

Diel spatial distribution and feeding activity of herring (*Clupea harengus*) and sprat (*Sprattus sprattus*) in the Baltic Sea

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Abstract

We analysed Baltic Sea pelagic fish (herring and sprat) spatial and temporal distribution, size distribution at different depths and time of the day and diel feeding pattern. In 1995 the study area was investigated by acoustic survey for 3 d, 3, 4 and 11 October, to investigate spatial and temporal distribution of pelagic fish. The area was divided in four different transects forming a survey quadrat of 15 nautical miles of side. The survey quadrat was ensonified each day four times in the 24 h. In 1997 the acoustic survey was conducted in the same area and in the same week of the year to analyse the diel feeding cycle of herring and sprat and their size distribution by depth and time of the day using pelagic trawls. Fish abundance, from 1995 survey, was statistically different among days and survey quadrats. However, from our data it is not clear whether the variation stems from random dispersion or directed movements occurring at the temporal small-scale. Pelagic fish were dispersed during the night at the surface and aggregated during the day at the bottom. They aggregated at dawn and dispersed at dusk at the surface. For herring this distribution pattern coincided with peaks of stomach fullness analysed in the 1997 survey, while sprat seemed to continue feeding during the whole day time. Larger herring were deeper in the water column than smaller individuals. Diel vertical migrations (DVM) of pelagic fish likely mirrored zooplankton diel vertical movements and it was reasonably in response to optimal predation conditions in the sea and possibly intertwined with predation avoidance and bioenergetic optimisation.

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Keywords: Baltic Sea; Pelagic fish; Diel vertical migrations; Diel aggregation patterns; Feeding activity

1. Introduction

Schooling behaviour is dependent on different environmental and physiological factors among which feeding and anti-predation risk represent crucial cues (Ona, 1990; see Pitcher, 1993 for a review). However, although spatial and temporal dynamics of fish school structure have been widely investigated in the past, most of the studies referred to tank or aquaria experiment (see Pitcher, 1993 for a review) while analyses in the field are limited (Hansson, 1993; Fréon et al., 1993, 1996; Torgesen et al., 1997; Orłowski, 1998, 1999, 2000; Stokesbury et al., 2000). In the last 30 years, the increased use of hydroacoustic surveys for stock assessment (MacLennan and Simmonds, 1992) has widened the possibility of spatial and temporal structure investigation of pelagic fish in the open sea. The general view is that pelagic fish

are highly dispersed at night and aggregated during the day (Blaxter and Holliday, 1969; Hansson, 1993; Fréon et al., 1996). Azzali et al. (1985) defined a model to describe the distribution of pelagic fish during dawn and dusk, arguing that fish disperse rapidly at dusk and aggregate slowly at dawn. This general result has been challenged by Fréon et al. (1996) who observed an opposite pattern analysing data from acoustic survey in the Mediterranean Sea.

Diel vertical migration (DVM) is behaviour common to both invertebrate and vertebrate aquatic organisms (e.g. Lampert, 1989; Levy, 1990a, b; 1991; Steinhart and Wurtsbaugh, 1999). Three major hypotheses (foraging, bioenergetics and predator avoidance) explain the adaptive significance of DVM in pelagic fish. They predict that either they would mirror prey daily movements (i.e. foraging), select water temperature (i.e. bioenergetics) in order to maximise their growth rate (Levy, 1990a, b; Wurtsbaugh and Neverman, 1988; Neverman and Wurtsbaugh, 1994) or reduce to a minimum the exposure to predators (i.e. predator avoidance) (Levy, 1987, 1990b; Clark and Levy, 1988). However, stud-

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ies on the vertical and horizontal structure of pelagic fish schools over the 24-h relating DVM with feeding behaviour in the marine environment are, to our knowledge, scarce in the literature (e.g. Blaxter, 1985), limited to tank experiment (Sogard and Olla, 1996) and lacking for the Baltic Sea.

Nevertheless, inferences on DVM of pelagic fish related to foraging may be done from lakes where DVM by zooplankton has been extensively studied (Levy, 1990a, b, 1991; De Stasio, 1993; Allison et al., 1996; Steinhart and Wurtsbaugh, 1999). Allison et al. (1996) showed peaks in feeding activity of pelagic fish (cichlids) at dawn and dusk in the Lake Malawi related to the DVM of their prey, i.e. zooplankton. Levy (1990b) and Stockwell and Johnson (1999) evaluated the relative importance of different factors explaining DVM of salmon in lakes arguing that a multifactor hypothesis (foraging, bioenergetics and predator avoidance) provided the most realistic explanation of the adaptive significance of DVM in pelagic fish.

The Baltic Sea pelagic ecosystem is constituted by the top-piscivores cod (*Gadus morhua*) and the major pelagic planktivores, herring (*Clupea harengus*) and sprat (*Sprattus sprattus*). Nekton is represented essentially by *Mysis* sp. while zooplankton is dominated by calanoid copepods, but cladocerans and rotifers can be abundant (Rudstam et al., 1994). Hansson et al. (1990) investigated DVM of zooplankton (occupying the deeper and darker water during the day and the upper water column in the night) in the Baltic Sea arguing that this phenomenon was essentially explainable by anti-predation behaviour.

In this paper we investigated pelagic fish (herring and sprat) (a) horizontal movements at the temporal small-scale (data from 1995 survey), (b) DVM and degree of aggregation (data from 1995 survey) and (c) size distribution at different depth and time of the day and diel feeding pattern (data from 1997 survey).

2. Materials and methods

2.1. Surveys design and collection of data

2.1.1. Survey 1995

In October 1995 an acoustic survey was conducted onboard the Swedish research vessel "Argos" in an area south of the Bornholm depth in the southern part of the Baltic Sea (Fig. 1). The 1995 survey was used to estimate the diel spatial distribution of pelagic fish. Recordings of acoustic data of fish were made by SIMRAD EK400 and EK500 38 kHz split-beam echo-sounders. These data were supplemented with geographical position from Global Positioning System in terms of geographical co-ordinates (latitude and longitude). The echo integrator data were collected from 10 m below the sea surface (transducer at 8 m depth) to 1 m above the seabed. Data were recorded using the Simrad BI500 software package on a SUN Sparc IPC computer and stored on DAT tapes. The echo sounder provides a mean integrated value for each 0.1 nautical mile (nm; 1 nm = 1.852 km).

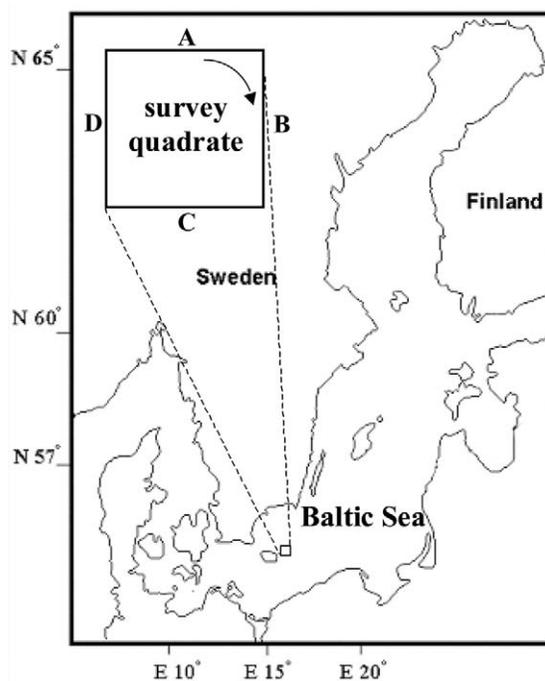


Fig. 1. Study area and sampling design during the 1995 survey. The survey quadrat, constituted by four transects (A–D), was ensounded four times each day (3, 4 and 11 October).

The area investigated was divided in four transects forming a survey quadrat of 15 nm per side (Fig. 1). The survey quadrat was ensounded four times during the 24-h (0–6, 6–12, 12–18, 18–24 h) with a standard vessel speed of 10 knots. The survey was conducted for 3 d on the 3, 4 and 11 October. During the experiment weather conditions were good with a stable high-pressure and variable wind, sunrise was at 05:00 UT (Universal Time) and sunset at 16:30 UT. All the hours mentioned in this study refer to UT. The moon was in its first increasing quarter. The area was chosen because of a high concentration of fish as estimated by the acoustic device. Profiles of water temperature ($^{\circ}\text{C}$), salinity (psu) and oxygen (ml l^{-1}) content were recorded at 0, 2.5, 5, 10, 15, 20, 30, 40, 50, 60, 70 and 80 m depth using a CTD (Conductivity Temperature Depth) probe.

2.1.2. Survey 1997

In the 1997 an acoustic survey was conducted onboard the Swedish research vessel "Argos" in the same area and in the same period of the year as in the 1995 survey (Fig. 1). The 1997 survey was conducted to estimate the diel feeding cycle of pelagic fish (herring and sprat) and analyse their species and size distribution by depth and time of the day. Individuals of herring and sprat were collected during the 24-h in 3 d using a pelagic trawl net. Fishing was performed with two different pelagic trawls (14–17 m vertical opening; 21 mm stretched mesh size in the cod-end). Size-selectivity of the two trawls used was not statistically different (Bethke et al., 1999). Standard fishing speed was 3–4.5 knots and hauls lasted for approximately 30 min (Bethke et al., 1999). Catches were sorted at species level and a sub-sample of

300 herring and 200 sprat individuals for each haul was measured (total length) to the nearest 0.5 cm for length-frequency distribution analysis. Individual fish were immediately frozen onboard and then processed in the laboratory. A random sample of about 100 herring and 50 sprat for each haul was collected for feeding analysis. In the laboratory, each fish collected was measured (total length) to the nearest 0.5 cm and weighed to the nearest 0.1 g and the stomachs investigated for fullness. A simple approach to calculate feeding cycle in the field is to estimate the proportion of fish with food in the stomach during the 24-h. It simply requires an estimate of the percentage of empty stomachs randomly collected. The effort to collect the data is irrelevant in comparison with other models, particularly when dealing with big sample areas such as the marine environment (Bromley, 1994).

3. Statistical analysis

3.1. Survey 1995. Spatial distribution of fishes during the 24-h

Processed S_a values were used as an index of fish abundance in the sea. In the southern Baltic Sea, herring and sprat constitutes more than 97% of the pelagic fish biomass (Orlowski, 2001). Therefore, the estimated S_a values were assumed to reflect essentially the biomass of herring and sprat and were used as an index of pelagic fish density in the sea. S_a values were transformed ($\ln S_a + 1$) to conform to assumptions of homogeneous variance, normality and linearity (Sokal and Rohlf, 1995). Data were divided into four depth strata (10–20, 21–40, 41–60, 61–80 m) and fish abundance at the different depth strata during the 24-h was compared using Variance Components Analysis and Factorial ANOVA in Statistica computer package (Statistica, 1995). HSD post-hoc tests (Sokal and Rohlf, 1995) were used for mean comparisons. To define changes in degrees of fish aggregation among different hours and depth strata we used the coefficient of variation (CV %) among point estimates of fish abundance as an index (Hilborn and Mangel, 1997). We assumed that when fish are dispersed the variance should be the lowest and when fish are highly aggregate the largest.

3.2. Survey 1997. Diel feeding cycle and species/size distribution of pelagic fish

We estimated the length–frequency distributions of herring and sprat and the proportion of the two species in the catch during the day (05:30–16:30) and night (17:30–04:30) at the surface (10–40 m) and at the bottom (41–80 m). Kolmogorov-Smirnov tests (K-S test) (Sokal and Rohlf, 1995) were used to compare length–frequency distributions. The significance level was set at 5% for all the statistical tests used in the analyses.

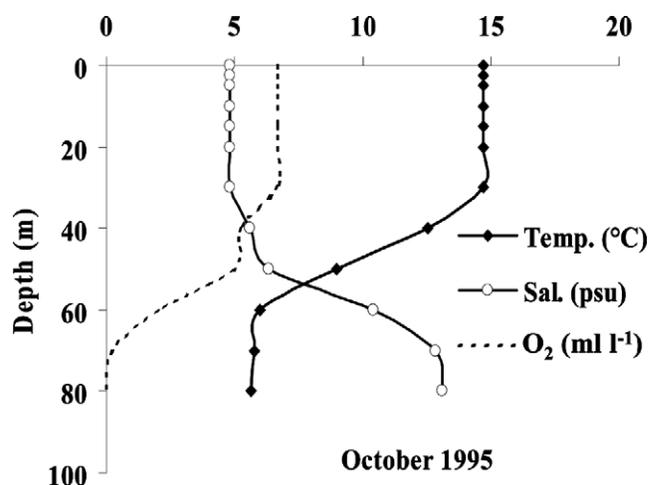


Fig. 2. Depth profiles of temperature, salinity and oxygen content in the study area during the 1995 survey.

4. Results

4.1. Survey 1995. Spatial distribution of fishes during the 24-h

Profiles of water temperature (°C), salinity (psu) and oxygen (ml l⁻¹) content are shown in Fig. 2. A thermocline occurred between 30 and 50 m, salinity was between 5–6 psu down to 40 m and increased to 13 at 80 m depth. Oxygen values were comprised between 6 and 7 ml l⁻¹ within 0–40 m decreasing to 0 ml l⁻¹ at 70 m depth. Overall, distinct variability was observed in both the horizontal and vertical distribution of fish abundance in space and time. Variables ‘day’ and ‘survey quadrat’ and their first interaction term significantly contributed while variable ‘transect’ did not contribute to explain the total variance of fish abundance during the experiment (Table 1). Fish abundance was significantly different among days (HSD-test), although without a defined pattern (Fig. 3). An increase in fish abundance occurred between the first (October 3) and the second day (October 4) followed by a significant decrease (HSD test; $P < 0.05$) in the third day (October 11) in all the different transects except in D. Here the difference between the second and third day was not significant (HSD test; $P > 0.05$). Fish abundance differed significantly (Table 1) also between different survey quadrats among days and transects but without a well-defined trend during the 24-h (Fig. 3).

The contribution of the variable ‘time’ to the total variance was not significant for any of the 3 d while ‘depth’ and ‘depth × time’ interaction term contributed significantly to the total variance (Table 1). Therefore, we used the 24-h as a single transect testing for diel differences in fish abundance at the different depth strata. Differences in fish abundance occurred among different depth strata during the 24-h (Table 1). Fishes were most abundant between 41 and 80 m (i.e. the deeper part of the thermocline) during the day (HSD test; $P < 0.01$). During the afternoon they migrated to the upper layer (10–40 m) and reached the largest values at the surface

Table 1

Results of Variance Components Analysis and Factorial ANOVA of the 1995 acoustic survey data. d.f. = degrees of freedom; MS = mean square; *P* = probability level, ns (not significant) = *P* > 0.05. {*n*}·{*n_x*} is the interaction factor between the different variables tested

All days	d.f. effect	MS effect	d.f. error	MS error	<i>F</i>	<i>P</i>
{1}day	2	54.9	8.0	10.3	5.34	<0.05
{2}survey quadrate	3	17.4	9.2	4.5	3.86	<0.05
{3} transect	3	5.3	8.0	10.0	0.53	ns
{1}·{2}	6	2.9	18.6	1.0	2.81	<0.05
{1}·{3}	6	8.4	18.0	1.0	8.39	<0.01
{2}·{3}	9	2.6	18.0	1.0	2.64	<0.05
{1}·{2}·{3}	18	1.0	6979.0	0.2	6.57	<0.01
October 3						
{1}time	23	25.5	79.6	106.6	0.24	ns
{2}depth	4	407.0	78.8	72.4	5.62	<0.01
{1}·{2}	79	69.0	12038.0	2.1	33.58	<0.01
October 4						
{1}time	23	37.0	80.1	122.9	0.30	ns
{2}depth	5	711.1	78.9	70.7	10.06	<0.01
{1}·{2}	78	86.0	12797.0	2.1	40.72	<0.01
October 11						
{1}time	23.0	12.3	81.7	20.9	0.59	ns
{2}depth	5.0	210.7	78.1	14.4	14.63	<0.01
{1}·{2}	78.0	14.6	11232.0	0.4	38.22	<0.01

(10–20 m) (i.e. above the thermocline), during the night (Fig. 4). Fish abundance in the upper stratum (10–20 m) was larger during the night when compared with deeper strata (HSD test; *P* < 0.01) except in October 3.

The coefficient of variation (CV %, considered as an index of fish aggregation) among point estimates of fish abundance increased sharply at dawn reaching the highest values during

the day. The CV % decreased after 14 h reaching the minimum values at night. This trend was common to all 3 d examined (Fig. 5). CV % was always larger in the upper layer (10–40 m) compared to the deeper layer (41–80 m) (ANOVA; *P* < 0.05) while no significant differences were detected within the upper (10–20 vs. 21–40 m) and the deeper (41–60 vs 61–80 m) layers (ANOVA; *P* > 0.05) (Fig. 5).

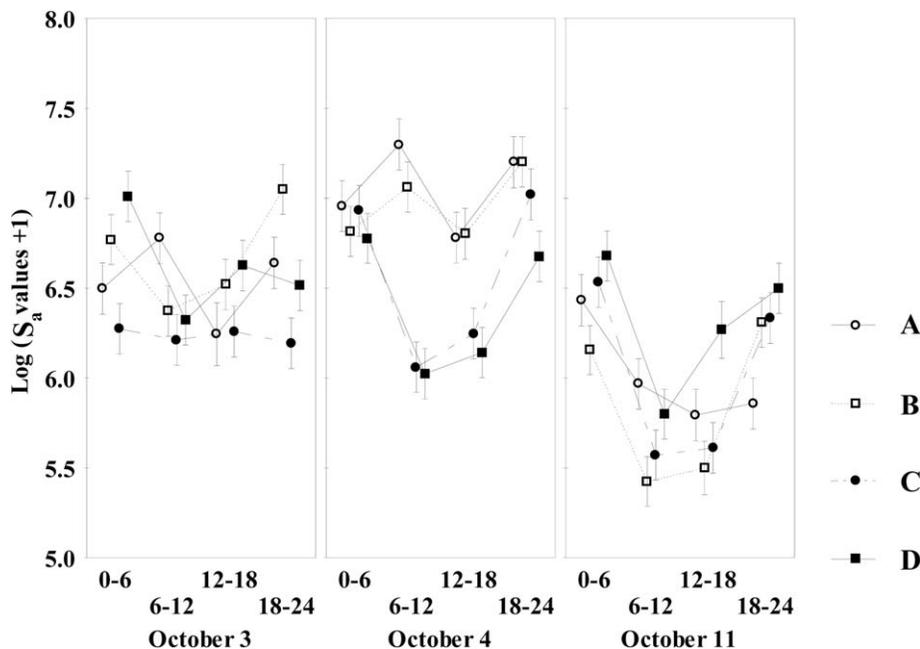


Fig. 3. Log transformed *S_a*-values estimated for the four transects (A–D) constituting the survey quadrate. The survey quadrate was ensouffled four times during the 24 h (0–6, 6–12, 12–18, 18–24 h) for 3 d during the 1995 survey.

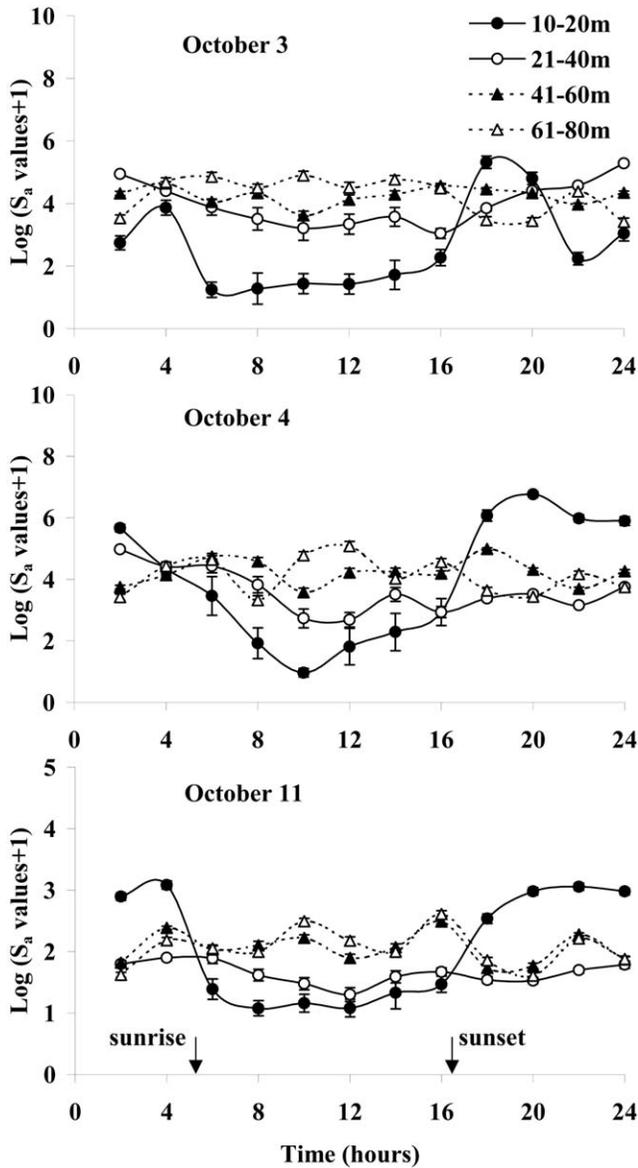


Fig. 4. Log transformed S_a -values (divided in four depth strata) estimated for 3 d over the 24 h during the 1995 survey.

Fig. 6 shows the degree of fish aggregation and dispersion as visualised by the echograms at dawn (a), during the day (b), at dusk (c) and during the night (d).

We also calculated the rates of change (increase or decrease) of CV % during the 4-h preceding (4–7 h) and following (16–19 h) the peaks of maximum aggregation (7 and 16 h, respectively). The rate of change (δ) of the CV % was calculated as:

$$\delta = \frac{cv_{1st} - cv_{4th}}{cv_{4th}}$$

where cv_{1st} is the first hour of the dawn (4 h) and dusk (16 h), and cv_{4th} is the last hour of dawn (7 h) and dusk (19 h).

The results of this analysis showed that δ was always larger (ANOVA; $P < 0.05$) at dawn compared to dusk in all days analysed (Fig. 7).

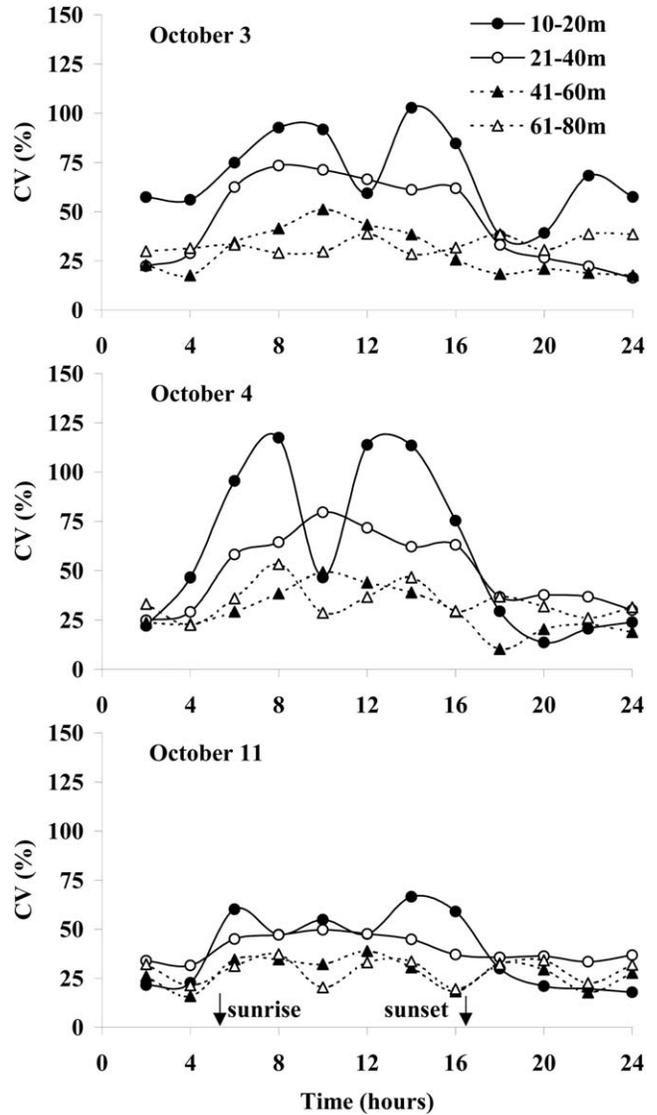


Fig. 5. Coefficient of variation (%) of log transformed S_a -values (divided in four depth strata) estimated over the 24 h for 3 d during the 1995 survey. High and low coefficient of variation (%) indicate fish aggregation and fish dispersion, respectively.

4.2. Survey 1997. Diel feeding cycle and species/size distribution of pelagic fish

The analysis of echograms showed in 1997 the same DVM pattern of pelagic fish as described for the 1995 survey (see section above) (data not shown). This pattern is common to all the other surveys conducted in the study area since 1979 (Nils Håkansson, pers. comm.).

Trawl stations data and percentages of herring and sprat in the catches are presented in Table 2. When comparing length–frequency distributions of herring and sprat during day and night at two different depths, herring length–frequency distributions were statistically different both during day and night. Larger herring individuals were more abundant at the bottom compared to smaller individuals (K-S test; $P < 0.05$) (Fig. 8a). On the other hand, sprat did not show any

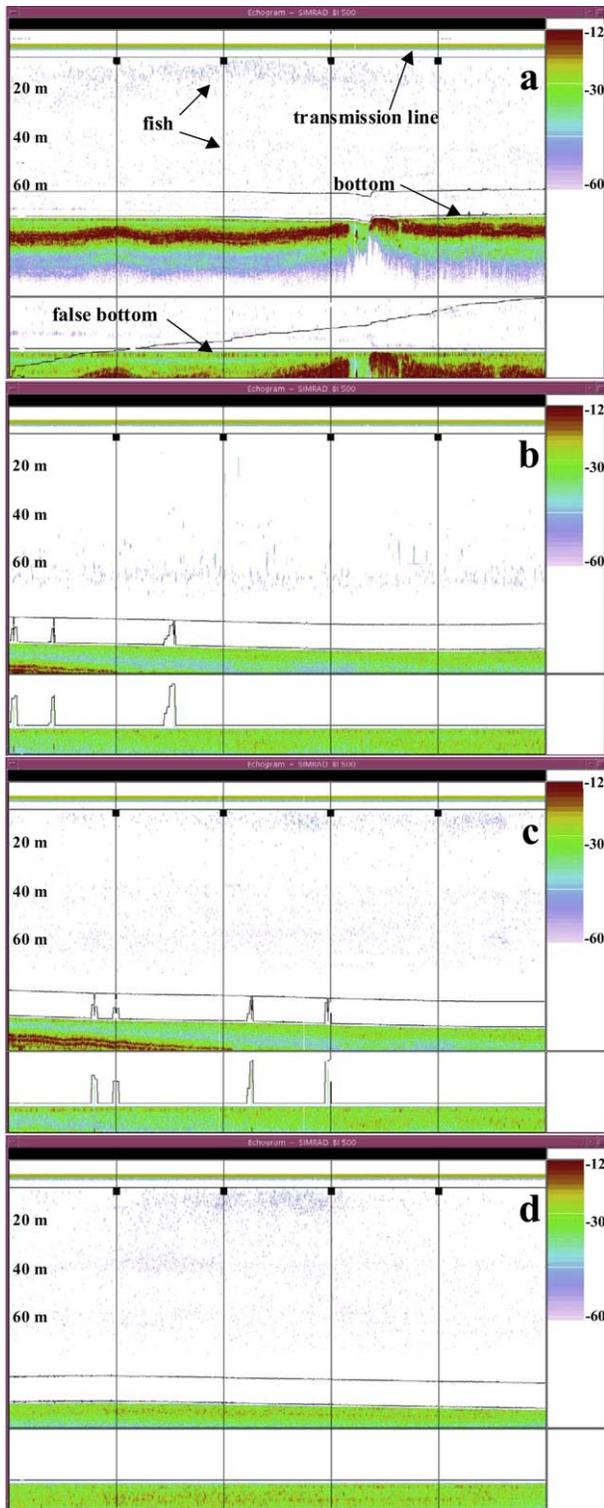


Fig. 6. Echograms of fish vertical distribution recorded during the 1995 survey at different time of the day: (a) dawn, (b) day, (c) dusk and (d) night. The colour scale on the right side of the echograms indicates the strength of the echoes. Red and blue colours indicate strong and weak echoes, respectively. The transmission line corresponds to the depth of the transducer (8 m).

statistical difference in length–frequency distribution at different depth either during the day or night (Fig. 8b).

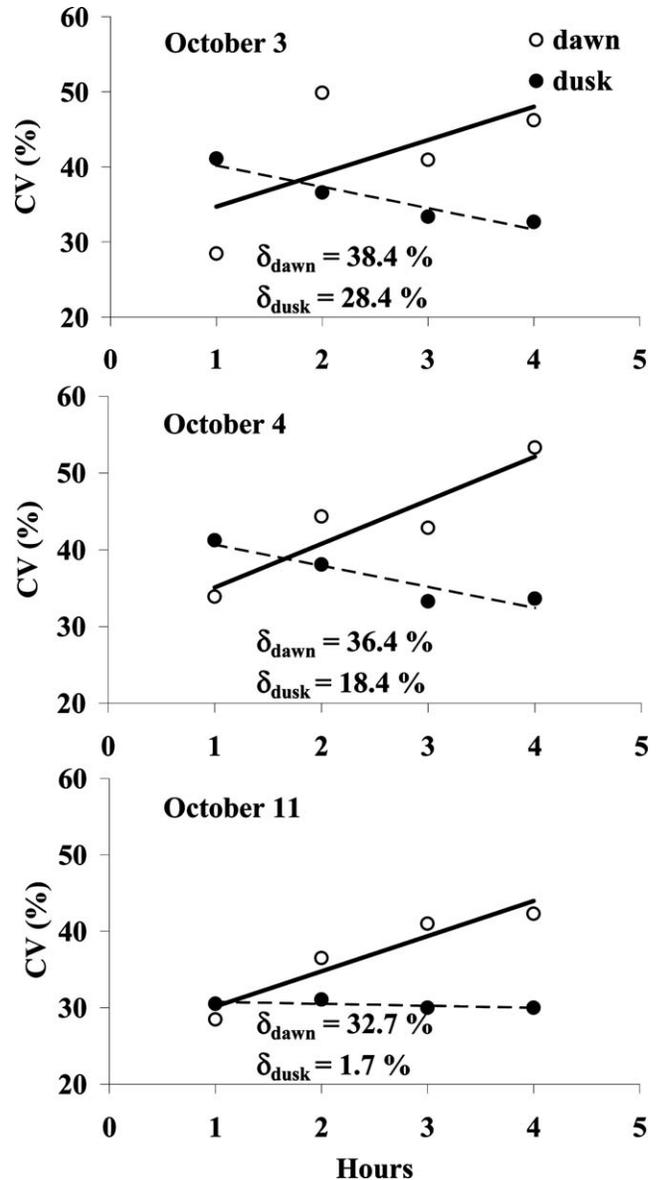


Fig. 7. Changes in the coefficient of variation (%) of log transformed S_a -values estimated during the 4h preceding (4–7) and following (16–19) the peaks of maximum aggregation estimated during the 1995 survey. High and low rate of change (δ) indicate rapid and slow fish aggregation (dispersion), respectively.

There was no statistical difference in the proportion of herring in the pelagic catch at different depth (surface and bottom) during either the day (one-sided test; $n_{tot} = 20$; $P = 0.46$; % herring = 26.31 and 28.36 at the surface and bottom, respectively) or night (one-sided test; $n_{tot} = 12$; $P = 0.21$; % herring = 29.26 and 54.58 at the surface and bottom, respectively). However, a larger proportion of herring was always present at the bottom both during the day and night.

Fig. 9 shows the proportion of herring and sprat individuals with food in the stomach during the 24-h. There were two peaks for herring, at dawn (~95%) (between 5 and 7 h) and at dusk (~60%) (between 16 and 18 h). The largest proportion of herring with empty stomachs was between 11 and 13 h. The data for sprat showed a peak during the morning (be-

Table 2
Summary of the 1997 trawl stations data. Only herring and sprat were considered in the catch analysis

Date	UT	Haul			Wind		Trawl data			Proportion in the catch		
		Latitude	Longitude	Bottom Depth (m)	Direction	Streight (m s ⁻¹)	Mean depth (m)	Duration (min)	Speed (knot)	Herring	Sprat	
											(Wet weight)	
970930	1526	633	N 56°28'	E 16°45'	58	N	4	42	29	3.9	0.27	0.73
970930	1721	634	N 56°27'	E 16°45'	58	N	9	45	19	4.0	0.07	0.93
970930	1948	635	N 56°22'	E 16°45'	60	NNW	7	35	14	3.9	0.20	0.80
970930	2103	636	N 56°22'	E 16°45'	60	NW	7	33	15	4.1	0.51	0.49
971001	1015	644	N 55°56'	E 17°03'	46	E	4	36	29	4.0	0.12	0.88
971001	1224	645	N 55°55'	E 17°09'	47	Var.	2	37	29	4.0	0.17	0.83
971001	1628	646	N 55°48'	E 16°31'	57	SW	4	37	30	3.8	0.31	0.69
971001	1753	647	N 55°47'	E 16°27'	57	SW	6	48	30	3.8	0.44	0.56
971002	1053	648	N 55°40'	E 14°29'	50	WNW	6	40	30	4.1	0.52	0.48
971002	1224	649	N 55°40'	E 14°29'	50	WNW	16	40	31	4.0	0.47	0.53
971002	1442	650	N 55°35'	E 14°36'	70	NW	15	53	30	3.8	0.76	0.24
971002	1619	651	N 55°35'	E 14°36'	70	NW	16	55	31	3.8	0.79	0.21
971002	2332	652	N 55°57'	E 15°24'	47	N	13	34	30	3.9	0.37	0.63
971003	0104	653	N 55°58'	E 15°24'	47	N	13	35	30	3.9	0.23	0.77
971006	1422	654	N 55°57'	E 15°23'	47	SSW	3	39	31	3.7	0.03	0.97
971006	1620	655	N 55°57'	E 15°22'	47	SSW	3	40	30	4.0	0.04	0.96
971006	2201	657	N 55°33'	E 15°03'	84	SW	4	37	30	3.8	0.17	0.83
971006	2326	658	N 55°33'	E 15°03'	84	SW	2	34	31	3.8	0.15	0.85
971007	0758	659	N 55°23'	E 15°20'	90	SSE	6	64	30	3.8	0.36	0.64
971007	0933	660	N 55°23'	E 15°21'	90	SE	7	71	30	3.7	0.26	0.74
971007	1111	661	N 55°21'	E 15°25'	92	SSE	7	64	30	3.5	0.13	0.87
971007	1233	662	N 55°21'	E 15°25'	92	SSE	7	66	30	3.4	0.24	0.76
971007	1855	664	N 55°28'	E 15°04'	75	SSE	5	57	30	4.5	0.05	0.95
971008	1855	665	N 55°36'	E 14°44'	75	W	7	22	30	3.6	0.10	0.90
971008	1106	666	N 55°36'	E 15°10'	75	WSW	10	60	30	3.7	0.29	0.71
971008	1331	667	N 55°35'	E 15°10'	75	WSW	7	54	30	3.7	0.26	0.74
971008	1854	668	N 55°30'	E 15°03'	76	SW	6	36	30	3.8	0.09	0.91
971009	0554	669	N 55°29'	E 15°02'	85	SW	8	61	30	3.5	0.12	0.88
971009	1801	670	N 55°28'	E 15°05'	75	SW	11	58	30	3.6	0.14	0.86

tween 8 and 10 h) and a minimum during the night. Differently from herring, a large proportion of sprat stomachs contained preys during the day-time. The proportions of sprat full stomachs were point estimates; therefore standard errors were not available.

5. Discussion

Acoustic techniques represent a powerful method to detect and estimate the abundance of fish in the sea (MacLennan and Simmonds, 1992). However, they present a number of important limitations to acknowledge when discussing results from acoustic surveys. One important problem is that when fish occurs in dense concentrations, non-linear effects may bias the accuracy of abundance estimates (MacLennan and Simmonds, 1992; Fréon et al., 1996; Orłowski, 2000). Differences between night and day estimates have been reported (e.g. Aglen, 1983; Unger and Brandt, 1989; Amin and Nugroho, 1990; Schalk et al., 1990) and they were plausibly due to the high degree of patchiness of pelagic fish during the day (Orłowski, 1999, 2000). Usually, in order to exclude or reduce the contribution of horizontal migration to the variation of fish abundance, the surveyed area is limited to a single

transect and the experimental time to some days. Hansson (1993) has shown, in a limited study area, that total fish abundances estimated with acoustic survey indicated no large-scale immigration or emigration between the study area and the surroundings. Our data showed that pelagic fish abundance was significantly different for different survey quadrates and days (temporal small-scale) but not for different transects (spatial small-scale). Moreover, no defined trend in pelagic fish abundance was present among days. Therefore, from our data it is not clear whether the variation stems from random dispersion or directed movements occurring at the temporal small-scale. Differences in fish abundance among survey quadrates could be due to bias in the S_a estimates caused probably by the non-linearity effect at different degrees of fish aggregation or by depth dependence of S_a estimates (Ona et al., 2001).

Hence, the lower values of fish abundance occurring during the day-time in some of the days and transects may be partially due to the high degree of fish aggregation as confirmed by the trend of the coefficient of variation among points estimates (a proxy for fish aggregation). On the other hand, when analysing the diel variation of pelagic fish abundance at the different depth strata, the contribution of the

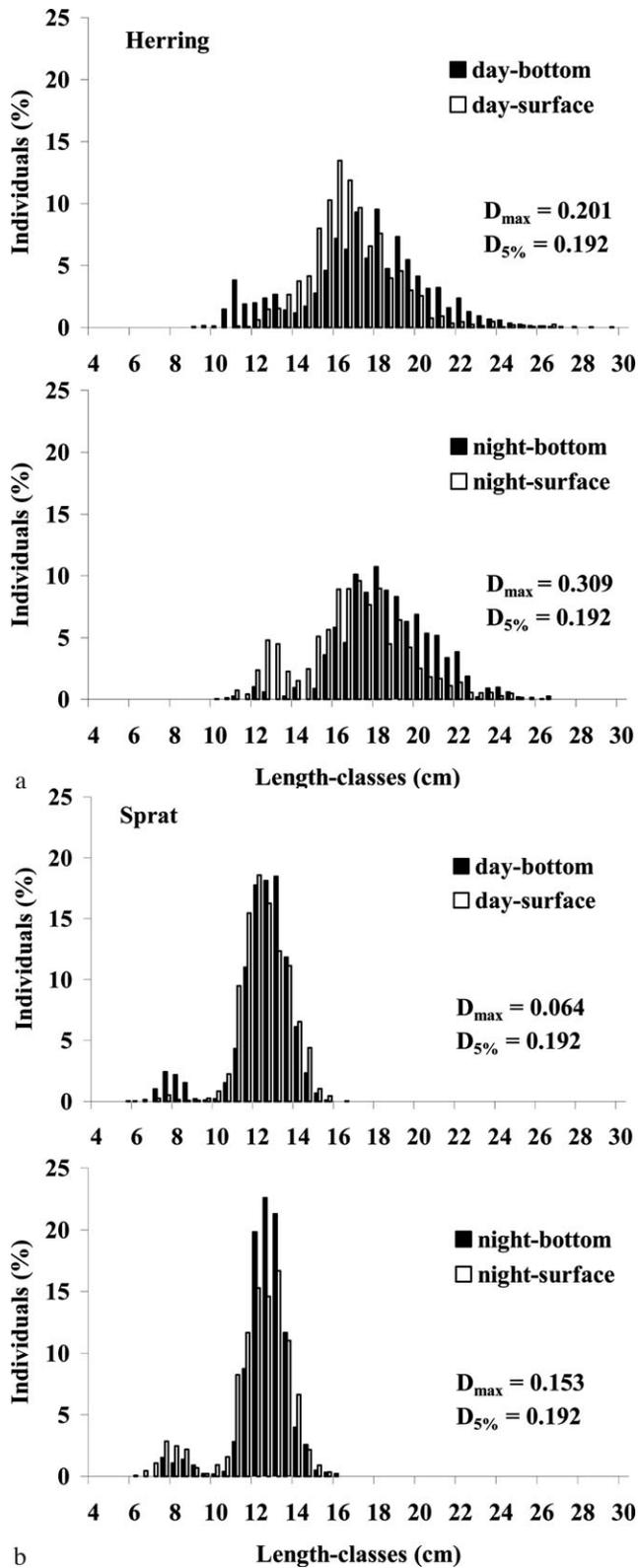


Fig. 8. Length–frequency distribution of herring (a) and sprat (b) during the day and night at the bottom and surface during the 1997 survey.

variable ‘time’ to the total variance was not significant for any of the 3 d. Therefore, although being aware of technical problems behind S_a values estimates, we assumed that diel

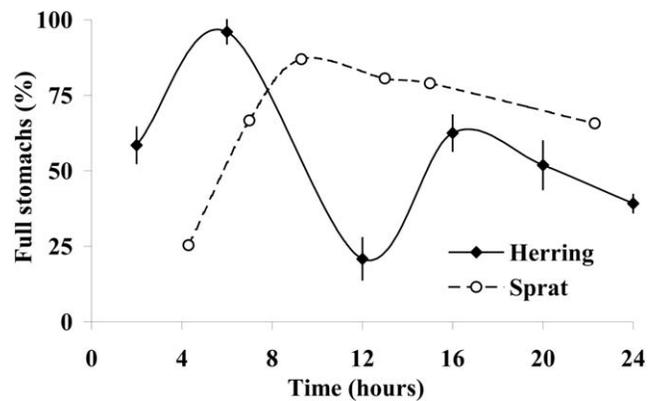


Fig. 9. Daily patterns of full stomachs (%) of herring and sprat sampled during the 1997 survey. Standard errors (bars) were not available for sprat.

trends of fish abundance at different depth were correctly described by S_a estimates. Thus, they reflected essentially the process of vertical migration of fish at the different depth strata during the 24-h and, in a minor extent, horizontal migration or immigration and bias in the acoustic estimates.

Defining school patchiness or aggregation is also a difficult task (Fréon et al., 1996). In this paper, we used the coefficient of variation between point estimates of fish abundance to elucidate diel patterns in pelagic fish patchiness at different depths. The results showed that fish aggregated fast at dawn at the upper layer (10–40 m). After the sunrise they migrated deeper forming denser schools and remained in the deepest layer (41–80 m) during the day. Nevertheless, the degree of fish aggregation was higher for fish stationed at the upper layer (10–40 m), this being possibly explainable as a fish anti-predation behaviour (e.g. Pitcher, 1993). Our results confirmed previous studies describing pelagic fish aggregation during the 24-h (e.g. Blaxter and Holliday, 1969; Fréon et al., 1996). Fréon et al. (1996) suggested that aggregation at dawn is fast due to visual cues and that fish actively swim together forming schools. Conversely, the model of Azzali et al. (1985) predicted that at dusk fish disaggregate fast while at dawn the reforming of the school takes longer. Our data agree with Fréon et al. (1996) showing on the surface a fast (likely to be mainly active) aggregation at dawn and a slower (likely to be mainly passive) dispersion at dusk. To better understand the observed patterns, we have chosen to discuss results from the 1995 acoustic survey with stomachs and length data of herring and sprat collected from the same area and period during the 1997 acoustic survey. We remind that the DVM pattern of pelagic fish, as indicated by the acoustic device, was the same for the two surveys and for all the surveys conducted in the study area since 1979. Stomachs analysis showed that the fast aggregation at dawn on the surface water well correlated to the highest values of stomach fullness in herring individuals. Zooplankton in the Baltic Sea perform large DVM moving to the surface during the night and to the bottom during the day plausibly to avoid zooplanktivorous fish visual predation (Hansson et al., 1990). This implies that zooplankton catchability is reasonably highest, due to fish optimal visual conditions, at the dawn and dusk

when zooplankton is distributed at the surface. This may explain why pelagic fish aggregate for feeding on the surface water at dawn, preying on zooplankton before it starts to migrate to deeper strata. The same pattern occurs at dusk when fish migrates to the surface from the deeper strata. Again, zooplankton is migrating from the bottom towards the surface at that time of the day and is again predated by pelagic fish as showed by herring stomach fullness index. A two-time feeding cycle (dawn-dusk) has been previously showed for young-of-the-year herring in the northern Baltic Sea (Arrhenius and Hansson, 1994a, b) and for cichlids in lake Malawi (Allison et al., 1996). Sprat, however, reached its peak in feeding activity later than herring and continued feeding during the day time. This could be explained by the different feeding preferences of the two species. Sprat feed exclusively upon zooplankton (Starodub et al., 1992) while herring (particularly large individuals) feed also upon nekto-benthos (Arrhenius and Hansson, 1994a, b). Nekto-benthos, compared to zooplankton, perform limited DVM and is closer associated to the dark bottom (Hansson et al., 1990). Since both herring and sprat are highly selective visual feeders (Blaxter and Hunter, 1982; Arrhenius, 1998; Viitasalo et al., 2001), the time available for herring for feeding could be less than for sprat and restricted only to dawn and dusk when nekto-benthos is in the water column and visible to them. On the other hand, sprat may possibly have more time available for feeding before zooplankton reach, during the day, the darkest layer of the water column. The proposed explanations could reflect in the different diel patterns of stomach fullness observed in this study. During the night, fish were dispersed in the upper water stratum (10–20 m) as well as zooplankton (Hansson et al., 1990) but they were not actively feeding.

According to our data, DVM of pelagic fish in the Baltic Sea is well explained in terms of trade-offs between the three major adaptive hypotheses (Levy, 1990a, b; Wurtsbaugh and Neverman, 1988; Neverman and Wurtsbaugh, 1994). During the day, pelagic fishes appeared at the surface for a short time, likely feeding at dawn and dusk on aggregating zooplankton before it moves down to the bottom, since the availability of plankton organisms in the upper layers is evidently higher and light condition reasonably optimal (Orlowski, 2000). On the contrary, fish spend most of the day-time at deeper areas probably to avoid predation by predatory fish and sea birds. During the night, when predation risk by sea birds is minimised, pelagic fishes were found at the surface water presumably selecting warmer water to maximise their growth rate (Levy, 1990a, b; Wurtsbaugh and Neverman, 1988; Neverman and Wurtsbaugh, 1994; Orlowski, 2000).

Interestingly, our data showed a statistical difference in length–frequency distribution of herring both during the day and night at different depths, with larger herring more abundant at the bottom than smaller individuals. The same trend was not true for sprat. Such differences in size distribution of the two species may again be explained by differences in their feeding habits (see above). As stated above, sprat and

smaller herring feed upon zooplankton (Starodub et al., 1992) while larger herring prefer nekto-benthos (Arrhenius and Hansson, 1994a, b). Therefore, larger herring individuals were found to be more abundant close to the bottom compared to smaller herring probably because feeding on nekto-benthos.

Concluding, results from this study showed that variability of fish distribution and abundance is large at the temporal small-scale although from our data it is not clear whether the variation stems from random dispersion or directed movements occurring at the temporal small scale. DVM of pelagic fish in the Baltic Sea is a well-defined process and it is correlated with their feeding behaviour including differences in diet habits among individuals of different size. Nevertheless, patterns of vertical diel migration of pelagic fish described in this study represent a more general ecological phenomenon. Fish vertical migrations mirrored in zooplankton diel movements in the water column likely in response to optimal predation conditions in the sea and plausibly intertwined with predation avoidance and bioenergetic optimisation.

References

- Aglen, A., 1983. Random errors of acoustic fish abundances estimates in relation to the survey grid density applied. Fisheries Acoustic Symposium, Bergen Norway, 21–24 June 1982. In: Nakken, O., Venema, S.C. (Eds.), FAO Fish. Rep., 300, pp. 293–298.
- Allison, E.H., Irvine, K., Thompson, A.B., Ngatunga, B.P., 1996. Diets and food consumption rates of pelagic fish in lake Malawi. Fresh water Biol. 35, 489–515.
- Amin, E.M., Nugroho, D., 1990. Acoustic surveys of pelagic fish resources in the Banda Sea during August 1984 and February–March 1985. Neth. J. Sea Res. 25, 621–626.
- Arrhenius, F., 1998. Food intake and seasonal changes in energy content of young Baltic Sea sprat (*Sprattus sprattus* L. ICES J. Mar. Sci. 55, 319–324.
- Arrhenius, F., Hansson, S., 1994. In situ food consumption by young-of-the-year Baltic Sea herring *Clupea harengus*: a test of prediction from a bioenergetics model. Mar. Ecol. Prog. Ser. 110, 145–149.
- Arrhenius, F., Hansson, S., 1994b. Erratum Re Arrhenius, F., Hansson, S., 1994a. Mar. Ecol. Prog. Ser. 114, 314. Mar. Ecol. Prog. Ser. 110, 145–149.
- Azzali, M., Buracchi, G., Conti, S., Gambetti, S., Luna, M., 1985. Relationship between the forms of pelagic fish distribution and nyctemeral periods. A tentative model of behaviour. Oebalia 11, 471–488.
- Bethke, E., Arrhenius, F., Cardinale, M., Håkansson, N., 1999. Comparison of the selectivity of different research trawls in the hydroacoustic surveys. Fish. Res. 44, 15–23.
- Blaxter, J.H.S., 1985. The herring: a successful species? Can. J. Fish. Aquat. Sci. 42 (suppl. 1), 21–30.
- Blaxter, J.H.S., Holliday, F.G., 1969. The behaviour and physiology of herring and other clupeids. Adv. Mar. Biol. 1, 261–393.
- Blaxter, J.H.S., Hunter, J.R., 1982. The biology of clupeoid fishes. Adv. Mar. Biol. 20, 1–225.
- Bromley, P., 1994. The role of gastric evacuation experiments in quantifying the feeding rates of predatory fish. Rev. Fish Biol. Fish. 4, 36–66.
- Clark, A.N.W., Levy, D.A., 1988. Diel vertical migration by juvenile sockeye salmon and the antipredation window. Am. Nat. 131, 271–290.
- De Stasio Jr, B.T., 1993. Diel vertical and horizontal migration by zooplankton: population budget and diurnal deficit. Bull. Mar. Sci. 53, 44–64.

- Fréon, P., Gerlotto, F., Soria, M., 1996. Diel variability of school structure with special reference to transition periods. *ICES J. Mar. Sci.* 53, 459–464.
- Fréon, P., Soria, M., Mullon, C., Gerlotto, F., 1993. Diurnal variation in fish density estimates during acoustic surveys in relation to spatial distribution and avoidance reaction. *Aquat. Living Resour.* 6, 221–234.
- Hansson, S., 1993. Variation in hydroacoustic abundance of pelagic fish. *Fish. Res.* 16, 203–222.
- Hansson, S., Larsson, U., Johansson, S., 1990. Selective predation by herring and mysids, and zooplankton community structure in a Baltic Sea coastal area. *J. Plankton Res.* 12, 1099–1116.
- Hilborn, R., Mangel, M., 1997. *The ecological detective. Confronting models with data.* Princeton University Press, Princeton, New Jersey.
- Lampert, W., 1989. The adaptive significance of diel vertical migration of zooplankton. *Func. Ecol.* 3, 21–27.
- Levy, D.A., 1987. Review of the ecological significance of diel vertical migration by juvenile sockeye salmon (*Oncorhynchus nerka*). Sockeye Salmon (*Oncorhynchus nerka*) Population Biology and Future Management. In: Smith, H.D., Margolis, L., Wood, C.C. (Eds.), *Can. Spec. Pub. Fish. Aquat. Sci.* 96, pp. 44–52.
- Levy, D.A., 1990. Reciprocal diel vertical migration behaviour in planktivores and zooplankton in British Columbia lakes. *Can. J. Fish. Aquat. Sci.* 47, 1755–1764.
- Levy, D.A., 1990. Sensory mechanism and selective advantage for diel vertical migration behaviour in juvenile sockeye salmon, *Oncorhynchus nerka*. *Can. J. Fish. Aquat. Sci.* 47, 1796–1802.
- Levy, D.A., 1991. Acoustic analysis of diel vertical migration behaviour of *Mysis relicta* and kokanee (*Oncorhynchus nerka*) within Okanagan Lake, British Columbia. *Can. J. Fish. Aquat. Sci.* 48, 67–72.
- MacLennan, D.N., Simmonds, E.J., 1992. *Fisheries acoustic.* Fish and Fisheries Series 5. Chapman & Hall, London 336 p.
- Neverman, D., Wurtsbaugh, W.A., 1994. The thermoregulatory function of diel vertical migration for a juvenile fish, *Cottus extensus*. *Oecologia* 98, 247–256.
- Ona, E., 1990. Physiological factors causing natural variations in acoustic target strength of fish. *J. Mar. Biol. Assoc. UK* 70, 107–127.
- Ona, E., Svellingen, I., Fosseidengen, J.E., 2001. Target strength of herring during vertical excursions. ICES Fisheries Acoustics, Science and Technology Working Group (FAST), Seattle, April 2001, 1–16.
- Orlowski, A., 1998. Acoustic methods applied to fish environmental studies in the Baltic Sea. *Fish. Res.* 34, 227–237.
- Orlowski, A., 1999. Acoustic studies of spatial gradients in the Baltic: implications for fish distributions. *ICES J. Mar. Sci.* 56, 561–570.
- Orlowski, A., 2000. Diel dynamics of acoustic measurements of Baltic fish. *ICES J. Mar. Sci.* 57, 1196–1203.
- Orlowski, A., 2001. Behavioural and physical effect on acoustic measurements of Baltic fish within a diel cycle. *ICES J. Mar. Sci.* 58, 1174–1183.
- Pitcher, T.J., 1993. *Behaviour of teleost fishes.* Fish and Fisheries Series 7. second ed. Chapman & Hall, London.
- Rudstam, L.G., Aneer, G., Hildén, M., 1994. Top-down control in the pelagic Baltic ecosystem. *Dana* 10, 159–173.
- Schalk, P.H., Zijlstra, J.J., Witte, J.I.J., 1990. Spatial and seasonal differences in acoustic recordings of the Banda Sea (Indonesia), obtained with a 30 kHz echosounder. *Neth. J. Sea Res.* 25, 611–620.
- Sogard, S.H., Olla, B.L., 1996. Diel patterns of behaviour in juvenile walleye pollock, *Theragra chalcogramma*. *Env. Biol. Fish.* 47, 379–386.
- Sokal, R.R., Rohlf, F.J., 1995. *Biometry.* third ed. W.H. Freeman and Company, New York.
- Starodub, M., Shvetsov, F., Hoziosky, S., 1992. The feeding of sprat in eastern Baltic. *ICES C.M.* 1992/J:26.
- Statistica, 1995. *Statistica for Windows.* Statsoft, Inc. and its licensors, 1984–1996.
- Steinhart, G.B., Wurtsbaugh, W.A., 1999. Under-ice diel vertical migration of *Oncorhynchus nerka* and their zooplankton prey. *Can. J. Fish. Aquat. Sci.* 56 (Suppl. 1), 152–161.
- Stokesbury, K.D.E., Kirsch, J., Brown, E.D., Thomas, G.L., Norcross, B.L., 2000. Spatial distributions of Pacific herring, *Clupea pallasii*, and walleye Pollock, *Theragra chalcogramma*, in Prince William Sound, Alaska. *Fish. Bull.* 98, 400–409.
- Stockwell, J.D., Johnson, B.M., 1999. Field evaluation of a bionergetics-based foraging model for kokanee (*Oncorhynchus nerka*). *Can. J. Fish. Aquat. Sci.* 56 (Suppl. 1), 140–151.
- Unger, P.P., Brandt, S.B., 1989. Seasonal and diel changes in sampling conditions for acoustic surveys of fish abundance in small lakes. *Fish. Res.* 7, 353–366.
- Torgesen, T., Kartvedt, S., Melle, W., Knutsen, T., 1997. Large scale distribution of acoustical scattering layers at the Norwegian continental shelf and the eastern Norwegian Sea. *Sarsia* 82, 87–96.
- Viitasalo, M., Flinkman, J., Viherluoto, M., 2001. Zooplanktivory in the Baltic Sea: a comparison of prey selectivity by *Clupea harengus* and *Mysis mixta*, with reference to prey escape reactions. *Mar. Ecol. Prog. Ser.* 216, 191–200.
- Wurtsbaugh, W.A., Neverman, D., 1988. Post-feeding thermotaxis and daily vertical migration in a larval fish (Lond.). *Nature* 333, 846–848.