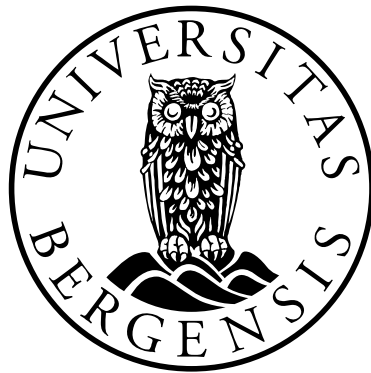# Behavioural effects of naval sonars on fish and cetaceans

Lise Doksæter

Dissertation for the degree philosophiae doctor (PhD)

at the University of Bergen

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1. Scientific environment

This work was done at the Institute of Marine Research (IMR) in close collaboration with the Norwegian Defence Research Establishment (FFI). Six months of the PhD was also spent at the Massachusets Institute of Technology (MIT) in Boston, USA.

The PhD was part of the project "Low frequency acoustics – potentials and dangers for marine ecosystems (LowFreq)"(project number 12200) under the IMR programme "Oil and fish", financed by the Norwegian Research Council and the FFI project Sonar and Marine Life funded by the Norwegian Ministry of Defense. Institutions participating in this project are IMR, FFI, MIT, University of Bergen (UiB), Kongsberg Maritime, Sea Mammal Research Unit at University of St.Andrews, Netherlands Organisation for Applied Scientific Research (TNO) and Woods Hole Oceanographic Institution (WHOI).

2.   Acknowledgements

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3. Abstract

Anthropogenic noise in the sea has increased during the past decades as a consequence of increased shipping traffic, oil and gas exploitation, and underwater construction work (Southall *et al*., 2007; Slabbekoorn *et al*., 2010). Such anthropogenic noise may affect marine animals by causing hearing injuries (Smith *et al.,* 2004; Popper *et al.,* 2007), masking of biological sounds (Richardson *et al*., 1995), or behavioural responses such as avoidance of the exposed habitat (e.g. Engås *et al.,* 1996; Morton and Symons, 2002). In 2006, the Norwegian Navy began to operate a new class of frigates, equipped with high-power sonars transmitting at frequencies overlapping with the hearing range of several species of fish and marine mammals found in Norwegian waters (Enger, 1967; Richardson *et al*., 1995). As naval sonar operations often coincide with the geographic distribution of these species, an examination of potentially negative effects was needed. My PhD work includes three papers on the effect of such sonars have on herring (*Clupea harengus*), and one paper concerning the effect of sonars on the diving behaviour of three species of cetaceans; killer whales (*Orcinus orca*), pilot whales (*Globicephala melas*) and sperm whales (*Physeter macrocephalus*).

In **paper 1,** herring were exposed to sonar signals at 1-2 kHz (Low Frequency Active Sonar, LFAS) and 6-7 kHz (Mid frequency Active Sonar, MFAS), and playbacks of recorded sounds produced by killer whales while feeding, during herring overwintering in the Lofoten area. Herring behaviour was monitored by two upward-looking echosounders, located 400 m apart, as the sonar source approached and passed the fish. No significant horizontal or vertical avoidance reactions were detected in response to the sonar transmissions, however, the killer whale feeding sounds induced both vertical and horizontal movements. The results indicate that sonar transmissions at 1-2 kHz and 6-7 kHz have negligible influence on herring at the source levels tested (197 and 209 dB re 1μPa, for LFAS and MFAS, respectively). The behavioural response during playback of killer-whale feeding sounds demonstrates the natural avoidance reaction, and the ability of the experimental design to reveal it.

In **paper 2**, herring schools were exposed to LFAS and MFAS sonar signals as well as playbacks of recorded sounds of feeding killer whales during herring summer-feeding migration in the Norwegian Sea. Herring behaviour was monitored by a high-frequency fishery sonar (110 kHz) following the moving schools. The schools did not dive nor change their packing density in response to the LFAS and MFAS signals at estimated maximum received sound pressure levels of 176 and 157 dB (re 1 µPa m) and sound exposure levels of 181 and 162 dB (re 1 µPa² s) for LFAS and MFAS, respectively. In contrast, killer-whale-feeding sounds induced diving responses by the herring. Based on these results combined with those from papers 1 and 3, and additional information from the literature, thresholds of behavioural responses and injury were estimated, and a simple model was constructed to estimate the accumulated effects of sonar on the herring population. It is concluded that naval sonars are unlikely to cause any behavioural changes or physiological injuries which would affect the herring population.

In **paper 3**, captive herring in a net pen were exposed to sonar signals at 1.0-1.6 kHz frequency, transmitted by a naval sonar source on a naval frigate. Experiments were conducted in all seasons. No behavioural reactions were detected, with maximum received sound pressure levels (*SPL*) of 168 dB re 1µPa, at a distance of 500 m between the herring and the frigate. However, the fish did exhibit a significant diving reaction when exposed to noise from an outboard engine at a much lower *SPL*. This showed that captive herring exhibit avoidance responses similar to wild herring. Further, it demonstrated that the experimental setup allowed such responses to be detected when they occurred.

In **paper 4**, diving behaviour of killer whales, pilot whales and sperm whales during exposure of MFAS and LFAS signals were studied during three field seasons of controlled exposure experiments. Diving behaviour were monitored before and during exposure by a digital tag attached on the animal, recording its vertical movement in addition to horizontal movement, vocalisation and received sound pressure level from the sonar. All three species tended to spend more time close to the surface during exposure, and less time diving. Changes in killer whale diving behaviour was strongly dependent on behavioural state, with whales in a feeding mode showing abrupt changes in diving behaviour, while no response were seen during travelling or socializing. Pilot whales showed only moderate responses at

high exposure levels. Sperm whales conducted normal deep feeding dives during MFAS exposure, but reduced foraging activity during LFAS exposure.

4. List of papers

Paper 1: Doksæter, L., Kvadsheim, P.H., Godø, O.R., Handegard, N.O., Donovan, C., Lam, F.P. and Miller, P.J.O. (2009). Behavioural response of herring (*Clupea harengus*) to 1-2 and 6-7 kHz sonar signals and killer whale calls. Journal of the Acoustic Society of America 125, 554-564.

Paper 2: Doksæter, L., Kvadsheim, P.H., Ainsely, M., Solow, A., Handegard, N.O., Nordlund, N. and Lam, F.P. Impact of naval sonar signals on herring (*Clupea harengus*) during summer feeding. Manuscript submitted to ICES Journal of Marine Sciences, November 2010.

Paper 3: Doksæter, L., Handegard, N.O., Godø, O. R., Nordlund, N. and Kvadsheim, P.H. Behavioural responses of captive herring to naval sonar signals (1-1.6 kHz) of a throughout a yearly cycle. Journal of the Acoustic Society of America (in press).

Paper 4: Doksæter L., Kvadsheim, P.H, Fahlman, A., Lam, F. P. and Miller, P. J. O. Assessing changes in dive behaviour during sonar exposure in sperm whales, killer whales and pilot whales. Manuscript.

Contents

5. Syntesis

5.1 Introduction

The silent ocean

The ocean is often referred to as silent, a highly misleading statement, because it is full of sounds (Wentz, 1964). These include sounds from earthquakes, ice cracking, wind-driven waves, and rainfall (Hildebrand, 2009). In addition to these physical sources, many sounds are produced by the animals living here e.g. snapping shrimps, grunting fishes, echo-locating dolphins, and singing whales (Fig.1, lower panel). Further, there is a wide variety of sounds created by human activities, often referred to as "anthropogenic noise" (Hildebrand, 2009). These originate from activities such as shipping, underwater construction, and explosions, or they may be transmitted intentionally into the sea for orientation or exploitation purposes, such as seismic-survey operations, fish-finding echosounders, and sonars operating over a wide range of frequencies for military and civilian purposes (Fig. 1, upper panel).
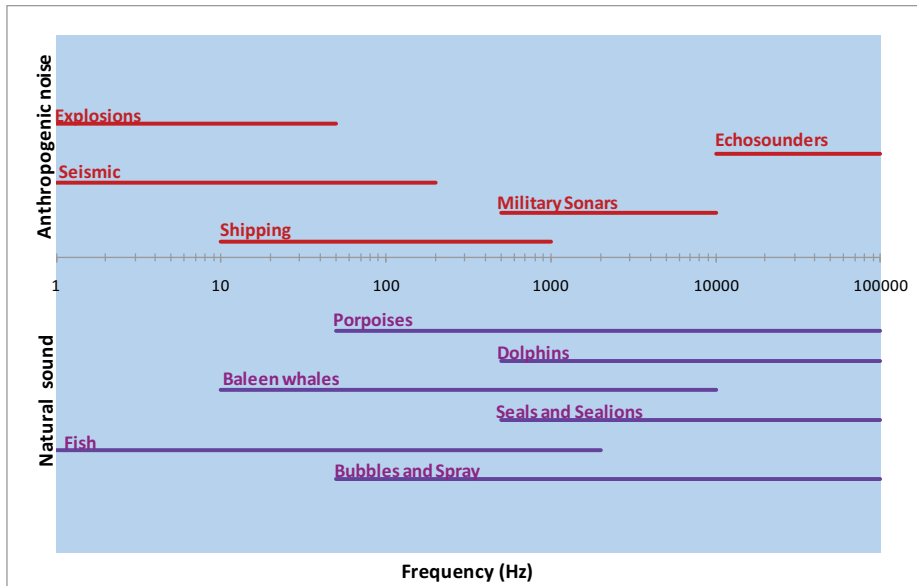
Fig. 1. Natural and anthropogenic sources of sound in the sea. Sources: Heathershaw *et al.*, 2001 (echosounders, seismic, military sonars); Hildebrand, 2009 (shipping, explosions, bubbles and spray); Verbom and Kastelein, 2002 (porpoises); Richardson *et al.*, 1995 (dolphins); Popper and Ketten, 2008 (baleen whales, fish); Frankel, 2002 (seals and sea lions).

The terms "noise" and "sound" are often used somewhat arbitrarily in the literature. Here I use "noise" for an anthropogenic source, and "sound" when the source is a natural physical process or biologically produced. The term "acoustic stimuli" is used when the source is unknown, or when it includes a combination of anthropogenic and natural sounds. Similarly, the term "background noise" is used for ambient noise of various uncertain origins.

The auditory scene

All animals use their senses to create an image of their environment. In the ocean, senses such as vision and olfaction function only over short distances. Vision depends on having sufficient light, which may only penetrate down to 40-m depth in coastal waters (Garrison, 2002). Sound signals, however, travel very well in water, spreading over long distances at a speed almost five times that in air. Intense low-frequency signals can be detected in the oceans halfway around the globe (Munk *et al.*, 1994). Hearing is thus a sense with great potential for providing marine animals with information about their environment at much greater distances than any other sense. Thus, the auditory scene is generally more important

than the visual scene for animals inhabiting the marine environment (Popper and Hastings, 2009a). The auditory scene consists of environmental sounds such as from raindrops at the surface and geological structures, as well as sounds from potential predators or mates. This creates a "soundscape" (Slabbekoorn and Bouton, 2008), providing fish and marine mammals with important information about their surroundings (Fay and Popper, 2000; Popper *et al*., 2003a), Fish also use sound in communication (Bass and McKibben, 2003), in orientation and in habitat selection (Simpson *et al*. 2004; 2005). The deep-diving cetaceans (whales and dolphins) spend much of their time in the dark, where sound is the main tool to gather environmental information, either through active echolocation (Au, 1993) or passive listening (Gannon *et al*., 2005). Sound also has a fundamental role in predator detection, inter-animal communication, and navigation (Richardson et al., 1995, Tyack 2000; Simpson et al., 2005). The acoustic scene has likely been a strong selective force in the evolution of hearing (Fay and Popper, 2000). Most of the fish and mammals inhabiting the marine environment have a very good sense of hearing (Popper and Ketten, 2009) which, however, needs further investigation both related to understand its biological importance and vulnerability to human disturbance.

Most fishes have optimum hearing sensitivity below 500 Hz, with some lesser capability up to 1 kHz (Chapman and Hawkins, 1973; Hawkins and Johnstone, 1978). Some species are sensitive to much higher frequencies, detecting sounds at several kHz (Popper and Fay, 1973; Fay, 1988) (Fig. 2a). This is probably due to a mechanical coupling between the swimbladder and the hearing organ, allowing these fishes to detect the pressure component of the signal in addition to the particle velocity which is directly detected by the inner ear (Popper *et al*., 2003).
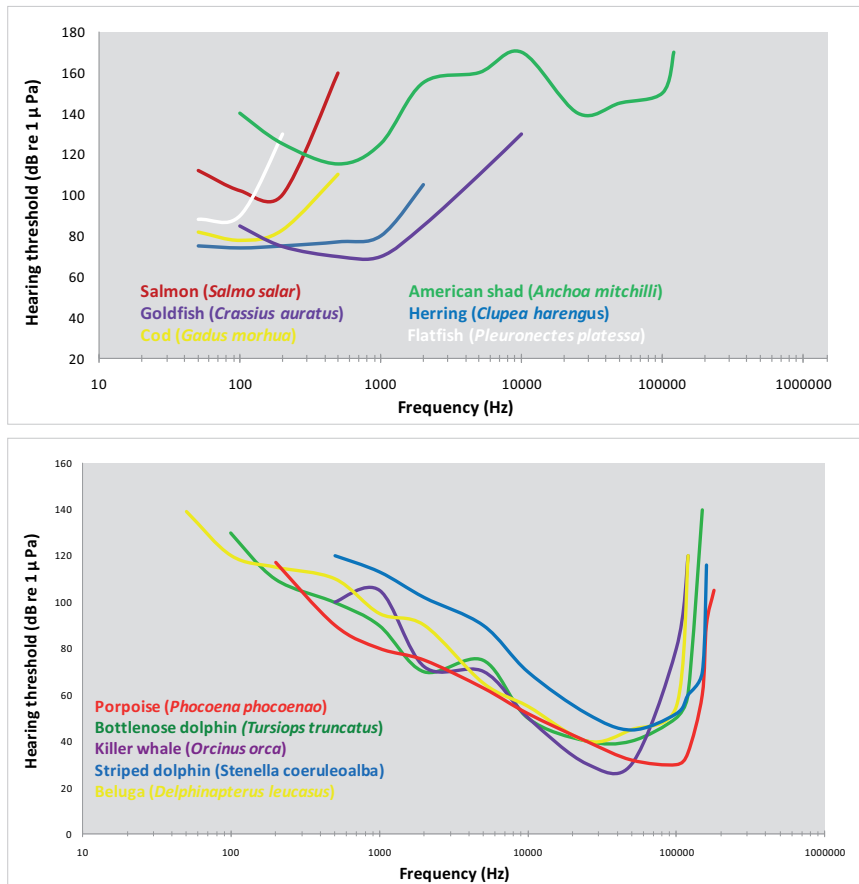
Fig. 2. Hearing curves for various species of fish (a) and cetaceans (b). Sources: Chapman and Hawkins (1973) (Cod); Hawkins and Johnstone, 1978 (salmon); Enger, 1967 (herring); Chapman and Sand 1974 (flatfish); Kenyon et al., 1998 (goldfish); Mann *et al*., 1998 (American shad); Szymanski *et al*. 1999 (killer whale); Ljungblad *et al*. 1982; Brill and Moore, 2001 (bottlenose dolphin); Johnson *et al*. 1989 (beluga), Kastelein *et al*., 2002 (porpoise); Kastelein *et al*., 2003 (striped dolphin).

Potential impact of anthropogenic noise

Any acoustic signals in the environment that alter the ability of animals to detect and analyse their auditory scene can potentially have a detrimental impact on their life and survival. The detection of a biologically-relevant sound depends on the level of any interfering signals (maskers) superimposed on the sound to be detected. Anthropogenic noise has in recent years become more and more pervasive and powerful, thus increasing the background noise level as well as the peak sound intensities in the sea (Jasny, 1999; Hofman, 2004). Much of this noise is produced in coastal and continental shelf waters, coinciding with important habitats

of marine animals (Hildebrand, 2009), and may thus interfere with their natural auditory scene. Such sounds may also induce a behavioural response of the animal, such as avoidance of the exposed habitat (Engås *et al.,* 1996; Engås and Løkkeborg, 2002; Allen and Read, 2000; Morton and Symonds, 2002), which could be either vertical or horizontal movement. This may result in the habitat being occupied by other, less sound-sensitive species, thus altering the ecosystem. The animals can also be affected through physiological-stress responses (Gilham and Baker, 1985; Popper and Hastings, 2009a). As the animal struggles to cope with the stressor, this may have negative consequences for important life functions such as predator avoidance (Mesa, 1994) and reproductive output (Legardere, 1982). Acoustic signals of high intensity may also cause direct physical injury leading to loss of hearing sensitivity (Popper *et al.,* 2005, Popper *et al.,* 2007). The hearing loss is measured by increased hearing thresholds which is either permanent (PTS) or temporary (TTS) (Scholik and Yan, 2002; Smith *et al*., 2004).

Naval sonars are among the most intense and widespread anthropogenic noise sources. Modern active long-range sonars used in anti-submarine warfare typically operate in the frequency band 1-10 kHz (Friedman, 2006). It is important to know how these may affect marine animals, due to their high source level, the long range of low-frequency signals, and the large number of such sonars that are deployed (Richardson *et al*., 1995).

Several stranding events of beaked whales have coincided in time and location with naval sonar operations (e.g. Simmonds and Lopez-Jurado, 1991; Frantzis, 1998; Jepson *et al*., 2003; Cox et al., 2006). Necropsy of some of these stranded animals found formations of nitrogen bubbles in several tissues (Jepson *et al*. 2003, 2005; Fernandez *et al*., 2005), a symptom often found in association with decompression sickness (DCS). This could have been caused by the sonar signals directly inducing bubble growth (Crum and Mao, 1996), or that the sonar noise caused a change in dive behaviour that will make them more vulnerable for bubble formation. Such behaviour include spending less time at the surface for nitrogen to dissipate, or conducting repetitive shallow dives (Jepson *et al*., 2003, Fernandez *et al*., 2004; Cox *et al*., 2006; Zimmer and Tyack, 2007). Other studies have documented sonar effects on vocal behaviour of humpback whales (Miller *et al*., 2000, Fristrup *et al*., 2003) and fin whales (Croll *et al*., 2001). There are few studies of sonar effects on fish, both with respect to species and the types of effects studied. The only documented cases are a minor

temporary threshold shift in hearing of rainbow trout (*Oncorhynchus mykiss)*, and avoidance behaviour and mortality of juvenile herring (*Clupa harengus*), cod (*Gadus morhua*) and wolfish (*Anarhichas lupus*) (Jørgensen *et al*., 2005).

Motivation of study

In 2006, the Royal Norwegian Navy introduced a new class of frigate, equipped with high-power sonars operating down to 1 kHz. These sonar frequencies overlap the hearing range of many marine animals in Norwegian waters, including all the cetaceans (Ketten and Popper, 2009), and some fish species, in particular clupeids such as herring (Enger, 1967). Operations in coastal and littoral waters are of high priority for the Royal Norwegian Navy. This implies that sonar noise-field will inevitably overlap with the distribution of many important species of fish and marine mammals along the Norwegian coast. These animals may be exposed over long periods of time, with potential impact on cornerstone Norwegian enterprises, like fisheries, aquaculture, and tourism.

Many studies on how sonar pulses might affect marine animals have focused on physiological effects (e.g. Jepson *et al*., 2003; 2005; Fernandez *et al*., 2004; 2005; Popper *et al*., 2007). However, a change in behaviour can be just as important, causing the animal to move away, either horizontally or vertically, from the area of exposure. From a conservation perspective, behavioural effects could potentially be most crucial, as these may impact life-cycle processes like migrations, and thus in the worst case harm the stock. Negative impacts on a top predator could affect the ecosystem by altering the predator-prey balance (Lima and Dill, 1990).

Behavioural responses of fish to anthropogenic noise include avoidance of the exposed habitat (Engås *et al*., 1996; Engås and Løkkeborg, 2002) as well as vertical escapement (Nøttestad and Axelsen, 1999). Such behavioural responses may increase energy depletion, reduce feeding or mating opportunities, and habitat abandonment (NRC, 2005). Most of the fish species in Norwegian waters are, however, not capable of detecting the frequencies of sonars operating in the 1-10 kHz frequency range (Chapman and Hawkins, 1973; Hawkins and Johnstone, 1978). Herring (*Clupea harengus*), on the other hand, can detect signals at frequencies up to 4 kHz (Enger, 1967), and are thus fully capable of hearing the lowest

frequency components of the sonar pulses. Herring are among the most numerous fish in the North Atlantic. This species has an important role in the ecosystem as prey for other animals on higher trophic levels (Holst *et al*., 2004), and is a commercially important fishery resource (Blaxter, 1985; Hamre, 1990). Throughout the year, the herring is distributed over most of the Norwegian Sea (Fig. 3); overwintering in the Lofoten area (Dragesund *et al*., 1997), spawning along the Norwegian coast in spring (Johannsessen *et al*., 1995; Røttingen and Slotte, 2001), and feeding in the Norwegian Sea in summer (Holst *et al*., 2004). In later years the herring overwintering areas has expanded to include offshore areas of continental slope area from Lofoten and northwards (Orellana, 2006). A study by Jørgensen *et al*. (2005) showed a strong behavioural response as well as mortality of captive juvenile herring exposed to naval sonar signals, but at very high intensities which implies that the effect zone around a transmitting source will be relatively small. Still, this raised concern as to how adult fish might respond. Negative effects on the herring may potentially reduce the stock, or change its distribution or migration patterns, with associated consequences for the fishery as well as for herring predators, such as killer whales. On this basis, and especially due to its role as a key species in the ecosystem, the herring has been given particular attention in my PhD work.
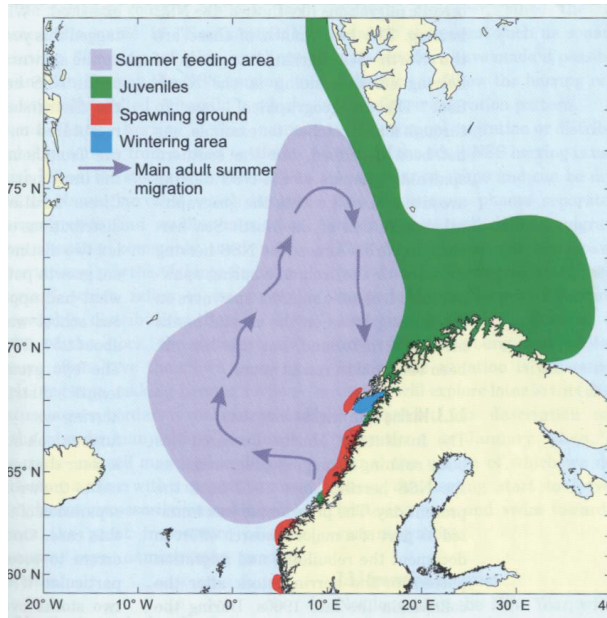
Fig. 3. Distribution of Norwegian Spring Spawning herring (*Clupea harengus*) throughout the year; spawning along the coast in spring (red), feeding in the Norwegian Sea in summer (purple) and overwintering in a sheltered fjord system in Northern Norway in winter (blue). Egg and larvae drift northwards from the spawning ground, and the juvenile period is spent in the Barents Sea (green). From Holst *et al*., 2004.

In breath-holding divers like the cetaceans, a changed dive pattern is an expected behavioural reaction to noise disturbance. This may be caused by the animal trying to escape to depths where the sound intensity is lower, or it can involve a predator-avoidance response if the signal is confused with predator-like sounds (Zimmer and Tyack, 2007), resulting in longer periods than normal being spent at the surface or at depth. This may have consequences for feeding, as well as physiological effects such as tissue nitrogen saturation and risk of bubble formation in supersaturated tissues if time spent at depths are not balanced by sufficient time at the surface (Ridgway and Howard, 1979). This may have consequences for feeding, as well as physiological effects such as tissue nitrogen saturation and risk of bubble formation in supersaturated tissues if time spent at depths are not balanced by sufficient time at the surface (Ridgway and Howard, 1979). The risk of bubble formation depend to some degree on the natural diving behaviour of the marine mammal. Deep-diving species are said to be more vulnerable than shallow-diving species (Zimmer and Tyack, 2007; Hooker *et al*., 2009).The sonar frequencies involved are probably audible to all the cetaceans inhabiting

Norwegian waters, including long-distance migrants feeding there in summer as well as resident species such as small odontocetes (Nøttestad and Olsen, 2004).

Killer whales (*Orcinus orca*), whose hearing sensitivity peaks around 10 kHz (Szymanski *et al*. 1999), are one of the few cetaceans resident in Norwegian waters. They are totally dependent on hearing and sound production during their advanced co-operative feeding and prey-localization activities (Van Opzeeland *et al*., 2005; Simon *et al*., 2006), making them vulnerable to the masking effects of high-intensity sonars. Killer whales are important top predators in the Norwegian Sea (Nøttestad and Olsen, 2004), and are considered specialist herring-feeders, following the herring concentrations throughout their annual migration cycle (Similä *et al*., 1996). Killer whales might thus be affected by naval sonar operations, both directly and indirectly, in the latter case by reduced prey availability if the herring were negatively affected. Pilot whales (*Globicephala melas*) are also among the most abundant odontocetes in the Northeast Atlantic (Buckland *et al*., 1993). They are important predators especially on the outer continental shelf (Payne and Heineman, 1993). Their main diet is believed to be squids (Desportes and Mouritsen, 1988), but they are highly opportunistic feeders, and various species of fish may also be important (Overholtz and Waring, 1991), such as herring (Gannon *et al*., 1997). Sperm whales (*Physeter macrocephalus*) are among the most numerous of the regular visitors to Norwegian waters, feeding in the deep waters of the shelf break (Christensen *et al*., 1992); and they have a significant impact on the deep-sea food web and nutrient cycling (Whitehead *et al*., 2003).

Killer whales are regarded as typical shallow-divers, with maximum dives to approximately 180 m depth (Nøttestad and Similä, 2001; Nøttestad *et al*., 2002). Sperm whales, on the other hand, are known as extreme deep-divers, regularly foraging down to depths of 2000 m (Watkins, 1993). Pilot whales, with their opportunistic diet, perform both shallow and deep dives (Heide-Jørgensen *et al*., 2002; Soto *et al*., 2008). Considering these different diving strategies among the three species mentioned, and since they are all important species along the Norwegian coast and in the Norwegian Sea (where the naval sonars operate), killer whales, sperm whales, and pilot whales are all included in my study of how cetacean diving behaviour may be affected by sonar exposure.

Objectives and tasks

The overarching objective of my study was to investigate whether the operation of naval sonars in the frequency range 1-7 kHz affect the behaviour of some important species of fish and whales in the Norwegian Sea. The following tasks were specified to achieve this objective:

- Study behavioural responses of herring to naval sonars during two different seasons and locations, representing different distribution regimes, activity levels, and physiological states; (1) overwintering in a small fjord area and (2) feeding migration within the open ocean. (papers 1and 2)

- Develop an adequate experimental setup for detailed studies of herring behaviour under controlled conditions, and use this to study herring reactions to naval sonar signals during all seasons of the year. (paper 3)

- Compare behavioural reactions between the different season on the basis of varying physiological states and motivation. (papers 1, 2 and 3)

- Use the results to assess how reactions to naval sonars may affect herring and cetaceans, and infer how sonar exercises should be conducted in the best way to mitigate harmful effects on the herring population. (paper 2, and discussion within this synthesis)

- Study changes in diving behaviour associated with sonar exposure, for three species of cetaceans with different natural dive patterns; pilot whales, sperm whales and killer whales. (paper 4)

5.2 Discussion

My PhD involves three studies of behavioural responses by adult herring to naval sonars. This is the first systematic investigation of such responses by fish species throughout all seasonal phases, under both free-field and controlled conditions. Further, it includes behavioural-response studies of three different species of cetaceans. In this overview I will first review the methodology for studying the behavioural responses of herring and cetaceans (chapter 5.2.1). Then, in chapter 5.2.2 I discuss some basic causes of behavioural reactions in fish and cetaceans, with particular emphasis on the most relevant results obtained in my studies. To broaden the perspective of the individual studies presented in the papers, and to relate the results to management issues, I will continue by discussing how single-exposure experiments, as those conducted here, can be used to predict potential effects on animal populations, and discuss this for the case of the herring (chapter 5.2.3). Finally, in chapter 5.2.4, I discuss the implementation of the results of the four papers through management decisions, and highlight the controversies and obstacles that arise when incorporating scientific results and advice in management practice.

5.2.1 Evaluation of Methodology

Herring

The design of an experimental setup for impact studies should be based on a well grounded hypothesis about reaction patterns. Avoidance reactions of herring may be a change in orientation or swimming direction, altered schooling dynamics or packing, or vertical and horizontal avoidance (Pitcher *et al*., 1996; Nøttestad and Axelsen, 1999). Vertical avoidance behaviour (e.g. a diving response) appears to be the most significant (Nøttestad and Axelsen, 1999; Wilson and Dill, 2002).

Based on these considerations, we expected reactions to sonar signals to be in the form of horizontal and vertical movements as well as changes in school density. Underwater acoustics provide an efficient way to study such horizontal and vertical movements of pelagic fish (Ona *et al*., 2007). Vessel-mounted echosounders have successfully been used to study herring-avoidance reactions to predators (Axelsen *et al*., 2000; Nøttestad and Axelsen,

1999; Nøttestad *et al*., 2002; Similä, 1997), as well as the avoidance of anthropogenic signals such as vessel noise (Olsen *et al*., 1983; Ona *et al*., 2007). However, in the case of our sonar-exposure study (papers 1 and 2), we had to use a large vessel to deploy the sonar source as close as possible to the herring, and at the same time to record their behaviour, thus a vessel-mounted echosounder was unsuitable. Stationary, bottom-mounted echosounders have successfully been used in studies of herring (Patel, 2007) and cetaceans (Doksæter *et al*., 2009). Such stationary instruments provide better temporal resolution than does a vessel-mounted echosounder (Patel, 2007), and they cover most of the near-surface blind zone that is inaccessible to vessel-based echosounders (Aglen, 1994). When the fish are relatively stationary, such as during the overwintering period (paper 1), or when they are captive (paper 3), stationary systems are suitable. However, when the fish are in continuous motion, e.g. during their migration (paper 2), stationary observation platforms are inefficient. Hull-mounted fish-finding sonars are designed to localize and monitor the behaviour of large schools in the commercially fishery. They allow school movements to be recorded in three dimensions (Misund *et al*., 1996). Such sonars have been used to study vessel-noise reactions by fish which are horizontally distant from the vessel (Misund *et al*., 1996, Soria *et al*., 1996, Gerlotto *et al*., 2004). They are also useful for observing school structures. For example, Soria *et al*. (1996) showed that schools close to the vessel were more compact than those further away, likely due to their response to the vessel noise. These early studies mostly got their results from video analyses of the sonar images. With the development of more advanced fish-finding sonars, digital records in the form of swimming speeds and directions, and school depths became available. These have been applied in studies of herring-migration patterns (Kvamme *et al*., 2003) and swimming speed and direction (Godø *et al*. 2004). However, these sonars do not provide the acoustic data directly, and this requires special signal processing (Brehmer *et al*. 2007). Such post-processing software has recently been developed as the SH 80 module of the Large Scale Survey System (LSSS) (Korneliussen *et al*., 2006). This has been applied in the Simrad SH 80 sonar. The software produces standardized outputs similar to an echosounder, allowing analysis and processing as with conventional echosounder data. Sonar methodology is still advancing, and fishery sonars may become increasingly important for scientific purposes, in studies of fish distributions and population-density estimation, as well as investigations of school behaviour.

Both the *in-situ* studies (papers 1 and 2) used established methodology, while in the captivity experiment (paper 3) we had to design a novel setup to achieve our objectives. This methodology, described in detail in paper 3, primarily targets to detect the vertical avoidance reaction in herring. We therefore used a particularly deep net pen equipped with echosounders and video camera to monitor herring behaviour at all time, a hydrophone recording received sound levels from the sonar as well as the ambient noise (see Fig. 1 in paper 3). This setup performed very well, and has the potential to become a standard method for similar experiments in the future.

To generalize the results and provide an overall estimation of the potential effects of naval sonars on herring, the three studies of overwintering and migrating herring, and that on captive herring in different seasons must be linked together. This task is not straightforward due to the variety of the observation methods which complicate their comparability. Echosounders and fishery sonars have traditionally measured quite different variables. The main output from an echosounder is the volume-backscattering coefficient, s_v ($\Sigma\sigma_{bs}/V$), representing the sum of echoes from all the targets (with individual backscattering cross-sections σ_{bs}) in a defined volume V (MacLennan et al., 2002). The traditional fishery-sonar output has been the mean depth, area, volume and swimming direction/speed of the target school, but not the direct acoustic backscatter (Brehmer et al. 2007). With the new LSSS SH 80 module, the mean s_v of the school is now also available from a fishery sonar. This sonar can follow the same targets for some time, independent of the ship`s movement, while a vessel-mounted echosounder will constantly detect new targets along the vessel track. A stationary echosounder on the seabed, used either on stationary fish layers as for the overwintering herring of paper 1, or on captive fish as in paper 3, will detect the same fish all the time. A fishery sonar and a stationary echosounder will hence both provide s_v values for the same fish structure (school or layer) over many transmission intervals.

The most significant and common avoidance response in herring, across seasons, physiological states, and geographical areas, is the vertical-escape reaction (Olsen *et al*. 1983; Pitcher *et al*., 1996; Nøttestad and Axelsen, 1999; Wilson and Dill, 2002; Ona *et al*., 2007). Vertical avoidance, measured as changes in the depth distribution during naval-sonar exposure, is therefore a sufficient basis for comparing the three studies. Paper 2 compares the vertical-avoidance reactions during the two field experiments, revealing no differences in the depth structure between sonar-exposure and control observations. Since captivity could

restrain the natural behaviour, control studies were conducted prior to all experiments to confirm that the herring were capable of vertical avoidance. All three studies thus include measurements of vertical-escape reactions, allowing comparison across the different seasons and physiological states investigated.

Cetaceans

The behavioural reactions of cetaceans to anthropogenic noise may be horizontal and vertical avoidance as well as changes in vocalisation (Nowacek *et al*., 2007). My work focussed on vertical avoidance i.e. changes in diving patterns.

Diving behaviour of marine mammals has traditionally been studied by time-depth recorders (TDR), giving a two-dimensional track of the depth against the time (e.g. Watkins, 1993; Hooker and Baird, 1999; Baird *et al*., 2002). Horizontal movements may be studied by tagging the whale either with radio- (e.g. Zimmer *et al*., 2003) or satellite-transmitters (e.g. Mate *et al*., 2005; 2007; Olsen *et al*., 2009), communicating the whale`s geographical position and behaviour while it is at the surface. Vocalizations can be detected by hydrophones operated from stationary platforms (Wahlberg, 2002; Oswald *et al*., 2003) or mounted directly on the animal (Madsen *et al*., 2005; Johnson *et al*., 2006; Soto *et al*., 2008). Newer technology allows the recording of all these observations within a single tag that can be attached to the animal, such as the digital tag (dtag) described by Johnson and Tyack (2003). These multi-sensory tags include stereo-hydrophone recordings, depth, pitch, and compass sensors, in addition to a radio-transmitter, allowing reconstruction of the animal's movements in three dimensions, as well as recording its vocalization. Dtags thus record all the observations relevant to evaluating behavioural responses to a noise disturbance, and have successfully been used to study the effects of seismic air-guns on sperm whales (Miller *et al*., 2009). We used such tags in the study of diving behaviour in response to the naval sonar (paper 4). They can also directly measure the noise-exposure level at the whale, characterizing the context in which a behavioural response occurs (Madsen *et al*., 2006). The dtag has, however, some limitations. The tagging procedure can be difficult and time demanding, limiting the number of replicate observations, and the tag must be successfully retrieved to get the data. Some animals may be particularly difficult or impractical to tag (e.g. smaller individuals, calves); those that were tagged may thus not be representative of the whole population.

Evaluating impacts on stimulated animals demands proper basic information about their natural behaviour. This may be highly variable, both between individual cetaceans and over time scales from the seasonal to the sub-daily, making it difficult to detect subtle responses. Some of this variability, however, can be eliminated by using pre- and post-exposure data as controls (Tyack, 2004; Miller *et al*., 2009), but long time series and large sample sizes are usually difficult to obtain. Longer time series of natural behaviours would therefore provide a good basis for evaluating how noise affects cetaceans. Exposure studies should therefore be conducted by combining tagging experiments with long-term studies of natural behaviour, to enhance the background information needed for reliable interpretation of the behaviours observed during short-term exposures (Bejder *et al*., 2006; Johnson *et al*., 2009). Studies of long-term behaviour require a different approach. Doksæter *et al*. (2009) show that stationary bottom-mounted echosounders may provide as efficient tools for long-term studies of cetacean diving behaviour and abundance, as they can operate continuously for more than a year. Such platforms may also have hydrophones to record the vocalization of whales, and if deployed well in advance of an exposure study, more reliable estimates of exposure impacts should result. Preferably, the operating frequency of the acoustic device should be outside the hearing range of the observed animals, which sometimes might conflict with the need for long-range observations.

5.2.2 Behaviour of fish and marine mammals in response to acoustic stimuli

In the studies of herring (papers 1-3) we found that the fish did not show any behavioural responses to the sonar, while other acoustic stimuli, such as playback of killer-whale feeding sounds, engine noise and a short-duration fence-strike noise caused strong vertical avoidance even though the sound intensity was less. Why did the fish react to the latter noises but not to the sonar signals? Are there any specific cues triggering reactions that are not present in the sonar signals? To try to answer these questions, here I review the literature to understand how and if we might predict the reactions of a marine animal to a certain acoustic stimulus, and I discuss this in relation to my results on herring and cetaceans.

Fish and cetaceans live in an environment that is full of various acoustic stimuli, and have to distinguish those that are of biological relevance. The animals act on the information they get from surrounding acoustic cues; anthropogenic noise is part of this "soundscape". Mankind has used the sea for a very long time, but only in the past 100 years has anthropogenic noise in the marine environment been at a level and so widespread that it may actually interfere with the flow of information from natural sounds (McDonald *et al*., 2006; Hatch and Wright, 2007). In particular for cetaceans, with their slow reproduction rate, no specific mechanisms to counteract anthropogenic noise have had time to evolve. The animal's behavioural responses will depend on how it assesses the perceived sound; if it is comparable to a natural alarming sound, which will trigger some form of response (Walter, 1969). Avoidance responses of animals to anthropogenic noise disturbance are often understood as anti-predator behaviour (Walter, 1969; Frid and Dill, 2002, papers 1 and 2). Prey species are, however, almost continuously exposed to cues associated with risk, and anti-predator behaviour may be costly to perform as well as competing with and diverting attention from activities such as foraging, mating or migration (e.g Lima and Dill, 1990; Lima, 1998, paper 2). The decision to perform avoidance behaviour is thus always a trade-off between the cost of that action and the risk of death (Walter, 1969; Frid and Dill, 2002, papers 1-3).

To predict reactions to anthropogenic noise, we must first know what sound characteristics that may trigger a reaction, and secondly the critical levels or doses at which a reaction will occur. This is complicated and has been frequently debated (e.g. Ona *et al*., 2007; Sand *et al*., 2008; Wahlberg *et al*., 2005; Madsen *et al*. 2006, paper 3), but is still not well understood (Handegard and De Robertis, in prep.; Southall *et al*., 2007, paper 3). The variability in reactions to the same stimulus adds further complexity. A reaction is often influenced by the internal physiological state of the animal and its motivation (Lima and Dill, 1990). Herring, for example, tend to react more strongly while overwintering than during feeding or pre-spawning periods (Skaret *et al*. 2005; Fernandes *et al*., 2000a,b), and walleye Pollock (*Theragra chalcogramma*) appear to be more reactive in winter than in summer (De Robertis *et al*., 2008). Another potentially important factor is learning (Fernö *et al*., in press.), e.g. cyprinids have been shown to avoid trawls after having escaped a previous capture attempt (Pyanov, 1993). The natural behaviour and habitat of an animal also influences its reaction pattern. For example, pelagic fish tend to be highly reactive (e.g. Chapman and Hawkins, 1969; Engås *et al*., 1996; Slotte *et al*., 2004, paper 3), while fish

living around underwater structures seem to react less (e.g. Pearson *et al*., 1992; Wardle, 2001). This may be explained by their vulnerability to predation. Pelagic fish are more easily detected, hence early avoidance will reduce the risk of being eaten. For bottom-dwelling fishes on the other hand, the best strategy will be not to react, as they are already hidden, and sudden movement is likely to alert the predator. Thus, to fully understand a reaction, we must know the processes occurring between the animal and its environment, such as the received sound level and other acoustic characteristics, as well as the processes occurring within the animal, such as its motivation and physiological state, and link these together (Browman, 2005).

Fish

Why did the herring react so strongly to the killer-whale playback, engine noise and fence-strike signals, while apparently ignoring the sonar transmissions?

To understand how an acoustic stimulus may trigger a reaction in fish, it is essential to determine how the sound is received and processed. The hearing sense of fish primarily depends on the otoliths within the inner ear. Most of the fish body is similar in density to the surrounding water, and the tissues oscillate with the sound field. Since otoliths are denser calcium-carbonate structures, sound waves cause relative movements between the otoliths and the surrounding tissue, and the entire organ thereby acts as an accelerometer (Chapman and Sand, 1974). The otoliths are surrounded by a close network of hair cells connected to nerves which detect the above-mentioned motion (Pumphrey, 1950). All fish have this sense, which is based on the particle motion of the sound wave, and is responsible for the low-frequency hearing capability (Chapman and Sand, 1974). Fish with a swimbladder may in addition detect the pressure component of a sound wave, due to oscillations of the air-filled bladder as the sound pressure changes. These oscillations may then be transferred to the inner ear through the body tissues (Sand and Hawkins, 1973), increasing the sensitivity to acoustic signals (Enger and Andersen, 1967; Chapman and Hawkins, 1973). This is particularly important for fish with a mechanical coupling between the swimbladder and the inner ear (Popper *et al*., 2003a); fish with such specialisations (e.g. herring) may detect sound frequencies over 3000 Hz (Mann *et al*., 2001; Popper *et al*., 2003a).

The next step in understanding fish reactions to acoustic stimuli concerns how they make behavioural decisions based on their perceptions. Hearing is important for communication, and a wide range of fish species produce sounds (Bass and McKibben, 2003). However, the most important property of fish hearing is that it gives a constant flow of information about the surrounding environment, ranging from distant sources like the wind and an approaching predator (Fay and Popper, 2000; Popper, 2003b). This has likely been a strong selective force in the evolution of fish hearing (Fay and Popper, 2000). Hearing senses developed before sound production related to communication (Popper and Hastings, 2009b). As anthropogenic noise is part of this "soundscape", reactions to these sounds are also to be expected, usually in the form of anti-predator responses. Killer whales are among the main predators on herring (Similä *et al*., 1996). Herring responses to killer-whale attacks have been studied in detail, revealing typical avoidance responses such as horizontal and vertical movements and school packing (Nøttestad and Axelsen, 1999; Nøttestad and Similä, 2001). Such reactions are therefore to be expected if the herring confuse the anthropogenic noise with the sound of a potential predator. Understanding if and why a fish will respond to certain human-generated acoustic stimuli is not straightforward. Løkkeborg *et al*. (2011) studied the effects of seismic air-gun noise on fish-catch rates, and found gear-dependent effects in commercial fisheries which included both reductions and increases in the catch rates of various fish species. The gillnet fishery on Greenland halibut (*Reinhardtius hippoglossides*) and redfish (*Sebastes marinus*) showed increased catches during seismic shooting, while long-line halibut catches fell. These apparently contradictory results may be explained by the more active swimming of halibut and redfish in response to the shooting, making them more vulnerable to the gillnets. Longlines, however, attract fish by baits, thus their catches depend on feeding motivation. These results indicate that seismic shooting may have a scaring effect on halibut, by making them more active while they devote less time to feeding. Catches of saithe (*Pollactius virens*) by both gillnets (Løkkeborg *et al*., 2011) and trawls (Engås *et al*., 1996), were reduced during seismic shooting, indicating that the fish emigrated from the shooting area. These studies show that different methods (i.e. gears) may give different results. Combined, the results demonstrate the importance of species-dependent natural behaviour, as the redfish is usually a relatively stationary, bottom-dwelling species; more activity would increase the gillnet catches, thus the more mobile saithe tend to move out of the area resulting in the observed reduction in gillnet catches.

My studies showed that herring did not react to the high-intensity sonar signal, but showed a strong diving response to the killer-whale playback (paper 1), to the broadband engine noise, and the "fence-strike" signal (paper 3). The latter was a low-frequency signal of very short duration, generated by striking the fence of the pen with a large wooden stick, and this signal caused the strongest response (paper 3). As the fish, the setup, and the study methods were exactly the same, the decision of whether to respond or not should be explained by characteristics of the acoustic signal. The sonar signals are likely perceived as sounds not associated with potential danger, whereas the engine noise, fence-strike and killer-whale playback could include features associated with risk. Such characteristics include the sound intensity, the exposure duration, peak-pressure, frequency content or modulation, signal rise-time, and repetition rate (Hildebrand, 2009). Paper 3 examines these characteristics for the "fence strike", engine noise, and sonar signals.

For humans, the intensity (received sound-pressure level [RL]) of a sound, often in combination with the duration of exposure (sound-exposure level [SEL]), may best explain reactions and the corresponding reaction thresholds (e.g. Miedema and Vos, 1998; Lercher *et al*., 2003; Nilsson and Berglund, 2006). Also in the case of fish, a relationship between the signal intensity and the behavioural response has been documented, e.g. *Sebastes* spp. showed stronger responses to seismic air-guns with increasing signal intensity (Parson *et al*. 1992). Gadiods exposed to seismic air-guns showed stronger and more long-term avoidance when the signals was stronger and more continuous, resulting in higher SEL (Engås *et al*., 1996; Løkkeborg *et al*., 2011). However, in our study (paper 3), the sonar signals had much higher RL as well as SEL compared to the fence-strike signal and the engine noise (see table III in paper 3). Due to the high variation in hearing sensitivity between frequencies, the spectrum of the signal is also important (e.g. Enger *et al*., 1993; Wilson and Dill, 2002). Herring is much more sensitive in the lower-frequency band (Enger, 1967; Blaxter *et al*., 1981), where the engine noise and "fence strike" signals have most energy, whereas the sonar signals are at higher frequencies where the sensitivity is low (see Fig. 4 in paper 3). However, even when compensating for the difference in sensitivity of 25 dB at most, the "sensation level" (RL as sensed by the fish) is still higher for the sonar signals. This demonstrates that even the perceived level of a sound is not always an adequate measure of how an animal is likely to respond, as also reported by Wahlberg and Westberg (2005). Engås *et al*. (1995) showed that herring reacted to authentic vessel noise, but not to

smoothed signals of the same noise at the same levels and frequencies, indicating that other characteristics are involved in triggering the reaction. The most intense behavioural reactions are often observed in response to brief sounds with a rapid rise time (Blaxter *et al*., 1981, Eaton *et al*., 2001), such as the fence strike signal. This was also documented by Handegard and Tjøstheim (2005), showing gadoids to be most reactive to a sudden increase in acoustic signals, and by Schwarz and Greer (1984) who showed that herring reacted more to irregularities in the sound signal than to a gradual increase of the signal intensity.

Another issue to consider is that in fish with a swimbladder, hearing is attributed to both the pressure and the particle displacement of the sound signal. While pressure-induced swimmbladder oscillation is the main stimulus at higher frequencies (Sand and Hawkins, 1973; Denton *et al*., 1979), particle motion dominates at lower frequencies, particularly below 20 Hz (Sand and Hawkins, 1973). Observations of strong avoidance reactions to sounds in the range 0-20 Hz has been demonstrated for salmon (*Salmo salar*) (Enger *et al*., 1993; Sand *et al*., 2001), gadoids (Handegard and Tjøstheim, 2005), and cyprinids (Sonny *et al*., 2006). These indicate that the particle motion of a signal induces the avoidance reaction. It has been suggested that near-field particle accelerations induced by the moving hull is the major stimulus causing the commonly observed vessel avoidance (Sand *et al*., 2008). The engine noise and the fence-strike signal both have strong components within the 0-20 Hz band, while the sonar frequencies are insignificant below 1 kHz (see Fig. 4, paper 3).

The lack of response to the sonar signals should also be considered as a potential habituation effect, i.e. there is decreased behavioural response to a repeated stimulus; the animals may learn to ignore a stimulus if it is considered irrelevant. Herring show weaker reactions with repeated exposure to vessel noise both in the wild (Vabø *et al*., 2002; Skaret *et al*., 2006) and in captivity (Schwarz and Geer, 1984). We do not know the history of these herring prior to capture, and cannot exclude the possibility that they may have been previously exposed to sonar signals, as the naval frigates operate in areas that coincide with the herring distribution. Weaker responses were observed during repetitive exposure to engine noise at two-minute intervals (paper 3), indicating some degree of habituation. However, after an hour with no exposure, the reaction was as strong as during the first exposure, indicating that any habituation was only short- term. No reaction was detected in response to the first sonar signals in any of the experiments, thus habituation seems an unlikely explanation of the lack of response to the sonar signals.

Thus, it seems likely that the strong reactions to the engine noise and fence-strike signals, and the lack of reaction to the sonar signals, is caused by several factors. The frequency spectrum of the signal, and thus whether the herring perceive it through pressure or particle movement, is likely to be most important. The intensity of the reaction may be predicted by the impulse characteristics of the sound, with brief signals with a rapid rise time (such as the fence-strike) causing the strongest reactions. In addition, any reaction is likely to be modified by factors such as the physiological state, motivation and life-stage of the fish, as discussed earlier.

Cetaceans

In my study of cetacean diving patterns, the strongest responses were seen during some of the killer-whale experiments, with immediate changes from deep foraging dives to a cessation of diving when the sonar transmissions began (paper 4). In spite of the strong changes in dive patterns seen in some experiments, there was no change in others. Why do responses to the same signal vary so much between experiments?

In contrast to fish, cetaceans likely have very limited sensitivity to particle motion (Finneran *et al*., 2002), but they generally have a much better sensitivity to the sound pressure, and they can hear over a wider frequency range (Fay, 1988; Richardson *et al*., 1995).

 As for fish, cetaceans use acoustic cues in the environment to orientate themselves, but additionally, sound production is probably more important for cetaceans. Sound production is used for social interactions, orientation, long-distance communication, and foraging (e.g. Richardson *et al*., 1995; Wartzok and Ketten, 1999).

Killer whales produce whistle tones and pulsed sounds. Whistles are narrowband sounds with most of the energy below 20 kHz, and are often used in social interactions such as mating, play, inter-animal dominance interactions, and maternal behaviour (Richardson *et al*., 1995). Pulsed calls are also important in social activities; for killer whales up to 95 % of these calls transmit energy between 500 Hz and 25 kHz, with the dominant frequencies being 1-6 kHz (Ford and Fisher, 1982). For killer whales in Norwegian waters, pulsed calls are particularly important for killer whales during their co-operative feeding (Van Opzeeland *et al*., 2005; Simon *et al*., 2006).

How do cetaceans perceive anthropogenic noise, and how can we predict their reactions? Compared to fish, most cetaceans have few predators, and anthropogenic signals do not necessarily trigger a fear response. However, the risk-disturbance hypothesis of Gill *et al*. (1996), forming the basis of predictions that prey may react to anthropogenic noise as if it were a predator, might still be useful. When a prey encounters a predator, this model applies economic principles to predict the responses of a disturbed animal in a way that describes changes in the intensity of the reactions, based on the perceived risk.

Due to the importance of animal-sound production, a more likely effect of anthropogenic noise is masking, which reduces the audibility of communication signals. Such masking has been reported for several cetacean species, and various behavioural reactions have been described. For example, both killer whales (Foote *et al*., 2004) and humpback whales (Miller *et al*., 2000) have been shown to increase the duration and intensity of their vocalization in response to underwater noise.

The difference in reactions between experiments may be due to variables outside our control. For the captive herring, we could control the environmental variables, RL, the seasonal phase and feeding conditions. Such control was of course not possible when studying cetaceans in the field. We had control of the source, sound level and frequency, but behavioural mode, season, location, physical environment and sound propagation conditions were thus highly variable between experiments. Since the signal was the same in all cases, acoustic characteristics such as frequency content and modulation, signal rise time and repetition rate cannot explain the different reactions. Uncontrolled variables, such as the source proximity (and hence the RL), the behavioural mode (feeding, travelling etc), previous exposure, and learning may be important factors influencing how the whales will react (Southall *et al*., 2007).

As for fish and humans, the natural place to start is the received level of the sound (RL) or the sound exposure level (SEL). The onset of behavioural reactions at specific RLs has been observed e.g. for bowhead whales (Richardson *et al*., 1999) and humpback whales (Todd *et al*., 1996). However, killer whales showed a marked change in diving behaviour during sonar exposure at an SEL of 100 dB (re 1 μPa² s) in one case, while in another experiment, the same sonar signals at SEL >150 dB (re 1 μPa² s), did not cause any reaction (paper 4). This is

consistent with the review of Southall *et al*. (2007) which found no clear relationship between the reaction onset and RL for odontocetes.

Wartzok *et al*. (2004) discussed the highly variable response of belugas (*Delphinapterus laucas*) in different locations, finding that their current activity and motivation to remain in the same area to be more significant than the sound-exposure level. The experiment causing severe changes in diving behaviour was done while the killer whales were actively feeding on herring at depth, while during all the no-response experiments, the whales were travelling (paper 4). Vocal communication between individual animals in the foraging group is crucial for successful hunting (Van Opzeeland *et al*., 2005; Simon *et al*., 2006). The masking of communication calls may thus have resulted in cessation of feeding, and hence a change in diving behaviour as the whales could no longer catch the herring by cooperative hunting. When travelling, killer whales are mostly silent (Shapiro, 2008), and are therefore not vulnerable to masking by sonar signals. This was confirmed by the experiments involving travelling whales which showed no change in their dive pattern. Similar results were found for bowhead whales (*Balaena mysticetus)* in response to seismic shooting; their reactions were highly dependent on whether the whales were feeding (Miller *et al*., 2005) or migrating (Richardson *et al*., 1999).

Based on this review, the reaction type or its severity, when cetaceans are subjected to acoustic stimuli, is not likely to be predictable from simple signal or source metrics, without considering the context. In the case of the different dive responses for killer whales seen in our experiments, the behavioural mode at the onset of the acoustic signal is likely to be of more importance than RL and SEL. When the whales depend on vocalization, some reaction may occur even at low-intensities of the interfering noise.

5.2.3 From small scale experiments to large scale population effects of sonar on the NSS herring stock

From papers 1-3, we conclude that naval sonars operating at the exposure levels tested (SEL up to 184 dB [re $1\mu Pa^2 s$]) did not cause any behavioural reactions in any seasonal phases and distribution areas. For the three species of cetaceans examined, changes in dive patterns

were detected for killer whales during feeding, but not during travelling, as well as some minor changes for pilot whales and sperm whales during LFAS transmissions (paper 4).

However, these exposure experiments (papers 1-4) were conducted on small scales with durations of hours to days using a small subsample of the total population, thus documenting the response (or lack thereof) on only a small part of the population in a limited time frame. In the context of management, the question is what population impacts could be expected from extensive operations of naval sonars: Could such operations cause changes in population characteristics such as growth, reproduction and survival (Tyack, 2008; NRC, 2005)? Impact could be altered habitat quality, including suitability of breeding and spawning sites, or energetic costs affecting growth and survival (Tyack, 2008).

The US National Research Council (NRC) has developed a four-step conceptual model of how to relate single acoustic disturbance events to potential population effects (NRC, 2005). This model, "The conceptual Population Consequences of Acoustic Disturbance (PCAD)" includes four steps to relate acoustic disturbances to effects on a population (Fig.3). Five groups of variables are of interest; sound disturbance, change in behaviour, life functions affected, vital rates and population effects (boxes 1-5 in Fig.3). The four steps describe the relationships between these variables, for example, how sounds of a given frequency affect the vocalization rate of a given species under specified conditions. The model is originally developed for marine mammals, but the concepts are basic, and may as well be applicable to fish. I will now use this model as a guide for discussing how the results of exposure experiments on adult herring (papers 1-3) can be applied to predict potential population effects. I will not do an equivalent examination of the population effects on cetaceans, mainly because effects on herring were the main objective of my study. Cetaceans were not studied to the same extent, the only focus being on their diving behaviour. Population effects on cetaceans should be examined on a later stage, after having documented effects on horizontal changes in behaviour as well as effects on vocalisation (e.g. Miller *et al*., 2011a,b).
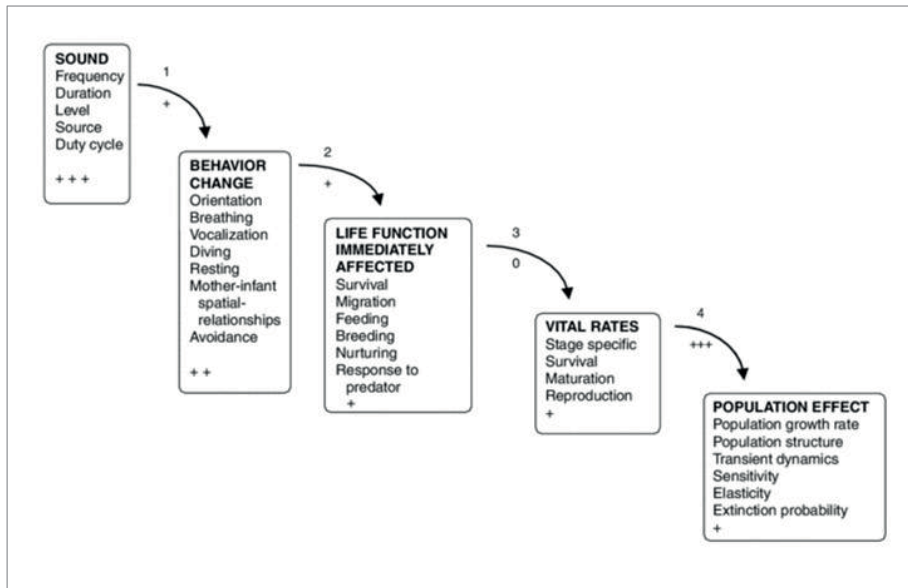
Fig. 3. The four steps involved in PCAD model. Each box lists variables with observable features (sound, behaviour change, life function, vital rates, and population effects) . The "+" signs at the bottoms of the boxes indicate how well the variables can be measured. The indicators between boxes show how well the "black box" nature of the transfer functions is understood; these indicators scale from "+++" (well known and easily observed) to "0" (unknown). (From NRC, 2005).

Step 1

The first step is to identify the noise disturbance, and relate it to the behaviour of the animal (box 1 and 2 in Fig.3). Since all three studies were conducted as controlled-exposure experiments, the noise disturbance, a naval sonar, is known (Tyack *et al*., 2004), and the herring behaviour can be accurately monitored by our methodology. We found no behavioural effects at the tested SEL, but we do not know what would happen if this level were exceeded. The tested SEL may therefore be treated as an upper threshold of ignorance, SEL_0 (paper 3). Higher levels could potentially cause a behavioural response. Another possibility is the consequence of swimbladder resonance. Jørgensen *et al*. (2005) demonstrated that sonar signals at similar frequency ranges as tested in our studies caused strong behavioural reactions and mortality in juvenile herring, which was likely caused by swimbladder resonance (cf. paper 3 and Jørgensen *et al*., 2005). The resonance frequency depends on the depth and the size of the fish (Løvik and Hovem, 1979). Adult herring with larger swimbladders will experience resonance in deeper waters than the juvenile fish studied

by Jørgensen *et al*. (2005). The adult herring in our studies had an average length of 28-30 cm (paper 3). In the frequency range 1-2 kHz (LFAS range), the swimbladders of herring of this size will experience swimbladder resonance at approximately 1 kHz when at 15 m depth, and 2 kHz at 40 m (estimated from Løvik and Hovem, 1979); the resonance frequency increases with the depth. The behavioural reactions observed by Jørgensen *et al*. (2005) showed higher swimming speeds and continuous changes in swimming directions, and in severe cases, significant mortality. These fish were held in small bags (30x40 cm) which did not allow any natural avoidance reaction, but the response indicated that such a reaction would also occur in nature. A change in behaviour could thus occur if herring were exposed to higher SEL or was subject to swimbladder resonance. Such a reaction in herring is likely to be diving and/or horizontal-avoidance reactions (Similä and Ugarte, 1993, Pitcher *et al*., 1996; Nøttestad and Axelsen, 1999), as in the control experiments described in paper 3.

Step 2

At this step, the change in behaviour is related to important life functions (box 3 in Fig.3), which in the case of herring are feeding, spawning, and migration between feeding and spawning areas. Avoidance reactions as described in step 1 have high energetic costs (Slotte, 1999), and severe energy-reserve depletion may have consequences for gonad development and hence reproductive success. Herring may not spawn at all in a year when their condition factor is low (Holst *et al*., 2004). Furthermore, fish in poor condition may undertake shorter migrations (Slotte and Fiksen, 2000), with the result that they do not reach the optimal feeding or spawning grounds. To quantify this step, one must determine the energetic cost of the behavioural change, e.g. higher activity levels, and estimate whether this can be compensated by increased daily feeding (Noren *et al*., 2011). After step 2, we have thus identified a potential change in behaviour, avoidance, which may have high energetic costs, and could result in reduced growth and reproductive successes for individual fish. Whether or not this may be compensated for, will depend on the duration and severity of the disturbance, leading to the next step of the model.

Step 3

The third step is to integrate the effects on the above-mentioned life functions on the vital rates of herring over daily and seasonal cycles (box 4 in Fig.3). Herring behaviour is strongly

time-dependent, both on a daily and seasonal basis. There are diel differences in the vertical structure (Huse and Korneliussen, 2000) and dynamics of schools (Slotte, 1999; Skaret *et al*., 2003). Herring behaviour is also highly variable between annual phases (overwintering, spawning, feeding, as described in paper 2), due to changes in the importance of feeding and spawning as a trade-off for risk avoidance (Fernö *et al*., 1998; Kvamme *et al*., 2003). Our experiments were conducted as successive blocks over about 12 hours, including both day-time and night-time observations (papers1 and 3). Free-field experiments were conducted during the overwintering and feeding seasons (papers 1 and 2), while those on captive fish were done throughout the year (paper 3). Both diurnal and annual differences should thus be detected if they are present. However, if a naval exercise continued for more than 12 hours or higher source level (SL) was used, this could result in behavioural responses since SEL_0 would be exceeded. Changes in vertical distribution involve a varying risk of swimbladder-resonance effects. The captivity experiments covered all the seasons, but the herring were limited to the net pen depth of 20 m, and swimbladder-resonance may only occur in the bottom of the pen when transmitting the lowest part of the frequency range. In the two field experiments, however, the herring were distributed at the depths naturally inhabited in the relevant seasons; 25-35 m during summer-feeding migrations, and from 10-200 m while overwintering. At the given frequency ranges (LFAS, MFAS) and fish sizes (28-30 cm), the field studies included exposure of fish in the resonance depth. However, all the studies included fish of different sizes, with corresponding differences in the depth-dependence of their resonance frequencies. The acoustic observation of collective movements may miss reactions made only by single or few fish. The possibility of such reactions by a few fish experiencing resonance cannot therefore be excluded.

To conclude step 3, I have found that no daily or seasonal cycles will be at risk when SEL is less than SEL_0, but this level can be exceeded during long term operations or with higher SL. Individual fish at resonance depth may also show a behavioural response with the risk of energy-depleting avoidance reactions.

Step 4

The final stage of the PCAD model is to compare the identified effects on the vital rates of individual fish (box 4 in Fig.3) to the effect on the population (box 5 in Fig.3).The effects

most relevant to herring is 1) population growth rate, 2) population structure and distribution, and 3) population sensitivity and elasticity.

For the first point, the growth of the population as a whole may be affected by reduced growth of individual adult herring, or reductions in reproductive output or recruitment. Individual-fish growth requires a positive balance between the costs of maintenance and acquisition of food. As have been identified in steps 1-3, costly avoidance reactions may interfere with this balance. Swimbladder-resonance may affect herring of a given size at a particular depth. Reductions in reproductive output may occur if spawning sites become unavailable, or if the fish are unable to spawn. Herring are most reactive to predators just before spawning, and they may not spawn at all if the perceived predation risk is high (Nøttestad *et al*., 1996). Recruitment is defined as the number of juveniles entering the adult population each year (Blaxter, 1974). Sonar effects on juvenile herring have been investigated by Jørgensen *et al*. (2005), who reported strong behavioural reactions, and substantial mortality when the fish were exposed to sound-pressure levels of 190 dB (re 1 μPa). However, as the natural mortality of juveniles is much higher than that of adult fish, Kvadsheim and Sevaldsen (2005) showed that the mortality due to that level of sonar exposure would, in a worst-case scenario, affect only 0.03 ‰ of the juvenile population, representing less than 1% of the natural daily juvenile mortality rate. Reductions in recruitment due to sonar exposure are hence unlikely to have any significant effect on the population level.

Secondly, the population structure and distribution is highly important to how large part of the population will be affected. This is estimated in paper 2, as the percentage of the population exposed to sonar intensities above SEL_0 in various operational settings and distribution regimes; high density concentrations during overwintering, and the much more dispersed distribution during summer feeding. In the overwintering phase, almost the entire population may be in an area of only 300-600 km^2, inside small fjord systems (Holst *et al*., 2004), with densities up to 30 fish m^{-3} (Nøttestad and Similä, 2001). In this habitat, a 24-h continuous sonar operation at SL above 220 dB (re 1 μPa m) could expose the entire population to levels above SEL_0 (Fig. 4, paper 2). During summer feeding, the herring are dispersed over the entire Norwegian Sea, occupying an area of 300 000 to 500 000 km^2 (Holst *et al*., 2004). For such a widespread distribution, less than 1% of the population could potentially be affected by a 24-h exposure to source levels below 225 dB (re 1 μPa m) (Fig.

4). If sonar intensities above SEL_0 cause avoidance responses and hence reduced growth rates, the risk of affecting a large part of the population is thus much higher for dense distribution regimes such as those found during overwintering.
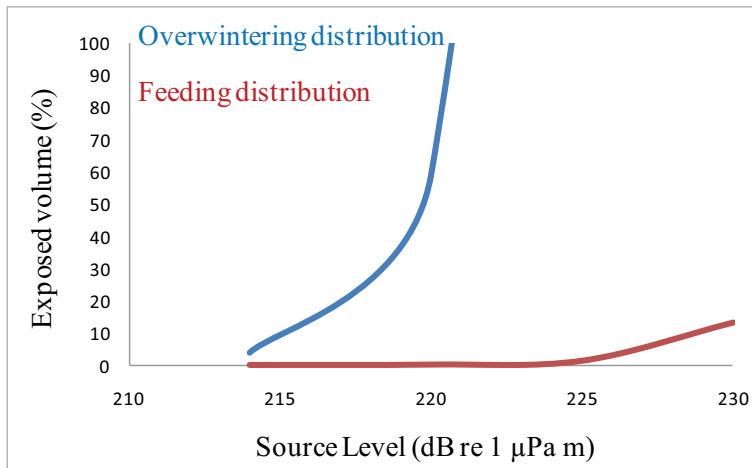

Fig. 4. Percent of the total volume occupied by the herring population that is exposed to *SEL* values above SEL_0 (184 dB [re 1 $\mu Pa^2 s$]) per 24 hours of active sonar transmissions at different *SL* values. This is shown for two scenarios of herring distribution: dispersed in summer-feeding areas in the Norwegian Sea (red); and concentrated in an overwintering area (blue). Calculations are based on a transmission duty cycle of 5 % and a ship speed of 4 m s^{-1}. Figure is based on data from paper 2.

Field experiments have not been conducted during the spawning season. Herring spawns along the Norwegian coast from about 59°N to 69°N, with the main aggregations in Møre between 62 and 64°N. This fish distribution falls between the high-density winter and the dispersed summer distributions which were used in the model calculations (paper 2). The spawning occurs over a period of two months (Holst *et al*., 2004). Although the fish densities in some local spawning areas may be similar to those during the overwintering phase, the fact that individual herring arrive at different times, and they depart soon after spawning, reduces the potential for any significant effect on the spawning population. Vertical distribution is also of importance, as the risk of swimbladder-resonance effects depends on the fish size, depth distribution, and the sonar frequency. Adult herring of the size examined

(~30 cm), will experience resonance at depths of about 15-40 m for the LFAS frequencies (1-2 kHz). Higher frequencies such as those of MFAS (6-7 kHz) will cause resonance at depths > 150 m (estimated from Løvik and Hovem, 1979). We cannot exclude the possibility of a few fish reacting if their particular combination of size, depth, and frequency exposure did cause resonance. However, such conditions were covered in the overwitering study, without detectable effects on the group of fish examined (paper 1). Since these fish make up only a small fraction of the exposed group, a population effect due to resonance is highly unlikely. Further, the field studies used frequency-modulated transmissions (FM signals), which means that any exposure at the resonance frequency will be very short. Continuous transmissions at one frequency (CW signals), as are also used by the Navy, may cause stronger effects.

Thirdly, the sensitivity and elasticity of the population to changes in these vital rates needs to be evaluated. The stock is likely to be most sensitive after spawning, during its migration towards the main feeding grounds, when the herring is in very low energetic condition (Holst, 1996), resulting in less ability to cope with stress factors such as noise disturbances (McEwen and Wingfield, 2003). However, due to the small proportion of the population potentially exposed at that time, the chance of any significant population effect is minimal. The overwintering phase is when the largest part of the population could be affected. In this phase, there is very little feeding, and the fish are mostly stationary in deep layers (Slotte, 1999), and may thus be less sensitivity to noise disturbances. During the spawning period, sensitivity may be high, as spawning may fail if the disturbance is significant (Nøttestad *et al.*, 1996). The stock is likely most sensitive after spawning during migration towards the main feeding grounds, when the herring is in very low energetic condition (Holst, 1996) with reduced ability to cope with a stress factor such as a noise disturbance (McEwen and Wingfield, 2003). However, due to the small proportion of the population potentially exposed in this phase, the possibility of a population effect is minimal. The overwintering phase represent the time of year when the largest part of the population may be affected. In this phase, feeding is highly limited, with the fish mostly staying stationary in deep layers (Slotte, 1999). Sensitivity to a sound disturbance may thus be less, as energetic costs of avoidance more easily can be compensated for by feeding. Sensitivity may also be high during spawning, as spawning may be skipped if the disturbance is high (Nøttestad *et al.*, 1996).

Additional considerations

All our studies and the issues discussed so far have focused on directly observable behavioural effects, treating the fish only as a harvestable resource that must be managed in a sustainable fishery that serves humans as a food supply, without considering the welfare of the fish. Even though fish do not show any behavioural reaction or change in distribution, this does not necessarily imply that they are not at all affected (Slabbekoorn *et al*., 2010). We know that humans living in noisy environments can experience stress. Being in noisy cities or in areas of heavy traffic, for example, involves costs with respect to physical and psychological welfare (Miedema and Vos, 1998; Nilsson and Berglund, 2006). Even moderate noise levels have been shown to negatively affect cognitive development and reading skills in humans (Lercher *et al*., 2003). Similarly, fish may also be stressed by repeated sound exposure (Smith *et al*., 2004, Wysocki *et al*., 2007), causing potential effects on growth and reproductive success (Pickering, 1993). Fish may appear to tolerate the disturbance, not showing any behavioural response, as moving away from the habitat may be too costly, or alternative habitats may be lacking (Gill *et al*., 2001). Fish and other marine animals have evolved to live in a dynamic environment, with resulting abilities to adapt to habitat perturbation to some extent (Costa, 2011). Allostasis is the ability of an animal to maintain its "normal" homeostatic mechanisms when it experiences a disturbance (McEwen and Wingfield, 2003), implying that the animal uses its energetic reserves etc. to maintain regular activities as far as possible. The animal could thus appear to behave normally despite being disturbed. When the level of disturbance becomes so severe that the animals can no longer cope with the stressor, this will result in changed behaviour and/or harm to important life functions. An alternative to directly studying the behavioural or physical effects of sound disturbances is therefore to monitor the secretion of stress-hormones in fish exposed to noise (NRC, 2005). This technique is generally far more complicated than traditional methods of behavioural or physiological investigations, but it could allow the detection of more subtle effects and stress conditions even at low sound levels.

Conclusions

Based on the PCAD model and my results, there is unlikely to be any large-scale population effect on adult herring due to sonar operations. On the other hand, the vulnerability of fish may increase during long naval sonar operations with high SL, especially when they are done in areas of dense fish concentrations, having specific combinations of low stock size,

sensitive periods, or with poor food availability. Swimbladder-resonance has been shown to cause behavioural effects, and in severe cases even mortality in juvenile herring. Swimbladder resonance will also occur for adult fish with specific combinations of fish size, depth distribution, and sonar frequency, but even if such effects as shown for juveniles also occur on adult fish, it is unlikely to cause any population effect. One should in addition consider the fish welfare, as stressors are not always reflected in observable behaviour. As regards the future, it would be useful to conduct a controlled captive-fish experiment to elucidate stressors and their effects in more detail. More investigation on effects of swimbladder-resonance on adult fish at different depths and frequencies are also needed to document potential similar effects as those seen on juvenile fish. To conduct such studies, a fish cage could be lowered to the depths of swimbladder resonance, and the behavioural effects of different acoustic signals and frequencies tested. Such a study would also permit blood samples to be collected from the exposed fish, revealing new insights through the measurement of stress-hormone levels.

5.2.4 Implementation of scientific results to management

One of the most important outcomes of noise exposure research is making recommendations on mitigation procedures and consequent regulations on sources of anthropogenic noise (Richardson *et al*., 1995). My results are intended for use in constructing regulatory guidelines for the sonar operations of the Norwegian Navy. I will here discuss some obstacles and controversies that may occur during this process, reviewing different mitigation strategies and regulatory approaches, and describing how my results are implemented in Norwegian regulations.

Controversies and conserns
Underwater noise is a controversial issue involving many stakeholders with different, and often contradictory, agendas; it is important to bear this in mind when regulations are formulated. Some stakeholders, for instance those in the oil or shipping industries, may fear the economic consequences of restrictive controls on noise emissions, and may thus attempt to slow progress, by expressing concerns based on the scientific uncertainty of existing

results (McCarty, 2004). Other stakeholders, such as environmental non-governmental organisations (NGOs), may try to promote restrictive regulations, often based on vague poorly-supported results from scientific research. It has been speculated that some review papers on anthropogenic noise effects may be biased, focusing on selected results that favours the sponsor of the research (Wade *et al*., 2010). Underwater noise pollution is also of public concern, and has been widely debated in the media. These issues place great responsibilities on the policy makers to form regulations based on rigorous scientific results, even in the face of loud protests. Since a vaguely formulated result may be interpreted in almost all directions, it is important that scientific results are presented in a clear and understandable way, without hidden uncertainties, so they can be correctly interpreted by the policy makers.

Focusing events

The type of scientific studies that are conducted, and hence which sound sources and species have become subject to regulations, have largely been influenced by so-called focusing events; defined as "key events that cause members of the public as well as elite decision makers to become aware of a potential policy failure" (McCarty, 2004). Such events have greatly influenced research programmes and enacted regulations of naval sonars. The first and perhaps the largest event attracting attention to naval-sonar issues ocurred in Greece in 1996. A number of Cuvier beaked whales *(Ziphius cavirostris)* stranded alive near to where a NATO research vessel was testing novel high-power, low-frequency, sonar systems (Simmonds and Lopez-Jurado, 1991), and it was claimed that the sonar transmissions had caused the strandings (Frantzis, 1998). This resulted in much public concern as well as debates among the scientific community. This, along with later strandings of beaked whales associated with navel sonar operations (e.g. Simmonds and Lopez-Jurado, 1991; Jepson *et al*., 2003; Cox *et al*., 2006), resulted in most subsequent scientific studies of naval sonar being focused upon marine mammals, particularly beaked whales.

Although the main international focus was on marine mammals, concerns of potential sonar effects on fish have been a national concern in Norway. Again, a particular focusing event elevated this issue to the public and governmental arenas. Vestfjorden in northern Norway has for several years been the main overwintering area for herring (Dragesund *et al*., 1997), but it is also an area used for multi-national naval sonar exercises. After one of these in 2000,

the World Wildlife Foundation (WWF) in Norway claimed that the naval operations had driven the herring away from Vestfjorden (WWF-Norway, 2001). Although these claims were not supported by any scientific research, and the sonars used in 2000 did not transmit frequencies within the audible range of herring, this publicity put the issue of sonar effects on fish, in particular herring, firmly on the scientific as well as the public agendas. This led to various research programmes that investigated the effects of sonars on marine life, such as those presented in papers 1- 4.

Mitigation tools

Mitigation guidelines worldwide are mostly based on some common approaches, involving noise reduction by careful planning of sound emissions (Richardson *et al*., 1995; Compton *et al*., 2008). They mainly comprise three components:

a) Time and area planning to avoid marine-mammal exposures

b) Implementation of operational procedures

c) Monitoring of animal locations to determine exclusion/safe zones around the sound source.

Time and area planning through temporal or spatial restrictions is a precautionary mitigation technique, often used when scientific knowledge is scarce. This implies that areas or times of the year which are ecologically significant, may be closed to noise producing human activities, such as seismic surveys or naval sonar exercises. This typically includes spawning areas or important feeding habitats.

Operational procedures may include the reduction of sound levels, ramp-up, or more general restrictions on how the sound source is used. Sound-level reduction can be done either by reducing SL or directing the sound away from the animals (e.g. downwards instead of horizontally). For an omni-directional sonar source, the latter will not be an option, but as shown in paper 2, reduced SL may greatly reduce potential impact on herring. NATO guidelines, for example, state that the minimum SL required for technical objectives to be met shall be used (Dolman *et al*., 2009). The "ramp-up" procedure; a gradual build-up of the acoustic signal to allow animals to move away, is a mitigation tool much used in both sonar- and seismic operations. However, its effectiveness may vary between species and circumstances, and there could be some degree of habituation (Barlow and Gisnier, 2006).

Another concern is that the initially low sound level could actually attract the animals, thus possibly doing more harm than good (Weilgart, 2007). Despite these weaknesses, the ramp-up is a standard mitigation tool in sonar operation. All studies in papers 1-4 used a 10-min ramp up in the exposure experiments. Use of the noise source may also be restricted, for instance if bad weather conditions prevented any monitoring of marine mammals.

Among the key provisions in many regulations are safety zones. These are generally determined as an area around the source where it is believed the RL would cause unacceptable effects such as hearing impairment (HESS, 1999). There are increasing demands for such zones to be adopted, based on knowledge of behavioural effects (Johnson, 2011; Southall, 2011). In the absence of relevant scientific results, the definition of safety zones is obviously difficult. These zones may therefore be decided arbitrarily, for example, the common 500 m safety distance around seismic sources, is solely based on the distance at which cetaceans can be reliably observed (Compton *et al*., 2008). In paper 2, such a safety zone for herring exposed to naval sonar was determined. Marine mammals may be excluded from a safety zone by visual or acoustical monitoring (Weir and Dolman, 2007; Dolman *et al*., 2009).

Following the controversy aroused by the beaked-whale strandings, the NATO Underwater Research Centre (NURC) adopted an environmental policy that specifically addressed underwater-sound issues. This resulted in NATO guidelines applicable to scientists, planners, and ship crew when conducting acoustic research at sea. These include maximum sound-exposure levels for both human divers and various marine mammals, but not for fish. The specified exposure levels are, however, not firmly based on scientific results. The guidelines do however only apply to naval research activities. Regular NATO naval operations are supposedly also regulated by similar guidelines, but they are confidential and thus of no value to reduce the concern of environmental groups. Most of the NATO member countries have developed their own guidelines, many including a safety zone between the sonar source and any observed marine mammals, but the size of these zones are not consistent between countries.

The Royal Norwegian Navy has its own guidelines. These apply both to research activities and regular naval operations involving 1-10 kHz active sonar transmissions with SL above 200 dB (re 1 μPa m). These guidelines cover issues concerning marine mammals, fish and

fisheries. They define safety zones around fishing and whaling vessels, and fish farms. The guidelines recommend against exercises in areas expected to have high densities of fish or marine mammals that may be affected by the sonar transmissions, and specify which species should be avoided. They define critical frequency bands and specific ramp-up procedures for active sonar operations. The present results on how herring behave in response to sonars have been central in the development of these guidelines.

These guidelines have been implemented in the software package SONATE, a decision-aid tool used by the Norwegian Navy to help reduce potential environmental impacts of naval exercises. SONATE is used during the planning and execution of sonar operations, with the aim of minimizing conflicts with activities such as fisheries, aquaculture, and tourism, as well as effects on marine life (Nordlund and Benders, 2008). In addition to the sonar-operation guidelines, SONATE contains cartographic information on animal distribution, fishing activity, and fish farms, providing the necessary background to ensure compliance with the guidelines. SONATE links the regulatory requirements to the maps, so that a sonar operator planning an exercise can easily see what rules apply at a specific time and place. This gives the sonar operator an overview of the biological concerns relevant to a given area or time period. SONATE incorporates a precautionary approach as basis; any area having a dense population of fish or marine mammals that may be expected to detect the sonar, will be marked as unsuitable for naval-sonar exercises. As more scientific results emerge, these areas will either remain restricted or be re-opened to naval activities, according to documented findings for the species in question. One example of such an area is Vestfjorden, were dense concentrations of herring may reside between October and January. This was initially marked as an area to avoid due to sonar transmissions at frequencies below 5 kHz is assumed detectable to herring. As a result of the work presented in paper 1, regarding sonar effects on overwintering herring, this area has been removed from the closed list. Similar adjustments have been made for other areas with dense herring concentrations, based on the results in papers 1-3. Such "clearances" are rather important, as the rich marine life along the Norwegian coast leaves very few suitable areas that do not have dense animal populations. Directing naval exercises to areas that are "safe", or at least have low environmental risk, is therefore an important task when mitigating sonar effects. The SONATE system is constantly updated with new distribution maps, and scientific results for different species are

incorporated as they emerge. The results presented in this thesis are, therefore, a good example of how scientific findings may be directly applied in mitigation actions.

6. Future perspectives

In general, a better understanding of the effects of noise on marine animals is needed (Nowacek *et al*., 2007; Popper and Hastings, 2009a, b). Such knowledge must form the basis for appropriate mitigation tools and procedures. For the purposes of management and mitigation, the most important issue is whether the noise disturbance has an adverse effect on the exposed populations (NRC, 2005). There is a need for further research to differentiate relatively harmless short-term responses, compared to long-term large-scale effects at the population level, focusing on knowledge of habituation, sensation, and tolerance (Richardson *et al*., 1995; Nowacek *et al*., 2007). Short-term studies may, however, be related to large-scale effects using the PCAD model, as has been discussed in chapter 5.2.3. The results of my PhD work indicate a need to investigate the potential effects of more intense acoustic stimuli on herring, and the relationship between these and swimbladder-resonance problems.

Applying scientific results in fishery and environmental management requires suitable mitigation tools, indicating a need for further studies on the effectiveness of different mitigation measures. When formulating mitigation guidelines, regulators often seek specific sound-level thresholds that would initiate a management action (Nowacek *et al*., 2007; Weilgart, 2007). Thus studies linking animal responses to particular RL values are of high importance.

Controlled-exposure experiments (CEEs) are somewhat controversial, but a powerful technique that allows researchers to have full control of the acoustic variables, and a robust way to link sound exposure with animal responses (Tyack *et al*., 2004). However, to elucidate the effect on the whole population with reasonable confidence, CCEs should be combined with long-term observations to evaluate the significance of animal responses over a variety of temporal and spatial scales.

Cooperation and collaboration between researchers is also a key consideration for the future. To obtain good scientific results, inter-disciplinary research is essential, combining fields such as behavioural ecology, physics, and oceanography to fully interpret and understand behavioural reactions and the impacts of acoustic stimuli on marine animals. In order for these scientific results to be implemented in mitigation guidelines, and possibly in

international legislation, much greater collaboration between scientists, managers, and industry is needed (Compton *et al*., 2008).

7. Conclusions

- Herring do not respond to naval sonar signals in the frequency band 1-7 kHz, at a received sound-pressure level (RL) up to 176 dB (re 1 µPa m), and accumulated sound-exposure levels up to 181 dB (re 1 µPa² s) (papers 1-3).

- The absence of any reaction is consistent over all seasons, distribution regimes, activity levels, and physiological states of adult herring, as documented through extensive *in-situ* field studies (papers 1 and 2), as well as highly controlled captive-fish studies of smaller-scale effects (paper 3).

- A suitable methodology for studying the detailed behaviour of captive herring has been developed (paper 3). This involves keeping the fish in a deep net pen, monitoring behaviour through vertically- and horizontally-looking echosounders, and video recordings. This setup allowed the herring to perform typical avoidance reactions, as well as proper recording and documentation of this behaviour.

- With sound levels exceeding those tested in the experiments described in papers 1-3, behavioural effects cannot be excluded, but it is highly unlikely that this will result in any effect at the population level, with the possible exception of densely aggregated herring exposed to sonars operating at source levels (SL) greater than 230 dB (re 1 µPa m) (paper 2).

- Herring did not react to the sonar signals, but strong avoidance reactions occurred in response to predator sounds (papers 1 and 2), engine noise, and the "fence-strike" signal (paper 3). These findings indicate that herring avoidance responses are mainly triggered by the low-frequency components of the perceived noise, perhaps in combination with its "suddenness" or impulsive character.

- Killer whales, pilot whales and sperm whales all tended to spend more time close to the surface and less time diving during LFAS (1-2 kHz) transmission. This type of change in diving behaviour does not result in any increased risk of bubble formation and Decompression Sickness (DCS) (paper 4).

- Changes in the diving behaviour of killer whales were highly dependent on their behavioural mode before sonar transmissions begin. During foraging behaviour, killer whales show severe responses by changing from deep-foraging dives to the shallow dives more normally associated with travelling (paper 4).

- Pilot whales showed only minor changes in diving behaviour during sonar exposure, with indications of postponing deep foraging dives when exposed to high sonar intensities (paper 4).

- Sperm whales tended to not perform foraging dives during LFAS exposure, but the low sample size of experiments on this species require further testing to prove this effect (paper 4).

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