SCHOOLING DYNAMICS OF SPAWNING HERRING *(Clupea harengus* L.) IN A BAY IN SOUTH-WESTERN NORWAY

by

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ABSTRACT

The schooling dynamics of herring (*Clupea harengus* L.) was investigated during spawning in Raunefjord, south-western Norway in 1994. A single school of Norwegian spring spawning herring (NSS) was tracked during daytime over a five day period in the spawning season, using multibeam scanning sonar and echosounder. Gillnet samples of the herring were collected daily from the school.
The school completed spawning in 3-4 days. It remained one unit throughout the period, but when spawning was initiated, the school divided vertically into two components, one pelagic and one demersal. Differing individual choices in the trade-off between survival and reproduction for fish prior to, during and after spawning may have caused vertical gradients of key factors such as food and predators to act as dividing forces. Prior to spawning, late matured and ripened individuals seeking downwards and early matured and spent individuals searching upwards probably caused the vertical school shape to be cylindrical. As spawning proceeded, fish from the demersal component spred outwards at the bottom, causing this component to take on the shape of a carpet, whereas the pelagic unit condensed into a somewhat tighter ball. When spawning was completed, the two components joined to form a loose feeding flake close to the surface.
Possible effects of timing and duration of the spawning period on acoustic survey estimates of spawning herring are discussed.

INTRODUCTION

The maturation cycle of Atlantic herring, which ultimately determines the time of spawning (Iles, 1964), have traditionally been considered to be relatively fixed (Cushing, 1969), generally within a 4-6 weeks interval (Dragesund, 1970; Dragesund et al., 1980; Lambert, 1987). However, in a recent study including a large historical material on New Foundland herring from 1970 to 1992, time of spawning appears to be strongly related to variation in sea temperature in January (Winters & Wheeler, 1996), and plasticity in the maturation cycle is suggested to be an adaptation to interannual variation in time of optimal larval conditions, according to match-mismatch theory (Cushing 1969, 1975).

Also, fish behaviour and large scale schooling dynamics on the spawning grounds have been reported to be more dynamic than previously anticipated. Nøttestad et al. (1996) concluded that schools migrate in and out of the spawning areas throughout the spawning period, and suggested that individual schools have shorter residential periods on the spawning grounds than 30 days, which has been the general opinion (Devold, 1967). However, to the authors knowledge, there has prior to this study not been reported *in situ* observations of a single school of herring throughout the entire spawning process. The duration of the process and the dynamic repertoire of herring schools in this crucial phase seems to be poorly understood, even though Aneer et al. (1983) have given a unique description of spawning behaviour of Baltic herring in the northern Baltic Sea, based on visual observations.

In this study, an overview of the schooling dynamics of a single school of herring, observed and sampled *in situ* throughout spawning, is presented. The results illustrate how spawning behaviour may be a potential source of error in acoustic abundance estimates of spawning herring.

MATERIALS AND METHODS

A school of NSS herring was tracked daily during daytime hours between 09:00 and 14:00 (UTC) in Raunefjord, south-western Norway in the period 25/4 - 29/4 1994. The school remained in the relatively small Bildøy Bay (figure 1) throughout the period, and was therefore readily located with sonar. The 96 GRT research vessel R/V "Hans Brattstrøm" of the University of Bergen was used in the investigation. A daily survey was conducted in the Bildøy area to locate the herring, and to investigate whether there were other fish schools and potential predators in the area.

Hydroacoustic recordings

The sonar used for the school tracking was a Kaijoo Denkij KCH 1827, a 180° multibeam scanning sonar with electronic beam orientation for recestion and transmission (Rotated Directed Transmission, RDT) and mechanical transducer tilt. Continuos tracking was attempted at 50-100 m vessel to school distance. However, in periods of low echo intensity and navigation problems due to shallow zones in the area, the school was occasionally lost, and the distance varied from 25 to 250 m. The majority of the observations were however done at a vessel to school distance between 50 and 100 m. The sonar image was recorded on video, and altogether 13 hours of sonar recordings were included in the material. Only recordings where the school had been tracked continuously for more than 10 minutes were analysed, in order to exclude sudden bursts due to vessel avoidance from the material and thereby obtaining the most realistic sonar image of the schools natural behaviour as possible.

Geographical position (GPS), swimming speed (V (ms^{-1})), horizontal school area (A (m^2)), relative density (D (%)), circularity (C (%)) and depth in the centre of the school (D_{sonar} (m)), was recorded every 60 ± 5 second, depending on whether or not the sonar image was clearly affected by bottom echoes or unfavourable tilt angles. If no acceptable image was observed within this 10 second interval, data were not collected. Data were collected from altogether 397 accepted observations. The geographical positions of the school was calculated trigonometrically from vessel position and horizontal distance & bearing to the school. Swimming speed was calculated using the geographical positions of the school from observation to observation for all recordings with less than two minute time difference. The horizontal area of the projected section of the school was measured with a light pen. Corrections were made for tilt angle (Misund, 1991), and for distance induced bias (linear regression, before correction: R^2 = 0,11; p<0,001, after correction: R^2 = 0,00; p>0,05). Relative density was defined as the percentage the densest part of the school (red area on the sonar screen) covered of the overall school area. Depth in the centre of the school, calculated trigonometric from vessel to school distance and tilt angle, was indicated on the sonar screen. Circularity was calculated using the formula given by Gerlotto et al. (1994). Net displacement velocity was calculated for each day from the first to the last recorded school position.

The echosounder, a Simrad EQ 50, was connected to a Hewlett Packard deskjet colour printer. Altogether 72 echograms of the school were printed within the time period of the sonar recordings. Minimum depth (D_{min} (m)), maximum depth (D_{max} (m)), horizontal extension (H (m)) and vertical extension ($V_{sounder}$ (m)) were measured manually from the echograms. Vertical extension was calculated as the difference between minimum and maximum depth, whereas depth in the centre of the school (m) was calculated as $D_{sounder} = D_{min} + 0{,}5 * V_{sounder}$. School shape was categorised into four dominating types, discriminated according to horizontal to vertical extension ratio (table 1). The vessel speed at the passing time was not recorded for all registrations. The horizontal extension of the school may therefore have been subject to some random error due to variation in passage speed. Large margins between the various categories were therefore applied to avoid incorrect categorisation. School recordings that did not fit any of the predefined categories were termed "Amorphous". Larger single fish echoes in the area were recorded as potential fish predators.

Fish samples and environmental data

Four gillnets were placed in one chain to sample individual herring from the school. The nets were set each afternoon in the central region of the Bildøy bay the first four days of the period. Samples of herring and bigger (≥ 50 cm total length) gadoids were collected from the nets each consecutive morning. The herring was weighed (total wet weight; 0,1 g resolution) and length measured (total length, 10 mm length groups). Stomach fullness was graded 1-5, 1 corresponding to empty stomachs and 5 to "full to the point of bursting", whereas gonad maturity index was classified according to the 8 point maturity scale of the International Council for the Exploration of the Sea (Anon., 1962). There was an even distribution between the sexes in the herring gillnet samples (49,8 % males and 50,2 % females, n=133). Total length (l) ranged from 250 mm to 360 mm, $\bar{l} = 305 \pm 19$ mm. Total wet weight (w) ranged from 148 g to 363 g, $\bar{w} = 232$ g ± 45 g. The samples were dominated by fish from 3 to 5 years of age, but also 6, 7 and 11 years old individuals (the strong 1983 year class) were present. Each sample contained 5-10 different gadoids such as cod (*Gadus morhua* L.), haddock (*Melanogrammus aeglefinnus* L.) and saithe (*Pollachius virens* L.). CTD profiles were taken both in the Bildøy Bay and in the connecting fjord system, and a standard weather report was provided from the nearest meteorological field station (DNMI, Flesland).

RESULTS

The average gonad maturation index in the samples progressed from a dominance of early maturing individuals in the first sample to a dominance of spent individuals in the last sample (table 2). Fish at all stages had food in their stomachs, but there was a slight positive correlation between stomach fullness and maturation stage ($r = 0{,}19$; $p<0{,}05$). There was a linear relationship between stomach fullness and maturation stage, but only 4% of the total variation could be explained by this relation (linear regression, $R^2 = 0{,}04$; $p<0{,}05$).

Only one herring school was recorded. The school was located within the Bildøy bay throughout the study period. The first day, echosounder recordings revealed that the school divided into two vertically segregated components, one pelagic and one demersal. Only the pelagic component could be detected by the sonar, and the sonar parameters therefore exclusively refer to this part of the school. The two subgroups were aligned vertically, with an intercomponent distance of 2-30 m, predominately between 10 and 20 m (figure 2). Towards the end of the period, the demersal components disappeared from the recordings, and only the pelagic unit was left, located directly underneath the surface.

The vertical shape of the pelagic and demersal component changed remarkably throughout the period (figure 3). The most common category or combination of categories was “Cylinder” the first day (47 %), “Amorphous/Carpet” the second day (42 %), “Ball/Carpet” the third day (30 %), (“Cylinder/Carpet” (24 %) and “Flake/Carpet” (19 %) the forth day and “Flake” the fifth day (48 %). There was a significant relationship between shape and depth (Tukey HSD test with unequal n, $p<0,001$) (table 3).

There was no linear relationship between vessel to school distance and depth (linear regression, $R^2 = 0,00$; $p>0,05$), indicating that swimming depth was independent of distance to the vessel. There was, however, a positive linear relation between school area and relative density (log [n] transformation and linear regression, $R^2 = 0,07$; $p<0,001$).

The school area increased significantly throughout the period (linear regression, $R^2 = 0,19$ $p<0,001$), whereas vertical extension from the echosounder and swimming depth for both sonar and echosounder showed a decreasing tendency (linear regression, $R^2 = 0,35$; $p<0,001$, $R^2 = 0,23$; $p<0,001$ and $R^2 = 0,30$; $p<0,001$, respectively).

Net displacement velocity was highest the first day (0,43 ms^{-1}), lowest the second day (0,01 ms^{-1}) and steadily increasing towards the end of the period (0,13 ms^{-1} the last day). School area (m^2), swimming depth (m) and vertical extension (m) were highly dynamic, whereas swimming speed, relative density and circularity showed little variation.

DISCUSSION

Most hydroacoustic studies have focused either on sonar or echosounder instrumentation, thus operating in two dimensions. However, the combination of sonar and echosounder in this study made it possible to get an overview of the 3D school dynamics. Even though the school was tracked with the sonar throughout the period, the demersal component could not be detected with this instrument. This layer was, however, easily identified with the echosounder. Also, vertical orientation and school shape could only be described properly using the echosounder. On the other hand, if schools are present close to the surface, bigger vessels than the one applied in the present study can have problems detecting the schools with the echosounder due to the upper dead zone, and in that case sonar may be the more practical instrument to use.

Observing a school strictly in 2D can also give a wrong impression of its dynamics. The relative density of the school increased with increasing school area. Increased area should normally be associated with increased volume, and thus diminishing school density. Decreasing interfish distance with increasing speed has previously been suggested to explain positive relationships between density and area in schools of herring, capelin (*Mallotus villosus*) and sandeel (*Ammodytes* sp.) (Cushing, 1977). In the present study, no change in swimming speed could be identified. However, school area increased throughout the period whereas the vertical extension, observed with the echosounder decreased in the same period. This clearly indicates that in the presented study, rather than increased swimming speed causing a tighter fish aggregating, the school was simply squeezing together vertically.

The depth estimates of the centre of the school seemed to be consequently somewhat deeper whith the sonar than whith the echosounder. A random error should be expected to be averaged out for multiple measurments, and a likely explanation is therefore sound wave refraction in the transition zone between brackish surface layer (25 psu) and saline sea water (32-33 psu). The overall impression of the school depth of the pelagic component was however fairly consistent between the two instruments. In conclusion, when investigating highly dynamic schools such as herring, both sonar and echosounder should be applied to get a representative impression of the dynamics and to obtain a better basis for evaluating possible sources of error.

Vessel avoidance could affect the schooling dynamics and thereby lead to a less representative impression of the herring's natural behaviour. Avoidance can be caused by noise from propellers and engines on the vessel (Olsen et al., 1983; Blaxter, 1985), and is among others reported for NSS herring (Olsen et al., 1983; Misund, 1991), North Sea herring (Misund & Aglen, 1992) and Baltic herring (Suuronen et al., 1996). Several authors have pointed out possible consequences for abundance estimation (Olsen et al., 1983, Fréon et al., 1992, Soria et al., 1996), but the knowledge about this important factor is yet not satisfactory. In this study, there was no relation between vessel to school distance and depth in the centre of the school, as should have been expected if the herring dove when the vessel came too close (Olsen et al., 1983). Neither did the echosounder indicate deeper school position than the sonar. The herring may have been habituated to the vessel, but in that case one should have seen a decrease in diving activity, and this was not the case. The behaviour of the herring has therefore probably not been affected by the boat to a large extent in this study, but the fish may have been habituated to boat traffic in the area prior to the investigation.

This study includes one school only, and the behaviour may vary between schools. Size segregation is reported for herring schools (Slotte, 1996), and bigger fish may be expected to swim somewhat longer and faster (Ware, 1978; Videler, 1993). However, size alone should not lead to fundamental changes in school shape and dynamics. Herring schools are groups of thousands of individual fish, and it seems unlikely that different schools consist of individuals that behave fundamentally different. Environmental factors should, however, be expected to affect behaviour, and the environment may thus influence behaviour differently on separate spawning grounds. In the study period, the Bildøy Bay consisted of cold, coastal water, which herring is seeking towards prior to spawning (Runnstrøm, 1941). Temperature and salinity changed relatively little with depth, and wind and wave activity were fairly low and constant throughout the period. Thus the environment could not have been extraordinary for spawning concerning the hydrographical conditions.

The spawning period has previously been estimated to 30 days from the schools enter the spawning area until spawning is initiated (Devold, 1967). The gonad maturation index of the herring samples in the present study indicated that spawning was completed within approximately 3-4 days. Spring spawning Balsfjord herring has been observed (visually) to complete spawning in three days (Kjørsvik et al., 1990), and Nøttestad et al. (1996) observed (acoustically) immigrating, emigrating, searching, spawning and feeding schools at the spawning grounds throughout the entire spawning period at the Karmøy spawning grounds in south-western Norway in 1994. They suggested that schools migrate in, spawn and migrate out again on a 4-6 day basis, indicating a considerably shorter spawning period than previously assumed. Even though they did not have observations on single schools throughout the process to support their hypothesis, their estimation is still consistent with the present study.

The duration of the spawning period may be influenced by school size. Pacific herring has been reported to distribute their spawning products repeatedly in brief periods, small schools (10-20 individuals) completing quicker (3 hours) than bigger (100-200 individuals) schools, spending 12 hours in the process (Stacey & Hourston, 1982). Furevik (1976) observed visually that a small, local herring stock in western Norway spawned within 12 hours, and Johannessen (1986) reported that the same stock completed spawning within a single day. NSS herring is reported to spawn on flat bottom substrate such as coarse gravel and rock (Bergstad et al., 1991), and the available area of spawning substrate could be an important limiting factor for school size. Variations in school size and available spawning substrate can therefore cause variations in residential periods between areas. Feeding has been observed on the spawning grounds of NSS herring (Nøttestad et al., 1996; Axelsen, 1997), and food availability can therefore also be an important factor. Schools of spent herring feeding on the spawning grounds may also increase the probability of multiple school encounters.

In the assessment of the spawning stock of the NSS herring, hydroacoustic surveys are used as indications of relative changes from year to year, Virtual Population Analysis (VPA) being the reference (Anon., 1996). The surveying is conducted night-time only when the herring are disperced in midwater shoals and layers (Anon., 1996), thereby avoiding bias due to close-to-bottom distribution (Ona & Mitson, 1996) and possibly another target strength when at greater depth during daytime (Ona, 1990). Normally, the transect lines are perpendicular to the coast (Anon., 1996), while the southbound migration towards the spawning grounds and the northbound migration away from the spawning ground are along the coast. If the residential periode on the spawning ground is in the order of 3-6 days, as suggested by our study and Nøttestad et al. (1996), there may be substantial migrations towards and away from the spawning areas during the acoustic survey of the spawning stock. With transect lines about perpendicular to the migration directions, a possible bias due to these migrations will be dependent on the progression speed (V_P) of the survey relative to the proportion (Q_T) and speed of the herring towards (V_T) and the proportion (Q_A) and speed of the herring away (V_A) from the spawning ground. For a survey progressing from north to south, this can be expressed by a slight modification of the equation given by MacLennan and Simmons (1992) as:

$$E(Q) = Q \times (1 + (V_T \times Q_T / Q - V_A \times Q_A / Q) / V_P)$$

where Q is the measured biomass and E(Q) is the expected biomass. Similar considerations have been made for North Sea herring (Hafsteinsson & Misund, 1995). However, the residential periods on the offshore spawning grounds are probably longer than indicated by the present study and by Nøttestad et al. (1996), possibly as long as 3 weeks (Slotte & Johannessen, 1996). If the acoustic survey is conducted during this period, the bias due to migration may be negligible.

At night time during spawning, the NSS herring spreads out in loosely arranged flakes, and this is favourable for the hydroacoustic abundance estimation techniques. However, there are great dynamics on the spawning grounds during daytime, both in the horizontal plane (Nøttestad et al., 1996) and in the vertical plane (Axelsen, 1997), and even though the spatial distribution may appear fairly stable, the herring may also be active at night. Coastal spring spawning herring on the western coast of Norway have been reported to spawn at night (Furevik, 1976). Northern anchovy (*Engraulis mordax*) (Hunter & Kimbrell, 1980) and Japanese sardine (*Sardinops melanostictus*) (Shiraishi et al., 1996) has been reported to spawn at night as well. If herring schools are as dynamic at night as they are in the day time, this can certainly affect the abundance estimates. School dynamics on the spawning ground at night should therefore be investigated further both in the horizontal and vertical plane, and potential effects on abundance estimation should be considered.

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Table 1. Criteria defining the different shape categories of the echosounder recordings (V: Vertical extension; H: Horizontal extension).

Category	Vertical orientation	Criterion
Cylinder	Pelagic	V : H 3:1
Ball	Pelagic	V : H = 1:1 ± 1:4
Carpet	Demersal	V : H 1:5, demersal
Flake	Pelagic	V : H 1:5, pelagic
Amorphous	Pelagic/ Demersal	Others

Table 2. Gonad maturation indexes (Anon., 1962) in the herring samples in percent (%).

Maturation stage	maturing (4)	ripe (5)	spawning (6)	spent (7)	resting stage (8)
Sample 1	47	40	13	0	0
Sample 2	0	71	29	0	0
Sample 3	0	3	21	77	0
Sample 4	0	10	10	76	4

Table 3. Vertical orientation of the different shape categories (n: number of observations).

Category	n	% Pelagic	% Demersal	$D_{sonar} \pm SD$	min	max	$V_{sounder} \pm SD$	min	max
Flake	15	100	0	3.1 ± 1.5	2	8	5.3 ± 2.2	3	11
Ball	16	100	0	11.8 ± 4.1	5	23	14.8 ± 3.9	8	24
Cylinder	20	90	10	20.8 ± 6.8	13	42	21.8 ± 5.8	13	36
Carpet*	37	0	100	39.2 ± 9.7	25	59	2.0 ± 0.0	2	2
Amorphous	20	55	45	28.7 ± 17	8	57	14.1 ± 8.9	3	34
All	108	69	31	24.6 ± 16	2	59	10.2 ± 9.0	2	36

*All recordings of "Carpet" were estimated to 2 m vertical extension.

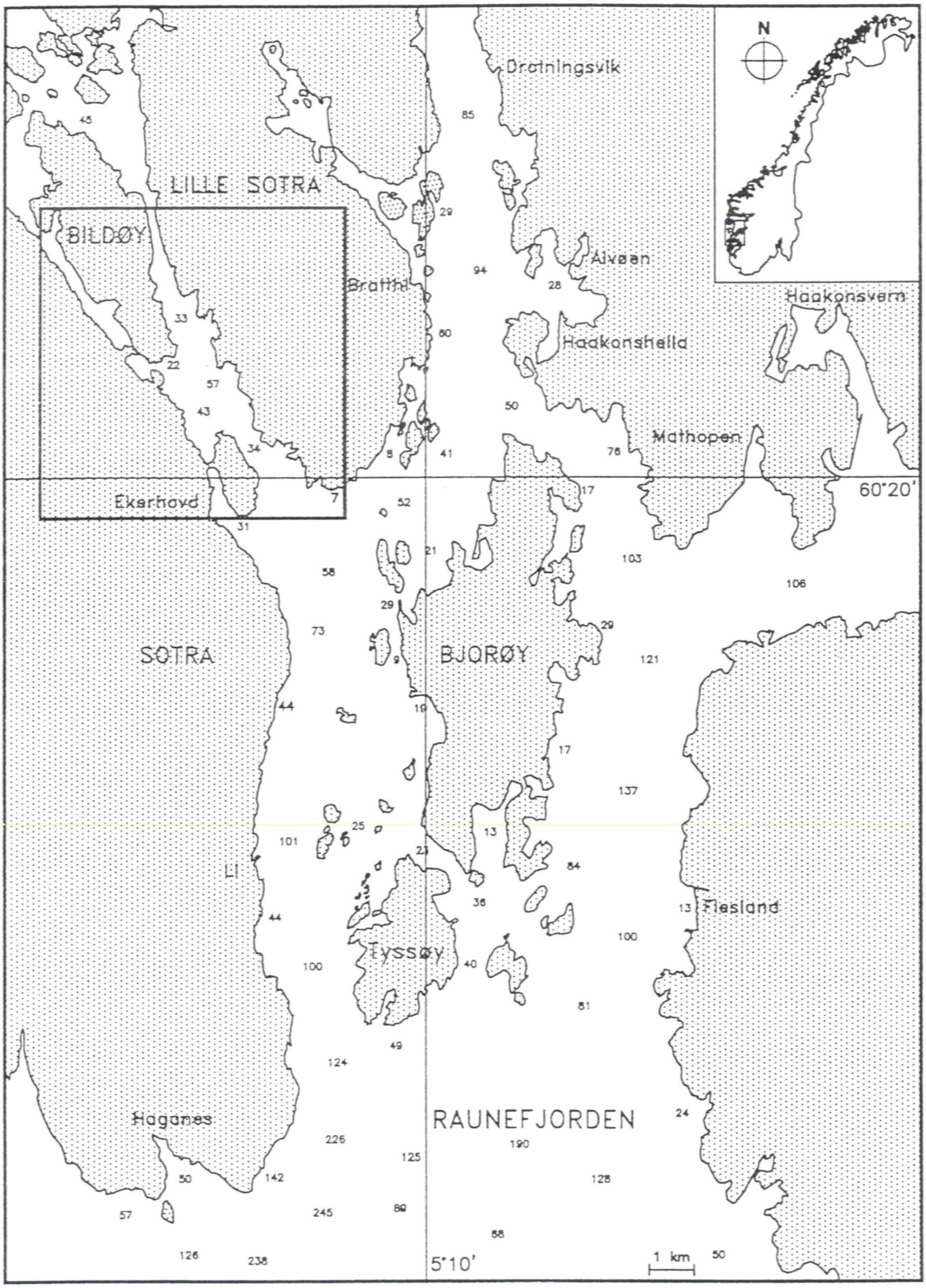

Fig. 1. Map over the Bildøy area (☐ - area of investigation, depths are in meters).

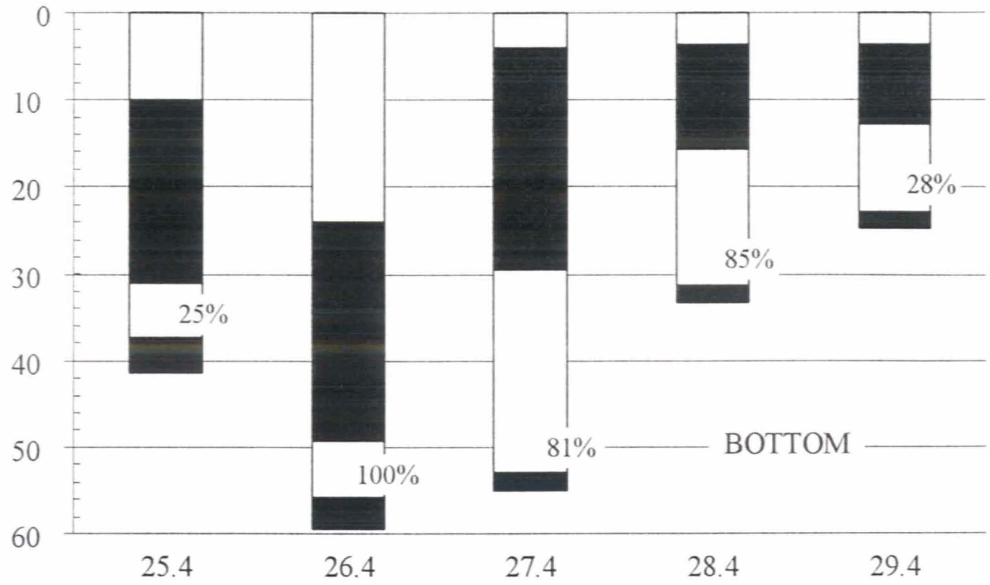

Fig. 2. Vertical orientation of the school components (n) in the water column (□) each day during the observation period (—: bottom (fitted)). Numbers indicate percentage of the observations with demersal component. Horizontal axis indicates the dates of the observations and vertical axis indicates depth (m).

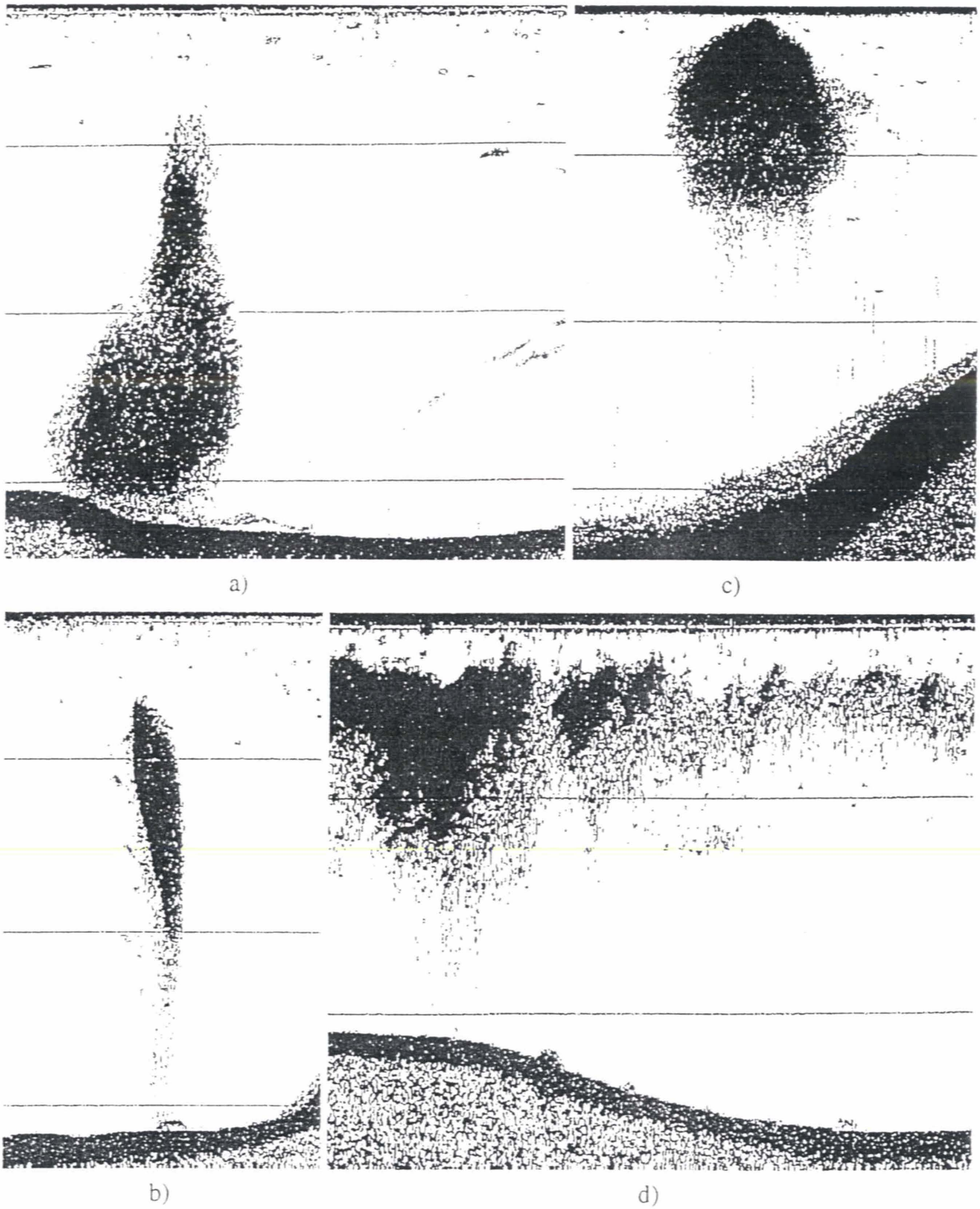

Fig. 3. Different school shapes observed throughout the period: a) "Amorphus" (early in the period); b) "Cylinder", a growing pseudopodium can be seen from the school towards the bottom (early in the period); c) "Ball/Carpet" (in the middle of the period); d) "Flake" (late in the period). Larger individual fish can be seen underneath and next to the school in a) and next to the school in c). Bottom depth is approximately 50 meters.