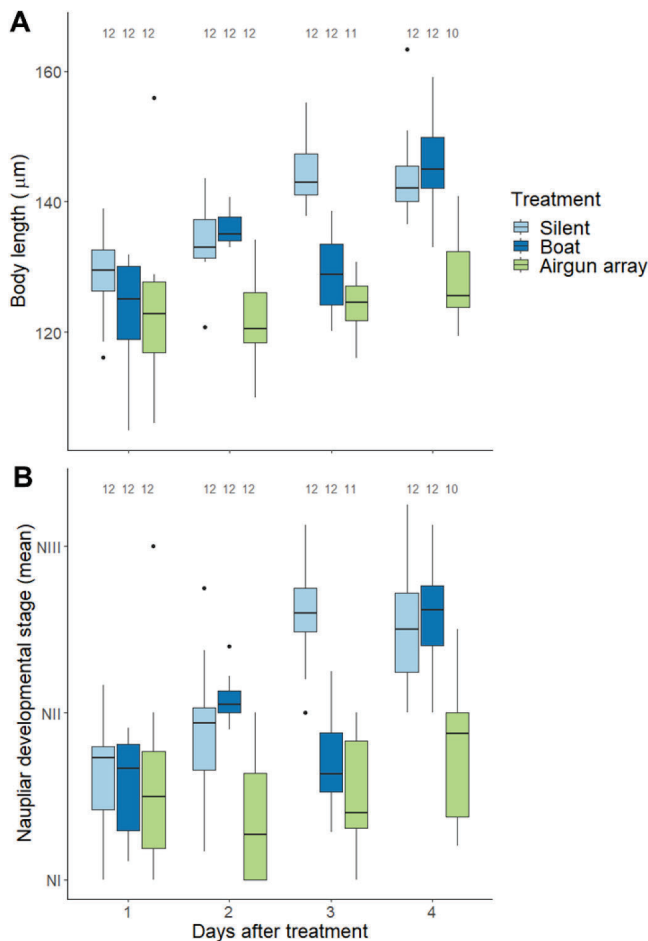


Fig. 6. The body length (μm) and developmental stage (NI–NIV) of *Acartia tonsa* nauplii after experimental exposure to a silent control, a boat control, or an airgun array from 1 to 4 days after exposure. A) Body length (μm) of the nauplii and B) naupliar developmental stage (NI–NIV), calculated as the mean proportion of stages for every aliquot. The total number of aliquots counted per treatment per day is noted at the top of the figure. The horizontal lines indicate the median, and boxes indicate the 25th percentile (lower quartile), and the 75th percentile (upper quartile).

(Payne et al., 2007), or zoea larvae of Dungeness crab weeks after exposure (Pearson et al., 1994). Fields et al. (2019) appear to be the only study to investigate delayed mortality (up to seven days after exposure) from airgun discharges in copepods. They found nominally (9%) higher mortality in exposed copepods, but only at a distance of <10 m from the source, in contrast to this study, in which elevated mortality was observed one day after exposure.

The airgun array exposed nauplii grew less and developed slower over four days than the boat and silent control groups. The slower development in the airgun array treatment nauplii was correlated with decreased growth. These results are consistent with the developmental delays and morphological abnormalities observed in scallop larvae after exposure to sounds recorded from an airgun array (de Soto et al., 2013). Developmental delays may also manifest at later life stages after exposure to various stressors during the early developmental stages and impact survival or fitness in later life stages (Gebauer et al., 1999; Pechenik, 2006). For example, gastropod larvae (*Crepidatella dilatata*) exhibited delayed development and decreased fitness after exposure to hypoxic conditions (Segura et al., 2014), and barnacles (*Balanus glandula*) grew slower after exposure to low food concentrations (Emlet and Sadro, 2006). The progression through developmental stages and increase in body length observed in the control groups in our study is more

similar to the development naturally observed in *Acartia tonsa* nauplii cultured in 10–15 °C water than is the development in the airgun exposed nauplii (Leandro et al., 2006). Slowed or arrested development at naupliar stages can reduce fitness or cause death (Gebauer et al., 1999). Thus, mortality could be affected long after seismic exposure. The population-level effects that this might have are uncertain.

4.2. The challenges of upscaling these results to a real-life seismic survey

Compared to a large seismic survey, the size and the number of airguns were much smaller in this study. Typically, 18–48 airguns are distributed in several subarrays during standard seismic surveys. The total chamber volume of an airgun array usually ranges from 1220 to 5300 inch^3 , covering survey areas of 1000–3000 km^2 (Hovem and Tronstad, 2012; Slabbekoorn et al., 2019). The source level of an airgun array may reach up to 260 dB re μPa at 1 m (Hildebrand, 2009). The modeled sound exposure level of such airgun arrays is 200 dB re $1 \mu\text{Pa}^2\text{s}$ near the source (Handegard et al., 2013), which is significantly higher than that in this study. The SEL generated at approximately 1 km by a large seismic array is equivalent to that measured at the closest distance in this study according to Handegard et al. (2013). However, since several properties of the sound will change with distance (Erbe et al., 2016), additional field studies such as those of McCauley et al. (2017) are warranted. Nonetheless, small-scale experimental studies such as this one provide a level of experimental control over both the exposure and the previous experience of the animals that is impossible to achieve in a field study.

Zooplankton will be exposed to airgun discharges when a seismic survey is conducted but over varying time durations and sound levels. In addition, seasonal, diel, and species-specific changes in copepod distribution, both within and among species (Hygum et al., 2000; Thor et al., 2005), can influence exposure level and, therefore, the impact of seismic discharges. The total duration of the exposure in this study was short compared to a real seismic survey. Seismic activity can run over several months, shooting both day and night. Our exposure time lasted ~ 2.5 h – i.e. individual zooplankton may not be exposed for much longer than a few hours during a survey, although this will depend on factors such as survey design and water current.

The areas where these surveys are conducted only comprise a small fraction of the areas where zooplankton are distributed. For example, on the Norwegian Continental Shelf, 16740 km^2 was covered with 3D/4D/4C seismic surveys in 2020 (NDP, 2021). In comparison, the Norwegian Continental Shelf comprises more than 2 million km^2 . Thus, regional population-level effects from a minute excess mortality ($\sim 14\%$ vs. $\sim 4\%$ mortality in the airgun and controls, respectively) in these areas seem unlikely. A model accounting for parameters such as ocean currents, seasonality, survey duration, area coverage, and vertical migration is needed to assess the potential population effects from seismic surveys on zooplankton.

5. Conclusions

The results of this study suggest that airgun array discharges affect the growth and mortality of *Acartia* in early naupliar stages. However, the degree of impact is likely to be stage- and species-specific and may be difficult to separate from background mortality. The growing demand for subsea minerals is driving exploration, which will ensure the continued use of seismic surveys in the coming decades. Understanding the potential impacts on key species and specific life stages is needed to inform the spatial locations and extent, and the seasonal timing, of these surveys.

Credit author statement

Emilie Hernes Vereide: Conceptualization, Methodology, Software, Formal analysis, Investigation, Resources, Writing - Original Draft,

Writing - Review & Editing, Visualization Project administration, Marina Mihaljevic: Investigation, Howard Browman, Conceptualization, Methodology, Writing - Original Draft, Writing - Review & Editing, Supervision, Funding acquisition, David M. Fields: Conceptualization, Methodology, Writing - Original Draft, Writing - Review & Editing, Funding acquisition, Mette Dalgaard Agersted: Josefin Titelman: Karen de Jong: Conceptualization, Methodology, Formal analysis, Investigation, Data Curation, Writing - Original Draft, Writing - Review & Editing, Supervision, Project administration, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgments

This study was a part of the project ZoopSeis (#302675) and in collaboration with SpawnSeis (#280367), funded by the Research Council of Norway. The authors thank the staff of the Austevoll Research Station (IMR), in particular Reidun Bjelland, Terje van der Meeren, and Glenn Sandtorv, for logistic support and advice. We also thank Lise Doksaeter Sivle and Kate McQueen for coordination on the seismic vessel, Tonje Nesse Forland for advice on the calibration of the hydrophones, and the Ecosystem Acoustics Group at IMR for feedback and comments.

References

- Booman, C., Dalen, J., Leivestad, H., Levsen, A., van der Meeren, T., Toklum, K., 1996. Effekter Av Luftkanonskyting På Egg, Larver Og Yngel. Undersøkelser Ved Havforskningsinstituttet Og Zoologisk Laboratorium UiB. Institute of Marine Research.
- Carroll, A.G., Przeslawski, R., Duncan, A., Gunning, M., Bruce, B., 2017. A critical review of the potential impacts of marine seismic surveys on fish & invertebrates. *Mar. Pollut. Bull.* 114 (1), 9–24. <https://doi.org/10.1016/j.marpolbul.2016.11.038>.
- Cervetto, G., Gaudy, R., Pagano, M., 1999. Influence of salinity on the distribution of *Acartia tonsa* (copepoda, calanoida). *J. Exp. Mar. Biol. Ecol.* 239, 33–45. [https://doi.org/10.1016/S0022-0981\(99\)00023-4](https://doi.org/10.1016/S0022-0981(99)00023-4).
- Christian, J.R., Mathieu, A., Thomson, D.H., White, D., Buchanan, R.A., 2003. Environmental Funds Project No. 144. Fisheries and Oceans Canada. In: *Effect of Seismic Energy on Snow Crab (Chionoecetes opilio)*. Calgary (106pp.).
- Cox, K., Brennan, L.P., Gerwing, T.G., Dudas, S.E., Juanes, F., 2018. Sound the alarm: a meta-analysis on the effect of aquatic noise on fish behavior and physiology. *Global Change Biol.* 24 (7), 3105–3116. <https://doi.org/10.1111/gcb.14106>.
- Day, R.D., Fitzgibbon, Q.P., McCauley, R.D., Baker, K.B., Semmens, J.M., 2022. The impact of seismic survey exposure on the righting reflex and moult cycle of Southern Rock Lobster (*Jasus edwardsii*) puerulus larvae and juveniles. *Environ. Pollut.* 309, 119699. <https://doi.org/10.1016/j.envpol.2022.119699>.
- Day, R.D., McCauley, R.D., Fitzgibbon, Q.P., Hartmann, K., Semmens, J.M., 2017. Exposure to seismic air gun signals causes physiological harm and alters behavior in the scallop *Pecten fumatus*. *Proc. Natl. Acad. Sci. USA* 114 (40), E8537–E8546. <https://doi.org/10.1073/pnas.1700564114>.
- Day, R.D., McCauley, R.D., Fitzgibbon, Q.P., Semmens, J.M., 2016. Seismic air gun exposure during early-stage embryonic development does not negatively affect spiny lobster *Jasus edwardsii* larvae (Decapoda: Palinuridae). *Science Reports* 6, 22723. <https://doi.org/10.1038/srep22723>.
- de Soto, N.A., Delorme, N., Atkins, J., Howard, S., Williams, J., Johnson, M., 2013. Anthropogenic noise causes body malformations and delays development in marine larvae. *Science Reports* 3, 2831. <https://doi.org/10.1038/srep02831>.
- Duarte, C.M., Chapuis, L., Collin, S.P., Costa, D.P., Devassy, R.P., Eguiluz, V.M., Erbe, C., Gordon, T.A.C., Halpern, B.S., Harding, H.R., Havlik, M.N., Meekan, M., Merchant, N.D., Miksis-Olds, J.L., Parsons, M., Predragovic, M., Radford, A.N., Radford, C.A., Simpson, S.D., Slabbekoorn, H., Staaterman, E., Opzeeland, I.C.V., Winderen, J., Zhang, X., Juanes, F., 2021. The soundscape of the Anthropocene ocean. *Science* 371 (6529), eaba4658. <https://doi.org/10.1126/science.aba4658>.
- Elliott, D., Tang, K., 2011. Influence of carcass abundance on estimates of mortality and assessment of population dynamics in *Acartia tonsa*. *Mar. Ecol. Prog. Ser.* 427, 1–12. <https://doi.org/10.3354/meps09063>.
- Emlet, R.B., Sadro, S.S., 2006. Linking stages of life history: how larval quality translates into juvenile performance for an intertidal barnacle (*Balanus glandula*). *Integr. Comp. Biol.* 46 (3), 334–346. <https://doi.org/10.1093/icb/ijc023>.
- Engås, A., Løkkeborg, S., Ona, E., Vold, A., 1996. Effects of seismic shooting on local abundance and catch rates of cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*). *Can. J. Fish. Aquat. Sci.* 53, 2238–2249. <https://doi.org/10.1139/cjfas-53-10-2238>.
- Erbe, C., Reichmuth, C., Cunningham, K., Lucke, K., Dooling, R., 2016. Communication masking in marine mammals: a review and research strategy. *Mar. Pollut. Bull.* 103 (1), 15–38. <https://doi.org/10.1016/j.marpolbul.2015.12.007>.
- Fields, D.M., Handegard, N.O., Dalen, J., Eichner, C., Malde, K., Karlsen, Ø., Skiftesvik, A. B., Durif, C.M.F., Browman, H.L., Ratilal, P., 2019. Airgun blasts used in marine seismic surveys have limited effects on mortality, and no sublethal effects on behaviour or gene expression, in the copepod *Calanus finmarchicus*. *ICES (Int. Council. Explor. Sea) J. Mar. Sci.* 76 (7), 2033–2044. <https://doi.org/10.1093/icesjms/fsz126>.
- Fritsch, L., Brown, A., Kim, R., Schwela, D., Kephelopoulou, S. (Eds.), 2011. Burden of Disease from Environmental Noise: Quantification of Healthy Life Years Lost in Europe. WHO Regional Office for Europe, Copenhagen, Denmark, p. JRC64428.
- Gebauer, P., Paschke, K., Anger, K., 1999. Costs of delayed metamorphosis: reduced growth and survival in early juveniles of an estuarine grapsid crab, *Chasmagnathus granulata*. *J. Exp. Mar. Biol. Ecol.* 238 (2), 271–281. [https://doi.org/10.1016/S0022-0981\(98\)00219-6](https://doi.org/10.1016/S0022-0981(98)00219-6).
- Gordon, J., Gillespie, D., Potter, J., Frantzis, A., Simmonds, M., Swift, R., Thompson, D., 2003. A review of the effects of seismic surveys on marine mammals. *Mar. Technol. Soc. J.* 37, 16–34. <https://doi.org/10.4031/002533203787536998>.
- Handegard, N.O., Tronstad, T.V., Hovem, J.M., Jech, J.M., 2013. Evaluating the effect of seismic surveys on fish — the efficacy of different exposure metrics to explain disturbance. *Can. J. Fish. Aquat. Sci.* 70 (9), 1271–1277. <https://doi.org/10.1139/cjfas-2012-0465>.
- Harrington, J.J., McAllister, J., Semmens, J.M., 2010. Assessing the short-term impact of seismic surveys on adult commercial scallops (*Pecten fumatus*) in Bass Strait. In: *Contract Report Australian Fisheries Management Authority*.
- Hildebrand, J.A., 2009. Anthropogenic and natural sources of ambient noise in the ocean. *Mar. Ecol. Prog. Ser.* 395, 5–20. <https://doi.org/10.3354/meps08353>.
- Hovem, J.M., Tronstad, T.V., 2012. Propagation of anthropogenic noise in the ocean. In: *35th Scandinavian Symposium on Physical Acoustics*. Gjølo, Norway.
- Hygum, B., Rey-Rassat, C., Hansen, B., 2000. Growth and development rates of *Calanus finmarchicus* nauplii during a diatom spring bloom. *Mar. Biol.* 136, 1075–1085. <https://doi.org/10.1007/s002270000313>.
- Kavanagh, A.S., Nykänen, M., Hunt, W., Richardson, N., Jessopp, M.J., 2019. Seismic surveys reduce cetacean sightings across a large marine ecosystem. *Sci. Rep.* 9 (1), 19164. <https://doi.org/10.1038/s41598-019-55500-4>.
- Kostyuchenko, L.P., 1973. Effects of elastic waves generated in marine seismic prospecting on fish eggs in the Black Sea. *Hydrobiologia* 9, 45–48.
- Leandro, S., Tiselius, P., Queiroga, H., 2006. Growth and development of nauplii and copepodites of the estuarine copepod *Acartia tonsa* from southern Europe (Ria de Aveiro, Portugal) under saturating food conditions. *Mar. Biol.* 150, 121–129. <https://doi.org/10.1007/s00227-006-0336-y>.
- McCauley, R.D., Day, R.D., Swadling, K.M., Fitzgibbon, Q.P., Watson, R.A., Semmens, J. M., 2017. Widely used marine seismic survey air gun operations negatively impact zooplankton. *Nature Ecology and Evolution* 1 (7), 195. <https://doi.org/10.1038/s41559-017-0195>.
- McQueen, K., Meager, J.J., Nyqvist, D., Skjæraasen, J.E., Olsen, E.M., Karlsen, Ø., Kvadsheim, P.H., Handegard, N.O., Forland, T.N., Sivle, L.D., 2022. Spawning Atlantic cod (*Gadus morhua* L.) exposed to noise from seismic airguns do not abandon their spawning site. *ICES (Int. Council. Explor. Sea) J. Mar. Sci.* <https://doi.org/10.1093/icesjms/fsac203>.
- Murphy, J.A., Cohen, R.E., 1978. A Guide to the Developmental Stages of Common Coastal. Georges Bank and Gulf of Maine copepods (*Technical Report*). NDP, 2021. In: Directorate, N.P. (Ed.), *Seismic, Norwegian Petroleum Directory*, no.
- Parry, G.S., Heislors, F., Werner, Asplin, D., Gason, H., 2002. In: *Assessment of Environmental Effects of Seismic Testing on Scallop Fisheries in Bass Strait*. Marine and Freshwater Resources Institute. Report No. 50.
- Parry, G.D., Gason, A., 2006. The effect of seismic surveys on catch rates of rock lobsters in western Victoria, Australia. *Fish. Res.* 79 (3), 272–284. <https://doi.org/10.1016/j.fishres.2006.03.023>.
- Payne, J., Andrews, C., Fancey, L., Cook, A., Christian, J., 2007. Pilot Study on the Effects of Seismic Air Gun Noise on Lobster (*Homarus americanus*).
- Pearson, W.H., Skalski, J.R., Sulkin, S.D., Malme, C.I., 1994. Effects of seismic energy releases on the survival and development of zoeal-larvae of dungeness-crab (*Cancer magister*). *Mar. Environ. Res.* 38 (2), 93–113. [https://doi.org/10.1016/0141-1136\(94\)90003-5](https://doi.org/10.1016/0141-1136(94)90003-5).
- Pechenik, J.A., 2006. Larval experience and latent effects—metamorphosis is not a new beginning. *Integr. Comp. Biol.* 46 (3), 323–333. <https://doi.org/10.1093/icb/ijc028>.
- Popper, A.N., Hawkins, A.D., 2019. An overview of fish bioacoustics and the impacts of anthropogenic sounds on fishes. *J. Fish. Biol.* 94 (5), 692–713. <https://doi.org/10.1111/jfb.13948>.
- Przeslawski, R., Huang, Z., Anderson, J., Carroll, A.G., Edmunds, M., Hurt, L., Williams, S., 2018. Multiple field-based methods to assess the potential impacts of seismic surveys on scallops. *Mar. Pollut. Bull.* 129 (2), 750–761. <https://doi.org/10.1016/j.marpolbul.2017.10.066>.
- R Core Team, 2022. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
- Schneider, C.A., Rasband, W.S., Eliceiri, K.W., 2012. NIH Image to ImageJ: 25 years of image analysis. *Nat. Methods* 9 (7), 671–675. <https://doi.org/10.1038/nmeth.2089>.

- Segura, C., Chaparro, O., Pechenik, J., Paschke, K., Osorio, S., Navarro, J., Cubillos, V., 2014. Delayed effects of severe hypoxia experienced by marine gastropod embryos. *Mar. Ecol. Prog. Ser.* 510, 59–71. <https://doi.org/10.3354/meps10906>.
- Slabbekoorn, H., Dalen, J., Haan, D., Winter, H.V., Radford, C., Ainslie, M.A., Heaney, K. D., Kooten, T., Thomas, L., Harwood, J., 2019. Population-level consequences of seismic surveys on fishes: an interdisciplinary challenge. *Fish Fish.* 20 (4), 653–685. <https://doi.org/10.1111/faf.12367>.
- Solé, M., Kaifu, K., Mooney, T.A., Nedelec, S.L., Olivier, F., Radford, A.N., Vazzana, M., Wale, M.A., Semmens, J.M., Simpson, S.D., Buscaino, G., Hawkins, A., Aguilar de Soto, N., Akamatsu, T., Chauvaud, L., Day, R.D., Fitzgibbon, Q., McCauley, R.D., André, M., 2023. Marine invertebrates and noise. In: *Frontiers in Marine Science*. <https://doi.org/10.3389/fmars.2023.1129057>, 10.
- Sullivan, B.K., Costello, J.H., Van Keuren, D., 2007. Seasonality of the copepods *Acartia hudsonica* and *Acartia tonsa* in Narragansett Bay, RI, USA during a period of climate change. *Estuar. Coast Shelf Sci.* 73 (1), 259–267. <https://doi.org/10.1016/j.ecss.2007.01.018>.
- Sunar, M.C., Kir, M., 2021. Thermal tolerance of *Acartia tonsa*: in relation to acclimation temperature and life stage. *J. Therm. Biol.* 102, 103116 <https://doi.org/10.1016/j.jtherbio.2021.103116>.
- Swaddle, J.P., Francis, C.D., Barber, J.R., Cooper, C.B., Kyba, C.C.M., Dominoni, D.M., Shannon, G., Aschehoug, E., Goodwin, S.E., Kawahara, A.Y., Luther, D., Spoelstra, K., Voss, M., Longcore, T., 2015. A framework to assess evolutionary responses to anthropogenic light and sound. *Trends Ecol. Evol.* 30 (9), 550–560. <https://doi.org/10.1016/j.tree.2015.06.009>.
- Thor, P., Nielsen, T.G., Tiselius, P., Juul-Pedersen, T., Michel, C., Møller, E.F., Dahl, K., Selander, E., Gooding, S., 2005. Post-spring bloom community structure of pelagic copepods in the Disko Bay, Western Greenland. *J. Plankton Res.* 27 (4), 341–356. <https://doi.org/10.1093/plankt/fbi010>.

Corrigendum

Corrigendum to: Effects of airgun discharges used in seismic surveys on development and mortality in nauplii of the copepod *Acartia tonsa*

[Environmental Pollution 327 (2023) 121469]

Vereide, Emilie Hernes^{1*}; Mihaljevic, Marina²; Browman, Howard I.³; Fields, David M.⁴; Agersted, Mette Dalgaard⁵; Titelman, Josefin⁶; de Jong, Karen¹

¹ Institute of Marine Research, Ecosystem Acoustics Group, Nykirkekaien 1, NO-5004 Bergen, Norway

² Institute of Marine Research, Austevoll Research Station, Sauganeset 16, NO-5392 Storebø, Norway

³ Institute of Marine Research, Ecosystem Acoustics Group, Austevoll Research Station, Sauganeset 16, NO-5392 Storebø, Norway

⁴ Bigelow Laboratory for Ocean Sciences, 60 Bigelow Drive, P.O. Box 380 East Boothbay, ME, USA 04544

⁵ Aarhus University, Department of Ecoscience, Frederiksborgvej 399, 4000 Roskilde, Denmark

⁶ University of Oslo, Department of biosciences, PO BOX 1066 Blindern, NO-0316 Oslo, Norway

The authors regret:

In the originally published version of this manuscript, there is an error in the reported received sound levels: sound pressure (peak-to-peak, kPa) and sound exposure level (SEL) (dB re 1 $\mu\text{Pa}^2 \text{ s}$). The error in the sound levels was caused by an error in the calibration script, which was found during sound analysis from another field study.

These corrections do not affect the interpretation of results.

In the following sections, the original and corrected values are reported:

Table 1:

Original:	Sound pressure: 48.9 kPa SEL: 180 dB re 1 $\mu\text{Pa}^2 \text{ s}$ (50 m), 166 dB re 1 $\mu\text{Pa}^2 \text{ s}$ (1100 m)
Corrected:	Sound pressure: 4889 Pa/4.9 kPa SEL: 162 dB re 1 $\mu\text{Pa}^2 \text{ s}$ (50 m), 132 dB re 1 $\mu\text{Pa}^2 \text{ s}$ (1100 m)

3.1 Sound measurements:

Original: The sound pressure level (kPa) ranged from 0.420 kPa at the furthest distance from the nauplii (~1200 m) to a maximum of 48.90 kPa at the closest distance (50 m) (Fig. 4A). The sound exposure level (SEL) was 152 dB re 1 $\mu\text{Pa}^2 \text{ s}$ furthest away and 183 dB re 1 $\mu\text{Pa}^2 \text{ s}$ at the closest distance (Fig. 4B).

Corrected: The sound pressure level (kPa) ranged from 42 Pa at the furthest distance from the nauplii (~1200 m) to a maximum of 4889 Pa at the closest distance (50 m) (Fig. 4A). The sound exposure level (SEL) was 132 dB re 1 $\mu\text{Pa}^2 \text{ s}$ furthest away and 162 dB re 1 $\mu\text{Pa}^2 \text{ s}$ at the closest distance (Fig. 4B).

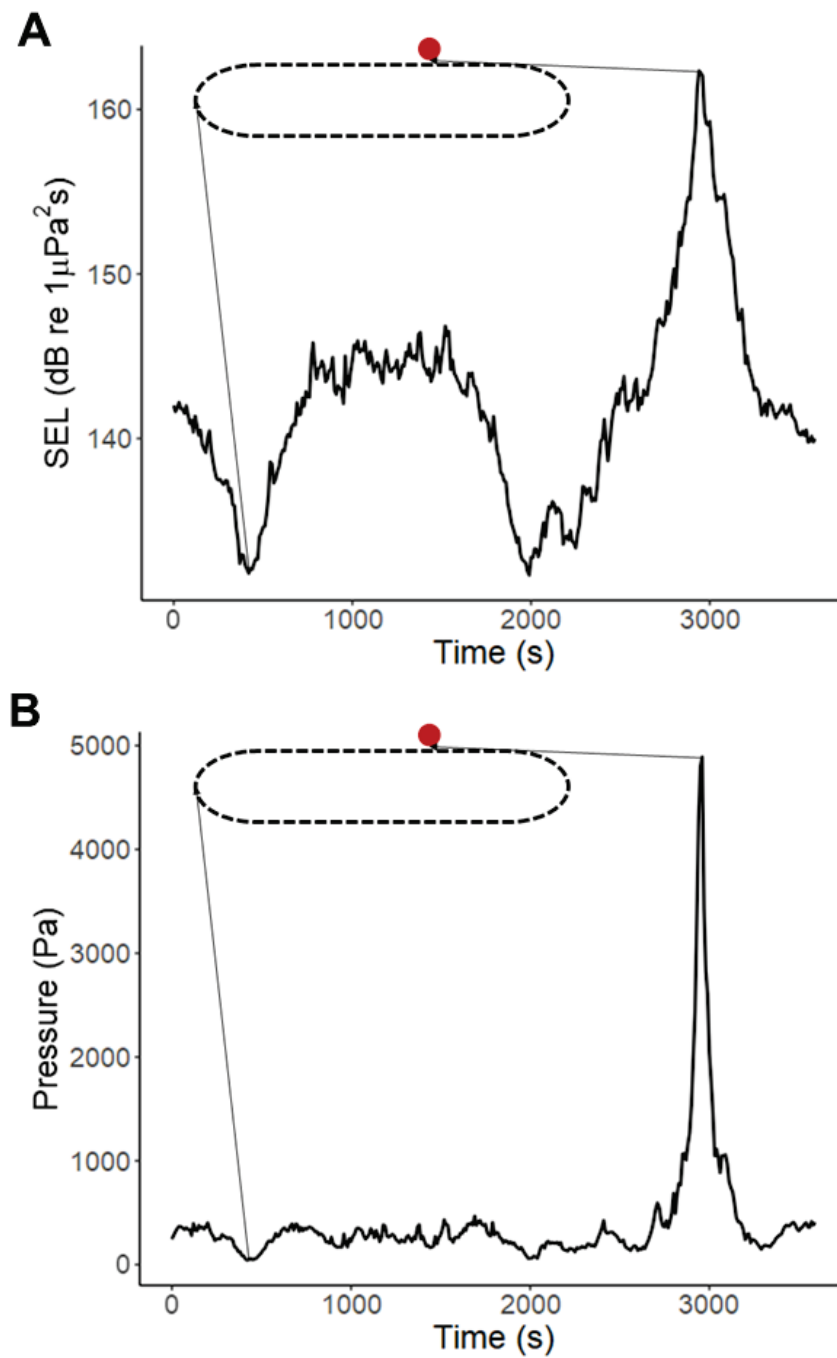
4.2. The challenges of upscaling these results to a real-life seismic survey

Original: The SEL generated at approximately 1 km by a large seismic array is equivalent to that measured at the closest distance in this study according to Handegard et al. (2013).

Corrected: The SEL generated at approximately 5 km by a large seismic array is equivalent to that measured at the closest distance in this study according to Handegard et al. (2013).

Fig. 4:

Corrected:



The authors would like to apologise for any inconvenience caused.

DOI of original article: <https://doi.org/10.1016/j.envpol.2023.121469>
Corresponding author: Emilie Hernes Vereide, +47 94174340
emilie.hernes.veraide@hi.no

V

