Unaccounted Mortality in Purse Seine Fisheries

Quantification and mitigation of slipping mortality

Maria Mikaela Tenningen



Dissertation for the degree philosophiae doctor (PhD) at the University of Bergen

2014

Dissertation date: 6 June, 2014

Contents

Scientific environment	3
Acknowledgements	4
Abstract	5
List of publications	8
Introduction	9
Purse seine fisheries	10
Slipping in purse seine fisheries	12
Northeast Atlantic mackerel and herring: distribution, fisheries and stock status	18
The scope and objectives of the thesis	22
Abstracts of papers	23
Discussion	26
An improved NEA mackerel assessment with tag recapture data	26
Slipping mortality	31
Why do fish crowded in the purse seine die?	39
Mitigation of slipping mortality	46
Purse seining in 2025	51
References	53
Papers I-IV	61

Scientific environment

The work was carried out at the Institute of Marine Research (IMR, Research Group Fish Capture). Funding has come from the Norwegian Ministry of Trade, Industry and Fisheries and The Norwegian Seafood Research Fund (FHF) mainly through the IMR project # 12168 (Overleving av pelagisk fisk etter trenging i not) and the FHF funded project #900688 (Tettheter av makrell og sild i not under kommersielt fiske).

Acknowledgements

I have now reached the point where I have the complete thesis in my hands, a point that I was not always sure I would reach. It has been an inspiring and enjoyable process, but at times also highly challenging. Thanks to my supervisors, colleagues, family and friends I have managed it.

First, I feel very fortunate to have had Aud as my main supervisor. With kindness, understanding and wisdom she has guided me through this process. I am also grateful for all the help and motivation from my co-supervisors, Arill Engås and Aril Slotte, especially during the challenging stages of writing the synthesis.

I would further like to thank my co authors, Héctor and Gavin, with whom it has been a pleasure to work with and Rolf Erik for helping me with the complex field of stress physiology.

I am grateful to everyone in the Fish Capture group for warmly welcoming me into the group and for providing an inspiring and fun working atmosphere. Special thanks to our group leader Bjørn Erik for his support and to the purse seine group (Aud, Jostein, Bjørn, Jan Tore and Mike) with whom I have shared many good moments on research cruises and who have taught me so much about purse seining and instrumentation. I would also like to thank my "new group" in Oslo and especially Jon Egil and Thomas for all the interesting conversations around the lunch table.

I would further like to thank Anders Fernø for his very helpful comments on the synthesis and Egil Ona for including me on the acoustic cruises that were not only fun but where I also had the opportunity to learn about underwater acoustics.

Having a good practical understanding of purse seine fisheries was a necessity in this work and I would thereby like to thank the skippers and crew on R/V Libas and R/V Endre Dyrøy who gave me the opportunity to experience and learn about the fisheries.

It has not always been easy to combine work and private life and I would like to thank my mother and my father and my parents-in-law, Liv and Arne, for always helping us with the children when needed and for all the support and encouragement.

Oliver and Jonatan, the stars in my life, you have kept my mind far away from work when at home.

Eirik, my love, for being you.

Abstract

Purse seining is an efficient fishing method that is used to catch most of the world's pelagic fish species. In some of these fisheries slipping is used to adjust catch size, increase catch value or to release illegal species and sizes. Slipping involves the release of fish from the net before they are brought on board. Little information is available on the frequency of slipping, but anecdotal information indicates that slipping is a common practice in some fisheries, including the Norwegian mackerel (*Scomber scombrus*) and herring (*Clupea harengus*) fisheries in some areas and seasons. Previous studies have shown that the mortality of mackerel and sardines slipped from the net may be high, especially if the density before slipping is high and the fish are held for a long time in the net. Paper II studied the mortality of herring crowded and released from a purse seine. The results showed a density-dependent mortality and a considerably higher tolerance to crowding compared to mackerel. Even so, a mortality rate above 50% was registered at high crowding densities, suggesting that herring slipped in a late phase of hauling may suffer unacceptably high mortality.

Identification of the main causes of slipping mortality is necessary for the adoption of appropriate mitigation measures and regulations. Physiological sampling of crowded herring in **paper II** showed that some fish display a maladaptive physiological stress response, including disturbances in their osmoregulatory balance, and energy exhaustion. A common assumption is that mortality occurs due to impairment of the skin barrier, leading to osmoregulatory deficiencies and substantial leakage of body fluids. **Paper III** showed that a loss of more than 25% of the scales can cause significant mortality in herring. Large quantities of scales can be observed in the water during the late phases of purse seining when the fish are crowded in the net, but to exactly what extent herring lose scales is not known. There is some evidence for scale loss not being a single cause of mortality, but the mortality is

rather a result of the synergistic effects of several stressors (scale loss, hypoxia, exhaustion and stress).

Slipping of dead or dying fish is illegal in Norway. The upcoming landing obligation in EU will have the same approach where fish can be released if high survival is ensured. Crowding experiments indicate that slipping in an early stage and in a careful manner can ensure high survival. There are currently no available estimates of fish densities inside the net during purse seining or any practical methods for monitoring the catches or the net during commercial fishing, which makes the regulation of slipping difficult. Paper IV described a method for monitoring purse seine net volume and estimating catch densities. The results indicated that even in large catches, lethally high densities of mackerel and herring are unlikely to occur up to the point when 80% of the net has been hauled. The results further showed that catch densities between purse seine sets vary significantly due to differences in net volumes and catch sizes. Regulations on how late in a haul slipping can be permitted will have to take such variations into account in addition to any differences in mortality rates caused by different environmental, fishing and biological conditions. In order to ensure that purse seines can continue to provide high-quality catches efficiently even with a precautionary limit to slipping, slipping regulations will have to be combined with technological solutions for improved identification of catch size, species and quality before the net is set or in an early stage of purse seining. In addition slipping techniques and gear modifications that raise survival rates will need to be developed and tested for survival.

Slipping mortality is a source of unaccounted mortality and contributes to biased stock assessment. The Northeast Atlantic mackerel stock is an example of how a high level of unaccounted mortality and a lack of fishery-independent indicators of stock biomass have resulted in unreliable estimates that were eventually rejected in 2013. In this fishery slipping is one source of mortality among many, but it is important to mitigate all the sources. In

paper I, a tag recapture data-set collected by the Institute of Marine Research was used to estimate mackerel stock size. The results indicate a stock size that has been as much as 2 to 2.3 times as large as the official estimate. The estimates involve some uncertainty that needs to be taken into account, especially related to variable tagging mortality and detector efficiency, but could potentially improve the current assessment if the data were included in the ICES stock assessment on a regular basis.

List of publications

Paper I

Tenningen, M., Slotte, A., and Skagen, D. 2011. Abundance estimation of Northeast Atlantic mackerel based on tag recapture data – A useful tool for stock assessment? Fisheries Research, 107: 68-74.

Paper II

Tenningen, M., Vold, A., and Olsen, R. E. 2012. The response of herring to high crowding densities in purse-seines: survival and stress reaction. ICES Journal of Marine Science, 69(8): 1523-1531.

Paper III

Olsen, R. E., Oppedal, F., Tenningen, M., and Vold, A. 2012. Physiological response and mortality caused by scale loss in Atlantic herring. Fisheries Research, 129-130: 21-27.

Paper IV

Tenningen, M., Peña, H., and Macaulay, G. J. 2014. Estimates of net volume and fish density during commercial purse seining. Manuscript. Submitted to Fisheries Research.

Introduction

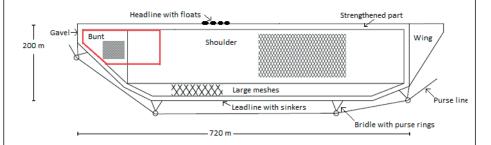
The vessel, a combined pelagic trawler and purse seiner, is heading out to the Norwegian Sea. Good herring catches have been reported and other vessels are already at the fishing grounds. Sonars scan the waters for herring schools. Once a school has been detected, the skipper inspects it by circling around it. This is a critical stage. In addition to determining swimming speed and direction of the school and planning how to set the net, the skipper must know the size of the school. The school should be large enough to avoid additional sets, but not too large and exceed the quota or the load capacity of the vessel. At times it can be very difficult to estimate school size due to the distribution or behaviour of the school. If the skipper decides to target the school, he shoots the net and within a few minutes the school is surrounded by the curtain of net. At this stage the fish may still manage to escape by diving under the net or the vessel where the net is still open. The net must be closed rapidly by hauling the purse line that runs along its bottom edge. Once the net has been pursed, hauling can begin and the sonar transducer that was retracted into the hull during pursing to avoid damage is lowered again. The skipper can then inspect what he has inside the net and see whether he actually managed to trap the whole school. But this is difficult due to air bubbles caused by propellers and thrusters, which disturb sound transmission. It may not be possible to get any idea of the catch until the fish are crowded by the vessel side and visible on the surface. At this stage the skipper may realise that there are too many fish in the net or that they are of low value due to their small size or poor quality. He may then decide to release, or slip, the whole catch or parts of it. If the skipper is satisfied, the catch is pumped onboard, stored in the refrigerated seawater tanks and the vessel steams back to port to deliver its catch.

Purse seine fisheries

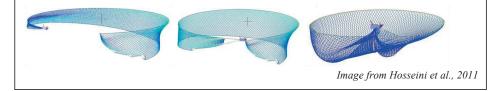
The above describes an ordinary fishing trip for a Norwegian purse seiner and outlines some of the challenges that may be faced and choices that need to be made during a purse seine set. In Norway, a fleet of around 400 purse seiners (ranging from small coastal to large oceangoing vessels) catches about 90% of the country's mackerel (*Scomber scombrus*), herring (*Clupea harengus*) and capelin (*Mallotus villosus*) quotas. In 2012 the catches of these species were 180, 610 and 360 thousand tonnes (kt) respectively (data from the Norwegian Directorate of Fisheries). Purse seining is also an important global fishing method, and schooling species (e.g. sardines, herrings, anchovies, mackerels and tunas) are caught all over the world with fleets ranging from small artisanal to large modern purse seiners (Ben-Yami, 1994). Purse seining accounts for about 30% of the world's total catches (Watson *et al.*, 2006), it is the most efficient method for catching aggregated pelagic species (von Brandt, 1984; Ben-Yami, 1994), and is one of the most energy-efficient fishing methods (Suuronen *et al.*, 2012) (see **Box 1**).

Box 1. Purse seining

The purse seine gear is a wall of netting with floats mounted on the headrope to keep the net at the surface, and with lead weights and purse rings on its lower edge. Net design varies according to vessel type and size, the behaviour of target species and the type of fishing grounds (Fridman, 1986). Below is an example of a Norwegian mackerel and herring purse seine.



The fishing process consists of three main phases: shooting, pursing and hauling. First, the wall of netting is shot in a circle around a school of fish. Second, the bottom of the net is closed by hauling the purse line. Third, the net is hauled onboard and stacked in the aft of the vessel ready for a new set. During hauling the catch is gradually accumulated in the strengthened part of the net (the bunt) and eventually taken on board either using a brail or a pumping system. To be able to capture the often fast swimming pelagic schools the net needs to be set in the right position according to the fish position, and swimming direction and speed (Misund, 1992). Fish schools are located by acoustic underwater devices, visual detection of the school or dolphins or birds following the school. Alternatively fish aggregating devices or light is used to attract and concentrate the targeted fish.



Slipping in purse seine fisheries

In purse seine fisheries, unwanted catches are sometimes deliberately released or 'slipped' from the net while still in the water (Lockwood et al., 1983; Kelleher, 2005). Slipping is usually carried out in a late phase of hauling when the fish are densely crowded by the vessel side by either letting down the gavel (horizontal end of the net) thereby making an opening in the net, or lowering the floatline (Lockwood et al., 1983). The most common reasons for slipping are excessively large catches that either exceed the quota or the load capacity of the vessel, low-value catches or illegal species or sizes. The Food and Agriculture Organization of the United Nations (FAO) includes slipping in the definition of discarding, i.e. the portion of the catch, which is thrown away or dumped at sea (Kelleher, 2005). Discarding is currently one of the main issues in fisheries management, and it has been estimated that 6.8 million t of fish, about 8% of world catches, are discarded (Alverson and Hughes, 1996; Hall and Mainprize, 2005; Kelleher, 2005). Fish mortality caused by discarding is generally regarded as a waste of resources, it may contribute to changes in ecosystem structure and functioning and if the mortality is not included in the total fishing mortality estimates in the stock assessment models, the result may be biased stock biomass estimates and quota recommendations that are not in accordance with the actual stock biomass (Alverson and Hughes 1996; Kelleher, 2005; Crowder and Murawski, 2011). Here, discarding and slipping are treated as two separate actions in order to distinguish between the different methods used to release the fish.

Slipping was first registered in the mackerel fisheries off the coast of Britain (Lockwood *et al.*, 1983) and has since been reported in sardine fisheries in Southern Australia (Mitchell *et al.*, 2002) and off Portugal (Stratoudakis and Marçalo, 2002) and in Norwegian mackerel and herring fisheries (Anon, 2002; Huse and Vold, 2010). A few attempts have been made to

estimate slipping quantities by placing observers on board purse seiners (Anon, 1999; Anon, 2002; Stratoudakis and Marçalo, 2002; Borges *et al.* 2008). Estimating the amount of slipping that takes place in a fishery, however, is challenging (Stratoudakis and Marçalo, 2002; Borges *et al.* 2008). Slipping is sporadic with large seasonal and regional variations, making the extrapolation of observed cases of slipping to whole fisheries difficult. The whole slipping process further takes place under water and it is difficult to visually estimate what quantities of fish are actually released. Finally, having observers on board the vessels may influence crew behaviour and slipping may be avoided when observers are on board. Anecdotal information based on registrations of dead fish on the seabed in areas where purse seiners have been fishing (although can also be result of net bursts) and reports of slipping in the fishing fields by onboard observers, scientists and fishermen suggest that slipping is widely used in some fisheries and in certain periods.

In the Norwegian mackerel and herring fisheries, catches are mainly delivered for human consumption and often to a highly quality-conscious market in which prices are strongly influenced by fish size and quality. Each vessel has its own quota and the focus is on maximizing the value of the catches. This is a powerful incentive to release low-value catches in favour of more valuable catches at times (Anon, 2002; Gezelius, 2006; Huse and Vold, 2010). Slipping has also frequently been reported from areas where the targeted fish form large dense schools, especially in the winter fisheries for Norwegian spring spawning herring. Controlling catch size can then be very difficult and skippers can end up with far more fish in the net than planned and unless excess catch can be pumped over to a nearby vessel they have no other choice than to release parts of the catch. Net bursts are also common when catches are very large, and this has been shown to result in high mortality (Misund and Beltestad, 1995).

In addition to quantifying the amount of fish slipped it is important to estimate the proportion of slipped fish that die. These two figures combined determine the magnitude of the problem. If most of the slipped fish survive it may not be too much of a problem, even if large quantities are released. Compared to many other fishing methods, purse seining can be regarded as a relatively gentle way of capturing fish. The fish are able to swim freely inside the net until a late phase of hauling. Slipping is also a gentler way of releasing fish than discarding, where fish are brought on deck and often handled before being released. This suggests that survival rates following slipping from purse seines may be higher than discarding in other fisheries. However, there are large differences in how well different species tolerate capture and release, and the small pelagic species that are targeted by purse seines are generally sensitive to interactions with fishing gears, with the result of high mortality (Chopin and Arimoto 1995; Suuronen et al., 1996a; Broadhurst et al., 2006). Previous studies have shown that especially mackerel (Lockwood et al., 1983; Huse and Vold, 2010), but also sardines (Mitchell et al., 2002; Marçalo et al., 2010) may experience high mortality following crowding and slipping in purse seines, particularly if they are held for a long time in the net and crowded to high densities before slipped.

Quantification of discard and slipping mortality is not straight forward. Fish may die as a direct effect of stress and injuries experienced during capture and release, or indirectly due to disease and predation (Chopin and Arimoto, 1995). Mortality can thus occur within hours, or up to several weeks after release (Lockwood *et al.*, 1983; Davis, 2002), making direct quantification of mortality rates under commercial fishing situations difficult. How well fish tolerate the capture and release is also influenced by environmental, fishing and biological conditions resulting in that mortality rates can vary under different conditions (Suuronen *et al.*, 1996b; Davis, 2002; Suuronen, 2005; Broadhurst *et al.*, 2006). Fish mortality after being released from fishing gears has commonly been studied in laboratory or field experiments, by

either exposing them to real or simulated fishing conditions or by exposing them to one or several capture and release stressors (e.g. net abrasion, crowding, handling, hypoxia, or air exposure), and then monitored for some days or up to several weeks (Suuronen *et al.*, 1996a; Broadhurst *et al.*, 2006). For some species and in some fisheries, indicators of discard mortality have been developed, these involve a measure of physiological or behavioural responses (see **Box 2**) (Davis, 2005), reflex impairment (Davis, 2007; Humborstad *et al.*, 2009), physical condition (Davis and Ottmar, 2006; Benoît *et al.*, 2010) or capture stressor intensity (Davis, 2002; Benoît *et al.*, 2013) that can be related to mortality. Such indicators allow mortality rates to be predicted immediately before or after release under commercial fishing situations and in a range of different fishing conditions (Benoît *et al.*, 2013). Understanding and identifying the main capture and release stressors that cause the mortality, how these vary under different conditions and how the fish respond to these stressors behaviourally and physiologically is important. By understanding the underlying mechanisms of mortality it will be possible to estimate mortality rates more accurately, identify indicators of mortality and appropriate mitigation measures and regulations can be applied.

Discard rates have been reduced in many fisheries through the introduction of more selective fishing gears, discards regulations and improved enforcement of regulatory measures (Kelleher, 2005; FAO, 2011). Growing public awareness and demand for sustainable and environmentally friendly fish stock harvesting have also been important in placing more pressure on reducing discards in fisheries (Bellido *et al.*, 2011). Gear modifications that improve selectivity (Isaksen *et al.*, 1992; Suuronen and Sardà, 2007) and monitoring instruments that provide detailed information on the composition and size of the catch (Misund, 1997; Graham *et al.*, 2004) have been important in reducing discarding in many trawl fisheries. In purse seine fisheries, such technological developments have so far been very few. Once a purse seiner has selected its target, the catch process itself is unselective,

using few or no devices for size or species selection. One of the few exceptions is the "medina panel" and the "back-down" manoeuvre, which have greatly reduced the mortality of dolphins in tuna fisheries (Barham et al., 1977). In Norway, sorting grids were considered for size selection in the mackerel purse seine fisheries, but the mortality rate of mackerel escaping through the grid was too high to recommend their use in these fisheries (Misund and Beltestad, 2000). There is now a sharper focus on slipping mortality in European purse seine fisheries for small pelagic species (Marçalo et al., 2006; Huse and Vold, 2010) and slipping regulations are being implemented. In Norway discards of fish, including slipping dead or dying fish, is prohibited, while the EU is in the process of introducing a landing obligation that provides an exemption if high survival of the discarded or slipped fish can be demonstrated (STECF, 2013). There is a growing need for improved catch-monitoring systems, for improved selectivity of purse seines and gear designs that allow for gentle releases of fish from the net. A great deal of effort is currently being put into the development of sonar technology that can provide more accurate information about schools (Gerlotto et al., 1999; Ona and Andersen, 2008). Physical sampling techniques at an early stage of hauling and purse seine net designs that facilitate quick and gentle release of unwanted catches without harming the fish are also under development (unpublished data, IMR). In tuna fisheries, fishing methods and gear modifications including the use of sorting grids that will reduce the number of unwanted species and sizes in the catches are also being developed (Gilman, 2011).

Box 2. The physiological stress response in fish

Fish possess a suite of adaptive behavioural and physiological strategies that have evolved to cope with challenges and stressors; the stress response (Pottinger, 2007).

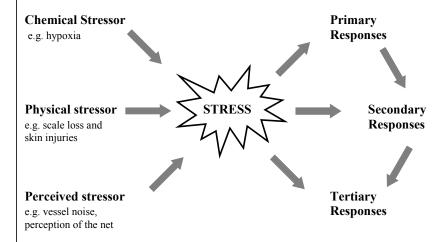


Image modified from Barton, 2002

Primary responses

When the central nervous system recognizes a real or a perceived threat catecholamine and corticosteroid hormones are rapidly released into the blood circulation (Barton, 2002).

Secondary responses

The primary responses stimulate secondary changes at blood and tissue level. Oxygen uptake and transport are increased (Wendelaar Bonga, 1997). Energy sources are mobilized and glucose is released into blood. Energy is reallocated away from growth and reproduction and toward activities that require energy to restore homeostasis, such as respiration, locomotion, hydromineral regulation and tissue repair (Wendelaar Bonga, 1997; Mommsen *et al.*, 1999). Cortisol also suppresses the stress-induced inflammatory / immune reaction that might otherwise lead to tissue damage (Mommsen *et al.*, 1999).

Tertiary responses

The secondary responses allow the fish to cope with stressors and help them to maintain or re-establish homeostasis, but some of them have negative side effects. The increased permeability of the gills cause a hydromineral imbalance as water and salt diffusion across the gills increase and additional energy is needed to cope with this osmotic imbalance. The suppressed immune defense, stimulated by cortisol, reduces the fish's resistance against infections and parasites. Further the reallocation of energy may, in

Northeast Atlantic mackerel and herring: distribution, fisheries and stock status

The Northeast Atlantic (NEA) mackerel stock is large and widely distributed, and it migrates over long distances between spawning, feeding and overwintering grounds (Figure 1a) (ICES, 2013a). The stock comprises three spawning components. The southern component spawns in Spanish and Portuguese waters from February to May, the western component spawns in the waters west of Ireland and the UK between March and July and the North Sea component centrally in the North Sea and Skagerrak between May and July (Iversen, 2002; ICES, 2013b). After spawning in late spring and summer, the adults from the southern and western components migrate to the Norwegian Sea for feeding, where they also mix with the North Sea component (Uriarte and Lucio, 2001). By the end of the summer the mackerel move further north and northwest to deeper waters for overwintering before they once again migrate to their respective spawning grounds in December – March (Reid, 2001).

The stock supports large and valuable fisheries in many European countries. Landings have ranged between 300 and 1 000 kt since 1969 (ICES, 2013a). The main fisheries include the EU trawl fleet, which targets mackerel west of the British Isles on their migration to the spawning grounds in December to February (35%), Russian freezer trawlers and, in recent years also Icelandic and Faroese trawlers targeting mackerel in the summer feeding grounds (38%), as well as the Norwegian purse seine fleet, which targets mackerel off the Norwegian coast and off the British Isles in August to November (20%). Mackerel are also fished throughout the year in Spanish and Portuguese waters.

Widely distributed and migrating stocks that are shared by many nations, such as the NEA mackerel, are difficult to assess and manage. The fish move between the fishing zones of several countries and the proportion of the stock present in each zone at any time varies with

the season and year. Reliable information on stock abundance and distribution patterns is essential for an international agreement on quota allocations between the fishing nations. Currently, both the abundance and distribution patterns of the NEA mackerel stock are uncertain. There is no international agreement on total allowable catches (TAC) and the quotas set by the different countries have consistently exceeded the TAC advice given by ICES (ICES, 2013a). The reason for the uncertainty of the stock size is the combined effect of unreliable catch data and a lack of fishery-independent estimates of abundance. As a result, in 2013 the quantitative assessment of the stock was rejected (ICES, 2013a) and this, together with a high fishing pressure, has placed the stock in a vulnerable position. There is thus an urgent need to improve the assessment model, develop a reliable age-structured fisheries-independent index of stock biomass and to reduce the unaccounted mortality sources that have produced the unreliable catch data. The sources of unaccounted mortality are believed to be unreported and illegal landings, discard and slipping mortality, escapee mortality (mortality of fish that escape the fishing gear) and a higher natural mortality rate than assumed in the assessment model (ICES, 2013b).

The Atlantic herring is another highly abundant pelagic species in the Northeast Atlantic that supports large purse seine and trawl fisheries. The herring population in the Northeast Atlantic is made up of several distinct stocks, the largest of which is the Norwegian Spring Spawning (NSS) herring (Holst *et al.*, 2004; ICES, 2013a). The NSS herring also migrates long distances between its spawning, feeding and overwintering grounds (Figure 1b) (ICES, 2013b). The stock spawns on the Norwegian coast between February and March. After spawning, the adult stock moves to the feeding grounds in the Norwegian Sea where it remains until late summer and partly mix with the NEA mackerel stock. It then moves to the currently oceanic overwintering grounds north of Vesterålen, where the herring form large dense schools (ICES, 2013b). The fisheries generally follow the migration of the stock; large

fisheries target herring on their spawning migration along the Norwegian coast at the beginning of the year, while Russian and Icelandic trawlers then catch herring in the summer feeding areas in the Norwegian Sea and the fisheries finally move to the overwintering grounds off the Norwegian coast. The stock is shared between Norway (60%), Iceland (15%), Russia (13%), the EU (6%) and Faroe Islands (6%), and landings have fluctuated between 100 and 1.7 million t since late 1980s (ICES, 2013b).

The NSS stock has been declining since 2009. It is now at a level of 5 million t and is expected to further decline in the near future (ICES, 2013a). The stock is managed sustainably and the recommended TAC for 2014 is 418 kt, which is a major reduction from the maximum TAC of 1.6 million t in 2009 (ICES, 2013a). The stock assessment utilises input from several survey indices and is thereby more reliable than the mackerel assessment (ICES, 2013a). Some uncertainty in the stock assessment is due to a discrepancy between survey indices and catch statistics (ICES, 2013b). According to ICES, levels of discard and slipping are insignificant in the fisheries (ICES, 2013a), but the quantities that die as a result of slipping and bursting nets are not known and should not be ignored, especially now that the stock abundance is declining.

The North Sea autumn spawning (NS) herring is also a large herring stock. It is distributed throughout the North Sea and spawns along the eastern coast of Great Britain between July and October (Figure 1c). Trawl and purse seine fisheries target NS herring in late spring and summer in the central and northern North Sea and in autumn and winter in the southern North Sea (ICES, 2013c). Total catches in 2012 were 405 kt, about 30% of which is taken by purse seiners (ICES, 2013c). The stock has been increasing since 2007, and in 2013 it produced catches at the same level as the NSS herring, with a quota recommendation of 482 kt for 2014 (ICES, 2013c). Discards are partly monitored and included in the assessment, but ICES is concerned about the lack of information on unallocated removals in the herring fisheries and

wishes observer coverage to be maintained in all fleets (ICES, 2013d). Slipping is known to take place in the summer fisheries, which target high quality matjes herring, i.e. young herring that have not yet spawned and have a high fat content (Anon, 1999).

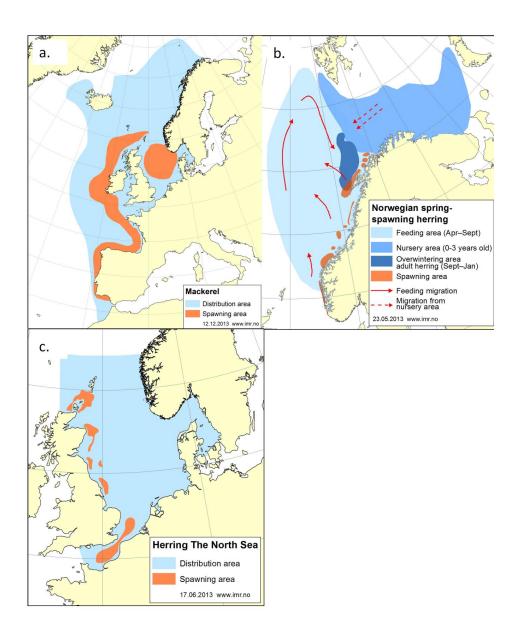


Figure 1. Distribution areas of NEA mackerel (a), Norwegian spring spawning herring (b) and North Sea herring (c), from IMR database.

The scope and objectives of the thesis

The work described in this thesis falls into two main areas. The first, focuses on unaccounted mortality in the NEA mackerel fishery and aims to develop an alternative estimate of stock biomass based on tag recapture data. The second and major part focuses on slipping from purse seines. Slipping is a source of unaccounted mortality in the NEA mackerel fishery, but is also likely to be a source of unaccounted mortality in herring purse seine fisheries. There is a need to both quantify and reduce this mortality and to be able to do that we need to understand why the fish die and how the mortality rates are influenced by different fishing conditions. In the final part, the focus is on applying the information available on the effects of slipping from experimental work to commercial fisheries and discussing potential mitigation measures that can be applied to purse seine fisheries where slipping is an issue on a more general basis. The work has been performed in close cooperation with other current projects at IMR that focus more on the technological development of the purse seine fisheries.

The main objectives of the thesis are to:

- estimate mackerel stock biomass based on tag recapture data and evaluate the usefulness
 of this method as a fishery-independent estimate of NEA mackerel stock biomass
- quantify the mortality of herring crowded to different densities in the purse seine and describe the physiological responses to crowding
- 3. investigate the importance of scale loss as a source of slipping mortality among herring
- 4. estimate fish densities in the purse seine during commercial fishing and use these estimates to discuss the usefulness of regulating slipping by having a limit to how late in a haul slipping can be permitted.

Abstracts of papers

Paper I

In the present study we utilize tag recapture data to estimate year class abundance and spawning stock biomass of mackerel (*Scomber scombrus* L.) in the Northeast Atlantic for the period 1986–2008. On average 20,000 jigged mackerel have been tagged annually with internal steel tags in the spawning area west of Ireland and the British Isles, and the tags have been recaptured in commercial catches screened through metal detectors. The spawning stock biomass estimates derived from two different tag-based models were highly variable but were on average 2 and 2.3 times higher than the ICES official estimate. The official estimate is considered uncertain and most likely an underestimate of the actual biomass, due to unregistered mortality in the fisheries and lack of fishery-independent, age-disaggregated data. Hence, tag-based estimates could potentially improve the current assessment if included in the ICES stock assessment on a regular basis. These estimates also involve some uncertainty that needs consideration, especially related to variable tagging mortality, detector efficiency and migrations of the stock.

Paper II

To study the effects of crowding in purse-seines on the survival and stress response of herring (*Clupea harengus*), large-scale field experiments were conducted in the North Sea during 2008 and 2009. The mortality was 28% at a crowding density of 221 kg m⁻³ and increased further with increasing density. Crowding densities <150 kg m⁻³ did not result in any additional mortality compared with the control group (0.9–2.0%). Smaller herring and herring with a lower condition factor were more vulnerable to the effects of crowding. Blood analyses showed a significant increase in cortisol, lactate, and blood ions in the crowded fish. Lactate

returned to control levels 2 d post-stress, whereas cortisol and blood ion levels continued to increase during the 4- to 5-d monitoring period. Furthermore, plasma glucose appeared to be substantially reduced at the end of the trial, indicating that the herring were incapable of restoring homeostasis and were approaching energy exhaustion. These results provide important information about the crowding densities that can be tolerated in the purse-seine fisheries for herring and will benefit future development of guidelines for purse-seine slipping operations.

Paper III

Slipping of crowded herring (*Clupea harengus*) from purse seines may lead to high mortalities. We suggest that scale loss during crowding may be one reason for the mortalities. To test this hypothesis, herring were transferred to 5 m tanks and subsequently de-scaled on 25% or 50% of the body surface. Recovery was monitored for mortality (over 7 days), behavior (days 1 and 2) and blood metabolites (days 0, 1, 2, 4 and 7). Most mortalities occurred between 1 and 4 days post treatment and increased with the degree of de-scaling reaching 60% in worst cases. Larger fish with good condition had better survival than smaller fish. Many de-scaled fish increased their swimming speed significantly. Some also deviated from the normal schooling behavior swimming with the current rather than against it. Descaling led to loss of osmoregulatory ability and presumably water loss as seen through increases in plasma ions and osmolality. Plasma glucose was reduced in de-scaled fish while plasma levels of cortisol and lactate were increased. An apparent bimodal response was observed in the blood data. While some fish recovered and returned to pre-treatment levels for most parameters within days, others were unable to recover. It is concluded that de-scaling may lead to mortality in herring. The mortality appears to be related to fish condition, loss of

osmoregulation and increased stress response and energy expenditure. Altered behavior may contribute to the mortality.

Paper IV

Slipping, the release of fish from the net while it is still in the water, is used to adjust catch size or increase catch value in many purse seine fisheries. High fish crowding densities prior to slipping have been shown to result in high mortality of the slipped fish. There are currently no available estimates of fish densities inside the net during purse seining or any practical methods for monitoring the catches or the net during commercial fishing, making the regulation of slipping difficult. In this study, a method for monitoring net volume during commercial purse seining is developed. The volume for eight separate purse seine sets was monitored during hauling using an omnidirectional fisheries sonar to image the net and hence create three dimensional representations of the net. An acoustic positioning system with transponders mounted in the net walls was used to monitor the location of various parts of the purse seine and to validate the sonar-based net borders. Net volume reduced from an average of 1 300 000 m³ when 5-15% of the net was hauled to an average of 130 000 m³ when 70-80% of the net was hauled, with significant variation between sets. Fish densities during hauling were estimated by dividing catch biomass with the available volume and were generally below 1 kg m⁻³ and exceeded 5 kg m⁻³ towards the end of the haul for larger catches. The results indicate that lethally high densities of mackerel and herring are not expected to occur during the first 80% of hauling even for large catches.

Discussion

An improved NEA mackerel assessment with tag recapture data

Several surveys a year are performed in order to map the distribution and estimate the abundance of the NEA mackerel stock (ICES, 2013b). Annual acoustic and trawl surveys are performed in the Norwegian Sea and off the Iberian Peninsula (ICES, 2013b), egg surveys have been carried out every third year since 1977 (Lockwood et al., 1981) and a Norwegian tag recapture programme has been running since 1969 (Hamre, 1978). All the survey-based estimates suggest that the stock biomass is significantly larger than the ICES official estimate (ICES, 2013a). The tag recapture-based estimates of spawning stock biomass (SSB) in paper I indicate that the stock in 1986-2008 averaged either 5 or 6.25 million t, depending on the model used, which is 2 or 2.3 times as high as the ICES official estimate for the same time period (ICES, 2013a). The discrepancy between survey-based estimates of SSB and the official estimates can at least partly be explained by unreliable catch data that have been used as input in the assessment model. Simmonds et al. (2010) estimated that the actual removals from the stock have been between 1.6 and 3.6 times as high as the officially reported catches. If underestimated catches are used as input in the assessment model the stock biomass will also be underestimated (ICES, 2013a). It might then be asked why the fishery-independent estimates of SSB do not play a larger role in the assessment, in order to reduce the dependency of catch data.

The egg survey-based estimates of SSB have been used as a relative index of SSB in the assessment since 1977 (Lockwood *et al.*, 1981; ICES, 2013a) and as the only fishery-independent source of information on stock size these have been very valuable. A disadvantage with this method is that data become available only every third year and are not

age-disaggregated. The international trawl survey carried out in the summer months, when the whole mackerel stock is expected to be present in the Norwegian is a relatively new, but promising method for estimating mackerel abundance and distribution (Nøttestad et al., 2013). Vessel avoidance is a challenge in this survey, because mackerel are distributed in loose aggregations close to the surface in the summer feeding grounds (Godø et al., 2004). A method has now been developed in which trawling is performed during a turn, in order to reduce the effects of vessel avoidance (Nøttestad et al., 2013). Multibeam sonar is also used in these surveys to map the mackerel distribution and for stock abundance estimates in addition to downward pointing echo sounders. The advantage of multibeam sonar is that several beams cover a large sector or a whole circle in each sound transmission, thus covering a far larger area than echo sounders, including the surface waters (Misund, 1997). However, detecting mackerel acoustically is rather challenging because this species lacks a swimbladder (which normally accounts for about 95% of the backscattering echo) and the reflected sound level is therefore very low (Gorska et al., 2005). The low school density in the summer further reduces the total backscatter. The methods are continuously being developed and improved, and in the near future the combination of sonar for mapping mackerel distribution and a trawl survey for estimating abundance has potential to provide reliable information on the mackerel stock.

Tag recapture based estimates

In **paper I** the Norwegian tag recapture data were used to estimate stock biomass. The tag recapture data have previously been used to study mackerel distribution, migrations and mortality rates (Iversen and Skagen, 1989; Uriarte and Lucio, 2001). The data were also used to estimate stock biomass until the late 1970s (Hamre, 1978). Tags were then recovered by magnets installed in reduction plants. As the use of mackerel changed from fish meal to

mainly human consumption, fewer tags were recovered and the tag data could no longer be used for stock assessment. In 1986 metal detectors were installed at Norwegian fish factories and about 20 000 t mackerel have been screened annually ever since. An average of 18 000 mackerel have been tagged every year, and the annual recaptures have ranged between 50 and 300. The data could thus be used to estimate stock abundance again. ICES has requested a fishery-independent index of stock abundance that is age-structured to allow tracking the abundance of year classes (ICES, 2013a). A time-series of at least five years is further required for the index to contribute meaningfully to an age-based assessment model (ICES, 2013a). The tag recapture data have potential to fulfil both these requirements.

Two different approaches were used in **paper I** to estimate mackerel abundance, the HAMRE (Hamre, 1978) and the MERKAN (developed by Dankert Skagen, IMR) models. Both models are based on the Lincoln-Petersen model (Ricker, 1975), which in turn is based on a first sample of fish caught, tagged and released back to the sea, n_1 , and a second sample, n_2 , when the number of recovered tags, m_2 , is registered. The population size (N) is then estimated by the equation $N=n_1*n_2/m_2$ and the rationale is that the fraction of marked fish in the second sample (m_2/n_2) should on average be equal to the fraction of the population that is marked (n_1/N) (Ricker, 1975; Pine *et al.*, 2003). This approach can provide absolute abundance at the time of tagging. Tag recoveries can be pooled from recaptures and samples taken over a long period of time, and no assumptions are required regarding natural or fishing mortality rates (Schwartz and Seber, 1999). This was the approach taken by the MERKAN program. The disadvantage is that some years of recaptures are required to produce reliable estimates and up-to-date estimates are therefore unobtainable. The HAMRE approach (Hamre, 1978) estimated abundance for the recapture year and several releases were pooled. This way up-to-date estimates could be obtained, but natural and fishing mortality rates, as estimated by the

ICES, were applied to the tagged individuals. This method can thus be influenced by biased stock mortality estimates.

The biomass estimates from both models fluctuated heavily in the first years of the study (1986-1990). Thereafter a steady decline in biomass (MERKAN: 5 to 3.5 million t and HAMRE: 6.5 to 5.5 million t) was shown from 1993 to 1997. In the years 2002 to 2006 the biomass was estimated to increase from about 4 to 6 million t by both models. This increase is in accordance with the egg survey estimates that have indicated a significant stock increases since 2004 (ICES, 2013b).

The Lincoln-Petersen model is simple, but several underlying assumptions may produce biased estimates if they are not fulfilled (Schwarz and Taylor, 1998; Pine et al., 2003). One of these is that the tagging procedure or having a tag attached does not increase mortality. In paper I, one of the main uncertainties in the estimates was the unknown tagging mortality rate. Lockwood et al. (1983) studied tagging mortality in mackerel, but the experiments did not include the effects on survival of dropping the fish from the vessel into the water, sea bird predation or the effects of weather conditions and sea state. A range of different tagging mortality rates were therefore applied to the data in paper I (30, 40 and 50% mortality). Another important assumption is the complete mixing of the tagged fish with the whole population that is being assessed. Migration and distribution studies indicate that the entire NEA mackerel stock is present in the northern North Sea and Norwegian Sea during the autumn and winter (Uriarte and Lucio, 2001) when the majority of catches were screened, and tagged fish were further allowed to mix with the population for one year before being included in the data set. This assumption ought therefore not to have caused any major problems. A third assumption is 100% reporting rate of recaptured tags. There are some concerns about the reliability of the metal detectors at some of the factories and tags may have been undetected. This would have resulted in that the stock biomass was overestimated. Some of the assumptions underlying the Petersen – Lincoln model were thereby violated in **paper I**, resulting in somewhat unreliable estimates of SSB.

IMR's mackerel tagging programme came to an end in 2011, but a new programme has since been introduced that employs radio-frequency identification (RFID) (ICES, 2013b), which uses radio waves to transfer data from electronic tags to reader systems at the mackerel landing plants. A computer program imports data on catch information and biological sampling data of released fish and screened catches, and estimates fish abundance by year class (ICES, 2013b). This system is thereby far more automatic and cost-effective than the traditional tagging programme and the method that was used for data processing. Between 2011 and 2013, more than 100 000 mackerel have been tagged and tag-reading systems have been installed in fish factories in Scotland, Ireland and Denmark, in addition to eight systems in Norway. This will markedly increase the number of catches screened, thus improving the accuracy of the SSB estimates (Ziegler, 2013).

Future NEA mackerel assessment

ICES is currently in the process of exploring alternative modelling approaches that can better deal with catch uncertainty in addition to trying to incorporate more stock size information in the model (ICES, 2013a). Which fishery-independent data sources will be included in the assessment and focused on in the future will be decided in the ICES mackerel benchmark meeting in 2014 (ICES, 2013a).

There is yet another way to improve the assessment, which is by reducing the unaccounted mortality sources and thereby producing more reliable catch data. Since 2005, unaccounted mortality in mackerel stock has fallen (ICES, 2013a). Illegal and unreported landings have been reduced through better control systems, while improved discard regulations and control

systems have probably cut down discarding at sea. In Norway, the purse seine is the main gear used to catch mackerel and there are some indications of slipping in the fisheries (Huse and Vold, 2010). This thesis focuses on this particular source of unaccounted mortality, not only in the mackerel fisheries, but also in the herring fisheries.

Slipping mortality

In 2004 slipping of dead or dying fish was prohibited in Norwegian fisheries ("Forskrift om utøvelse av fiske i sjøen" §48) and the challenging task of enforcing the regulations in purse seine fisheries began. How could it be determined whether a slipped fish would survive? Slipping mortality has been shown to have a latency of hours or even days (Lockwood et al., 1983), and fish that swim out of the net apparently in good condition may actually die later. To find solutions to this problem, the Institute of Marine Research launched a study of the survival of mackerel following slipping, with the support of Norwegian fisheries managers. The effects of different crowding densities and durations on mackerel survival had already been studied in small-scale experiments (Lockwood et al., 1983), but there was some debate about how well the results represented the commercial situation. To validate these results, Huse and Vold (2010) carried out large-scale field experiments in 2006 and 2007. A mortality rate of 80 - 100% was registered in mackerel that were crowded for 10 minutes at densities at which they started to evince a panic reaction and swim at high speed just under the surface. This was an easily recognisable type of behaviour, and was expected to be associated with densities just before the catches start to be pumped. These results have been important in forming the current regulations on slipping in the mackerel fishery.

There was also a need to enforce the regulations in the herring purse seine fisheries. Slipping and net bursts were frequently reported from the fishing grounds, and previous experiments had shown that few herring survived a simulated net burst (Misund and Beltestad, 1995), while the mortality of small herring that escaped from pelagic trawl codends was particularly high (Suuronen *et al.*, 1996b). There was reason to suspect that slipping was a cause of mortality also in the herring fisheries. In 2007 Norwegian fisheries managers asked for a study of herring following slipping, and these experiments are presented in **paper II** and discussed in more detail below.

Choice of method

The survival of fish that are released or escape from the fishing gear can be studied in the field under commercial conditions (Suuronen *et al.*, 1996a; Mitchell *et al.*, 2002) or on a smaller scale in the laboratory (Olla *et al.*, 1997; Davis *et al.*, 2001; Marcalo *et al.*, 2010). Due to delayed mortality (Davis, 2002), a monitoring period is usually needed to register mortality rates. In the field, fish may be transferred into net pens, cages or tanks, where they are monitored for some days or weeks. As an alternative, tagging may be used where tag recapture rates of fish exposed to capture and release stressors are compared with the recapture rate of unstressed fish (Hueter *et al.*, 2006). The methods used in survival studies generally involve some form of fish transfer or handling, which may cause unintended additional stress and mortality. These unintentional effects can be difficult to separate from those caused intentionally as a part of the study. Mortality rates therefore often differ between studies, depending on the methods used (Chopin and Arimoto, 1995).

Experiments carried out in the laboratory are generally cost-effective when large numbers of replicates can be obtained and the variability in the survival estimates can be captured. The

effects of individual stressors and the combined effects of several stressors and how these are modified by environmental and biological conditions can be systematically studied (Davis, 2002; Broadhurst *et al.*, 2006). The problem is that it is virtually impossible to create realistic fishing stressors in the laboratory (Suuronen, 2005). How well sample populations in the laboratory represent wild populations may also be questioned. Mortality during transfer to the laboratory may be selective in that only the strongest fish survive, resulting in a sample that is not representative of the wild population. Fish held under laboratory conditions also experience sensory-deprivation, which can result in behavioural and physiological responses that do not resemble normal responses in the field (Suuronen, 2005).

In field experiments, conditions are generally more realistic although there may be problems related to holding experimental fish in tanks or net pens for monitoring. The conditions may not be quite the same as they would be in the wild, e.g. temperature, availability of light, pressure and stocking density (Broadhurst *et al.*, 2006). Wild fish have not been acclimatized to captivity like fish used in laboratory experiments, and captivity may therefore be an additional stressor. At the same time, fish may be in a more protected environment in which natural predation is reduced or absent. Well-designed control groups are necessary to reveal any artificial effects of handling and captivity, but these will not be able to detect confounding effects of captivity on already stressed or injured fish (Suuronen, 2005). Long-term mortality due to behavioural impairment (Davis, 2005; Marcalo *et al.*, 2013) or infections and disease (Chopin and Arimoto, 1995) is usually also not captured when fish are monitored for relatively short periods of time.

An open-sea large-scale method was developed in mackerel crowding experiments (Huse and Vold, 2010), in which the fish were transferred from a purse seine through a transfer channel into net pens. In the net pens fish were crowded by raising the bottom of the pen in order to reduce the available volume. After a short period of crowding (10-15 min.) the pens were

released to create their full volume again and left to drift freely for a monitoring period of 4-5 days. The method was challenging and vulnerable to weather conditions, and some trial and error was needed before it produced reliable results, i.e. low control group mortalities. The main advantages were that the experiments closely resembled real fishing conditions, they were on a relatively large scale and no transportation and very little fish handling was required. The limitation was that only a few successful replicates were obtained. Because the main aim of the herring crowding experiments in **paper II** was to obtain reliable estimate of slipping mortality that could be used into management, we chose to use this method in the experiments, but focusing on obtaining a larger number of replicates than in the mackerel experiments, in order to control for variability in the mortality rates.

Responses to crowding

The experiments in **paper II** produced three successful replicates with two crowded groups and one control group in each replicate. Insignificant mortality was registered at densities below 150 kg m⁻³ (10 minute crowding phase). Mortality rates then increased with crowding density, and a rate of about 50% was found at the maximum crowding density of 480 kg m⁻³. Mortality rates of crowded herring are clearly lower than those of crowded mackerel (Lockwood *et al.*, 1983; Huse and Vold, 2010). Sardine crowding mortality measured in field (Mitchell *et al.*, 2002) and in laboratory experiments (Marçalo *et al.*, 2010) appears to be nearer the range of that of herring, but crowding density was not measured in these experiments, which makes comparisons difficult.

Measuring the physiological stress response can sometimes provide indications of the type and severity of stressors involved (Davis *et al.*, 2001; Herbert and Steffensen, 2006). Measures of stress will also provide a description of how fish respond physiologically to the

stressor and about the physiological basis of death. Immediate rises in blood cortisol and lactate levels were registered in the blood of herring following crowding (paper II), responses similar to those previously registered among captured and crowded mackerel (Pawson and Lockwood, 1980). In both the herring and mackerel experiments, blood lactate levels returned to control levels within a few days. This was either an indication that fish could cope with the higher lactic acid levels or that fish struggling with high lactic acid had died before they could be sampled again. Lactic acid is the end-product of anaerobic metabolism, and it rapidly dissociates into lactate, some of which leaks into the bloodstream (Wood, 1991; Kieffer, 2000). High and rising ion concentrations in the blood appeared to be closely related to the observed mortality among the crowded herring (paper II) and mackerel (Pawson and Lockwood, 1980). Ion regulation is frequently disturbed during a stress response, as gill permeability is increased in order to increase oxygen uptake (Wendelaar Bonga, 1997). The ion balance may also be disturbed if the protective barrier of the skin is damaged (Bouck and Smith, 1979; Quilhac and Sire, 1998). In paper II, glucose levels in herring blood were very low by the end of the monitoring period (4 days post-stress) indicating energy exhaustion. In conclusion, the stress response among the crowded herring in paper II suggest that some of the herring received injuries or trauma during crowding that they could not cope with, which resulted in a maladaptive stress response that ultimately ended in exhausted energy resources and death.

The stress response is difficult to interpret and it is often impossible to identify a relationship between stressor intensity and the observed response or mortality rate (Davis and Schreck, 2005; Marcalo *et al*; 2010). How fish respond to stressors is complex and is influenced by a number of factors (Pottinger, 2008). Besides the physiological changes that fish undergo during a stress response, they also display behavioural responses (Schreck, 1981). An adaptive behavioural response (e.g. swimming away from a stressful situation, hiding or

reducing swimming speed to save energy) may reduce the energy demand on the physiological system that must respond to the stressor, while an ineffective behavioural response (e.g. trying to swim away when it is not possible) may increase the energetic demand on the physiological system and magnify the stress (Schreck, 1981). Caution is thereby needed when interpreting the physiological response, and physiological parameters may be most useful when combined with other sources of information such as stressor type, behavioural responses and physical injuries.

Individual herring coped differently with crowding. While some of the fish died, others survived. Wide variations were also registered in the initial physiological responses to crowding, suggesting that fish were either exposed to the stressors to different degrees or that individual herring were differently able to cope with the same stressor. The mortality rate among smaller herring seemed to be somewhat higher than among larger fish. This has also been observed in previous experiments, in herring escaping from the trawl codend (Suuronen *et al.*, 1996b) and may explain some of the variation observed by us.

Responses to slipping

In addition to crowding in the net prior to slipping, the way in which fish are slipped from the net, e.g. whether they can swim freely out of the net or are forced out, is likely to influence survival. How the fish are slipped depends on gear design, the skipper's way of operating the gear and environmental conditions. Ambient light, for example, may be important in guiding the fish out of the net. Rough sea may cause large net motion and reduce the opening hole, increasing the risk of net abrasion. Live capture and storage of herring and mackerel is an example of how fish can be "slipped" in a careful manner. High survival rates and good fish quality are necessary during live capture, and the fishermen that use this method have long

experience in transferring fish from the seine and into storage pens. In survival experiments on slipped sardines Mitchell *et al.* (2002) looked at the combined effect of slipping and crowding without registering very high mortalities, thereby concluding that quick and careful release of fish could be carried out with low mortality. In our experiments (**paper II**), and in those of Huse and Vold (2010), the effects of crowding were the main focus, but the effects of slipping were also measured in the process. The initial transfer of fish from the seine to the net pens was actually identical to slipping, carried out in a very careful way. The high survival rates in the control net pens indicate that if herring and mackerel are carefully slipped under good weather conditions, survival can be close to 100%.

Variation in survival rates

Fishing is carried out under a wide range of environmental conditions, targeting fish in various biological states and using different operational methods and gear designs. These variable conditions and situations result in variation in how the fish cope with capture and release stressors (Arimoto and Chopin, 1995; Suuronen, 2005).

Environmental factors such as ambient light levels (Olla *et al.*, 1997; Olla *et al.*, 2000; Suuronen *et al.*, 1995) and water temperature (Davis *et al.*, 2001; Suuronen *et al.*, 2005) have been shown to influence how well fish orient to and avoid the net and how well they cope with stressors. The ability of herring and mackerel to avoid fishing gear may be impaired under low ambient light levels (Blaxter and Batty, 1987; Misund, 1992), while sardine survival following slipping was estimated to be 20% lower at water temperatures of 23 °C than at 18 °C (Marçalo *et al.*, 2010). On the other hand, swimming speed and endurance were reduced (Beamish, 1966; He and Wardle, 1988) and wound healing was slower at lower temperatures (Silva *et la.*, 2005). Sea-state may also be an important factor during purse

seining. Visibility may be reduced, and the net may move more in rough seas, making it difficult for fish to orient and avoid hitting the meshes. The degree of crowding in the net is influenced by gear dimensions, how the skipper operates the gear and catch size (Ben-Yami, 1994; Suuronen, 2005; Ruttan and Tyedmers, 2007). Individual fish are also likely to respond differently to fishing stressors. The stress response is energy-intensive, and individuals that are in better condition and have more available energy to invest in the stress response have better chances of survival. Fish condition varies with the seasons and years, but also between individuals due to size, sex and maturity stage (Mello and Rose, 2005; Casini *et al.*, 2006).

We were aware of the potential effects of environmental and biological conditions on herring survival, and that the experiments were likely to represent only the specific conditions experienced there and then. However, it was not possible to carry out many survival experiments under a range of different conditions due to the high cost of the experiments and the limitations imposed by weather conditions. In view of the sensitivity of the method to weather conditions, the choice fell on the summer herring fishery in the North Sea. The North Sea herring fishery in June is a highly quality-conscious fishery that targets matjes herring. The price for high-quality matjes herring may be more than twice as high as for ordinary fillet quality, and there are indications that slipping is frequently employed in this fishery to optimise catch quality. It was thereby natural to start the investigations in this fishery, but there was some concern that survival might have been overestimated due to the good condition of the fish in the North Sea during the summer. However, crowding experiments performed in March 2011 on spawning NSS herring (Vold et al., 2012) showed very similar mortality rates as those registered for NS herring in the summer, although 10% mortality was registered at a crowding density of 92 kg m⁻³, indicating that survival rates may not be significantly affected by seasonal variations in fish condition.

Conclusions

The experiments carried out in paper II provide estimates of herring tolerance to different crowding densities and show a close relationship between crowding density and mortality rate. Such data may be very useful for determining maximum permitted densities before slipping. The results are also likely to be realistic estimates of survival rates, but perhaps only under the specific conditions of the experiment. During commercial purse seining, around half of all herring and mackerel catches are made at night, the weather may be rough and catch sizes differ between sets and are usually much larger than the biomasses we used in our crowding experiments. We do not know how these factors influence the survival rates. Environmental and biological conditions and operational information was registered in the crowding experiments in paper II, but it is unlikely that enough replicates can ever be obtained to provide a full understanding of the effects of these variables on survival. It might be more sensible to use the information gathered in the field as a basis for controlled experiments in the laboratory, where the effect of single or a combination of stressors on fish survival, and how survival is influenced by different environmental and biological conditions, can be studied. This approach is recommended by Davis (2002) and has been successfully applied to estimate sardine slipping mortality by Marçalo et al. (2010, 2013).

Why do fish crowded in the purse seine die?

The mortality of fish crowded in purse seines is a function of crowding density and time (paper II; Lockwood *et al.*, 1983; Marçalo *et al.*, 2010). In aquaculture, fish holding densities are known to influence water quality, fish behaviour and physiology, and high densities may result in stress, injuries, infections and disease, reduced growth and higher mortality (Portz *et*

al., 2006). During purse seining, fish are allowed to school freely inside the net until a relatively late phase of hauling, but at some point the reduced net volume will aggregate the fish into higher densities than those that are natural for the species. It becomes more difficult for the school to maintain its structure, swimming is restricted and the school formation finally breaks down (Lockwood et al., 1983; Mitchell et al., 2002). The increasing aggregation of the fish alters the surrounding environment (water quality) for the worse and the fish may experience stress and suffer physical injury. Apart from the crowding itself, the whole catch process may be perceived as stressful and may lead to physical exhaustion. Why fish die, and what are the main stressors that cause the mortality following a short but intense crowding phase during purse seining, are not well understood.

Scale loss and skin injuries

The mortality of small pelagic species caused by crowding and contact with fishing gears has usually been associated with scale loss and skin injuries (Lockwood *et al.*, 1983; Misund and Beltestad, 1995; Suuronen *et al.*, 1996a; Mitchell *et al.*, 2002; Marçalo *et al.*, 2010). Scales and skin provide the fish with a physical barrier that protects them from the external environment (Bullock and Robertis, 1974). If the skin or scales are removed or damaged the protective barrier is lost and the fish become exposed to disease and infections. Water may also leak through the skin causing osmoregulatory disturbances (Bouck and Smith, 1979), but the physiological mechanisms associated with skin injury are unclear (Smith, 1993). A stress response (Box 2) is usually triggered when injury is suffered. During the stress response the immune system is suppressed, increasing the risk of infections, and the osmoregulatory balance is disturbed by the increased permeability of the gills. Losing small amounts of scales, however, is a natural part of the lives of most fish and the lost scales are rapidly regenerated without negative effects (Bereiter-Hahn and Zylberberg, 1993).

No signs of infections were observed on the skins of the crowded herring in **paper II**, but injuries and scale loss were registered on many fish. Large quantities of scales were observed in the water during crowding, which is a common sight during commercial fishing. We therefore decided to study the effects of scale loss on herring survival, physiology and behaviour in laboratory experiments (**paper III**). Scales were removed from either 25 or 50% of the body surface, followed by a seven-day monitoring period.

The results from the scale removal experiments in **paper III** show that when scales were removed from 25% of the body surface the mortality rate was between 7.5 and 35%. When scales were removed from 50% of the body surface, the mortality rate rose to 30-60%. Control group mortality was between 0 and 10%. Higher levels of cortisol, ions and lactate and lower glucose levels were recorded in the blood of the de-scaled herring, indicating a general stress response similar to that observed among the crowded herring in **paper II**. There was a tendency towards greater differences in these parameters with time, and in many cases treatment appeared to create bimodal groups, with some fish being similar to control group fish while others approached the values of the moribund fish, which were clearly experiencing a maladaptive stress response. These results indicate that there are individual differences in how well herring cope with scale loss. Higher lactate levels further coincided with registrations of altered behaviour (faster and less oriented swimming) and we speculated whether skin injuries may have damaged the sensory system on the body surface, leading to the alterations in behaviour.

The experiments in **paper III** demonstrate that scale loss can cause significant mortality and that the mortality rate rises in line with the amount of scales lost. To understand the importance of scale loss during crowding and slipping, data on normal scale loss rates during commercial purse seining are needed. We currently lack such data, but some data are available from experimental conditions. Scale loss was quantified in a sample of herring in

crowding experiments in 2011 (Vold *et al.*, 2012; Svalheim, 2012). The scale loss among herring crowded to 80-370 kg m⁻³ was generally less than 10% and only a few fish among the most crowded groups reached levels of 50% or higher. No relationship was identified between mortality rate and scale loss, and it was concluded that scale loss could not alone explain the observed mortality among crowded herring. Herring scale loss following a simulated net burst was estimated to be 35-50% (Misund and Beltestad, 1995) while sardine scale loss following simulated purse seining and slipping in the laboratory was observed to be significantly higher among fish that died than among survivors (Marçalo *et al.*, 2010). Unlike Svalheim (2012), Misund and Beltestad (1995) and Marçalo *et al.* (2010) concluded that scale loss was a significant cause of mortality.

There are several ways of quantifying scale loss and it is not only the number of scales lost, but also the depth of the injury that determine the severity. The deeper the injury is, the longer it will take to heal. If only the scale is lost with no damage to the scale pocket in which it is located, regeneration will be rapid (Quilhac and Sire, 1998). Svalheim (2012) looked at histological samples of the skin of crowded herring and found that the scale pockets were mainly intact. It may thereby seem as though a few herring in a purse seine catch experience high scale loss rates, while the majority experience low, sublethal, rates.

Physical exhaustion

Physical exhaustion has often been related to the mortality of small pelagic fish that have escaped from the trawl (Suuronen *et al.*, 1996a; Turunen *et al.*, 1996; Kvalsvik *et al.*, 2002). Exercise that leads to exhaustion involves high intensity swimming that is primarily powered by white muscle fibers and supported by anaerobic metabolism (Milligan, 1996). The size of the energy stores, accumulation of metabolic end-products (e.g. lactate and metabolic protons)

and recovery rate (e.g. lactate clearance rate and glycogen recovery rate) determine how long anaerobic swimming can be maintained (Wood *et al.*, 1983; Milligan, 1996; Kieffer 2000). Physical exhaustion can be lethal, and cellular acidosis, i.e. lactic acid accumulation in the cells, has been suggested as the cause of mortality (Wood *et al.*, 1983).

During purse seining the role of physical exhaustion is not expected to be as severe as during trawling because fish are allowed to swim freely in the net. However, mackerel and herring have been observed to increase their swimming speed in the early stages of encounters with purse seines (Misund, 1992). Video recordings of herring in the purse seine before they were transferred to the net pens in the experiments described in **paper II** show dense schools swimming at high speed and making many manoeuvres, a similar response as observed among herring attacked by whales (Domenici *et al.*, 2000a; Nøttestad *et al.*, 2002). Marcalo *et al.* (2006) found rising stress levels among sardines as the net was hauled, well before fish were crowded in the net, suggesting the existence of an early stress response to purse seining. Herbert and Steffensen (2006) registered elevated lactate levels, about 11 mmol 1⁻¹, among herring exposed to severe exercise, levels that correspond to those measured among some of the crowded herring (**paper II**). Fish caught by purse seine thereby appear to experience some degree of physical exhaustion, but unlikely at a lethal level.

Hypoxia and reduced water quality

High fish densities will cause changes in water quality (e.g. reduced dissolved oxygen, increased CO₂, reduced pH and increased concentrations of ammonia) unless the water flow rate is high enough to replenish dissolved oxygen and remove fish wastes (Portz *et al.*, 2006). If the fish are also being stressed, the changes may be magnified as a result of greater oxygen consumption. Dissolved oxygen is essential for aerobic activity, and if the oxygen level is

below the species' aerobic limits, the fish will need to exploit anaerobic metabolic pathways which are inefficient and can only be maintained for short periods (Portz et al., 2006). In the herring crowding experiments in paper II, the oxygen level in the water dropped from nearly 100% to about 45% within ten minutes. Previous studies suggest that these may be levels at which herring are able to maintain aerobic metabolism. Herring have been shown to cope with a reduction in oxygen saturation as low as 30% in their natural environment (Dommasnes et al., 1994) and even lower in the laboratory (Domenici et al., 2000b). The laboratory experiments showed increased swimming speed at oxygen saturation levels of between 15 and 34%; swimming speed was then reduced as oxygen was further reduced and finally the school broke up at an oxygen saturation of 12 - 25% (Domenici et al., 2000b). Physiological sampling indicated that the response to hypoxia was an adaptive stress response that allowed them to maintain aerobic metabolism with no indications of respiratory distress at the measured oxygen levels (Herbert and Steffensen, 2006). Even though herring appear to tolerate hypoxia well, it is not certain that they cope equally well with a sudden reduction in oxygen in the field. Hypoxia may be more severe under commercial fishing conditions, with large catches, than in the crowding experiments reported in paper II.

Elevated concentrations of ammonia, urea, residual organic nitrogen and phosphate were measured in the water during the crowding phase of a purse seine set (Stratoudakis *et al.*, 2003). The increased ammonia and urea were explained by excretion of nitrogen waste, perhaps enhanced by stress reactions among the crowded fish, and the increased dissolved organic nitrogen and phosphates were explained by the combined effects of skin abrasion, regurgitation of stomach contents and forced evacuation of partly digested food. Ammonia is toxic to fish and increases gill ventilation, erratic and quick movements, loss of equilibrium and even mortality (Portz *et al.*, 2006).

Synergistic stress

A fish that is coping with one stressor will have reduced capacity to handle additional stressors because it is already using energy to cope with the first (Schreck, 1981). The effects of single capture and release stressors can thus be magnified when they occur simultaneously with others. Hypoxia that under normal conditions would not pose any threat to the fish, may become detrimental if it is combined with other stressors that increase oxygen demand. The sensory perception and the ability to maintain position within the school may be reduced when fish are exhausted, increasing their risk of colliding with other fish or with the net. Environmental conditions during the fishing situation may also influence how fish cope with stressors, and a small change in environmental conditions may cause mortality rates to tip from high survival to very low survival. These synergistic effects may explain much of the variability observed in survival rates. Such interactions are particularly difficult to create in the laboratory and if taken into account may lead to the level and variability of mortality rates being undertestimated.

Conclusions

Currently available information indicates that mortality caused by high crowding densities is a result of the combined effects of many stressors. Differences in environmental and fishing conditions affect the relative intensities of different fishing stressors, e.g. crowding may be more intense when catches are large and hypoxia may be more severe when water temperatures are high. The main causes of mortality may thus differ depending on the capture situation. The position of the individual fish inside the net is also likely to determine relative stressor intensities, e.g. fish in the middle of a school may be more likely to suffer from hypoxia, while a fish at the edge of a school may be at higher risk of skin injuries and scale loss from net abrasion. Finally, even if fish are crowded under exactly the same conditions,

experiencing exactly the same stressor intensities, individuals may respond and cope differently, partly due to differences in condition and available energy, but also to genetical differences. Individuals may have different perceptions of and sensitivity to the stressors, and therefore choose different coping strategies (Wendelaar Bonga, 1997).

The response of mackerel to capture stressors has been less studied compared with herring. Even though mackerel and herring appear to have a fairly similar stress response to crowding, as indicated by blood parameters, their mortality rates are very different. In behavioural terms, they also react differently to capture stressors; mackerel display a more consistent panic response at the surface when crowded above a certain limit in the net, while herring only occasionally display such behaviour. Hypoxia causes altered patterns of behaviour, such as erratic swimming (Portz *et al.*, 2006), and the panic behaviour that is characteristic of crowded mackerel may indicate that this species does not have the same ability as herring to compensate for the lack of oxygen and increased oxygen demand during crowding and stress.

Mitigation of slipping mortality

As discussed above, slipping following high crowding densities in the purse seine can result in high mortality rates. This was shown in **paper II** for herring and has previously been shown for mackerel (Lockwood *et al.*, 1983; Huse and Vold, 2010) and sardine (Marçalo *et al.*, 2010). There is political and public pressure in Norway to regulate and mitigate slipping mortality. Purse seiners catch about 1 million t fish a year in Norway, about 60% of the total Norwegian catches, and because discarding is banned it is important to ensure that fish do not die as a consequence of slipping. The Marine Stewardship Council (MSC), which operates a certification and eco-labeling programme for the sustainability of wild fisheries stocks, also

takes slipping into account in certification of NEA mackerel and herring purse seine fisheries. The MSC has requested that efforts should be made to quantify and reduce slipping mortality in these fisheries. However, the challenge lies in implementing slipping regulations in practice. On one hand, slipping mortality needs to be avoided, while on the other hand it is important that the industry can continue to deliver good-quality, high-value catches (Gezelius, 2006; Suuronen and Sardà, 2007).

The enforcement of slipping regulations in Norway

In Norwegian mackerel fisheries there is a limit for how late in the hauling of the net slipping is allowed, a "point of no return". The point of no return was originally set to the start of pumping of the catch onboard the vessel; it was later changed to the time at which fish displayed panic behaviour on the surface. When the results from the survival experiments on mackerel (Huse and Vold, 2010) were published, it was realised that this was still too late, and slipping mackerel at this stage would result in high mortality. In 2011, as a result of meetings between fisheries managers, fishermen and scientists, a new regulation whereby it is illegal to slip fish after 7/8 of the net has been retrieved was implemented in the mackerel fishery. All vessels had to place a white buoy at the float line at this position of the net so that the regulation would be easy to observe and enforce. Implementation of the 7/8 net rule is an important step towards a reduction of slipping-related mortality. The problem is that even though crowding experiments have demonstrated a relationship between crowding density and mortality, there is no practical way to measure fish densities during commercial purse seining. In addition to uncertainty related to the position of the point of no return, it may be asked whether a static point of no return that is the same for all catch sizes, net designs and

dimensions and under all conditions would be a sensible solution. In practice, purse seining is a highly dynamic process and no two sets are identical.

Purse seine monitoring for improved guidelines on slipping

Fish density in the purse seine is determined by net volume, catch size, and school behaviour, and information on net volume and how it reduces during hauling is therefore important when considering constraints on slipping. In **paper IV**, a method for monitoring purse seine shape and volume during commercial fishing was developed. The studies are a first step towards developing a method to study crowding densities in the net and for the development of real-time net monitoring methodology. The approaches presented in the paper can be used to evaluate the usefulness of having the point of no return at 7/8 hauled net in the mackerel fishery and to identify an appropriate point of no return for the herring fisheries, for which no definite limit to slipping has yet been set.

A high-frequency omnidirectional fishery sonar (Simrad SH80) on board the F/V "Libas" was used in the experiments. Omnidirectional sonars cover a 360° fan in each transmission and can be tilted from +10° above horizontal to -60° below horizontal. In theory, a complete horizontal transect of the net can be obtained at each transmission. The whole net was scanned by systematically tilting down the sonar until the bottom of the net was identified. Several net border slices that covered the whole net were then combined to reconstruct the three dimensional shape of the net. The volume of each net reconstruction was estimated and related to hauling proportion (i.e. the percentage of net hauled). Fish densities in the net were estimated by dividing catch biomass by net volume estimates during hauling. It was assumed that the fish are evenly distributed within the whole available net volume. In the early stages of hauling this is certainly not the case, but it may be a valid assumption once the volume begins to restrict normal schooling behaviour and densities approach detrimental levels.

The limit for slipping in the mackerel fisheries (7/8ths net) is reached when about 88% of the net has been hauled. The aim was to estimate densities up to this point and beyond, if possible. Unfortunately no net measurements could be made for the last 20% of hauling, due to the low resolution of the sonar and signal distortion caused by the air bubbles produced by the bow thrusters, main propellers and vessel heave. The results do, however, indicate that lethally high densities of mackerel and herring are not expected to occur during the first 80% of hauling even for large catches.

The net volume estimates were also used to simulate catch scenarios where fish densities were estimated in a range of potential catch sizes from start of hauling and until 90% of the net was hauled. The catch scenarios indicated that fish densities at the current limit to slipping in mackerel fisheries (7/8ths or 88% hauled net) would be about 20 kg m⁻³ in a 1000 t catch and about 10 kg m⁻³ in a 500 t catch. Slipping before this stage can hence be expected to result in low crowding-induced mortality based on mortality rates estimated for mackerel (Lockwood *et al.*, 1983; Huse and Vold, 2010) and herring (**Paper II**; Vold *et al.*, 2012). A slipping limit at 88% hauled net in the mackerel fishery thus appears to be precautionary. While for herring the limit could be later in the hauling due to its higher tolerance to crowding.

However, the volume estimates are somewhat uncertain, data is lacking from the last part of hauling and variation in volume between sets is not accounted for in the catch scenarios. The catch scenarios should thereby be treated with caution and were mainly presented to demonstrate the usefulness of the approach when discussing slipping limits.

The use of acoustics during purse seining is not straightforward. The vessel is often surrounded by air bubbles that disturb the acoustic beam that is transmitted and received. In our experiments, the net dimensions were determined as best estimates from the sonar images, but these were subject both to human error in how the images were interpreted and

uncertainty caused by the relatively low resolution of the sonar. The volume measurements could be improved by using a higher-resolution sonar deeper in the water column or at a different position, where air bubble disturbance is lower. Alternatively, a system based on positioning sensors and a dynamic model could be developed (De Cew *et al.*, 2013).

From the fisherman's point of view a precautionary limit to slipping is problematic and may result in loss of catch value and/or violation of the regulations. In most cases, fish densities will not be high enough at this stage for it to be possible to obtain a physical sample of the catch or to visually determine catch biomass, species, fish quality or size and determine whether there is a need to slip. Variation in fish densities between sets could be taken into account by having a flexible limit to slipping, but that would require real-time monitoring either of fish densities directly or of net volume, combined with reliable estimates of catch sizes.

To ensure that fish do not die following slipping a better understanding of fish behaviour in relation to the net is needed, particularly if net volume and catch size are used to determine slipping limits. Is the panic behavior observed among crowded mackerel a direct result of net volume, or do other stimuli play a role? Do the fish occupy the whole net volume at the point at which they start dying? These are questions that will need to be answered. Furthermore, variation in mortality rates caused by varying environmental, fishing and biological conditions need to be taken into account in determining limits to slipping. To ensure that purse seines continue to catch high-quality catches efficiently, even with a precautionary point of no return, slipping regulations need to be combined with technological solutions in order to improve identification of catch size, species and quality in the early stages of purse seining or even before the net is set. Slipping techniques and gear modifications that ensure high survival also need to be developed and tested. Many of these are currently under development and are expected to become available in due course.

Purse seining in 2025

The purse seiner is heading to the herring fishing grounds in the North Sea. It is June and the skipper's aim is to catch high-quality matjes herring. The catch thereby needs to consist of herring with a high fat content and total catch should not exceed 150-200 t, in order to maintain high quality during capture, landing and processing.

The vessel is equipped with the latest sonar technology that has been under development for many years. Much more accurate estimates of school biomass and composition can be obtained before shooting the net than were possible in 2013. Even individual fish size can be estimated under optimal conditions. Thanks to the improved sonar technology, not only has the need to slip been reduced, but fishing efficiency has also improved due to more accurate identification and monitoring of appropriate schools.

The skipper detects a school, decides to target it and successfully captures it. He can now use a sonar specifically designed to monitor the fish inside the purse seine to confirm the precatch information. This sonar is particularly useful in cases when pre-catch identification of schools is inaccurate when schools are large and dense or form loose aggregations. Because fish quality is crucial in matjes herring the skipper also needs a physical sample of the catch to explore the fat and stomach contents. He shoots a small sampling trawl into the net and hauls a sample of fish on board. It is still early in the haul and well before the precautionary limit to slipping. New purse seine design allows for careful slipping and the skipper knows well how to operate the gear in order to ensure high survival. If the quality proves to be poor he can therefore still release the catch without significant mortality and without violating the fishing regulations. North sea herring in this season are in good condition and can tolerate high crowding densities; however new information on school behaviour in the net and net performance under different environmental conditions show that slipping is more risky when

the weather is rough and therefore under certain conditions when the risk for mortality is high slipping is forbidden. Especially under these conditions the fisheries are efficiently monitored by the coastal guard to ensure compliance with the regulations. It is also in the interest of the skipper that the fishery is sustainable and responsible to ensure valuable fisheries also in the future and he also wishes to comply with the regulations. This time he has caught a high quality catch and steams home to deliver.

References

- Alverson, D. L., and Hughes, S. E. 1996. Bycatch: from emotions to effective natural resource management. Reviews in Fish Biology and Fisheries, 6: 443-462.
- Anon. 1999. Investigation of the extent and nature of discarding from herring and mackerel fisheries in ICES Sub-Areas IVa and VIa. Final Report for Study No. 96/082. 23pp.
- Anon. 2002. IPDEN: Investigation of Pelagic Discarding Extent and Nature. Final Report for Study No. 99/071. 31pp.
- Barham, E. G., Tabuchi, W. K., and Reilly, S. B. 1977. Porpoise rescue methods in the yellowfin purse seine fishery and the importance of the Medina panel mesh size. Marine Fisheries Reviews, 39(5): 1-10.
- Barton, B. A. 2002. Stress in fishes: a diversity of responses with particular reference to changes in circulating corticosteroids. Integrative and Comparative Biology, 42: 517-525.
- Beamish, F. W. H. 1966. Muscular fatigue and mortality in haddock *Melanogrammus aeglefinus*, caught by otter trawl. Journal of the Fisheries Research Board of Canada, 23: 1507-1521.
- Bellido, J. M., Begoña Santos, M., Grazia Pennino, M., Valeiras, X., and Pierce, G. J. 2011. Fishery discards and bycatch: solutions for an ecosystem approach to fisheries management? Hydrobiologia, 670: 317-333.
- Ben-Yami, M. 1994. Purse seining manual. Food and Agriculture Organization of the United Nations. Fishing News Books, Oxford. 416 pp.
- Benoît, H. P., Hurlbut, T., and Chassé, J. 2010. Assessing the factors influencing discard mortality of demersal fishes using a semi-quantitative indicator of survival potential. Fisheries Research, 106: 436-447.
- Benoît, H. P., Plante, S., Kroiz, M., and Hurlbut, T. 2013. A comparative analysis of marine fish species susceptibilities to discard mortality: effects of environmental factors, individual traits, and phylogeny. ICES Journal of Marine Science, 70(1): 99-113.
- Bereiter-Hahn, J., and Zylberberg, L. 1993. Regeneration of teleost fish scales. Comparative Biochemistry and Physiology, 105A(4): 625-641.
- Blaxter, J. H. S., and Batty, R. S. 1987. Comparisons of herring behaviour in the light and dark: changes in activity and responses to sound. Journal of the Marine Biological Association of the United Kingdom, 65: 1031-1049.
- Borges, L., van Keeken, O. A., van Helmond, A. T. M., Couperus, M., and Dickey-Collas, M. 2008. What do pelagic freezer-trawlers discard? ICES Journal of Marine Science, 65: 605-611.

- Bouck, G. R., and Smith, S. D. 1979. Mortality of experimentally descaled smolts of coho salmon (*Oncorhynchus kisutch*) in fresh and salt water. Transactions of the American Fisheries Society, 108: 67-69.
- Brandt von, A. 1984. Fish Catching Methods of the World, 3rd edn., Fishing News Books Ltd, Farnham, Surrey, 432 pp.
- Broadhurst, M. K., Suuronen, P., and Hulme, A. 2006. Estimating collateral mortality from towed fishing gear. Fish and Fisheries, 7: 180-218.
- Bullock, A. M., and Roberts, R. J. 1974. The dermatology of marine teleost fish. I. The normal integument. Oceanography and Marine Biology Annual Reviews, 13: 383-411.
- Casini, M., Cardinale, M., and Hjelm, J. 2006. Inter-annual variation in herring, *Clupea harengus*, and sprat, *Sprattus sprattus*, condition in the central Baltic Sea: what gives the tune? Oikos, 112(3): 638-650.
- Chopin, F. S., and Arimoto, T. 1995. The condition of fish escaping from fishing gears a review. Fisheries Research, 21: 315-327.
- Crowder, L. B., and Murawski, S. A. 2011. Fisheries bycatch: Implications for management. Fisheries, 23(6): 8-17.
- Davis, M. W. 2002. Key principles for understanding fish bycatch discard mortality. Canadian Journal of Fisheries and Aquatic Sciences, 59: 1834-1843.
- Davis, M. W. 2005. Behaviour impairment in captured and released sablefish: ecological consequences and possible substitute measures for delayed discard mortality. Journal of Fish Biology, 66: 254-265.
- Davis, M. W. 2007. Simulated fishing experiments for predicting delayed mortality rates using reflex impairment in restrained fish. ICES Journal of Marine Science, 64(8): 1535-1542.
- Davis, M. W., Olla, B. L., and Schreck, C. B. 2001. Stress induced by hooking, net towing, elevated sea water temperature and air in sablefish: lack of concordance between mortality and physiological measures of stress. Journal of Fish Biology, 58: 1-15.
- Davis, M. W., and Ottmar, M. L. 2006. Wounding and reflex impairment may be predictors for mortality in discarded or escaped fish. Fisheries Research, 82: 1-6.
- Davis, M. W., and Schreck, C. B. 2005. Response by Pacific halibut to air exposure: lack of correspondence among plasma constituents and mortality. Transactions of the American Fisheries Society, 134(4): 991-998.
- DeCew, J., Fredriksson, D. W., Lader, P. F., Chambers, M., Howell, W. H., Celikkol, B., Frank, K., and Hoy, E. 2013. Field measurements of cage deformation using acoustic sensors. Aquaculture Engineering, 57: 114-125.
- Domenici, P., Batty, R. S., and Similä, T. 2000a. Spacing in wild schooling herring while encircled by killer whales. Journal of Fish Biology, 57: 831-836.

- Domenici, P., Steffensen, J. F., and Batty, R. S. 2000b. The effect of progressive hypoxia on swimming activity and schooling in Atlantic herring. Journal of Fish Biology, 57: 1526-1538.
- Dommasnes, A., Rey, F., and Roettingen, I. 1994. Reduced oxygen concentrations in herring wintering areas. ICES Journal of Marine Science, 51(1): 63-69.
- FAO, 2011. International guidelines on bycatch management and reduction of discards. Rome, 73 pp.
- Fridman, A. L. 1986. Calculations for fishing gear design. Fishing News Books Ltd, Farnham, Surrey, 241 pp.
- Gerlotto, F., Soria, M., and Fréon, P. 1999. From two dimensions to three: The use of multibeam sonar for a new approach in fisheries acoustics. Canadian Journal of Fisheries and Aquatic Sciences, 56(1): 6-12.
- Gezelius, S. S. 2006. Monitoring fishing mortality: Compliance in Norwegian offshore fisheries. Marine Policy, 30: 462-469.
- Gilman, E. L. 2011. Bycatch governance and best practice mitigation technology in global tuna fisheries. Marine Policy, 35: 590-609.
- Godø, O. R., Hjellvik, V., Iversen, S. A., Slotte, A., Tenningen, E., et al. 2004. Behaviour of mackerel schools during summer feeding migration in the Norwegian Sea, as observed from fishing vessel sonars. ICES Journal of Marine Science, 61(7): 1093-1099.
- Gorska, N., Ona, E., and Korneliussen, R. 2005. Acoustic backscattering by Atlantic mackerel as being representative of fish that lack a swimbladder. Backscattering by individual fish. ICES Journal of Marine Science, 62: 984-995.
- Graham, N., Jones, E. G., and Reid, D. G. 2004. Review of technological advances for the study of fish behaviour in relation to demersal fishing trawls. ICES Journal of Marine Science, 61: 1036-1043.
- Hall. S. J., and Mainprize, B. M. 2005. Managing by-catch and discards: how much progress are we making and how can we do better. Fish and Fisheries, 6: 134-155.
- Hamre, J. 1978. The effect of recent changes in the North Sea mackerel fishery on stock and yield. Rapports et procès-verbaux des réunions / Conseil permanent international pour l'exploration de la mer, 172: 197-210.
- He, P., and Wardle, C. S. 1988. Endurance at intermediate swimming speeds of Atlantic mackerel, *Scomber scombrus* L., herring, *Clupea harengus* L. and saithe, *Pollachius virens* L. Journal of Fish Biology 33: 255-266.
- Herbert, N. A. and Steffensen, J. F. 2006. Hypoxia increases the behavioural activity of schooling herring: a response to physiological stress or respiratory distress. Marine Biology, 149: 1217-1225.

- Holst, J. C., Roettingen, I., and Melle, W. 2004. The herring. *In* The Norwegian Sea Ecosystem. Ed. by H. R. Skjoldal *et al.* Tapir Academic Press, Trondheim, Norway. 559 pp.
- Hosseini, S. A., Lee, C-W., Kim, H-S., Lee, J., and Lee, G-H. 2011. The sinking performance of the tuna purse seine gear with large-meshed panels using numerical method. Fisheries Science, 77: 503-520.
- Hueter, R. E., Manire, C. A., Tyminski, J. P., Hoenig, J. M., and Hepworth, D. A. 2006. Assessing mortality of released or discarded fish using a logistic model of relative survival derived from tagging data. Transactions of the American Fisheries Society, 135(2): 500-508.
- Humborstad, O-B., Davis, M., and Løkkeborg, S. 2009. Reflex impairment as a measure of vitality and survival potential of Atlantic cod (*Gadus morhua*). Fishery Bulletin, 107(3): 395-402.
- Huse, I., and Vold, A. 2010. Mortality of mackerel (*Scomber scombrus* L.) after pursing and slipping from a purse seine. Fisheries Research, 106(1): 54-59.
- ICES. 2013a. Report of the ICES Advisory Committee 2013. ICES Advice, 2013. Book 9. 389 pp.
- ICES. 2013b. Report of the Working Group on Widely Distributed Stocks (WGWIDE), 27 August–02 September 2013, ICES Headquarters, Copenhagen. ICES CM 2013/ACOM:15.
- ICES. 2013c. Report of the ICES Advisory Committee 2013. ICES Advice, 2013. Book 6, 447 pp.
- ICES. 2013d. Report of the herring assessment working group for the area south of 62 N (HAWG), 12-21 March 2013, ICES Headquarters, Copenhagen. ICES CM 2013/ACOM:06.
- Isaksen, B., Valdemarsen, J. W., Larsen, R. B., and Karlsen, L. 1992. Reduction of fish by-catch in shrimp trawl using a rigid separator grid in the aft belly. Fisheries Research, 13(3): 335-352.
- Iversen, S. A. 2002. Changes in the perception of the migration pattern of Northeast Atlantic mackerel during the last 100 years. ICES Marine Science Symposia, 215: 382-390.
- Iversen, S. A., and Skagen, D. W. 1989. Migration of Western Mackerel to the North Sea 1973 1988. ICES CM 1986/H:20.
- Kelleher, K. 2005. Discards in the world's marine fisheries. An update. FAO Fisheries Technical Paper. No. 470. Rome, FAO. 131 pp.
- Kieffer, J. D. 2000. Limits to exhaustive exercise in fish. Comparative Biochemistry and Physiology, 126(A): 161-179.

- Kvalsvik, K., Misund, O. A., Engås, A., Gamst, K., Holst, R., Galbraith, D., and Vederhus, H. 2002. Size selection of large catches: using sorting grid in pelagic mackerel trawl. Fisheries Research, 59: 129-148.
- Lockwood, S. J., Nichols, J. H., and Dawson, W. A. 1981. The estimation of a mackerel (*Scomber scombrus* L.) spawning stock size by plankton survey. Journal of Plankton Research, 3: 217-233.
- Lockwood, S. J., Pawson, M. G., and Eaton, D. R. 1983. The effects of crowding on mackerel (*Scomber scombrus*): physical conditions on mortality. Fisheries Research, 2: 129-147.
- Marçalo, A., Araújo, J., Pousão-Ferreira, P., Pierce, G. J., Stratoudakis, Y., and Erzini, K. 2013. Behavioural responses of sardines *Sardina pilchardus* to simulated purse-seine capture and slipping. Journal of Fish Biology, 83: 480-500.
- Marçalo, A., Marques, T. A., Araújo, J., Pousão-Ferreira, P., Erzini, K., and Stratoudakis, Y. 2010. Fishing simulation experiments for predicting the effects of purse-seine capture on sardine (*Sardina pilchardus*). ICES Journal of Marine Science, 67(2): 334-344.
- Marçalo, A., Mateus, L., Duarte Correira, J. H., Serra, P., Fryer, R., and Stratoudakis, Y. 2006. Sardine (*Sardina pilchardus*) stress reactions to purse seine fishing. Marine Biology, 149: 1509-1518.
- Mello, L. G. S., and Rose, G. A. 2005. Seasonal cycles in weight and condition in Atlantic cod (*Gadus morhua* L.) in relation to fisheries. ICES Journal of Marine Science, 62(5): 1006-1015.
- Milligan, C. L. 1996. Metabolic recovery from exhaustive exercise in rainbow trout. Comparative Biochemistry and Physiology, 113A(1): 51-60.
- Misund, O. A. 1992. Predictable swimming behaviour of schools in purse seine capture situations. Fisheries Research 14(4): 319-328.
- Misund, O. A. 1997. Underwater acoustics in marine fisheries and fisheries research. Reviews in Fish Biology and Fisheries, 7: 1-34.
- Misund, O. A., and Beltestad, A. K. 1995. Survival of herring after simulated net bursts and conventional storage in net pens. Fisheries Research, 22: 293-297.
- Misund, O. A., and Beltestad, A. K. 2000. Survival of mackerel and saithe that escape through sorting grids in purse seines. Fisheries Research, 48: 31-41.
- Mitchell, R. W., Blight, S. J., Gaughan, D. J., and Wright, I.W. 2002. Does the mortality of released *Sardinops sagax* increase if rolled over the headline of a purse seine net? Fisheries Research, 57: 279-285.
- Mommsen, T. P., Vijayan, M. M., and Moon, T. W. 1999. Cortisol in teleosts: dynamics, mechanisms of action, and metabolic regulation. Reviews in Fish Biology and Fisheries, 9(3): 211-268.

- Nøttestad, L., Fernö, A., Pitcher, T., Mackinson, S., and Misund, O. A. 2002. How do whales influence herring school dynamics in the cold front area in the Norwegian Sea? ICES Journal of Marine Science, 59: 393-400.
- Nøttestad, L, Utne, K., Oskarsson, G. J., Debes H. et al. 2013. Cruise report from the coordinated ecosystem survey (IESSNS) with M/V "Libas", M/V "Eros", M/V "Finnur Fridi" and R/V "Arni Fridriksson" in the Norwegian Sea and surrounding waters, 2 July 9 August 2013. Working Document presented to ICES Working Group on Widely distributed Stocks (WGWIDE), ICES Headquarters, Copenhagen, Denmark, 27 August 2 September 2013, 42 pp.
- Olla, B. L. Davis, M. W., and Rose, C. 2000. Differences in orientation and swimming of walleye pollock *Theragra chalcogramma* in a trawl net under light and dark conditions: concordance between field and laboratory observations. Fisheries Research, 44: 261-266.
- Olla, B. L., Davis, M. W., and Schreck, C. B. 1997. Effects of simulated trawling on sablefish and walleye pollock: the role of light intensity, net velocity and towing duration. Journal of Fish Biology 50: 1181-1194.
- Ona, E., and Andersen, L. N. 2008. Field calibration of a 3D scientific fisheries sonar: accuracy matters when measuring sensitive pelagic fish schools. Sea Technology, 49(2): 61-65.
- Pawson, M. G., and Lockwood, S. J. 1980. Mortality of mackerel following physical stress, and its probable cause. Rapports et Procès-Verbaux des Réunions du Conseil Permanent International pour l'Exploration de la Mer, 177: 439-443.
- Pine, W. E., Pollock, K. H., Hightower, J. E., Kwak, T. J., and Rice, J.A. 2003. A review of tagging methods for estimating fish population size and components of mortality. Fisheries Research, 28(10): 10-23.
- Portz, D. E., Woodley, C. M., and Cech Jr., J. J. 2006. Stress-associated impacts of short-term holding on fishes. Reviews in Fish Biology and Fisheries, 16: 125-170.
- Pottinger, T. G. 2007. The stress response in fish mechanisms, effects and measurement. *In* Fish Welfare. Ed. by E. J. Branson, Wiley-Blackwell, Oxford. 316 pp.
- Quilhac, A., and Sire, J-Y. 1998. Restoration of the subepidermal tissues and scale regeneration after wounding a cichlid fish, *Hemichromis bimaculatus*. Journal of Experimental Zoology, 281: 305-327.
- Reid, D. G. 2001. SEFOS shelf edge fisheries and oceanography studies: an overview. Fisheries Research, 50: 1-15.
- Ricker, W. E. 1975. Computation and interpretation of biological statistics of fish populations. Fisheries Research Board of Canada Bulletin, 191.
- Ruttan, L. M., and Tyedmers, P. H. 2007. Skippers, spotters and seiners: Analysis of the "skipper effect" in US menhaden (Brevoortia spp.) purse-seine fisheries. Fisheries Research, 83: 73-80.

- Schreck, C. B. 1981. Stress and compensation in teleostean fishes: response to social and physical factors. *In* Stress and Fish. Ed. By A. D. Pickering. Academic Press, London. 367 pp.
- Schwarz, C. J., and Seber, G. A. F. 1999. Estimating Animal Abundance: Review III. Statistical Science, 14 (4): 427-456.
- Schwarz, C. J., and Taylor, C. G. 1998. Use of the stratified-Petersen estimator in fisheries management: estimating the number of pink salmon (*Oncorhynchus gorbuscha*) spawners in the Fraser River. Canadian Journal of Fisheries and Aquatic Sciences, 55: 281-296.
- Silva da, J. R. M. C., Cooper, E. L., Sinhorini, I. L., Borges, J. C. S., Jensch-Junior, B. E., *et al.* 2005. Microscopical study of experimental wound healing in Notothenia coriiceps (Cabecuda) at 0 degree C. Cell and Tissue Research, 321(3): 401-410.
- Simmonds, J., Portilla, E., Skagen, D., Beare, D., and Reid, D. G. 2010. Investigating agreement between different data sources using Bayesian state-space models: an application to estimating NE Atlantic mackerel catch and stock abundance. ICES Journal of Marine Science 67(6): 1138-1153.
- Smith, L. S. 1993. Trying to explain scale loss mortality: A continuing puzzle. Reviews in Fisheries Science, 1(4): 337-355.
- STECF. 2013. Scientific, Technical and Economic Committee for Fisheries Landing obligation in EU fisheries (STECF 13 23). Publications Office of the European Union, Luxembourg, EUR 26330 EN, JRC 86112, 115 pp.
- Stratoudakis, Y., and Marçalo, A. 2002. Sardine slipping during purse-seining off northern Portugal. ICES Journal of Marine Science, 59: 1256-1262.
- Stratoudakis, Y., Marçalo, A., Vale, C., and Falcão, M. 2003. Changes in seawater nutrient concentrations during purse seine fishing for sardine *Sardina pilchardus* off northern Portugal. Marine Ecology Progress Series, 265: 235-242.
- Suuronen, P. 2005. Mortality of fish escaping trawl gears. FAO Fisheries Technical Paper, 478, 70 pp.
- Suuronen, P., Chopin, F., Glass, C., Løkkeborg, S., Matsushita, Y., Queirolo, D., and Rihan, D. 2012. Low impact and fuel-efficient fishing Looking beyond the horizon. Fisheries Research, 119-120: 135-146.
- Suuronen, P., Ericson, D., and Orrensalo, A. 1996a. Mortality of herring escaping from pelagic trawl codends. Fisheries Research, 25: 305-321.
- Suuronen, P., Lehtonen, E., and Jounela, P. 2005. Escape mortality of trawl-caught Baltic cod (*Gadus morhua*) the effect of water temperature, fish size and codend catch. Fisheries Research, 71: 151-163.
- Suuronen, P., Perez-Comas, J. A., Lehtonen, E., and Tschernij, V. 1996b. Size-related mortality of herring (*Clupea harengus* L.) escaping through a rigid sorting grid and trawl codend meshes. ICES Journal of Marine Science, 53: 691-700.

- Suuronen, P., and Sardà, F. 2007. The role of technical measures in European fisheries management and how to make them work better. ICES Journal of Marine Science, 64: 751-756.
- Suuronen, P., Turunen, T., Kiviniemi, M., and Karjalainen, J. 1995. Survival of vendace (*Coregonus albula* L.) escaping from a trawl codend. Canadian Journal of Fisheries and Aquatic Sciences, 52(12): 2527-2533.
- Svalheim, R. 2012. Skin morphology in Norwegian spring spawning herring (*Clupea harengus* L.) and scale loss following crowding in a purse seine. Master's thesis, University of Bergen, 61pp.
- Turunen, T., Suuronen, P., Hyvärinen, H., and Rouvinen, J. 1996. Physiological status of vendace (*Coregonus albula* L.) escaping from a trawl codend. Nordic Journal of Freshwater Research, 72: 39-44.
- Uriarte, A., and Lucio, P. 2001. Migration of adult mackerel along the Atlantic European shelf edge from a tagging experiment in the south of the Bay of Biscay in 1994. Fisheries Research, 50: 129-139.
- Vold, A., Isaksen, B., Saltskår, J., Tenningen, M., Totland, B., Aasen, A., and Olsen, R. E.
 2012. Dødelighet av vårgytende sild etter trenging i not, Rosfjorden i Vest-agder,
 21.03 04.04.2011 (Tokt 2011 805). Rapport fra Havforskningen Nr. 10-2012.
 Bergen, Norway, 22 pp.
- Watson, R., Revenga, C., and Kura, Y. 2006. Fishing gear-associated global marine catches. I. Database development. Fisheries Research, 79: 97-102.
- Wendelaar Bonga, S. E. 1997. The stress response in fish. Physiological Reviews 77(3): 591-625.
- Wood, C. M. 1991. Acid-base and ion balance, metabolism, and their interactions, after exhaustive exercise in fish. Journal of Exploratory Biology, 160: 285-308.
- Wood, C. M., Turner, J. D., and Graham, M. S. 1983. Why do fish die after severe exercise? Journal of Fish Biology 22: 189-201.
- Ziegler, P. E. 2013. Influence of data quality and quantity from a multiyear tagging program on an integrated fish stock assessment. Canadian Journal of Fisheries and Aquatic Sciences, 70: 1031-1045.