

How and why acoustic detectability and catchability of herring change with individual motivation and physiological state in a variable environment: a multi-scale study on a local herring population in southwestern Norway

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The understanding of distribution and aggregation in herring (*Clupea harengus*) can be enhanced by integrated multi-scale studies in small ecosystems. Hydro-acoustics, underwater cameras, herring and predator gillnet samples and oceanographical measurements were used to quantify herring schooling dynamics. During autumn (September) after an active feeding period, the herring was distributed in small and dense schools, mostly close to land and in relatively shallow water (< 30 m depth). During the late overwintering period in February altogether 5-7 rather dense and geographically stationary herring schools were found mid-pelagic in deeper waters (> 40 m depth). All recorded herring schools were then vertically extended in the water column within the most variable temperature and oxygen profiles, presumably enabling individuals to adjust maturation rate to prevailing environmental conditions and synchronize spawning of individuals within the school. From late February prior to spawning, only one major pelagic school was observed, extraordinarily stationary at the only inlet to the inner basin. The pre-spawning herring aggregation was fairly easy to detect acoustically for more than one month. Just prior to spawning and during spawning, herring spread out and became extremely difficult to detect acoustically. Only underwater cameras and bottom set gillnets could then be used to identify herring and selected spawning areas. We argue that the dramatic seasonal changes in acoustic detectability and catchability we observe is best understood and predicted based on detailed knowledge of how herring react to a changing environment according to their physiological state and motivation. Such factors should also be taken more systematically into account when performing acoustic surveys in large marine ecosystems. We need to study in more detail the vital underlying processes behind the substantial variability observed in acoustic detectability and catchability of pelagic planktivorous fish species during their annual life cycle in order to better understand and quantify variability in acoustic surveys, and thereby improve our acoustic abundance estimation.

Keywords: acoustic detectability, catchability, environmental factors, herring, motivation, physiological state

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Introduction

Norwegian spring-spawning herring (*Clupea harengus* L.) is probably the most studied fish species in the northeast Atlantic (Holst et al. 2004, Nøttestad et al. 2004). Nevertheless, a

major challenge in studying herring and other planktivorous schooling species is to be able to perform well-defined and controlled experiments at relevant scales within their natural environment and ecosystem (Nøttestad et al. 2004). The variable spatial distribution, dispersion level and migrations of schooling populations are mainly explained by variations in motivational factors like hunger level and environmental factors like plankton distribution, predation and temperature distribution (Corten 1999, Dalpadado et al. 2000, Nøttestad et al. 2004) as well as learning processes (Fernö et al. 1998). Herring may be distributed very differently vertically and horizontally during seasons of spawning, feeding and wintering due to differences in how they aggregate and school (Fernö et al. 1998, Mackinson et al. 1999, Nøttestad et al. in press). During the last few decades there have been dynamic and partly unpredictable changes in the selection of wintering and spawning areas, migration routes and distribution patterns during feeding (Holst et al. 2004). Acoustic monitoring of such a stock is highly influenced by how fish aggregate and the dynamics of these aggregations (Gerlotto & Fréon 1988, Fréon & Misund 1999). There has been a rapid development in hydro-acoustic technology over the past decades (Ona 1990, MacLennan & Holliday 1996, MacLennan & Simmonds 2005). However, pelagic fish behaviour plays a major role in hydro-acoustic fish stock assessment surveys (Fernö & Olsen 1994), and a bottleneck in interpreting acoustic data now lies in our understanding of fish behaviour (Fréon & Misund 1999). To understand more about fish distribution and population dynamics it is necessary to know how the individual fish respond to different ecological factors (Wootton 1999, Axenrot et al. 2004).

Marine ecosystems like the Norwegian Sea (Skjoldal 2004) are complex and dynamic. Nevertheless, individual organisms are the basic building blocks and if we aim at understanding ecosystems we need to know how individuals behave and interact and why they apply such behaviours. Even when the ultimate target of our research is to understand the large-scale picture (km's), our knowledge of fish schooling in marine ecosystems may ultimately rely on our ability to build theories about how individual fish make decisions (Nøttestad et al. 2004). Understanding essential processes and mechanisms behind schooling dynamics has crucial implication for acoustic abundance estimation and stock assessment, due to the fact that acoustic detectability may vary enormously with changing individual behaviour and interactions between individuals (Fréon & Misund 1999). Tilt angle of individual fish, density, vertical distribution and dispersion level have been shown to significantly affect the precision and reliability of biomass estimation in pelagic fish populations (Ona 1990, Fréon & Misund 1999, Vabø 1999). Furthermore, collecting data and gaining knowledge on physiological state and individual motivation should to a large extent explain how and why herring schools change in size, density, structure and location. Schooling dynamics of pelagic fish and thus variability in acoustic detection ought to be explained by external factors from the physical and biological environment as well as internally driven processes such as gonad maturation influencing local interactions and positioning between individuals.

The scientific echosounder is the basic tool used in fisheries acoustics and has provided considerable information about the formation and characteristics of fish schools in the wild (MacLennan & Simmonds 2005). Nevertheless, it can be important to combine echosounder investigations with sonar observations, as the school-detection ability of sonar can be more than 30 times higher (Misund 1997). When herring is geographically isolated and occur in high concentrations it is difficult to detect these aggregations on an ordinary acoustic survey with the use of echosounder, without the active use of sonar technology. Sonar is important for several reasons: 1) active avoidance behaviour of pelagic fish towards the vessel and thus the echosounder, 2) shallow distribution in the upper acoustic dead zone of the echosounder

(0 - 10 m), 3) deep distribution close to the bottom during spawning within the acoustic dead zone (Skaret et al. 2003, Axenrot et al. 2004) and 4) distribution close to land in more shallow waters where the research vessel cannot cover fish distribution acoustically with an echosounder. Thus, studying pelagic fish behaviour in their natural environment presents numerous complications and need complementary tools. In addition, factors assumed to significantly alter the target strength and thereby strongly influence acoustic detectability include stomach fullness, gonad maturation, fat content, swimming depth (Ona 1990, 2001) and tilt angle of individual fish (Nakken & Olsen 1977, Olsen et al. 1983, Jørgensen 2003). Detectability has been defined as “the proportion of the true abundance of a target species within the ensonified volume (surface to bottom) that is detected by an echosounder and included in integration” (Lawson & Rose 1999), and can be viewed as a major source of bias and imprecision in acoustic abundance estimates in fish, as well as a bias in terms of the inability of echosounders to detect all fish present. Detection probability is determined primarily by physical properties of the acoustic beam and pulse, and how these relate to the distribution, aggregation and behaviour of the fish.

Acoustic applications are now widespread in fisheries science to assess the abundance, distribution, and behaviour of fish, plankton and other marine organisms (Walsh et al. 2001). Schooling has been identified as a problem for hydro-acoustics for several reasons (see Aglen 1994, Appenzeller & Legget 1992, Fréon & Misund 1999, Sawada et al. 1992, MacLennan 1990, Ona 1990, Machias & Tsimenides 1996). The behaviour of the fish may thus greatly affect the level and precision of hydro-acoustic fish abundance and biomass estimates. Fish behaviour is generally very dynamic and changes both seasonally and diurnally (Huse & Ona 1996, Fréon & Misund 1999). Herring perform for instance extensive diel vertical migrations (Blaxter & Hunter 1982, Olsen 1990, Huse & Ona 1996, Petitgas & Lévênez 1996, Aglen et al. 1999). This type of behaviour may result in that the fish occur close to the surface or close to the bottom, causing underestimation of fish abundance as the fish become practically invisible for echosounder detection (Aglen et al. 1999) and can lead to bias through temporal and spatial variation in detectability (Fréon et al. 1993, Demer & Hewitt 1995, Michalsen et al. 1996). Furthermore, numerous types of pelagic aggregations have been observed during daytime, from dense schools to scattered bottom layers (Skaret et al. 2003, Nøttestad et al. 2004) and such variation significantly influence acoustic detectability and catchability.

Small-scale process studies are required where well defined and controlled field experiments on behavioural, environmental and ecological measures can be conducted to account for variability and systematic changes in acoustic detectability. Lindåspollane in southwestern Norway is a small well-defined ecosystem covering about 7 km², representing a unique link between studies in the laboratory and the open ocean and is referred to as a natural “research aquarium” (Lie & Dahl 1981), providing a simple, enclosed and small ecosystem with favourable weather- and current conditions. The area has a postglacial history established approximately 8000 years ago, and contains a local herring stock believed to have existed in the area for more than 5000 years. Specific quantitative hypothesis on a range of scientific issues can be put forward and tested within this system.

This study considers an ecosystem approach focusing on individual trade-offs in relation to the motivation and physiological state (maturation) concentrated around the spawning period. In this paper the scientific concept is our main focus, rather than the quantitative results on acoustic variability of herring throughout their annual cycle. This study takes into account both internal and external factors of the fish behaviour underlying the observed acoustic properties, more than direct measurements on detailed acoustic properties of e.g. target

strength and tilt angle distribution on individual fish. Our aim is to combine and integrate acoustic, environmental, biological and behavioural aspects, with the main objective to understand the behavioural background for variable acoustic detectability and be able to decide when and why acoustic abundance estimation on herring should be performed.

Material and methods

Lindåspollane in southwestern Norway is a small well-defined ecosystem covering about 7 km² (Figure 1). The area has a postglacial history established around 8000 years ago. The average depth inside the poll is approximately 35 m. Maximum depth is about 100 m and the bottom topography is rather varied with islands and bays. There exist a major narrow channel, 7.5 m wide with a shallow sill, which is 3.5 m deep (Figure 1). The area is characterised by little boat traffic and limited human activities except in summertime, protected for severe wind and wave conditions and very suitable for experimental studies. Ice coverage up to 5 cm thick during winter may sometimes constrain the scientific activities in the area.

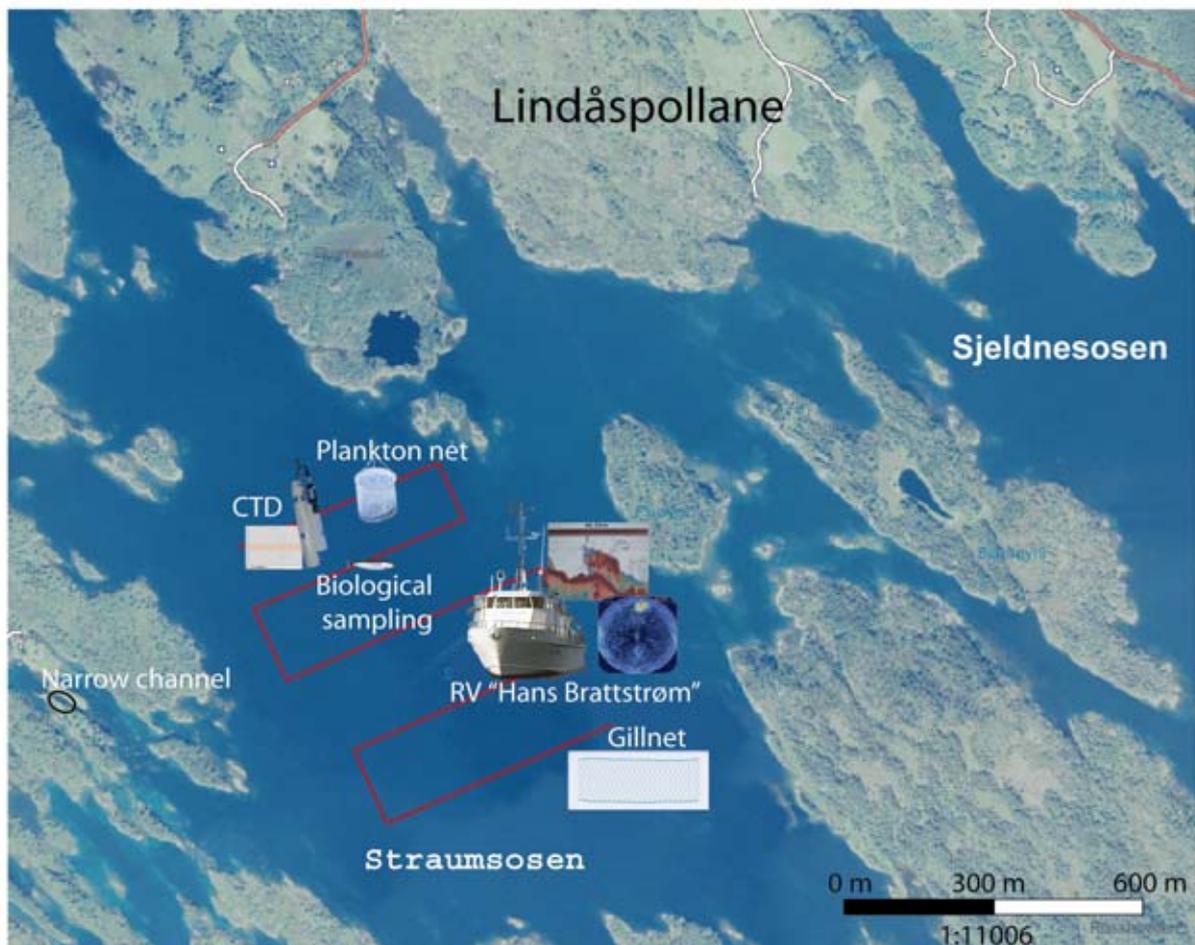


Figure 1. Map over the study area in Lindåspollane, southwestern Norway including R/V "Hans Brattstrøm" with applied methodology (cruise tracks) and technology including scientific echosounder, multi-beam sonar, CTD probe with oxygen sensor, WP2 (180 µm) plankton net, herring and predator gillnets.

The ecosystem is characterised by a large biodiversity in flora and fauna. The local Lindås herring is the key species in terms of ecological importance and biomass within this defined ecosystem. The herring is mainly protected and only small-scale gillnet and hand line fishing

are legal. There exists a whole range of other fish species and potential predators on herring inside the poll including cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), saithe (*Pollachius virens*), whiting (*Merlangius merlangius*), pollack (*Pollachius pollachius*), flounder (*Platichthys flesus*), plaice (*Pleuronectes platessa*), sea trout (*Salmo trutta*) and mackerel (*Scomber scombrus*), which are occasionally caught in gillnets and by angling. Some of these species have also been observed with underwater video camera. Marine mammals and seabirds are also periodically present in Lindåspollane. Sea otters (*Enhydra lutris*), shags (*Phalacrocorax aristotelis*), gulls (*Laridae* sp.), common eider ducks (*Somateria mollissima*), white tailed eagle (*Haliaeetus albicilla*) and grey herons (*Ardea Cinera*) are potential predators on herring eggs, larvae, juveniles and adults on a seasonal basis.

R/V “Hans Brattstrøm” is 24.3 m long and 6.5 m wide (79 GRT). The normal cruising speed is 13 knots but can reach more than 20 knots. The research vessel is well equipped with Simrad EK60 38 kHz ES12-B connected to a General Purpose Transceiver (GPT) and logging as BI60 data on a Dell Pentium IX processor. Garmin GPS 76 linked to PC for continuous logged dGPS position, speed and distance. Prior to the cruises we performed a copper sphere calibration procedure (Foote 1983). We applied 2000 W and 1ms pulse length. A CTD cast was done for calibration settings, including temperature and sound velocity profile. A Kaijo Denki KCH-1827 (emitting frequency = 163 kHz) multi-beam sonar was used for exploratory studies of herring schools and for qualitative meso-scale studies on schooling behaviour. The RGB video-signal from the sonar was recorded to a Panasonic DVD-player. A SAIV Minisoft SD200W CTD probe with oxygen sensor was applied, for accurate water temperature, salinity and oxygen profiles for the whole water column. A WP 2 zooplankton net (1 m², 180 µm) was used to collect the plankton community. Zooplankton species were taxonomically identified using a WP2 net at two distinct depths (normally 0 - 25 m and 0 - 10 m). Gillnets for herring (35 mm mesh size) and predators such as saithe and cod (57 and 79 mm mesh size) were used to sample different species of fish within the poll. The nets were 25 m long and 6 m deep. Close to the acoustic and visual area of the herring, two gillnets were set overnight at 25 - 30 m depth and two gillnets set overnight at 0 - 6 m depth, simultaneously covering the upper water column and the bottom area. Herring gill nets were used repeatedly to catch and collect adult herring specimen throughout the spawning season, which was applied by a separate small boat (Vernøy 430 SL). A local fisherman helped us with systematic geographical sampling of fish using predator and herring gillnets, in order to estimate the changes in physiological state and time to spawning as well as stomach content of herring and predators. Full biological measurements and calculations on length, weight, age determination from otoliths and scales, maturation stage, stomach fullness and content, fat content and condition factor for up to 100 selected herring individuals per sample were made. A SIT (high resolution, wide angle) underwater camera was used for underwater filming of herring schools, other fish species and bottom substrate. A LICOR sensor recorded light levels underwater. Surface filming of various scientific activities were performed using a Sony DCR-TRV-50 mini DV format and digital photography with Nikon D70 an Olympus Camedia still-camera.

Population size of adult and juvenile herring was estimated according to standard acoustic abundance estimation methodology with active use of sonar detection targeting herring schools when herring was most stable and accessible for acoustic abundance estimation. An estimated gadoid biomass was also performed along the adaptive cruise track within Lindåspollane.

Results

There were exceptionally calm wind and wave conditions favourable for acoustic measurements throughout our repeated investigations in Lindåspollane between September and April. Occasional ice-cover in some areas during wintertime prohibited a complete coverage. The geographical distribution of herring schools in Lindåspollane was dynamic, but there was a partly recognizable pattern over time from late autumn in September to post-spawning in April the following year (Figure 2). The time periods for our observations could be divided into five different behavioural and physiological stages/phases in the annual life cycle of adult herring:

- 1) In September the major herring concentrations were distributed in small, narrow (< 30 m bottom depth) and difficult accessible areas for systematic echosounder recordings among small islands close to land.
- 2) In January/February approximately 5 - 7 distinct overwintering herring schools were easily detected on sonar and echosounder in the central and deeper (> 40 m bottom depth) part of the outer basin in Straumsosen.
- 3) In late February/March only one large and surprisingly stationary school was detected acoustically prior to spawning for more than one month at the entrance to the second basin in Spjeldnesosen.
- 4) In late March just prior to spawning the large pre-spawning herring school disappeared and divided into several small spawning locations at the bottom in more shallow waters and bays.
- 5) After spawning the herring spread out in scattered shoals/dispersed aggregations close to surface while feeding on mainly small copepods (*Pseudocalanus*).

There was a clear environmental gradient within Lindåspollane during our study period. Tidal driven currents flowing twice a day in and out of the channel dominated the water circulation pattern inside the outer part of the poll, resulting in a presumably restricted exchange of organisms. The current speed was measured where the pre-spawning aggregation was located and showed current speed of < 5 - 10 cm/s with the current following the direction of the systematic tidal cycle in and out of the poll.

The zooplankton density varied between 139 - 5341 ind/m³ from early winter to after spawning and included *Microcalanus*, *Oithona*, Copepod nauplii and *Pseudocalanus* (stage I-II and IV-VI). Herring initiated feeding right after spawning and typically selected the largest and most nutrient-rich zooplankton species and individuals from the samples, including the *Pseudocalanus* (IV-VI) and *Oithona*.

Lindåspollane is best covered acoustically when combining vertical echosounder transects with horizontal omni-directional sonar detection of schools and fish aggregations along the cruise track. The sonar identified the schools at a distance of 50 - 400 m depending on bottom depth and vertical school distribution. The procedure was then to pass over the respective schools with the echosounder at a relatively slow speed (3 - 5 knots).

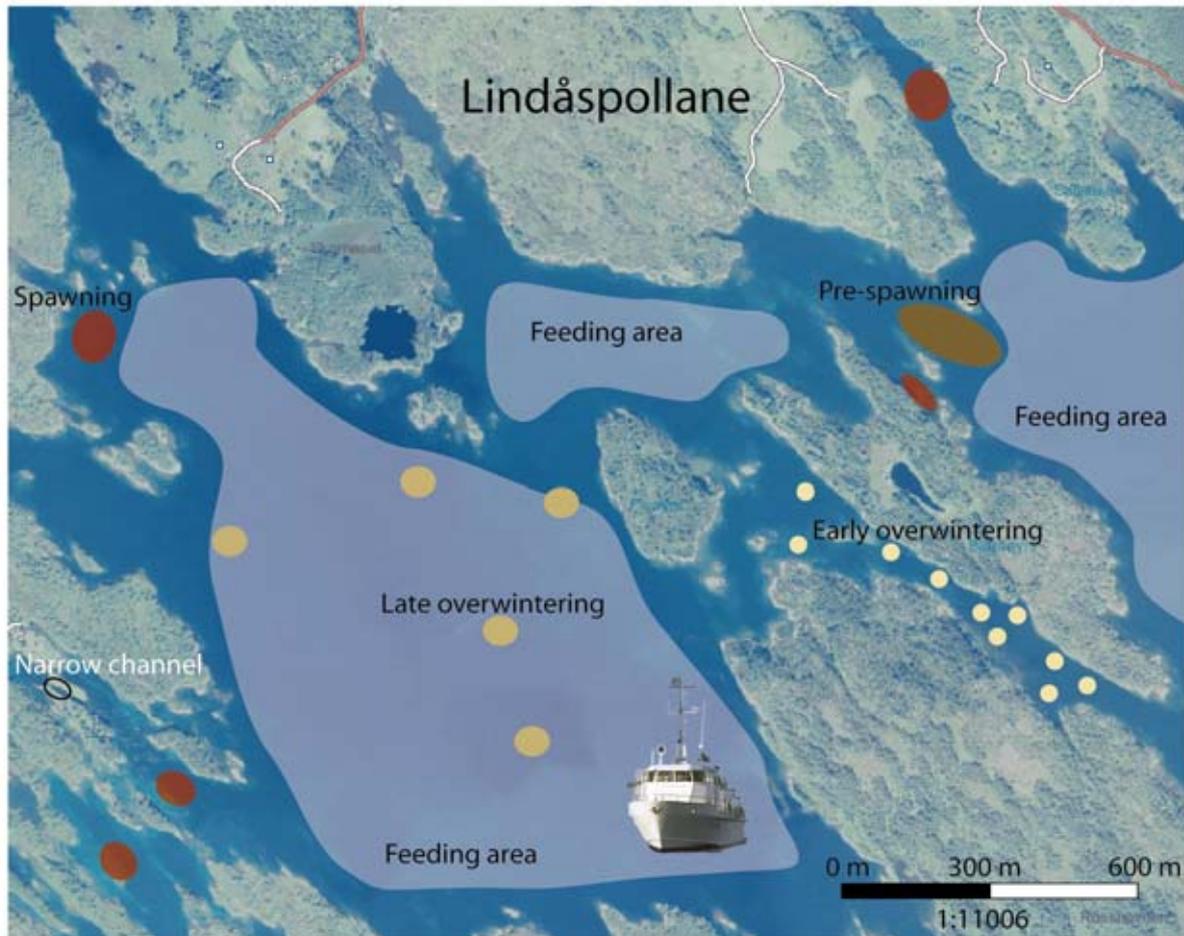


Figure 2. Illustration of horizontal herring school distribution in Lindåspollane during a dynamic period from September to April the following year. The distribution map is based on two consecutive years, 2005 and 2006, of repetitive collected acoustic, visual, biological and oceanographical data: 1) early overwintering (September), 2) late overwintering (January/February), 3) pre-spawning (March), 4) spawning (late March-early April) and 5) feeding period (April->). The fish species were confirmed by repeated gillnet fishing and underwater video-observations. Spawning areas were confirmed by repeated biological sampling of herring and predators, which ate freshly spawned herring eggs. A 10 kg cod caught at one particular spawning site, had eaten a large haddock (about 1.5 kg), which in turn had eaten a substantial amount of freshly spawned herring eggs. Feeding areas are based on visual observations at the surface; gillnet samples and underwater video observations.

It takes approximately eight hours to cover about 7 km² of the major areas in the three major basins within Lindåspollane. A preliminary abundance estimation of the adult and juvenile local herring population showed a population size in February 2006 of about 168 tons of adult herring when the vast majority of the fish was concentrated in one large school prior to spawning (Table 1).

Table 1. Preliminary abundance estimation of adult and juvenile herring as well as gadoid biomass estimates inside Lindåspollane along the adaptive acoustic cruise track with echosounder and multi-beam sonar in February 2006.

<i>Species</i>	<i>~ Sv (dB)</i>	<i>~ L (cm)</i>	<i>TS (dB)</i>	<i>N (fish/m³)</i>	<i>NASC (m²/nm²)</i>	<i>N (fish)</i>	<i>Biomass (tons)</i>
Adult herring	-35.2	30.0	-40.2	3.05	147442	673437	168.4
Gadoid	-52.9	40.0	-35.50	0.18	41941	7667	1.9
Juvenile herring	-44.3	18.0	-42.32	8.44	117555	28190	7.1

Data on vertical extension, upper and lower school depth, centre of school and bottom depth were recorded and calculated for the respective schools to link this information to our behavioural understanding and consequences for acoustic detectability (Table 2).

Table 2. Brief summary of number, size, location and vertical distribution of herring schools during different time periods linked to their physiological state and interpreted internal motivation. The table illustrates how changing environment and predation strongly influence the three dimensional fish distribution, aggregation and behaviour, which in turn strongly affect acoustic detectability. School dimensions are calculated from sonar and echosounder recordings as well as underwater video observations. Data on fish length, weight and age were gathered through standard biological analyses. Data on feeding motivation is based on herring stomach samples, stomach fullness and prey identification, while quantification of maturation is based on gonad stage determination from selected herring individuals in different seasons.

<i>Parameter</i>	<i>Overwinter September</i>	<i>Pre-spawning February/March</i>	<i>Spawning March/April</i>	<i>Post-spawning April-></i>	<i>Behavioural and physiological trade-offs</i>
Estimated school size (tons)	Small 10 > S > 2	Large S > 100	Medium 100 > S > 10	Very small S < 1	Trade-offs: feeding, spawning, predation
School height (m)	2-9	10-15	1-3	1-5	Maturation stage, feeding, anti-predator behaviour
Swimming depth (m)	15-25	10-18	5-10	0-20	Maturation stage, predator avoidance, feeding
Distance to bottom (m)	5-20	3-15	0-1	10-80	Maturation stage linked to motivation for spawning
Feeding	No	No	No	Yes	Surface feeding motivation linked to accessible food
Estimated number of schools (N)	<10	1	>5	>30	Multiple trade-offs: predation, spawning and feeding
Maturation stage (3-8)	3.5-4.1 early mature	4.2-5.5 late mature	5.6-6 spawning	8 post-spawning	Physiology, pheromones and environment
Size (cm)	28-34	26-36	28-34	26-33	Maturity stage, experience
Weight (g)	193-347	158-474	220-430	130-280	Weight, condition factor
Age (years)	3-10+	4-10+	5-10+	3-10+	Learning, experience
Acoustic detection	Medium	High	Very low	Low	Spawning motivation, multiple trade-offs

Biological sampling results varied occasionally significantly from one day to another due to variable individual behaviour, motivation, maturation, light regime, physical environment and

predation pressure. Age distribution varied with water depth according to sampled herring at the surface as compared to the bottom. The older herring were distributed significantly deeper ($p < 0.05$) in the water column than younger individuals. During the pre-spawning period the herring with different gonad-somatic index (GSI) and maturation stage had significantly different depth preferences ($p < 0.001$), with the most mature individuals occupying the deeper part of the school, while less mature individuals preferred to swim higher up in the water column.

Two temperature-, salinity- and oxygen- profiles linked to vertical distribution of herring schools during the late overwintering period are shown in Figure 3. Temperature, salinity and oxygen profiles were conducted at six different stations with bottom depth varying from 29 - 49 m.

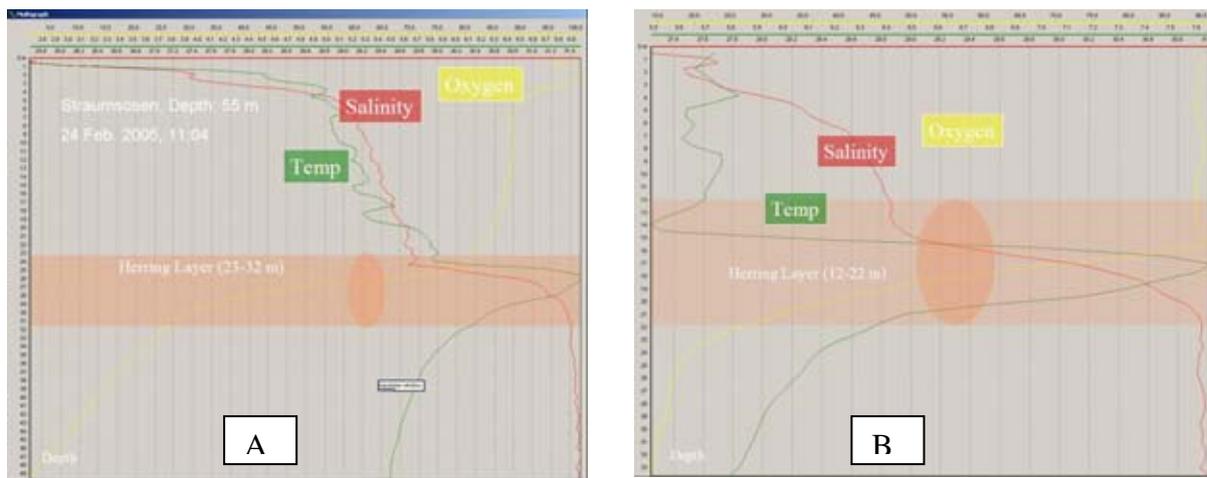


Figure 3 A, B. Illustration of two different vertical herring distributions in late overwintering period linked to temperature, salinity and oxygen profiles in Linådpollane in late February 2005. Note the close connection between vertical school alignment and the highest and most variable temperature and oxygen values.

The temperature varied between a minimum of 2°C close to the surface up to 7.5°C. The salinity varied between 25.0 and 31.4. Oxygen saturation varied between 0 (anoxic conditions) in the inner basin to >100% saturation in outer areas with good flow conditions. In all six cases the main density centre of the observed school was distributed at maximum temperature values, as well as in the most variable temperature and oxygen maturation ranges. Consequently, all major pre-spawning herring schools in Lindåspollane stayed in the most dynamic range according to temperature (thermocline) salinity and oxygen, at variable distance to the bottom as indicated when comparing Figure 3A with Figure 3B.

Discussion

Proximate (how) and ultimate (why) questions in fish behaviour need to be explored in relation to acoustic abundance estimation of all fish species in question. The biases imposed by behavioural dynamics on different spatial-temporal scales in the system are better understood when trying to identify relationships with such proximate and ultimate factors. The individuals are the key starting point to understand how and why acoustic detectability varies over time in ever-changing dynamic fish aggregations. It is the individuals and second-to-second interactions between individual fish that dictate the dynamics in the school responsible for most variation in acoustic signatures of fish targets. Our aim is to zoom out from an individual point of view, via the school organization and behaviour to the population

level when we study spatial and temporal clustering of schools and large-scale aggregation of animals. Seasonal dynamics and acoustic measurement during nighttime provide us with diurnal shifts in acoustic detectability, due to sudden changes in behavioural trade-offs influencing the behavioural and motivational output (Vabø 1999). Herring has wide capabilities of adaptation both physiologically, e.g. to different temperature and salinity, and behaviourally, e.g. by timing of spawning or choice of spawning grounds.

The overwintering and pre-spawning period is crucial for herring in order to mature timely and synchronously and thus be able to successfully spawn in the spring. Large-scale herring population surveys with calibrated echosounder and sonar recordings are vital for multi-scale data collection of abundance, distribution, aggregation and migration of herring within Lindåspollane. It is essential to understand how fish respond and behave throughout the year, depending on the annual cycle related to access for food, abundances of predators and maturation cycle. It is furthermore important to determine fluctuating environmental conditions throughout a season and between seasons to shed light on factors influencing spatio-temporal distribution, aggregation, tilt-angle distribution and degree of variability. Biological sampling of herring and gadoids caught in gillnets, as well as zooplankton samples at selected depths, enabled us to determine and understand changes in predation pressure and feeding motivation of herring. Such information can be useful to explain observed changes in herring population dynamics important for quantitative acoustic data collection.

Our results show that age distribution and maturation in herring varies with depth. Similar results have been found by Godø and Weststad (1993), where detectability varied with differences in age composition and local density. Skaret and Johnsen (in prep) found very similar differences in maturation stage with depth at the main Norwegian spring-spawning herring spawning sites off Møre as were observed in Lindåspollane. This clearly illustrates the similarities and transfer value between small-scale ecosystems and large-scale ocean systems. Their study also suggests that behaviourally mediated, systematic variation in detectability can be the major source of bias in acoustic density estimates. Patterns of variation in detectability may be complex and the plasticity of fish behaviour is often poorly understood. Spatial and temporal variability in the physical setting is important in understanding fish stocks.

The vertical migration may be understood on the basis of a trade off between energy saving and predator avoidance (Bayly 1986, Clark & Levy 1988). The different behavioural characteristics in different depth intervals and time of the day lead to different combined effects of behavioural bias. The TS of individual fish is known to be a highly variable and sensitive parameter (Midttun & Hoff 1962, Love 1971, 1977, Nakken & Olsen 1977, Foote 1980b, Dawson & Karp 1990, Ona 1990). The swimbladder and volume may vary seasonally as a result of various physiological factors such as gonad development and the stomach and fat contents of the fish (Ona 1990). Since herring is a physostomous fish, it is generally accepted that it is not able to secrete gas into the swimbladder (Brawn 1962, Fahlen 1967, Ona 1984, Blaxter & Tytler 1978, Blaxter & Batty 1990, Ona 1990), although this has been questioned (Nøttestad 1998). The TS is therefore believed to be a depth-dependent variable that follows the diurnal vertical migration patterns as increased pressure causes compression on the swimbladder volume. TS vary considerably with the tilt angle of the fish (Midttun & Hoff 1962, Love 1971, Nakken & Olsen 1977, Foote 1980a, MacLennan et al. 1989) and tilt angle changes during vertical migrations.

In the various life-history stages of the herring, both physiological states and motivational behavioural states vary (Nøttestad 1999), and this probably results in corresponding differences in TS, tilt angle distributions and reactions to survey vessels (Mohr 1971, Olsen et al. 1983). Such knowledge could be used in relation to *in situ* measurements to improve our understanding and handling of links between behavioural characteristics and acoustic aspects. Variability in depth position, tilt angles and target strength can be explained by individual variability, but this variability is not necessarily a problem in acoustic abundance estimation if it is known and uniform around a well-defined mean (MacLennan & Simmonds 2005). Biases related to behaviour such as horizontal migration, bottom and surface dead-zone problems, and acoustic shadowing due to dense aggregations and schooling (MacLennan & Simmonds 2005) are regarded as the most serious behavioural within-beam errors (Aglen 1994).

Since spawning stock estimates are made during overwintering before spawning, it is important to gain knowledge of the behaviour of herring in this period in order to evaluate possible effects of behaviour on acoustic target strength (Huse & Ona 1996). Pre-spawning herring in Lindåspollane swam slowly around in schools interrupted by occasional low-intensity reactions to potential gadoid predators. The schools stayed in a restricted area and kept in depths with peaks in temperature and decreasing oxygen concentration with strong gradients of these environmental factors. The adaptive significance of the behaviour of animals can often be explained by multiple trade-offs between different demands and activities (Sih 1993). Herring generally trade-off predator avoidance and feeding, resulting in different school characteristics and migration patterns (Fernö et al. 1998, Nøttestad et al. 2004). During the spawning season reproduction also becomes crucial and can take precedence over feeding and even anti-predator behaviour (Nøttestad et al. 1996, Skaret et al. 2003). The wintering and pre-spawning periods represent a trade-off between predator avoidance, energy conservation and maturation up until spawning.

During the pre-spawning stage when herring has reached the spawning ground they should be expected to behave in order to maximise reproductive output. Firstly, they should use as little energy as possible on other activities than reproduction. Although herring have been observed to feed by filtering on high prey concentrations shortly before spawning (Axelsen et al. 2000), they generally endure a period of several months with no food intake before spawning (Nøttestad et al. 1996, Slotte 1999). This was confirmed in the present study where herring had empty stomachs in spite of relatively high abundance of zooplankton. It thus becomes crucial to effectively allocate the available energy resources into reproductive activities and products. Secondly, the rate of maturation determining the time of spawning should be tuned to the dynamics in the external environment with regard to temperature and food abundance in order to provide optimal conditions for the larvae at hatching. The individual fish in a school should also synchronise spawning in order to encounter sexually mature mates, prevent school splitting and restrict the time at the spawning site and at the risky habitat on the bottom (Axelsen et al. 2000, Skaret et al. 2003). Last, but not least, the fish should avoid being predated on. Cod and haddock are visual feeders on herring and herring eggs, and these predators have been repeatedly documented to feed on herring in Lindåspollane. Hence, herring in the pre-spawning stage should be expected to avoid being eaten using a minimum of energy while staying in water masses that synchronise spawning within an optimal time window.

A crucial decision is where to spend the time before spawning. With regard to the horizontal dimension the herring schools kept close to known spawning grounds (Lie et al. 1978, Johannessen 1986). The fish were observed to swim slowly around, a swimming activity

presumably related to the vertical dynamics. Herring as a pelagic and physostome species (Ona 1990) must compensate by swimming to avoid sinking to the bottom. We observed herring with extended pectoral and pelvic fins, permitting gliding behaviour and thus slower descent. Groups of herring were in addition occasionally observed to swim steeply upwards. Herring in a wintering situation have earlier been observed to perform "rise and glide" type behaviour, presumably to avoid sinking and save energy (Huse & Ona 1996).

The observed schools during the late overwintering period stayed at 13 - 31 m centre depth. Herring had empty stomachs from September until late March prior to and during spawning, and should therefore not have any motivation related to feeding to swim high in the water column with highest food concentrations. However, herring are neutrally buoyant at shallow depths and will expend increasing amounts of energy as their depth increases. The preference for relatively deep waters must thus be associated with some benefits. No clear diel rhythms were found so the light level does not seem crucial, although we have very few acoustic night-time observations presumably due to dispersal of schools at low light levels. The distance to the bottom varied between schools. The school depth was, however, strongly linked to the environment in the sea. All observed schools stayed in layers with maximum temperature and decreasing oxygen levels characterised by strong gradients. We can partly predict herring vertical distribution pattern from the temperature profiles prior to spawning due to their preferences for depths with highest temperature and largest range in temperature. This indicates that the fish selected water masses increasing maturation rate, and the gonadosomatic index was found to increase within an interval of two days. The fish were spread out in the vertical dimension around the depth with highest temperature. Different temperature preferences between individual fish could explain the vertical extension of the herring schools, which is in contrast to the usually observed horizontal shape of fish schools. The depth range within a school could permit synchronisation of maturation of individual fish. Ambient temperature strongly influences maturation in fish (Hay 1985). The vertical extension of the schools was 10 - 12 m, and fish moving within the school might experience a temperature range of 1.5 - 2.5°C. By staying in a depth with strong gradients, the individual fish in the school can select water of different temperature; swimming to warmer waters to speed up maturation and conversely moving to colder waters if too close to spawning. In fact, most herring schools have earlier been observed to spread out in the vertical dimension just prior to spawning (Axelsen et al. 2000). In line with the present observations this was explained by individual variations in the strength of attraction to the bottom spawning substrate in fish with different maturation states. Consequently, these mechanisms might substantially influence acoustic detectability of herring.

Only a few herring were found in the stomachs of the gadoid predators indicating that the risk of predation was relatively low. Most predatory fish in the area were presumably too small to constitute a serious threat, and the herring avoided potential predators by slowly swimming away. Yet the risk of predation for an individual herring and the consequences for its behaviour is difficult to estimate. The herring schools stayed in waters where the oxygen levels rapidly decreased with depth. Whereas all schools stayed around the peak in temperature, the schools encountered different oxygen levels, strongly indicating that temperature is the main factor determining the depth. The behaviour of maturing herring at the spawning site in Lindåspollane is primarily shaped by energy conservation and regulation of maturation. The fish do not feed and seem to do as little as possible except for avoiding occasional predatory attacks. The most adaptive behaviour in this situation seems to be to wait in the pelagic compensating for the steady sinking. This will influence acoustic detectability due to variable tilt angle during sink and glide.

Conclusion

This process-oriented study in a small self-contained marine ecosystem investigation was performed during a dynamic time period for herring. We have demonstrated how the individual state and motivation of herring linked to the prevailing physical and biological environment greatly influences the overall schooling dynamics of herring, thus affecting acoustic detectability and furthermore catchability. A prerequisite to understand and predict observed diurnal and seasonal changes in acoustic detectability and catchability of a herring population is to focus on individual behaviour within herring schools. We emphasise the transfer value of results obtained from small-scale studies for large-scale open ocean ecosystems. After all, the dynamics and seasonal changes in the three dimensional behaviour of herring within this small-scale system (7 km²) is surprisingly similar to herring dynamics in a large-scale marine ecosystem (> 1 mill km²). The best periods to perform herring abundance estimation in Lindåspollane will be during late overwintering and pre-spawning when herring schools are stationary and easily detectable by echosounder surveys. These results represent information of fish behaviour and distribution that could be valuable for future survey planning and improved analyses of hydro-acoustic data from regular fisheries surveys. We ought to gain detailed knowledge of the species behaviour and physiology in order to better understand how and why acoustic detectability and catchability vary during different periods in the life cycle of herring.

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