

# **Distribution and activity of pelagic fish – acoustic studies in the Baltic Sea**

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Doctoral Thesis in  
Marine and Brackish Water Ecology



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# Abstract

Fisheries agencies around the Baltic Sea use hydroacoustics to assess stock sizes of herring and sprat. These assessments rely on the assumption that the acoustic properties of Baltic clupeids are the same as North Sea herring. This may lead to biased results, as system-specific differences in salinity and fish fat content may influence acoustic target strength. The acoustic properties of the Baltic clupeids were explored and a new relationship between target strength and fish length was developed (paper I). The intercept of this new relationship is 3.4 dB higher than normally used by the agencies. Applying this new relationship would reduce the acoustic stock biomass estimates by approximately 50%.

Diel variation in the vertical distribution of fish may influence acoustic abundance estimates. Fish body posture may influence target strength and if fish concentrate near the surface or bottom this may affect detectability by an echo sounder. A seabed-mounted, upward pinging echo sounder was used to study diel variation in vertical distribution, acoustic size distribution and abundance of fish (Paper II). Differences between day and night were substantial and it was concluded that night time acoustics are to be preferred, at least in our study area. The seabed-mounted echo sounder was also used to study fish swimming activity and vertical distribution in relation to light intensity and water temperature (paper III). Four phases of fish distribution were distinguished over the diel cycle (day, night, dawn and dusk). Acoustic tracking was used to estimate the swimming speed of individual fish. The speed varied among the diel periods and the greatest difference was observed between day and night with twice as high swimming speed during the day. Regression models were developed to investigate the effects of fish size and environmental factors (water temperature, light intensity at the sea surface and *in situ*, measured at the depth of the fish) on swimming speed. Fish size, light intensities and temperature were all significant variables in the models, with fish size being generally most important. These results have clear implications for fish bioenergetics models. Such models should account for seasonal, light-driven cycles in the activity-induced respiration estimates, in particular when modelling populations at high latitudes.

Vertical and horizontal fish distributions were studied from spring through autumn during two consecutive years (paper IV). The seasonal dynamics in vertical distribution patterns were consistent between years. Prior to thermocline formation, fish of all sizes concentrated near surface where water temperatures were higher than in the underlying water mass. During the summer period of pronounced thermal stratification, larger fish were found deeper than small individuals (including young-of-the-year fish), which remained close to the surface. In the autumn, when the thermal stratification diminished, the small fish moved somewhat deeper while larger individuals dispersed throughout the water column. Fish showed clear horizontal patchiness, but horizontal distributions were not significantly related to wind directions.

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## List of papers

- I. Didrikas, T. and Hansson, S. 2004. *In situ* target strength of the Baltic Sea herring and sprat. *ICES Journal of Marine Science* 61: 378-382. © (2004) International Council of the Exploration of the Sea. Published by Elsevier Ltd.
- II. Axenrot, T., Didrikas, T., Danielsson, C. and Hansson, S. 2004. Diel patterns in pelagic fish behaviour and distribution observed from a stationary, bottom-mounted, and upward-facing transducer. *ICES Journal of Marine Science* 61: 1100-1104. © (2004) International Council of the Exploration of the Sea. Published by Elsevier Ltd.
- III. Didrikas, T. and Hansson, S. Effects of light intensity on the vertical distribution and activity of pelagic fish – studies with a seabed-mounted echo sounder. Manuscript.
- IV. Didrikas, T., Axenrot, T. and Hansson, S. Pelagic fish distribution in relation to water temperature and wind direction: a study in a Baltic Sea coastal bay. Manuscript.

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# **My contributions to the papers**

## **Paper I**

I took part in the collection of some data sets (4 of 15), performed data analyses and developed the regression models after discussions with the co-author. I wrote most of the paper after discussions with the co-author.

## **Paper II**

I collected the data during field work together with T. Axenrot. I analysed most of the data (vertical fish distribution and fish tracking). The outline of the paper was developed through discussions among the co-authors and I wrote parts of the results and discussion sections.

## **Paper III**

The field work required for this paper was conducted by me and different colleagues. The data analyses, outline of the paper and writing of the manuscript was mainly done by me, but in close cooperation with the co-author.

## **Paper IV**

I participated in the data collection in one of the two years, analysed vertical distributions and wrote parts of the introduction, results and discussion sections. The manuscript as a whole has been thoroughly scrutinised and modified after discussions among all the authors.

# Introduction

The present level of marine fisheries is very intensive (Pauly & Christensen, 1995). Overfishing has become a major problem that is likely to have serious ecological consequences or even to result in to the collapse of whole ecosystems (Pauly *et al.*, 1998; Steele & Schumacher, 2000; Jackson *et al.*, 2001). Overfishing is not only a problem in remote ocean areas, but also in the Baltic Sea. A common problem for fisheries management is that commercial catches are used in assessing stock sizes, and biases in such assessments have resulted in very serious overfishing problems (e.g., Hansson, 1999; Kuikka *et al.*, 1999). To help avoiding these kind of problems, and manage fisheries within sustainable levels, reliable and fishery independent data are urgently needed. Hydroacoustics is one of the few techniques with which fisheries independent quantitative assessments of fish stocks can be made (MacLennan & Simmonds, 1992).

Hydroacoustic techniques have undergone rapid development during the last decades (e.g., MacLennan & Simmonds, 1992; MacLennan & Holliday, 1996) and scientific echo sounders are routinely employed in the assessments of many fish stocks. Besides providing us with estimates of fish abundances, this technique is used for various other purposes. It is, for example, possible to “observe” fish *in situ*, independent of light conditions and depth. Hence, studies of behaviour (e.g. swimming speed) under different conditions are possible. This facilitates, for example, analyses of activity responses to changes in food availability, light, temperature, etc. However, hydroacoustic techniques also face problems and uncertainties, especially related to fish behaviour (Fréon & Misund, 1999).

This thesis has two main objectives. The first is to improve our knowledge on the acoustic properties of Baltic Sea clupeids (herring and sprat). The second is to use acoustic technique to address ecological questions concerning the distributions and behaviour of pelagic fish.

In Paper I, a new relationship between acoustic target strength (TS) and fish length for Baltic Sea herring and sprat was proposed. This relationship is crucial to derive estimates on fish abundances and biomass from acoustic data. To study fish behaviour and vertical distribution over the diel cycle, I used a seabed-mounted upward pinging echo sounder (papers II and III). Paper II discusses the possible effects of behaviour and distribution on the quality of acoustic fish biomass estimates. In paper III, I studied the effects of light intensity on the vertical distribution and activity of fish. Paper IV discusses seasonal dynamics in the vertical and horizontal distribution of fish in relation to water temperature, wind direction and fish size.

## Acoustic target strength

Measurement of fish abundance is probably the most common application of hydroacoustics in fisheries research. The target strength is a pivotal parameter for the conversion of the integrated acoustic energy to absolute fish abundance (MacLennan, 1990). The target strength of the fish is a number which indicates the size of the echo and consequently the size of the fish. Due to practical reasons, and probably also tradition, the target strength to fish size regression equations includes only length as independent variable. However, the target strength is also influenced by biological factors such as the tilt angle (the body posture of the fish relative to the echo sounder; Nakken & Olsen, 1977; Blaxter & Batty, 1990; Ona, 2001), the physiological status of the fish (Ona, 1990, 2003; Ona *et al.*, 2001) and the depth at which it occurs (Edwards & Armstrong, 1983; Mukai & Iida, 1996; Mukai & Foote, 1997; Ona, 2003). These complicating factors are rarely included in the equation that describes the relationship between fish size and echo strength. Properties of the echo sounder, such as the sound frequency (e.g., Holliday & Pieper, 1995), also influence the echo strength, and TS equations (relation between fish size and echo strength) are often given for specific frequencies.

## Biological factors affecting target strength

Variation in the behaviour of fish, their morphology, ontogeny and physiological status can, through changes in the target strength, lead to substantial errors in acoustic abundance and size structure estimates (Hazen & Horne, 2003). In fish with a swim bladder, this tissue is responsible for most of the reflected sound (90-95% of the backscattered energy, Foote, 1980) and factors that influence the size and shape of the swim bladder also influence the TS value of the fish. It is unfortunate that the target strength of fish is determined by such a labile organ. The volume of the swim bladder depends on the size of the fish, but also on the magnitude of its inflation. In order to provide neutral buoyancy, the swim bladder should occupy approximately 5% of the body volume in a fully marine species and 7% in a freshwater species (c.f. Blaxter & Batty, 1990). The volume may, however, change rapidly in response to vertical movements (pressure changes). The fat content of the fish also influences the swim bladder volume. Ona (1990) found an inverse relationship between the fat content and the swim bladder volume in herring. Fat content varies with e.g. gonad maturation stage and feeding conditions, and the swim bladder cross-section and hence the target strength may thus vary seasonally. Machias & Tsimenides (1996) proposed that in subtropical conditions where the reproductive period is long (for Mediterranean sardine it lasts almost half a year), the effects of the gonads on the swim bladder cross-section can be as important as that of the fish

length on the swim bladder size. The stomach fullness can, in the same way as variation in the size of the gonads, modify the size and shape of the swim bladder. For physostomous and filter-feeding planctivores, such as sardine, this seems to have little or no influence (Machias & Tsimenides, 1996), while gadoids, when food is available in great quantity, will feed until the stomach is fully expanded and the swim bladder is deformed as to be almost unrecognisable (Ona, 1990).

## Fish tilt angle and target strength

Experiments with caged fish (e.g., MacLennan, 1990) as well as *in situ* TS measurements together with target tracking (e.g., Huse & Ona, 1996; McQuinn & Winger, 2003) have shown that the diurnal change in target strength correlates well with the tilt angle of the body. However, target strength changes much more rapidly with tilt angle than would be expected from geometrical considerations alone (Nakken & Olsen, 1977). When an acoustic pulse is reflected by a long, thin target such as a swim bladder, the energy in the reflected wave will change as the target tilts. There are two reasons for this effect. First, the cross-section of the target, as seen from the transducer, decreases as the tilt increases. Second, while the target strength varies as the cosine of the tilt angle, the echo energy may change much more rapidly because of interference between wavelets reflected from different parts of the target. This interference effect is only important when the acoustic wavelength is comparable to, or smaller than, the length of the target (MacLennan & Simmonds, 1992). For example 70, 200 and 710 kHz frequency echo-sounders transmit respectively 2, 0.7 and 0.2 cm long sound waves. Thus, the target strength of objects smaller than these sizes is not influenced by the tilt angle. It should be noted that for fish these sizes generally refer to swim bladder size, not the total fish length.

It should not be assumed that the swim bladder necessarily lies horizontally within the fish. In some species it is angled upwards at the anterior end. This angle can be quite steep, for example 18° in the deep-bodied fish Atlantic menhaden (Batty *et al.*, 1990) and approximately 7° in herring (Blaxter & Hunter, 1982). This explains why Nakken & Olsen (1977) found the highest target strength of saithe when the fish tilt angle was between -4 to -11° (i.e. head down). There are also extensive photographic observations of tilt angles of commercial fish *in situ* and in cages, made as part of target strength measurements (Batty *et al.*, 1990; Huse & Ona, 1996). There is evidence of both a wide scatter of a tilt angles under all conditions and a tendency for mean tilt angles to be positive at night (i.e. the fish tend to be head-up). This may result from the fish being negatively buoyant and less active at night and thus requiring a head up posture to obtain lift and maintain depth when swimming slowly (Ona, 1990; Huse & Ona, 1996).

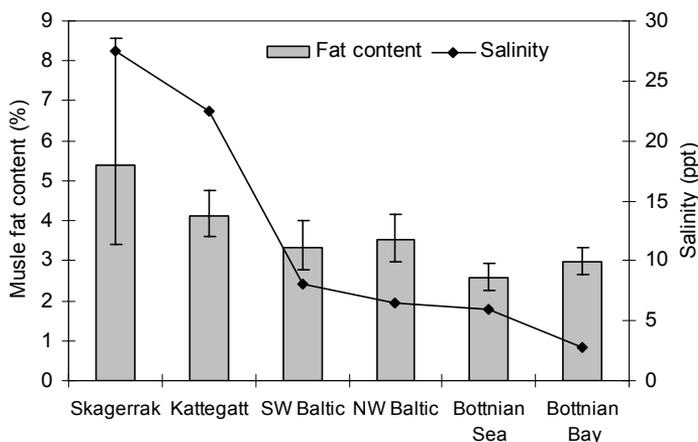


Figure 1. Fat content (average with 95% confidence intervals) of herring muscle and average surface water salinity in Skagerrak, Kattegat and different parts of the Baltic Sea (based on Bignert, 2002).

## Target strength studies of Baltic Sea fish

Fisheries agencies around the Baltic are using TS to fish length relationship which is based on the assumption that Baltic Sea herring has the same TS to size relationship as North Sea herring (ICES, 1997, Table 1). Using this assumption may be inadequate because of differences between the areas in salinity and in the fat content of the fish (Fig. 1). In paper I we present new TS to fish length relationships for the Baltic Sea herring and sprat, which were derived using *in situ* data. Our relationship had an intercept, which is 3.4 dB higher than that recommended by ICES (International Council for the Exploration of the Sea). Based on the equation that we found, the clupeid biomass should be only half of that estimated from the TS relationship recommended by ICES. However, this difference does not necessarily imply that the ICES general estimates of herring and sprat stocks are wrong. In the ICES working groups, acoustic abundance estimates have been used as an index of the relative abundance for tuning the standard stock assessment models (e.g. XSA – Extended Survivor Analysis method is used to tune VPA – Virtual Population Analysis models). Present scepticism to an increased use of acoustic data in determining pelagic fish stock sizes is motivated by uncertainties concerning the accuracy of the method (but not its precision), for example our inadequate knowledge of the target strength to fish size relationship.

A year after our paper I was published, Peltonen & Balk (2005) proposed TS-length relationship for herring in the Bothnian Sea (Northern Baltic).

Table 1. Target strength (TS, dB) to fish length (L, cm) relationships (with slope fixed to 20) from different studies on Baltic Sea clupeids.

Equation	System	Frequency, kHz	References
$TS=20 \log_{10} L - 66.3$	Split beam	38	Didrikas, 2005
$TS=20 \log_{10} L - 63.9$	Split beam	38	Peltonen & Balk, 2005 (Bothnian Sea)
$TS=20 \log_{10} L - 67.8$	Combined single & split beam	38 & 70	Didrikas & Hansson, 2004
$TS=20 \log_{10} L - 71.2$	Not defined	38	ICES, 1997
$TS=20 \log_{10} L - 69.9$	Single beam	70	Rudstam <i>et al.</i> , 1988
$TS=20 \log_{10} L - 70.8$	Single beam	38	Lassen & Stæhr, 1985
$TS=20 \log_{10} L - 73.4$	Single beam	120	Lassen & Stæhr, 1985

Their regression equation had a surprisingly low slope of 16.8. However, when fixing the slope to 20, which is almost a standard assumption in fisheries acoustics, their data produced an equation which suggests that a fish of a given size has a TS value that is 7.3 dB higher than derived from the standard equation used by ICES. The difference was thus in the same direction as reported in paper I.

In 2005 we were requested by the ICES Study group of Target Strength Estimation in the Baltic Sea (SGTSEB) to collect and analyse relevant acoustic data from around the Baltic Sea, and derive new TS to fish length relationship. From the ten datasets that were made available, we derived an equation with a TS value 4.9 dB higher (slope fixed to 20) than that traditionally used by ICES (Didrikas, 2005, see Table 1). The parameters in “the ICES TS-length relationship” are further challenged even by studies from the North Sea, where Ona (2003) derived target strengths that were 4.6 dB higher than expected.

The differences between acoustic and XSA biomass estimates for herring in the Baltic Proper, derived by different ICES working groups, vary over time but estimates are very similar for some years (Fig. 2). Applying the TS to fish length regression proposed in paper I and in most of the other studies lately carried out in the Baltic Sea (Table 1), would produce biomass estimates that are substantially below those reported by ICES. Such discrepancies hardly would be welcomed by the fisheries management community. A possible explanation to the low hydroacoustic biomass estimates is an avoidance reaction by the fish. There is no clear consensus on the importance of vessel avoidance, but it appears to depend on vessel size, noise signature, fish species, spawning period, bottom depth, distance

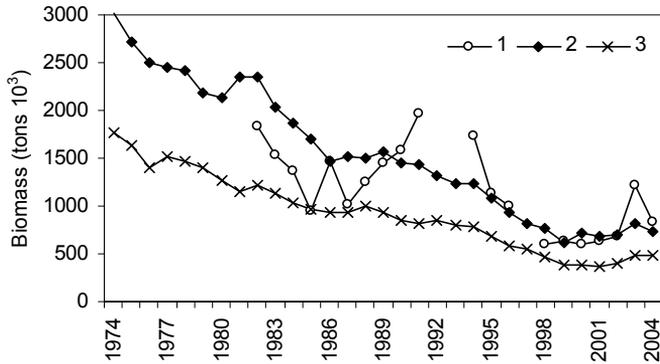


Figure 2. Acoustic estimates of the total herring biomass (1), corresponding biomass from the Extended Survivor Analysis (XSA, 2) and spawning stock biomass (3) from XSA in the Baltic Proper (ICES 25-29 & 32 subdivisions, excluding Gulf of Riga, redrawn from ICES, 2005).

between the fish and the vessel, etc. (e.g., Olsen *et al.*, 1983; Fréon *et al.*, 1993; Fernandes *et al.*, 2000; Mitson & Knudsen, 2003; Skaret *et al.*, 2005). However, avoidance reactions of the Norwegian spring spawning herring have been observed down to 150 m depth (Vabø *et al.*, 2002). With an average depth of 55 m and hypoxia/anoxia deeper than 70-100 m (e.g., Elmgren, 2001), avoidance might be a crucial factor effecting acoustic biomass assessments in the Baltic Sea. When avoiding a vessel, fish can try to escape by swimming either horizontally or vertically. In the first case, less fish would occur in the acoustic beam of the echo sounder and consequently registered fish biomass would be underestimated. In the second case, diving fish would shift their tilt angle (see above) and this would bias TS estimates. However, this bias is at least partly accounted for when the TS to fish length relationship is based on *in situ* data. Another possible explanation to low acoustic fish abundances compared to population model estimates, is that a considerable fraction of the stock is in the “blind zones” at the surface or close to the bottom (see below).

## Results from studies with a seabed-mounted inverted echo sounder

Attempts to study the behaviour of pelagic fish in their natural environment present many difficulties. Fish can seldom be visually observed without being disturbed, especially at night. Furthermore, fish often move over large waters, and can occupy different areas and depth layers over the diel cycle and seasons (e.g., Neilson & Perry, 1990; Fréon & Misund, 1999;

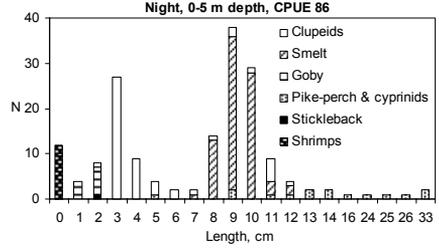
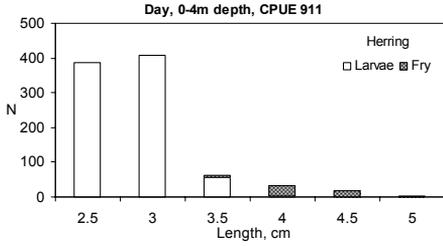
Fabi & Sala, 2002). Hydroacoustic techniques provide means to overcome some of these problems, but they also introduce complications concerning e.g. species identification, fish avoidance of research vessels, uncertainties related to fish behaviour, etc. However, using a seabed-mounted transducer minimizes possible fish avoidance or attraction reactions, and allows studies close to the sea surface and monitoring over extended periods of the time (e.g., Arrhenius *et al.*, 2000; Cech & Kubecka, 2002; Trevorrow, 2005).

In conventional, downward pinging acoustics, the transducer of the echo sounder is towed at the depth of 1-2 m or mounted on the ship's hull at depth of 2-6 m. For a technical reasons (the transducer near field), a range of 0.2-2 m from the transducer is excluded from the analysis. Therefore, there is an upper "blind zone" of 1.5-8 m. For other reasons, there is a blind zone above the bottom and the range of this zone depends on pulse length, beam width and bottom depth (Ona & Mitson, 1996). Conventional vertical acoustic assessment thus requires that the fish should be distributed from a few meters below the surface to a small distance off bottom (c.f. Fréon & Misund, 1999; see also Ona & Mitson, 1996). In our regular mobile surveys the upper blind zone is 2-3 m and the bottom blind zone is <1 m.

In paper II we presented a study with a seabed-mounted, upward pinging transducer. This study was addressed to determine the diel changes in pelagic fish behaviour and distribution, and how this influences acoustic estimates of fish biomass and size. Most of our results suggested that night-time acoustics are to be preferred. Patchiness was less at night, resulting in lower variation of acoustic backscattering ( $s_A$ ). The frequency of single fish echoes was also higher at night, which is valuable if TS values are used to determine the fish size distribution. The vertical distribution of fish was also more favourable at night, with fewer individuals in the blind zones close to the surface and close to the bottom. We estimated that about 9% of the total acoustic backscattering occurred in the upper 3 meters at night, but it was not clear to what extent backscattering might be influenced by wind-induced air bubbles in the surface layer (e.g., Dalen & Lovik, 1981).

The acoustic backscattering in the upper 3 meters is a relatively small compared to the integrated backscattering over the total water column, but it does not imply that the targets close to the surface are of limited significance for our understanding of the pelagic ecosystem. The targets close to the surface may represent different species or size classes. Mid-water trawling in the Himmerfjärden bay (Fig. 3) in the beginning of August showed that herring larvae (length >25 mm) were abundant in the upper layer (0-5 m), while at the same depth in late September we caught metamorphosed young-of-the-year (YOY) herring and sprat. Acoustic data from this depth interval

### 3 August, 2004



### 30 September, 2004

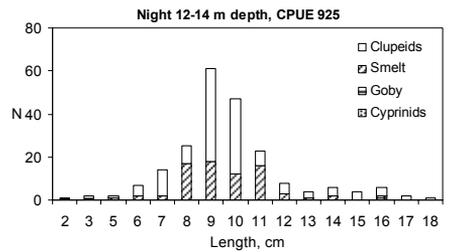
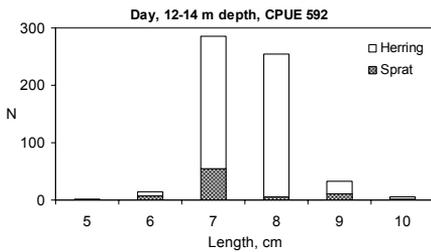
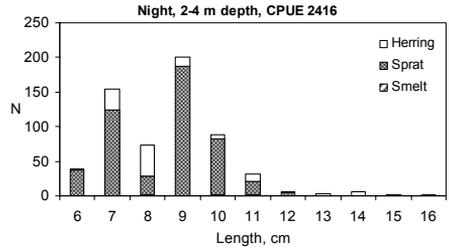
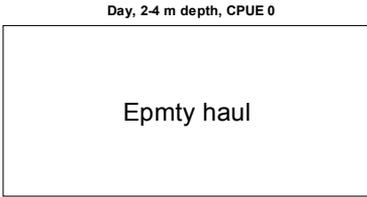


Figure 3. Species composition and length distributions in trawl catches from the Himmerfjärden bay.

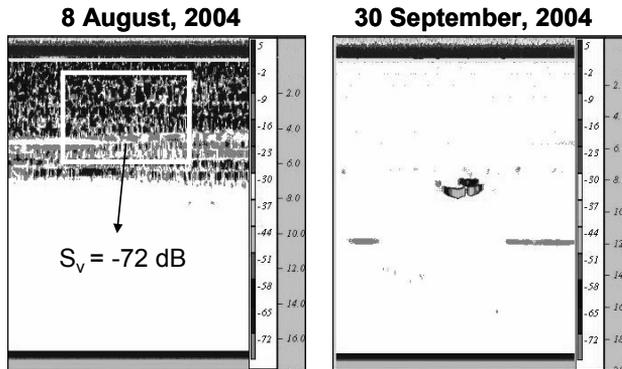


Figure 4. Example of echogram showing the layer with low volume back scattering strength ( $S_v$ ) and very few single echo detections, presumably formed by herring larvae on 8 August, 2004 (left panel). This layer was not observed in September (right panel).

in July-August (both day and night) showed a layer with a volume backscattering strength ( $S_v$ ) of  $-75 - -60$  dB and very few single echo detections (Fig. 4). I hypothesise that this backscattering was derived from larval herring that were too small to be efficiently detected as single echoes with our 70 kHz echo sounder. The acoustic data from September did not have this diffuse backscattering layer and no larval fish were caught in the trawl. Comparison of the day and night trawl hauls (Fig. 3) showed that herring larvae constantly remained at the surface layer through the diel cycle, whereas at night this layer was also invaded by their older conspecifics and other fish.

We observed day and night differences in the TS distribution of the tracked fish from 2001 and 2002 (Fig. 4 in Paper II). Similar differences were present in the August survey of 2004 (Fig. 5). In the late September survey 2004, day and night TS distributions were more alike, but still had a tendency towards weaker echoes at nights. The high TS peak of  $-58 - -59$  dB was registered at nights in July-August through all years resulting in bimodality of TS distributions. This peak was not that pronounced in the late September survey, but occurred both day and night (Fig. 5). These differences between day and night can have several explanations. They can originate from changes in the fish assemblage. They can also be caused by changes in fish behaviour over the diel cycle. Fish swimming speed is lower at night (Paper III) and if they are negatively buoyant, they may tend to swim with the head up to maintain depth and the tilt angle would then reduce their TS value (e.g., Huse & Ona, 1996).

Schooling is a salient characteristic of clupeids. Except for a period during the larval stage, all their life activities are conducted within schools

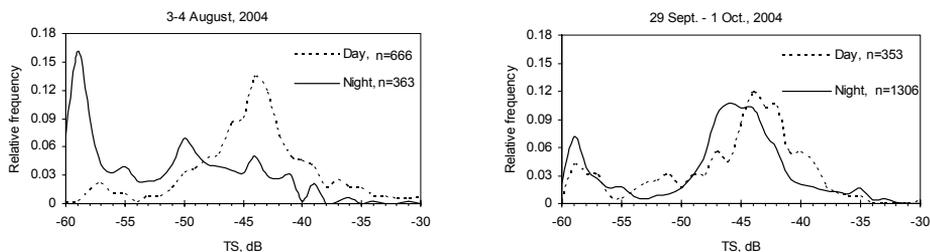


Figure 5. Relative frequency distribution of the mean target strength (TS; arithmetic mean grouped in 1 dB bins) from tracked fish. Data from August and September-October, 2004

(Blaxter & Hunter, 1982). At night-time, fish schools commonly disperse and extend in aggregations and layers. Apart from being a social assembly of fish in one particular area, such groupings display no strict coordination among individuals. Pitcher (1983) proposed that such fish aggregations should be termed “shoals”. Schooling has been identified as a problem for hydroacoustics for several reasons: it is statistically unfavourable due to large dispersion and skewness in the distribution function of collected data (Aglén, 1994), and it may result in acoustic “shadowing”, resulting in underestimated fish biomasses (Appenzeller & Legget, 1992). On the other hand, schools are easy to detect. Furthermore, the tilt angle distribution is supposed to become narrower and on average more horizontal when fish are schooling (day) and this is expected to result in higher average target strength (c.f. Fréon & Misund, 1999). However, at high fish densities the probability increases that echoes from several fish are misinterpreted as the echo from a single but larger fish (Sawada *et al.*, 1992; see also Gauthier & Rose, 2001). In paper II we showed that the processes of formation and disintegration of schools happened rapidly and coincided with day and night transition periods. In paper III we used Simpson’s evenness index to detect changes in vertical fish distribution patchiness, which is strongly influenced by schooling. Analysis of the index showed that the fish distribution became more even (fish entered night phase) on average two hours after sunset and it became more patchy (fish entered morning phase) on average about one hour before sunrise. If acoustic surveys are to be conducted during night conditions, this means at least for clupeids in our study area, that they should not start before two hours after sunset and should be completed at the latest one hour before sunrise.

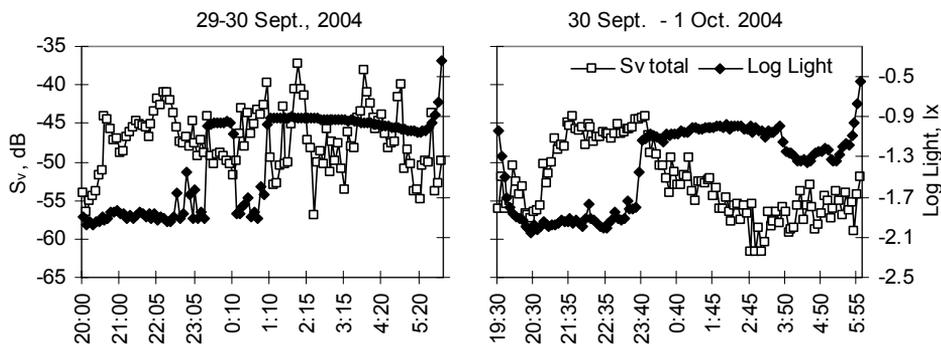


Figure 6. Effects of moon light at night (Log Light, lx) on volume backscattering strength ( $S_v$ , dB) in the depth layer 1-5 m.

## Light and fish activity

The changes in behaviour patterns can be referred to as activities, and the swimming of fish is one such obvious activity. Light is generally recognized as a critical cue that affects this and other activities (e.g., Helfman, 1993; Anras *et al.*, 1997). Light is sometimes even considered a top-down factor on marine pelagic food web structures, as it is crucial for the visual and selective foraging efficiency in many fish (Aksnes *et al.*, 2004). Clupeids usually perform diel vertical migrations, occurring closer to the surface at night. This can be related to a light intensity preference, but may also be initiated by changes in brightness (Blaxter & Hunter, 1982). It has even been reported that fish can change their vertical or horizontal distribution in response to the differences in night light intensity (moon phase, Luecke & Wurtsbaugh, 1993; Gaudreau & Boisclair, 2000).

We observed changes in fish vertical distributions and schooling in response to the diel light cycle (Papers II and III). On one occasion we also saw indications that the fish responded to a change in moonlight at night (Fig. 6). In the beginning of night, when there was no clear moonlight, fish formed quite a solid layer at 1-5 m depth. Later, when moon illumination increased, the concentration of fish decreased and the layer became more dispersed. However, this clear reaction was only observed on one night, while in the night before with similar moonlight conditions, the fish concentration in the surface layer was variable and showed no clear trend.

For most fish, the metabolic cost of swimming is substantial and must be accounted for in energy budgets (Krohn & Boisclair, 1994). In bioenergetics models this is often done by applying an activity multiplier to the respiration equation (Hanson *et al.*, 1997). At low latitudes, the seasonal

difference in day length is reasonably modest, but it increases with distance from the equator and can be considerable at high latitudes. For this reason, the activity multiplier in bioenergetics models may need to be modified when applied to fish at high latitudes (Van Tassell, 2002). Data on swimming speed are often obtained experimentally (e.g., Boisclair & Leggett, 1989; Hughes & Kelly, 1996), but it can then be difficult to account for the magnitude and variability of activity under natural conditions (Boisclair & Leggett, 1989). Such information can be obtained by direct *in situ* observations, although this is often difficult. Nonetheless, several studies have been published on fish activity measurements from *in situ* observations with video (e.g., Krohn & Boisclair, 1994), telemetry (e.g., Anras *et al.*, 1997; Thorstad *et al.*, 2004) and stationary hydroacoustics (e.g., Arrhenius *et al.*, 2000; Pedersen, 2001; Mehner, in press). In paper III we used acoustic tracking to estimate individual fish swimming speed and size (target strength). Swimming speed was different among all diel periods (day, night, dawn, dusk) and the highest (twofold) difference was observed between day and night. We developed regression models to investigate effects of fish size and environmental factors (water temperature, sea surface light intensity and *in situ* light intensity at the depth of the fish) on swimming speed. For all diel phases combined, the model explained 48% of the variation in swimming speed, with fish size, sea surface light intensity and temperature being the significant variables. In analyses of the different phases separately, fish size was always the most important variable. At night and in the morning, the sea surface light intensity was a better predictor of activity than the *in situ* light intensity at the depth at which the fish occurred. In contrast, the *in situ* light intensity explained more of the variation in swimming speed by day and in the evening than did the surface light intensity.

## Temporal and spatial distributions of fish

The temporal and spatial distribution of fish differs among species, and sometimes also between populations and life stages of a species (Fréon & Misund, 1999). The distribution of fish is governed by habitat selection or migration. A habitat is selected based on different quality aspects of a location, including physico-chemical factors, food availability, and the presence of the other animals (e.g. predators, competitors and suitable mates, Wootton, 1999). Changes in habitat selection occur and can be analysed on various scales in time (e.g. instantaneous, circadian, seasonal or interannual) and space (e.g. coastal – offshore, shallow – deep water, demersal – pelagic environment). The scale applied in a study may also influence the results (e.g., Maravelias & Haralabous, 1995). Factors that influence habitat selection can be divided in ultimate (long-term, functional) and proximate

(short-term, immediate response, causation) cues (Noakes, 1992), of which mainly the latter are in focus here.

Habitat selection and migrations are crucial in understanding fish distribution and ecology at individual, species and community levels, but they are also of primary interest in fish stock assessment and management because they are key factors for the identification of stock units in relation to the exploitation (Fréon & Misund, 1999). Fish, especially pelagic species, live in a three-dimensional environment, which to fish is much more heterogeneous than it may appear to humans. Generally, the most important abiotic factors believed to determine distributions are light intensity, temperature, oxygen, salinity, currents, bottom depth and nature of the seabed. Among corresponding biotic factors are food availability, presence of predators and differences in the physiological requirements of different life stages. It is thus relevant to study fish habitat selection and migrations in both horizontal and vertical perspectives. Some factors may influence both horizontal and vertical distributions, while other factors are relevant mainly for the distribution along one spatial dimension.

Fish are generally ectotherms, but they are able to thermoregulate by selecting areas of favourable water temperature (e.g., Batty, 1994). Most pelagic fish can detect temperature variations smaller than 0.1° C, which allows them to orientate towards areas favourable to their metabolism or to detect remote thermal fronts where prey may be more abundant (c.f. Fréon & Misund, 1999). The distribution and movements of prey are often considered the major factors that determine the vertical distribution of fish. The thermocline may act as a limiting factor (barrier) for vertical habitat selection (Perry & Neilson, 1988; Swartzman *et al.*, 1994, 1995). However, the significance of the thermocline may vary depending of other environmental factors, such as absolute temperature, prey density, distance to the bottom, etc. (e.g., Ciannelli *et al.*, 2002; Swartzman *et al.*, 2002; Gray & Kingsford, 2003).

In paper IV we studied vertical and horizontal fish distributions from late spring to autumn, and related spatial patterns to water temperature, wind conditions and fish size. Data were collected biweekly at night, for two consecutive years. These kinds of data give instantaneous pictures of fish distributions at night, but naturally provide no information on possible diel migrations or distributions during the major daylight feeding period. In late spring and beginning of summer, before the thermal stratification, fish of all sizes occurred predominately close to the surface, where water temperature was higher than in the deeper water mass. During the summer stratification, most of the larger fish moved deeper, while small fish remained in the upper layers. In the autumn, after the disintegration of the thermocline, the small fish moved somewhat deeper, while larger fish dispersed more or less over the whole water column. The summer vertical distribution was probably

governed by different thermal preferences of small and larger individuals, as well as predator avoidance and feeding conditions for those that were able to feed at night. In addition to these factors, seasonal differences in vertical distributions were probably also influenced by spawning migrations and the growth of YOY individuals (Axenrot & Hansson, 2004). Although fish schools were generally absent at night, there was substantial patchiness in the horizontal distribution. We were unable, however, to identify annual or seasonal trends in the distributions of patches, neither could we explain the locations of patches from wind data.

## Future perspectives

Applying the new target strength to fish size relationships (see Table 1) in acoustic assessments of herring biomass, at least in the Baltic Proper, would result in considerably lower estimates and substantial differences in stock size compared with estimates obtained through virtual population modelling (XSA). This would complicate the practical management of the fishery. However, if the acoustic estimates are correct, then herring stock size is much smaller than assumed today, and the fishing intensity much higher, making the risk for serious overfishing imminent. It is thus important that we understand why there is such big difference between acoustic and modelled stock size. It is known that the ability of fish to avoid ships can bias acoustic biomass estimates (Fréon & Misund, 1999), in particular in shallow waters, such as the Baltic Sea (e.g., Vabø *et al.*, 2002). Therefore, we need better understanding of the reactions of fish to approaching research vessels.

In papers III and IV we discussed fish distributions in relation to various abiotic and biotic factors. Some of the environmental parameters, such as water temperature, salinity, etc. are relatively easy to measure. However, assessments of prey densities (e.g. mysids and zooplankton) and the temporal and spatial variation in these densities are usually much more complicated and time demanding. Because of this, really adequate data on prey densities are often limited. During my PhD studies, my colleagues and I made some efforts to assess mysid densities with hydroacoustics (using two frequencies, 70 & 200 kHz), but due to technical constraints and time limitation it was not possible to finish this work. I hope that rapid development of hydroacoustic techniques and post-processing software will provide us with the means required to quantify not only fish, but also the pelagic invertebrates that constitute the basis for most of the higher trophic levels in marine ecosystems.

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