International Council for
the Exploration of the Sea

Fish Capture Committee
C.M. 1990/B:40

Session R

Dynamics of moving masses: Variability in packing density and shape among pelagic schools

By

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Abstract

The packing density and external shape of herring, saithe and sprat schools in the North Sea and along the Norwegian coast are measured acoustically. The packing density was inversely related to the fish size, but species and regional differences among the schools were detected. There were great variations in packing density from one school to another, and a new 'cell'-integration technique revealed even greater packing density variations within single herring schools. The schools were shaped as flattened discoides close to the surface or sea bottom and more spherical midwater, but there were great variations among the schools, and no clear species, geographical, or fish size influence on the school shape. The great variations in density, and to a certain extent in shape, are explained by the dynamics of a moving mass of polarized and syncronized individuals. Methods for adjusting the horizontal beamwidth of sonars, and egde-effects when integrating schools, are outlined.

Introduction

Traditionally, fish schools were regarded as compact, egalitarian units, with equally spaced and syncronously behaving individuals (Parr 1927; Breder 1951, 1976; Shaw 1978). More dynamic school structures appeared when the three-dimensional position of individuals in small, enclosed schools were monitored. Partridge (1981) observed that individuals moved about considerably within saithe schools, but the syncrony and polarization were maintained as individuals matched changes in swimming speed and headings of their nearest neighbours within time lags of about 0.1 s. The individuals pack denser when they swimm faster (Pitcher and Partridge 1979, Partridge 1981), and to a certain extent when the number of school members increases (Partridge et al. 1980). The relative interfish distance between schooling juveniles is greater than that of larger fish (Van Olst and Hunter 1970), and individuals prefer to swimm alongside school members of similar size (Pitcher et al. 1984). Another feature of the dynamic school structure is formation of subgroups (Breder 1951; Shaw 1978). Acting more and less independently, subgroups may form appendages from the school (Radakov 1973) or open up empty spaces within the school (Pitcher and Partridge 1979).

Statistically, however, a certain packing structure is apparent within schools (Partridge et al. 1980). Herring tend to take up positions 45° in front of or behind and 30° above or below its neighbour. Saithe is schooling with the same elevation tendency, but more alongside its neighbour in the horizontal plane, while schooling cod swim side by side and randomly spaced. Individuals are usually spaced less than one bodylength apart (Cullen et al. 1965, Pitcher 1973, Pitcher and Partridge 1979), even if the interfish distance is slightly influenced by the relative position between neighbours in space (Partridge et al. 1980). This high packing density in enclosed schools are generally one order of magnitude greater than measured acoustically or from fotos of freeswimming schools (Radakov 1973; Serebrov 1976, 1984; Cushing 1977), but a few exeptions where compatible densities have been recorded exist (Smith 1970, Graves 1977). Whether the discrepancy reflects different packing behaviour in artificially and natural environment, or are caused by lower resolution of the measuring methods used in the field, is considered in this investigation.

The polarised, well coordinated swimming behaviour is not an all-time occupation as schools usually resolves in more loose aggregations at night (Whitney 1969; Hunter 1968), or during feeding and spawning (Radakov 1973, Devold 1969). Presence of predators (Radakov 1973; Seghers 1974; Major 1978; Pitcher & Wyche 1983; Abrahams & Colgan 1985), time of day (Volkova 1973), level of background noise (Moulton 1960), and amount of dissolved oxygen (MacFarland & Moss 1967), are also claimed to affect the structure of schools. The schooling behaviour may in addition change with season as Hergengrader & Hasler (1968) and Koltes (1984) have documented for yellow perch and Atlantic silverside, respectively. These species were rather inactive and behaved individually during winter, but were found in active, well-organized schools during spring and summer.

In the present investigation, the average internal density of pelagic herring, sprat and saithe schools is measured by conventional echo integration technique, and the results are compared to the 'compactness' reported on enclosed schools. The influence of fish length, species specific packing behaviour, school size, school shape, sea temperature, swimming behaviour, as well as seasonal and geographical differences on the internal density of schools are studied. To improve the resolution of the acoustic measurements, some of the schools were recorded by a newly developed, computerized echo integrator, with options for producing outprints at short intervals. As this gave the opportunity to measure the internal density in different regions of schools, the principal questions were: To what extent does the density vary within a school? Are there distinct regions suggesting the existence of subgroups within a school? How is the internal density distribution related to the size of the school?

Partridge et al. (1980) claim that the function of an internal school structure is to enable the individuals to perform well coordinated manouvres to avoid attacking predators as the individuals take up positions that maximizes the information flow about swimming movements of their neighbours. An additional antipredator advantage of schooling might be obtained if the external school structure minimizes the probability of being detected by searching predators. As the minimum area to volume proportion is obtained by a sphere, many authors suggested that a seldom observed spherical school shape would be optimal (Breder 1959, 1976, Cushing & Harden-Jones 1968, Radakov 1973), while Partridge & Pitcher (1979) argues for the more common discoid shape. We have investigated the shape of the recorded schools according to these hypotheses, and also analyzed if the shape changes with the depth and swimming behaviour of the schools. The variation in the external structure is considered as this might reflect the schooling ability of a species (Partridge et al. 1980), and since seasonal and geographical differences may be expected. A particular interest is payed to this aspect, as school geometry measurements may be a useful method in abundance estimation of pelagic species (Anon 1974, Hewitt et al. 1976), especially if consistent relations between the geometric dimensions and biomass of the schools exist (Misund 1988, 1990, Misund & Øvredal 1988).

Materials and Methods

The school recordings of the different species have been collected during four cruises along the Norwegian coast and two in the North Sea (Table 1). The cruises were run by the vessels R/V "Eldjarn" (1340 GRT, 3600 HP) or R/V "Fjordfangst" (20 GRT, 180 HP), both equipped with multi-beam sonar and echo integration systems (Table 2 and 3). Before the start of each cruise, the echo integration systems were calibrated according to standard methods (Foote et al. 1987) while the vessels were anchored in sheltered bays near Bergen. To reduce the probability of system saturation, the echo integrators were operated with lowest possible attenuator. Similarly, the sonars were set at moderate gain steps to avoid side-lobe detection of the schools.

At sea, only distinct recordings appearing as high intensity spots on the sonar displays were categorized as schools. I believe that this 'sonar' definition of schools compares well with Pitcher's (1983) heuristic definition, stating that schools are characterized by individuals in syncronized and polarized swimming. As individuals must swim close to each other to conduct such behaviour, they will be recorded by low resolution sounders as a single unit. At night, the schools usually resolved in looser organized schools (Shaw 1961), which appeared as rather scattered and extended sonar recordings. The school recording sessions were therefore limited to daytime only, when the light level was well above the critical level for schooling (Class et al. 1986; Whitney 1969).

When the horizontally guided sonar recorded a new school in front of the vessel, an 'acoustic dimensioning and density recording phase' began (Fig. 1). A video recorder, tapeing the sonar display via a time generator, was started, and the vessel was manoeuvred to a course pointing directly at the school (often this required a slowing down of the speed and a U-turn of the vessel). R/V "Eldjarn" was run with a speed ranging from about 5.0 to 11.5 knots in these measurement situations, while R/V "Fjordfangst" kept a more or less constant speed of 5 knots during the recording sessions. The Simrad SM 600 sonar was run with automatic tracking of the targets in true motion mode, in which data on bearing, horizontal distance vessel-to-school (R), school depth (D), school speed, and echo quantity, are presented on the sonar display. When using the Furuno CH-12 sonar, the distance (R), direction, and depth (D) of the school were continuously monitored by the sonar marker. If the vessel was manoeuvred accurately, and the school performed little avoidance, a distinct school recording appeared as a high intensity spot on the display of the vertically mounted echo sounder, and as a 'jump' in the echo integration output for the actual depth interval. Position, time of day, integrator value (M), depth (D), and vertical extent (H), were noted imidiately for each school recording.

The sonar picture of a school recording were playbacked at still picture intervals of 10 seconds. The lengthwise (lw) and crosswise (cw) extents (Misund 1990) of the school projection were measured by a ruler directly on the monitor screen. Horizontal distance vessel-to-school (R), tilt angle of the sonar (α), and depth (D) of the school recording were noted for each interval. Swimming speed horizontally (V_H), radially to the vessel (V_R) and vertically (V_V) of the North Sea-recordings in front of the approaching vessel were quantified as described by Misund (1990). The real dimensions of the school projection were calculated by:

(1) Crosswise extent:

$$CW = (cw \cdot s) - 2R\tan(BW_s/2) \quad (m)$$

(2) Lengthwise extent:

$$LW_1 = (lw \cdot s) - ((ct_s)/2) \quad (m)$$

$$LW_2 = ((lw \cdot \cos\alpha) \cdot s) - (ct_s)/2) \quad (m)$$

s: sonar scaleing factor (sonar distance/screen distance)
c: speed of sound (~ 1500 m/s)
BW_s: horizontal beam angle of the sonar
t_s: sonar pulselength
1: Simrad SM 600
2: Furuno CH-12

The transect length (tl), was measured on the echosounder recording of the school, and the real dimensions and fish density calculated by:

(3) Vertical extent

$$H = h - ((ct_e)/2) \quad (m)$$

(4) Transect length

$$TL_A = tl \cdot (V/p_V) - D(2tan(BW_e/2)) \quad (m)$$

$$TL_B = 185.2 \cdot (tl/QNM) - D(2tanBW_e/2)) \quad (m)$$

(5) Fish density

$$p = (C_I \cdot M \cdot K_{NM})/(4\pi\sigma_{BS}K_{NM}^2 TL \cdot H) \quad (n/m^3)$$

A) Simrad EY-M
B) Simrad EY200 or EK400
t_e: Echo sounder pulse length
v: vessel speed
p_s: paper speed of the echo sounder
QNM: 0.1 nautical mile interval
BW_e: beam angle (alongship) of the echo sounder
C_I: system calibration constant
K_{NM}: number of meter in one nautical mile
σ_{vs}: back scattering cross section of the fish calculated by $TS_{clupeoid} = 20 \log L - 71.9$ or $TS_{gadoid} = 20 \log L - 67.4$ (Foote 1987)

During the North Sea cruises, fishing trials on school recordings were carried out by a standard pelagic trawl, in some occations by a bottom trawl. The herring and saithe recordings along the Norwegian coast were sampled by purse seines. Length down to the nearest 0.5 cm, sex, gonad maturation stages, and weight, were measured on subsamples of about 100 individuals from eventual catches. For calculation of target strength, the length was averaged from all subsamples within a region or within subregions when this was considered most appropriate (especially for the North Sea cruises).

When using the Simrad EY-M, the target strength of the fish was adjusted for the frequency of that echo sounder by addition of $4.5(\log f_a - \log f_b)$, where $f_a = 70$ kHz, and $f_b = 38$ kHz (MacCartney and Stubbs 1971). The sea temperature profile was measured by a CTD-sonde or a Nansen water sampler at least once in the different regions (Fig. 2).

20 of the herring schools recorded in Gratangen 1989 were 'cell-integrated'. These schools were first measured by the ordinary 'acoustic dimensioning and density measuring'-method, which gave knowledge about their depth extent. For 'cell-integration', the PC-integrator was set to

produce outprints at intervals of 3 echo sounder pings for 15 pelagic depth channels. For 15 of the schools (Group B), the depth interval was set to 2 m for each channel, while 5 larger schools (Group A) required channel intervals from 4 to 7 m to be completely covered. The 'cell-integration' was started shortly before the school was recorded on the echo sounder, and stopped as soon as the school was transected. As the echo integrator outprints were normalized to one nautical mile, the 'cell'-densities were calculated by:

(6) Fish density

$$p = (C_I \cdot M \cdot K_{NM})/(4\pi\sigma_{BS}K_{NM}^2 \cdot CR \cdot CD) \quad (n/m^3)$$

CR: sailed distance for intervals of 3 pings (ca. 5 m)
CD: depth interval per depth channel

The beamwidth of the sonar will cause a range-dependent distortion of the sonar projection, which usually has been corrected by subtracting half the beamwidth (-3dB points) as in equation 1 (Smith 1970; Anon 1974; Hewitt et al. 1976). The width of the beam emitted from the Simrad SM600 transducer si 9°, while the sonar presentation is based on 17 beams, each of 5° width (Bodholdt 1982). As this cause some uncertainty about which beamwidth-correction to be used, an attempt will be made to investigate this controversy by statistical analysis of the collected sonar data.

If a proper beamwidth-correction has been made, the ratio between crosswise and lengthwise school extent (CW/LW) should be range-independent. An underlying assumption is that the schools were keeping the same orientation relative to the approaching vessel so that the lengthwise extent is independent of the horizontal distance vessel-to-school. This is not the case, neither for all the school observations in the North Sea (Spearmans rank correlation coefficient (r_S) between R and LW = 0.24, $p < 0.05$, N = 634), nor the 1988-observations alone ($r_S = 0.15$, $p < 0.05$, n = 372), or just the 1989-observations ($r_S = 0.39$, $p < 0.05$, N = 262). This indicates eighter a range-dependant change in the orientation of the school relative to the approaching vessel (LW-extent decreases, CW-extent increases), the school pack denser as the distance to the vessel decreases (both LW- and CW-extent decreases), only parts of the school are insonified at shorter ranges, or the LW-extents are underestimated, as the slant distance vessel-to-school (R_S) decreases and the tilt angle increases. Since the horizontal beamwidth still is uncertain, only the last possibility can be tested.

This can be done by investigating if there are LW-recordings close or equal to the maximum projectable size at a given slant distance and tilt angle. It is difficult to formulate a general expression for this relationship, but when assuming a circular school shape (Fig. 3), a numerical solution is obtained by combination of the equations (the expressions are illustrated in Fig. 3):

I) $LW_{max} = R_x - R_y$

II) $R = R_s \cos\alpha = (R_x + R_y)/2$

$$50 \leq R \leq 500 \text{ or } R_{ymin} = 50,\ R_{xmax} = 500$$

Figure 4a shows the resulting LW_{max}-extent for a given tilt angle and slant distance, while the LW-extents recorded in the North Sea related to corresponding tilt angle and slant distance are given in Figure 4b. The difference between the maximum LW-extent and the recorded LW-extents are shown in Figure 4c. There are two cases only were the difference is smaller than 10 m. If these two LW recordings are omitted, then the other LW-recordings from the North Sea are still significantly rank correlated to the distance vessel-to-school ($r_S = 0.24$, $p < 0.05$, n = 633), which is also the case if all LW-recordings made at a horizontal distance vessel-to-school less than 150 m are omitted ($r_S = 0.23$, $p < 0.05$, n = 470). This indicates that underestimation of the LW-extents close to the vessel is not the reason for the observed range dependence in the LW-recordings from the North Sea.

Supposing, therefore, that the CW- and LW-extents are equally dependant of range, the task is to determine a horizontal beamwidth so that the CW/LW proportion is range independent. This is done by correcting for the beamwidth in the range 5° to 15° in equation 1 for the North Sea-recordings, and observing the effect on the CW/LW-ratio (Fig. 5). If the beamwidth is anticipated to be 5°, then the CW/LW-ratio is bigger than 2.0, and significantly rank-correlated to horizontal distance vessel-to-school, both for the 1988-recordings, the 1989 recordings, and the pooled 1988-89 recordings. By increasing the anticipated beamwidth to 9°, the similar CW/LW-ratios are in the range 1.64 to 1.84, and both the 1988 recordings and the pooled 1988-89 recordings are still significantly rank correlated to the distance. At 12° beamwidth, there is no significant range-dependency in the CW/LW-ratios, which now are between 1.03 and 1.12.

However, for the following analyzis, the horizontal beamwidth of the Simrad SM 600 sonar will be set to 10°. For the North Sea recordings, this gives CW/LW proportions ranging from 1.42 to 1.57, and still a weak, but significant range-dependency for the 1989 proportions, while the 1988 and the pooled 1988-89 proportions are range independent. Based on the statistical analyzis, a beamwidth choice of 12° may seem more correct. However, the measurements are done by a ruler on displayed school-projections, and technically it seems most correct to choose a beamwidth that is a multiplum of the display beamwidth and which also more or less fulfils the statistical criteria. For the recordings made by the Furuno CH-12 sonar, the specified 6° beamwidth gives a significant, negative rank correlation between the CW/LW proportion and distance for the recordings obtained in Gratangen in 1989 ($r_S = -0.18$, $p < 0.05$, $N = 191$). This is, however, not the case for the recordings made in Lofoten in 1989 ($r_S = 0.07$, $p > 0.05$, $N = 148$), nor the pooled Lofoten and Gratangen recordings ($r_S = -0.04$, $p < 0.05$, $N = 339$). This gives no reason to doubt the 6°-transducer beamwidth of the Furuno sonar. The negative Gratangen-proportion are caused by recordings of a few schools with large LW-extents that were measured at relative long distance vessel-to-school.

Analoge to the preceeding considerations, how should the range distortion be treated in the analyzis of the 'cell-integrated' schools? A straight forward solution would be to apply equation 4 to subtract $D \cdot (\tan(BW_e/2))$ from the extents of the first and last 'cells' in each depth interval. These 'edge'-cells are determined by subracting a threshold noise-contribution (equal to 0.03 herring/m^3) that are set 2% higher than maximum echo-contribution in 1290 apparently 'empty' integration cells before and after school recordings (average noise equal to 0.025 herring/m^3). The average distance sailed for each integration outprint (3 pings) was 4.8 m (SD = 0.9 m, N = 4320) when recording 5 large schools at pulse repetion rates of about 93/min, and 3.9 m (SD = 0.6 m, N = 7515) when recording 15 schools in shallower water at pulse repetition rates of about 110/min. Correcting the range-distortion by the traditional method would therefore reduce the extent of each edge-cell by about one fourth at 15 m depth, and exclude therm totally at depths greater than 70 m. As 95% of the recorded school-'cells' with densities larger than the threshold were within that depth interval, such correction may remove important information about the density distribution towards the edges of the schools.

Packing densities close to the noise threshold seems unrealistic for schooling herring, however, and to find criteria for adjusting the school-edge recordings, the density distribution for the edge elements of the 'cell'-integrated schools are calculated (Fig. 6a). A symmetry in the recorded densities in the elements at the front and rear of the school is apparent. The average density increases fivefold from element 1 to 2, but only by a factor of 1.4 from element 2 to element 3. A corresponding density decrease is observed at the rear of the schools. Despite this symmetry, the average density in element 1 and N is significantly different (Wilcoxon 2-sample test, $p < 0.05$), similarly between element 2 and N-1 ($p < 0.05$), while the average density does not differ between element 3 and N-2 ($p > 0.05$). The depth of the integration-cells in each edge-element catagory, does not influence the recorded density ($-0.09 \leq r_S \leq 0.13$, $p > 0.05$, Fig. 6a). Due to the volume overlap of neighbouring integration cells caused by the geometry of the echo sounder beam, a close connection of recorded densities from one cell to the next is to be expected. As apparent from Figure 6b and 6c, this is the case when relating the densities in element 2 and 3 ($r_S = 0.73$, $p < 0.05$) or N-1 and N-2 ($r_S = 0.78$, $p < 0.05$), while there are more loose, but still significant, correlations between the densities recorded in element 1 and 2 ($r_S = 0.61$, $p < 0.05$) or in element N-1 and N ($r_S = 0.55$, $p < 0.05$). In the latter cases, a relative low density recording in element 1 or N are often followed or preceeded by much higher densities in element 2 or N-1. This indicates that the many density recordings just above the threshold (0.03 herring/m^3) in element 1 or N are marginal school recordings, and may be the result of school detection way out of the -3 dB-points in the main lobe or even in the first side-lobe. For the later school structure analyzis, such marginal density elements will therefore be removed by setting a lower limit to 0.1 herring/m^3, which is the mode in the density distributions both for element 1 and N.

Results

The daytime pelagic trawl catches in the North Sea were usually obtained from single schools as were the purse seine catches along the Norwegian coast. Figure 7 shows that the length of the herring, sprat, or saithe, in these cathces, was quite homogeneous, even if there is some variation from one school to the other. The interval of variation increases from 3-4 cm only at an average length of 7 cm to 5-14 cm at average lengths around 30 cm. Relatively, however, the variation decreases with increasing length ($r_S = -0.56$, $p < 0.05$, $N = 68$) as the coefficient of variation drops from around 0.1 for 7 cm average length to about 0.05 for average lengths around 30 cm. By considering the few samples of saithe and sprat and taking account of the length differences, there is no indication of an obvious difference in the length homogenity between schools of the different species.

The internal structure of the schools is first studied by the reflected acoustic energy per unit school volume (calculated by eqn. 5 without inserting the length dependent, clupeoid and gadoid specific back scattering cross section). This measure, which is proportional to fish density, shows a great variation (up to a factor of 100) from one school to another recorded in the same region, season, and of similar sized individuals (Fig. 8a). The acoustic school structure measure differs significantly between the species (Table 4), but is also significantly different for the various regions and for the actual length groups of a species recorded in these regions.

Generally, the estimated packing density decreases as the length of the schooling individuals increases (Fig. 8b), but there are still significant differences between the species and different regions (Table 5). For the length groups below 20 cm of herring, the over 50% lower average density of the Troms 1989-recordings compared to that of about similar sized North Sea-recordings, is remarkable. Within the 20 to 28 cm average length interval of herring, the average density varies from 0.9 to 5.1 fish/m^3, even for neighbouring length groups (25.3 and 25.2 cm, respectively) in the same region (North Sea 1988). Except for the Møre 1987-recordings, with an average density of 4.7 herring/m^3 (average fish length 28.1 cm), there was little variation in the average density (from 1.3 to 1.9 herring/m^3) for schooling herring above 28 cm recorded along the Norwegian coast.

The sea temperature in the range 5.3-13.0° in the actual depth has no general effect on the packing density of the schools (Table 5), which is the case also for the area, shape (CW/H), vertical extent, and swimming depth of the school. At the regional level, however, significant rank correlations between packing density and shape, swimming depth, sea temperature, and area of the herring schools, exists (Table 6). There is tendencies towards higher packing densities in more disc-shaped schools, both in the North Sea- and Troms-recordings, while the opposite is the case for the Lofoten-recordings. The packing density seems to decrease as the swimming depth increases, both at the Møre 1987- and North Sea 1989-recordings, while there is an opposite tendency for the Møre 1988-recordings. The schools with the largest area seem to have the highest density of the Møre 1988- and Gratangen-recordings. The highest densities were found in warmest waters in Møre 1987 and North Sea 1988, while the contrary tendency was recorded in Lofoten 1988. The swimming speed (V_H), vessel avoidance behaviour (V_R, V_V), or time of day, did not influence on the packing density of the North Sea herring schools (Table 7). For these schools, the length dependency explains nearly 50% ($r_2 = 0.46$) of the recorded school-to-school variation in packing density.

The preceeding results on internal school structure refer to average estimates, one packing density value is obtained for each school recorded. Of the 20 'cell-integrated' herrings schools in Gratangen 1989, from 32 to 358 elements with packing densities above the lower 0.1 fish/m^3-limit were recorded for each school. This revealed a considerable variation in the internal structure of the schools (Fig 9), and measured as number/m^3, the density varied by a factor up to 240 (maximum packing density recorded was 24 herring/m^3). Estimated as interfish distance (possible when assuming a cubic lattice organisation of the school members), the density varied by a factor of about 6 only. In general, the density in about 25% of the elements was within the average density category (1-3.5 fish/m^3, Fig. 10), and only 5% of the cells recorded had densities in the highest category (8.2 - 24.0 fish/m^3).

Distinct high density regions were found in 13 of the schools, however, and in the largest schools two such regions were detected (Fig. 11). It is possible that separate regions, where the packing density is above the average category, represent sub-group formations within the schools. In that case up to seven sub-groups were detected in the largest schools. The extent of this high density regions seems to increase somewhat in proportion to the size of the schools (Fig. 11). In eight of the schools, one or two empty regions were recorded.

The 'cell-integrated' schools were recorded from two groups, one (A) of large schools found in the outer, deep part of the Gratangen fjord, and another (B) of various sized schools recorded in the shallow (about 60 m deep), inner part. The two parts of the Gratangen fjord are connected by a shallow (about 5 m deep) ridge, which caused different vertical temperature distributions in these localities (Fig. 12a). Most of the vertical extent of the group B schools were within a depth zone (20-40 m) where the temperature dropped 4°C, while the group A schools were distributed within a rather homogeneous temperature regime. Averaging the packing density of the 'cell-integrated' schools for each depth layer, revealed that the highest packing density were generally found in the upper part of the schools in both groups. The bimodal appearance of both density distributions is striking, but for the 15 group B schools it may be caused by the pooling of 7 positively and 8 negatively skewed density distribution (Fig. 12b).

The scaling of the horizontal and vertical dimensions of the 'cell-integrated' schools to the same level (Fig. 11), revealed distinct variations in their external structure. The school surface is not smooth, and appendages and inward bends are common, especially in the group B schools. Generally, however, all school recordings were projected with a rectangular shape at the sonar displays, but a few irregular or parabolic shaped herring schools were recorded in the Norwegian fjords. When averaging the measurements of crosswise and lengthwise extent for each school, and relating them to the vertical extent, great variations, both in size and shape, among the schools appeared (Fig. 13). A general trend is that the horizontal dimensions is significantly bigger than the vertical (Table 8), and that the crosswise extent is the greatest. Usually, there are quite close and significant rank correlations between the dimensions, indicating that they increase somewhat proportionally as the schools become bigger. Nevertheless, in some of the regions the vertical extent seems to reach an asymptote (at about 50 m for the Møre 1987-, the North Sea 1988- and the Lofoten 1988-recordings, and 30 m for the Troms 1989-recordings).

The school shape does not differ significantly among the species or the different length groups of a species in the various regions (Table 9 and 10), but regional differences are found for the crosswise to vertical proportion. The swimming depth influences significantly the shape of the school, and both the crosswise-to-vertical and lengthwise-to-vertical proportion decreases at greater depths ($r_S = -0.34$, $p < 0.05$, and $r_S = -0.37$, $p < 0.05$ for CW/H and LW/H rank correlated to depth, respectively). This general tendency of a change from flattened, discoid shaped schools towards more spherical schools at greater depths, is especially clear for the Troms 1989-, Gratangen 1989-, and the Lofoten 1988-recordings (Fig. 14). For the North Sea recordings, the tendency is also present down to about 80 m depth. Beyond that depth, the North Sea schools tend towards a more flattened, discoid shape again, probably because they, in most of these cases, were swimming close to the bottom. Although not significant, the depth dependence seems present also for the shape of the Møre 1988-recordings, but the shape of the Møre 1987-recordings is not influenced by their swimming depth. The shape of the North Sea school is generally not influenced by time of recording, horizontal swimming speed, or vessel avoidance behaviour (Table 11). The indication of a positive correlation between vertical swimming speed and school shape are caused by little vertical avoidance of schools close to the surface (Aglen & Misund 1990).

Discussion

The length variation of the individuals in herring, saithe, or sprat schools, is quite small. The relative and the range of length variation is inversely related, the former decreasing the latter increasing with increasing fish size. This length homogenity is probably caused by size sorting mechanisms like the individuals preference for schooling together with neighbours of similar size (Pitcher et al. 1985), indicating an hydrodynamical advantage (Weihs 1975), on asymmetrical payoffs during foraging and responses to predators (Pitcher et al. 1986).

The packing density is closely and inversely related to the size of the schooling individuals. This indicates that the real distance between neighbours increases with their size, but relative to the bodylength this distance is probably quite length independent. This indication is in agreement with Partridge's (1981) hypothesis that the individuals position themselves to maximise the information flow of their neighbours' movements, both through the visual and acoustio-lateralis sense system (Partridge & Pitcher 1980). The recorded packing densities were generally one order of magnitude lower than can be predicted by a length-to-density relationship proposed by Pitcher & Partridge (1979), based on observations of cod, herring, and saithe when schooling in a gantry. They are more comparable to, but mostly somewhat lower than can be calculated from a length-to-density conversion given by Serebrov (1976) on the basis of acoustic and photographic density measurements of freeswimming schools of various species. The discrepancy becomes almost negliable when comparing with densities predicted by Serebrov's (1984) revised relationship. On the basis of this similarity, it is tempting to conclude that the packing density of freeswimming schools is generally much lower than of aquaria schools. There are, however, some visual observations of freeswimming schools of various species with much higher packing densities than we have recorded (Smith 1970; Graves 1977; Sætre & Gjøsæther 1975). In addition, most of the sources of errors connected to the acoustic method will contribute to underestimate the fish density in schools (Aglen 1989). Most serious is probably vessel avoidance reactions, bringing the schooling fish into unfavourable aspect angles (Olsen et al. 1983, Olsen 1990) or more or less out of the path of the vessel (Misund 1990). Then there is the extinction of the emitted sound energy within the school (Røttingen 1976; Foote 1978), which Thoresen (1990) has found to underestimate the density of large herring concentrations by about 30%. The target strength of the physostomous glupeoids is also probably depth dependent (Olsen & Ahlquist 1987), but a general relationship is not yet established.

The high packing densities recorded in some regions of the herring schools when improving the resolution by the 'cell'-integration method are, however, at the same level as predicted by the Pitcher & Partridge (1979)-relationship. Since schooling herring organizes an internal structure that resembles a cubic lattice (Partridge et al. 1981), the interfish distance in the high density regions is estimated to about 1 bodylength. About such nearest neighbour distance is commonly reported for both herring and other species when schooling in an enclosed environment (Cullen et al. 1965; Pitcher 1973; Partridge et al. 1980), and also observed visually in some freeswimming schools (Graves 1977; Meyer et al. 1979; Sætre & Gjøsæter 1975). Our results therefore implies that equally high packing densities may be found within freeswimming schools as in enclosed schools, but the average density of wild schools are lower. This may indicate that individuals in enclosed schools respond to environmental artifacts by a more strict packing behaviour, but also that regions with such tight packing is a feature of wild schools. Alternatively, the on average lower density of wild schools may be effected by a higher feeding motivation of these individuals compared to that of regularly and well feed fish in captivity, since hunger tend to loosen a strict school structure (Keenlyside 1955; Morgan 1988; Robinson & Pitcher 1989a & b). In our case, this explanation seems less likely, as the packing density (on average 1.7 fish/m^3) of prespawning and nonfeeding herring off Møre in the winter 1988 was quite similar to the density in schools of heavily feeding, maturing herring, recorded in Lofoten autumn 1988 and Gratangen autumn 1989 (on average 1.2 and 1.5 fish/m^3, respectively).

Despite the length dependency, the packing density varied by a factor of 100 from one school to the other of the same species, region, and lengthgroup. To a certain extent, such variation can be explained by the recording procedure. Differences in the accuracy of navigation and vessel avoidance reactions among the schools (Misund 1990) can result in a more representative measure of one school than of another. External school structure features not accounted for by the rather coarse dimensioning procedure, may also cause unequal biases in estimated volume and corresponding packing densities among the schools. However, it is probable that a large amount of the packing density variation among the schools is real. It is also likely that the behavioural causes of such variation is the same as those causing the great internal variation (by a factor up to 240) of the 'cell-integrated' herring schools. This is because variation in the internal density distributions of the schools obviously will cause differences in their average packing density. That the internal density variation of the Gratangen schools was caused by large length variations of the individuals is not likely, as the relative length variation within these schools of in average 33 cm long herring was 5% only with a minimum length of 26 cm and maximum length of 37.5 cm. Nevertheless, there could be an uneven size distribution of the individuals throughout the schools, both because of a tendency to school next to similar sized individuals (Pitcher et al. 1985), and since the largest individuals may occupy the central and safest regions, as observed in American sand lance schools (Meyer et al. 1979). For the North Sea schools, at least, the internal structure variation is not caused by differences in horizontal swimming speed, even if Partridge et al. (1980) observed that schooling saithe pack denser as the swimming speed increased. The internal organization of the North Sea schools seems neither influenced by differences in their vessel avoidance behaviour, nor the different times of day at which they were recorded. The density distribution within the 'cell-integrated' Gratangen schools seems also little influenced by sea temperature, as the internal density variation of the group A and group B schools, which were swimming in a homogeneous and varying temperature regime, respectively, was quite similar.

A tempting explanation is therefore that large internal variation is caused by dissipation of dissolved oxygen within the school. In schools of migrating *Mugil Cephalus*, MacFarland & Moss (1967) observed that the amount of dissolved oxygen declined towards the rear of the schools where the highest packing densities and tendencies towards loosening of the school structure, surface rolling, and leaving of small subgroups, were observed. The higher densities at the rear was probably not an effect of, but rather the cause of, the lower dissolved oxygen content. The school structure changes was therefore more likely the result of predator - prey interactions taking place at the rear, since migrating *Mugil Cephalus* suffer heavy predation (Peterson 1976). The oxygen explanation is therefore not plausible in our case, especially as the high density regions of the Gratangen schools were more or less randomly distributied.

Is the high density regions functional units? Shaw (1969) noted that when a small harengula school changed direction, 3-4 individuals in three groups scattered within the school initiated the change. On the other hand, it is often observed that several fish at the edges can alter direction, and leave the school without any affect on the rest of the school, and usually the outbreakers soon join in again (Shaw 1969). According to this, the high density regions of the Gratangen schools could act as core units, determining the overall school movements. That this is the case seems rather unlikely, however, as the size of the units appears to grew somewhat in proportion to the dimensions of the school. Also during predator threats, the probability of survival would be greatest if the schooling individuals follow the movements of those at the edges, who have a visual perception of the predators, and could monitor their actions (Magurran & Higham 1988; Pitcher 1986; Godin & Morgan 1985).

A characteristic feature of the school structure is the great internal dynamic (Partridge 1981). The individuals move about considerably within the schools which results in rapidly change of neighbours and small differences in swimming speed between them. Since the school members match changes in speed and direction of their nearest neighbours within small time lags (Partridge 1981; Hunter 1969), this may cause short term variation in speed and levels of arousal among different regions of a moving mass of individuals . If individuals pack denser at greater speeds or higher levels of arousal (Pitcher & Partridge 1979; Partridge et al. 1980), then this may cause equally packing density variation between regions of the school. As relative small changes in nearest neighbour distances may create large changes in number of fish per unit of volume, such variation may be especially pronounced in freeswimming schools with a much lower overall density compared to more compact "aquaria" schools. The internal speed and density variations may be especially apparent when large schools change direction, comes across patches of food, or respond to predators. High density regions or empty lacunas may thereby be the result of the moving mass dynamic within the school, which also causes the formation of subgroups. Such moving mass dynamic may explain the large density variation within the 'cell'-integrated schools, and also among the schools of similar sized individuals within a geographical area. As our cell-integration procedure gives an approximate point recording of the schools, the instataneous density variation within the schools may be especially clear. An underlying assumption for the moving mass dynamic hypothesis is, however, that the linearity of the fisheries acoustics (Foote 1983) exists also at short integration intervals. The internal school structure may be quite homogeneous when the individuals react to external stimuli like vessel generated sound (Freon et al. 1990). The great internal density variation of the Gratangen schools may therefore indicate that they were little influenced by the vessel.

Even if there were great school to school variations, the packing density differed among the species and geographical areas. The SA per unit volume analysis showed that the different reflecting properties of saithe usually gave higher values than that of herring and sprat, but when converting the reflected echo energy to fish density, it appeared that the relative interfish distance in schools of the three species is much alike. This is different from Pitcher & Partridge (1979) and Partridge et al. (1980), who found a smaller nearest neighbour distance in saithe schools than in herring schools. The geographical area difference in packing density of the schools seems not to be caused by differences in sea temperature, swimming depth, stage of maturation, or stomack filling. However, the presence of predators also affects the structure of schools (Pitcher 1986), and a systematic knowledge of the activity of predators around the schools in the different areas were not obtained. The packing density variation among the schools in the different areas and also among different subareas with neighbouring lengthgroups in the North Sea may therefore be the result of different predation exposure. This may also be the reason for the school shape difference among the areas, which after all were rather small (detected for CW/H only).

The only area in which an obvious predation activity took place was on the herring schools in Troms 1989. Schools of large saithe hunted the schools of small herring, forced them occationally to the surface where a heavy predation, both by the saithe and sea birds, was observed. Unexpectedly, when viewed against these circumstances, the packing density was much lower when compared to schools of about similar sized North Sea herring. A probable explanation is that the low density of the Troms 1989-schools are a risk balancing outcome of a conflict situation between feeding and predator avoidance (Sih 1980). The individuals were hungry at the same time as they often experienced predator attacks. This results in a loosening of the school structure with tendencies towards individual food search behaviour (Robinson & Pitcher 1989a & b), but the individuals can still respond to a sudden saithe attack by strict schooling and avoidance tactics within a minimum of time.

The swimming depth of the schools has a significant effect on their external structure, with flattened, discoid schools towards the surface, more sperical schools midwater, and tendencies towards flattened bottom schools. If external school shape is a result of natural selection to minimize the detection probability by searching predators, then our results show that the discoid shape has been selected for when schooling close to the boundaries, while the circular school shape is adaptive in midwater. Thus, depending on the swimming depth, both the traditional, circular school hypothesis (Breder 1959; Cushing & Harden Jones 1968; Hamilton 1971) and the discoid school hypothesis (Pitcher & Partridge 1979) are supported. The results can also be interpreted as that the circular school shape is the usual, but that a discoid shape results from interactions with the surface or sea floor (Breder 1976; Meyer et al. 1979; Kühlman & Karst 1967). It is also probable that environmental gradients, especially in sea temperature and ambient light, can influence on the shape of the schools. The group B-schools in Gratangen 1989 was clearly influenced by such factors, as their vertical extent was from about 20 to 40 m deep, irrespective of horizontal size. In four of the other regions there were also clear tendencies towards an asymptote for the vertical extent. But as argued by Pitcher (1986), the function of schooling is probably not to adopt a certain shape that avoids being detected by searching predators, rather it is to avoid predators when they are attacking.

That nearly all school projections were rectangular are probably due to the low resolution and shape distortion of the sonars (Misund 1990), as pelagic schools are seldom observed to have a regular geometry (Squire 1978; Radakov 1973). The parabolic shape observed in some occasions in the Norwegian fjords may be an adaption to a combined feeding - migration behaviour, as reported for hunting giant bluefin tuna (Partridge et al. 1983). The shape of the schools varied also considerably from one school to another. A large extent of this variation is obviously the result of differences in the horizontal dimensions as the vertical extent in many of the areas reached an asymptote. As with the internal density, variation in external structure may also to a certain extent be the result of the moving mass dynamic. Differences in speed, density, and movement direction among regions of the school, will clearly affect the external shape. Appendages, inward bends, and an irregular surface, as recorded for the Gratangen-schools, are therefore probably common features of the external school structure. Nevertheless, the polarization and synchrony among the individuals probably smooths out the variation in internal and external structure over time, and creates the impression of schools as cohesive, homogeneous units.

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Table 1. Seasons and areas for the school recordings of the different species. (IM: immature, M: maturing, PS: pre-spawning, S: spawning, F: full, SF: some filling, E: empty, no. of lengthgroups in brackets).

Species	Season and year	Area	No. of schools	Stage of maturity	Stomach filling	Average fish length (cm)	Vessel
Herring	Sept 1987	Møre (fjord)	47	M	F	28.1(1)	"Fjordfangst"
	March 1988	Møre (coast,fjord)	41	PS	E	29.3-30.0(2)	"Eldjarn"
	July 1988	North Sea	113	IM-PS	E-F	7.3-27.5(10)	"Eldjarn"
	Sept 1988	Lofoten (fjord)	71	M	SF	32.3(1)	"Fjordfangst"
	July 1989	North Sea	87	IM-PS	E-F	23.8-29.3(9)	"Eldjarn"
	Sept 1989	Troms (fjord)	63	M	SF	9.6-18.7(3)	"Fjordfangst"
	Oct 1989	Gratangen (fjord)	79	M	SF	33.0(1)	"Fjordfangst"
Sprat	July 1988	North Sea	16	S	SF	12.9-14.0(2)	"Eldjarn"
	July 1989	North Sea	3	IM	SF	11.0(1)	"Eldjarn"
Saithe	Sept 1987	Møre (fjord)	5	IM	SF	36.7(1)	"Fjordfangst"
	Sept 1989	Troms (fjord)	7	M	SF	57.8(1)	"Fjordfangst"

Table 2. Acoustic equipment used for the school recordings.

Vessel	Year	Sonar	Echo sounder	Echo integrator
"Fjordfangst"	1987	Furuno CH-12	Simrad EY-M	Simrad QM
	1988	Furuno CH-12	Simrad EY-200	Simrad QD
	1989	Furuno CH-12	Simrad EY-200	PC
"Eldjarn"	1988-89	Simrad SM600	Simrad EK-400	Nord-10*

*Blindheim et al. 1982

Table 3. Technical specifications of the sonars and echo sounders used for the school recordings.

	Sonars		Echo sounders		
	Furuno CH-12	Simrad SM600	Simrad EY-M	Simrad EY-200	Simrad EK-400
Frequency (kHz)	150	34	70	38	38
Beamwidth					
horizontal	6°	9°(5°)	-	-	-
vertical	4.5°	7°	-	-	-
alongship	-	-	11°	8°	8°
awarthship	-	-	11°	8°	8°
Pulselength (ms)	2.4-5.6	3-9	0.6	1.0	1.0

Table 4. Results of nested linear model using SA/unit volume as dependent variable.

	d.f.	Mean Square	F-value	p	r^2
Model	31	$2.5 * 10^{-5}$	9.47	<0.001	0.38
Source					
species	2	$1.8 * 10^{-5}$	6.96	0.001	
region (species)	8	$5.1 * 10^{-5}$	18.88	<0.001	
length (species, region)	21	$1.7 * 10^{-5}$	6.28	<0.001	

Table 5. Results of nested linear model with continous effects (shape, depth, school area, sea temperature, and vertical extent) using packing density as dependent variable.

	d.f.	Mean Square	F-value	p	r^2
Model	36	2157.8	11.53	<0.001	0.50
Source					
species	2	854.3	4.56	0.011	
region (species)	8	1531.3	8.18	<0.001	
length (species, region)	21	3163.3	16.90	<0.001	
school area	1	29.6	0.16	0.691	
school shape (CW/vert)	1	211.6	1.13	0.288	
swimming depth	1	28.1	0.15	0.698	
vertical extent	1	1.7	0.07	0.923	
sea temperature	1	151.4	0.81	0.369	

Table 6. Rank correlations between packing density and shape (CW/vert), swimming depth, sea temperature, and area of the schools (*: $p < 0.05$).

	Shape			Depth			Area			Sea temperature		
Region	Herring	Sprat	Saithe	Herring	Sprat	Saithe	Herring	Sprat	Saithe	Herring	Sprat	Saithe
Møre 1987	0.05	0.2	-	-0.34*	0.15	-	0.02	-0.46	-	0.40*	-	-
Møre 1988	-0.11	-	-	0.39*	-	-	0.53*	-	-	0.28	-	-
North Sea 1988	0.29*	-	0.43	-0.46*	-	-0.37	0.11	-	0.02	0.39*	-	-
North Sea 1989	0.51*	-	-	-0.14	-	-	0.23	-	-	0.10	-	-
Lofoten 1988	-0.37*	-	-	0.21	-	-	-0.10	-	-	-0.24*	-	-
Gratangen 1989	0.21	-	-	-0.14	-	-	0.27*	-	-	-0.14	-	-
Troms 1989	0.44*	0.25	-	-0.01	-0.61	-	0.01	-0.77	-	0.03	-	-0.53

Table 7. Linear model with continous effects (hour, V_H: horizontal swimming speed, V_R: radial horizontal swimming speed, V_V: vertical swimming speed) of the North Sea school recordings using packing density as dependent variable.

	d.f.	Mean Square	F-value	p	r^2
Model	23	448.6	6.98	0.001	0.62
Source					
length	19	541.8	8.42	<0.001	
hour	1	1.3	0.02	0.887	
V_H	1	5.1	0.08	0.779	
V_R	1	1.4	0.02	0.882	
V_V	1	16.9	0.26	0.608	

Table 8. General school shape.
(r_s: Spearmans rank correlation coefficient, WSR: Wilcoxon signed rank test, N: number of schools, S: $p < 0.05$, NS: $p > 0.05$)

	CW/H				LW/H				CW/LW				
Species & region	Mean	SD	r_s	WSR	Mean	SD	r_s	WSR	Mean	SD	r_s	WSR	N
Herring													
Troms 1989	4.7	3.8	0.28	S	3.6	4.2	0.43	S	1.7	1.2	0.34	S	70
Gratangen 1989	2.4	1.5	0.46	S	1.8	1.2	0.41	S	1.5	0.7	0.72	S	70
Lofoten 1988	2.8	2.7	0.26	S	3.4	6.7	-0.01^{NS}	S	1.4	0.8	0.24^{NS}	NS	71
Møre 1987	1.8	1.7	0.46	S	1.9	1.4	0.39	S	1.2	1.1	0.02^{NS}	NS	52
Møre 1988	1.7	1.0	0.32^{NS}	S	1.0	0.5	0.34^{NS}	NS	1.9	0.7	0.75	S	41
North Sea 1988	2.6	2.3	0.41	S	2.2	2.0	0.40	S	1.5	1.2	0.59	S	116
North Sea 1989	3.4	2.7	0.46	S	2.7	2.4	0.46	S	1.5	0.8	0.69	S	90
Saithe													
Møre 1987													
Troms 1989	3.2	2.7	0.70	S	2.5	1.4	0.67	S	1.5	1.1	0.40^{NS}	NS	17
Sprat													
North Sea 1988-89	2.6	2.2	0.38^{NS}	S	2.6	2.2	0.49	S	1.1	0.4	0.77	NS	12

Table 9. Results of nested linear model with depth as continous effect and CW/H as dependent variable.

	d.f.	Mean Square	F-value	p	r^2
Model	32	20.8	3.51	<0.001	0.2
Source					
species	2	0.5	0.08	0.920	
region (species)	8	29.4	4.95	<0.001	
length (species, region)	21	6.7	1.14	0.306	
depth	1	126.9	21.37	<0.001	

Table 10. Results of nested linear model with depth as continous effect and LW/H as dependent variable.

	d.f.	Mean Square	F-value	p	r^2
Model	32	18.0	1.68	0.012	0.11
Source					
species	2	3.8	0.36	0.698	
region (species)	8	17.6	1.65	0.109	
length (species, region)	21	5.5	0.52	0.964	
depth	1	206.5	19.28	<0.001	

Table 11. Rank correlations between the school shape and time of recording, horizontal swimming speed (V_H), radial horizontal swimming speed (V_R), and vertical swimming speed (V_V) (S: $p < 0.05$).

Shape	Time	V_H	V_R	V_V
CW/H	-0.01	-0.05	0.01	0.14
LW/H	-0.03	-0.06	0.06	0.19^S

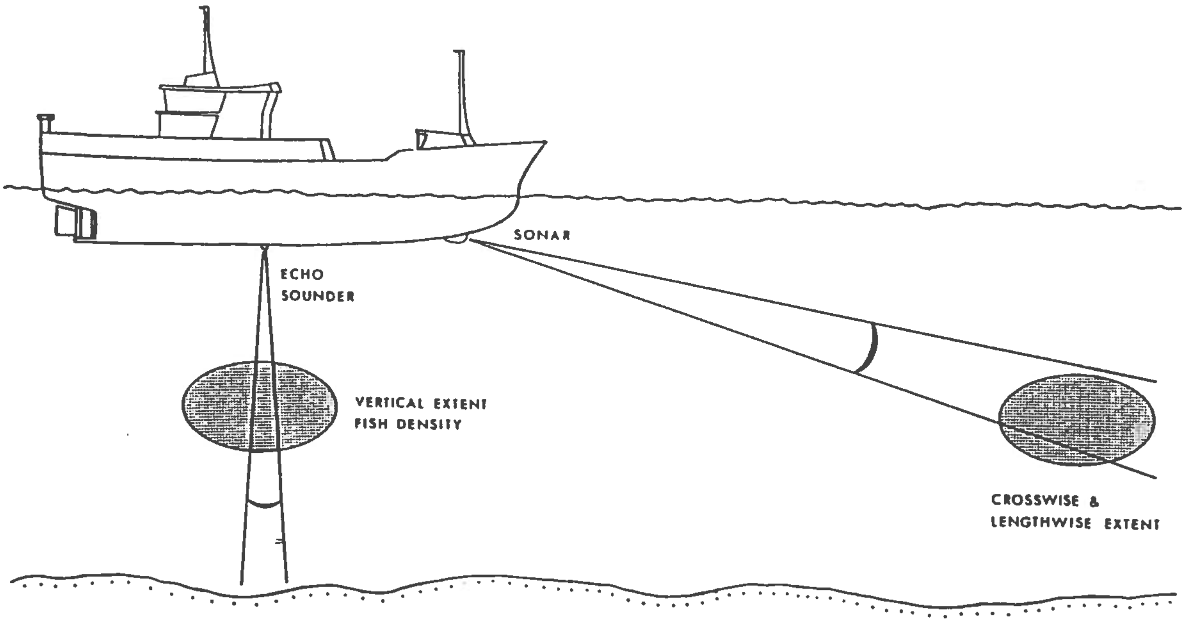

Figure 1. Acoustic dimensioning and density measurement of schools.

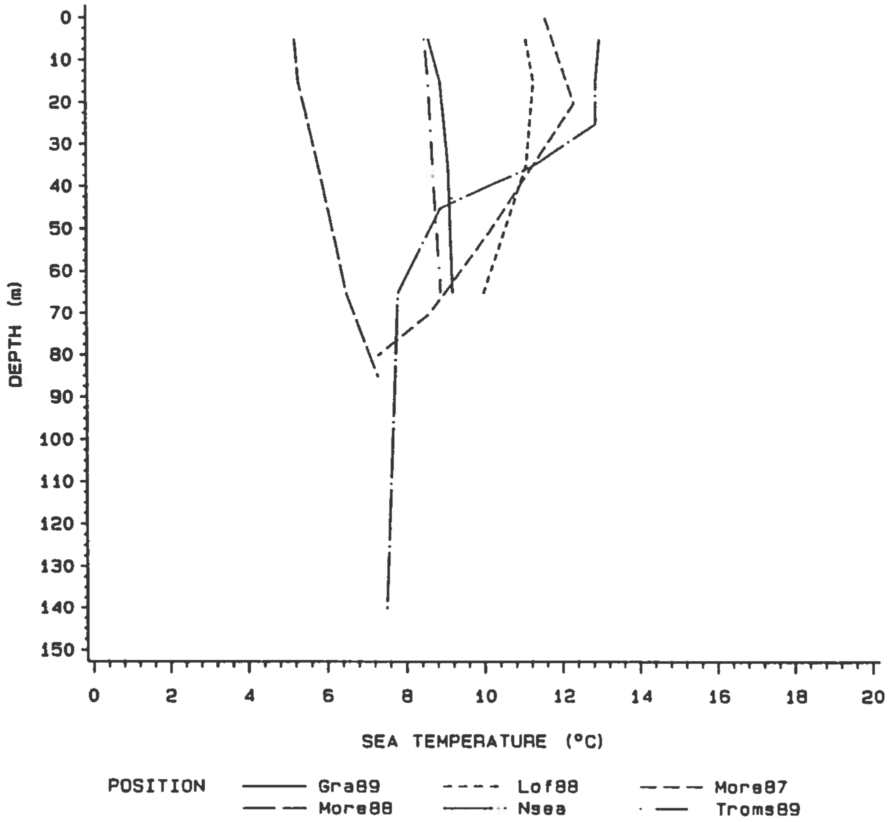

Figure 2. Sea temperature profiles for the actual regions and seasons.

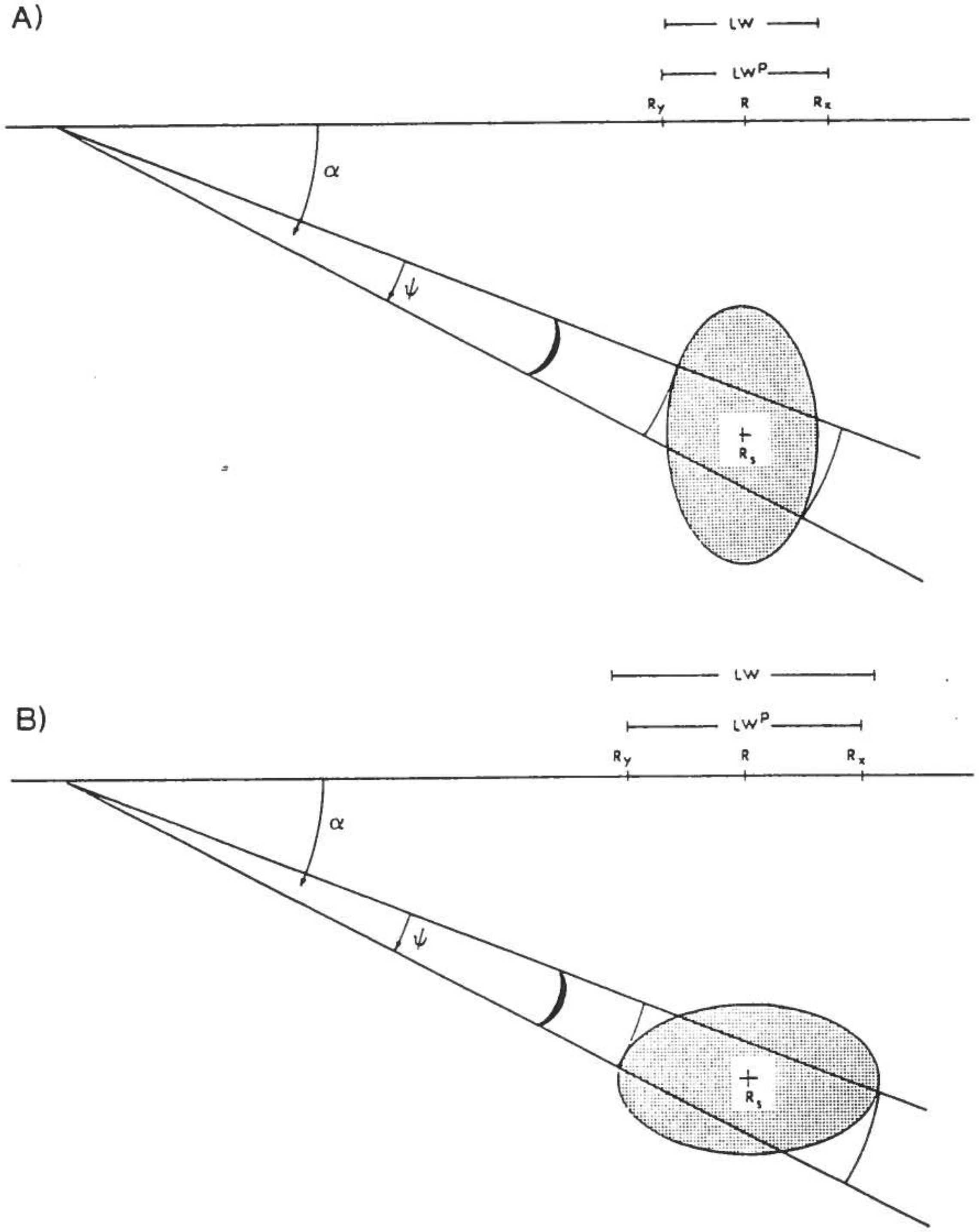

Figure 3. Sonar projection of elliptical schools with the greatest dimension along the vertical (A) and horizontal (B) axis. (LW: real lengthwise dimension, LW_P: sonar projected lengthwise dimension, R_S: slant distance vessel-to-school, R: horizontal distance vessel-to-school, R_X, R_y: distance to beginning and end of school projection, respectively, α: tilt angle, ψ: vertical beamwidth).

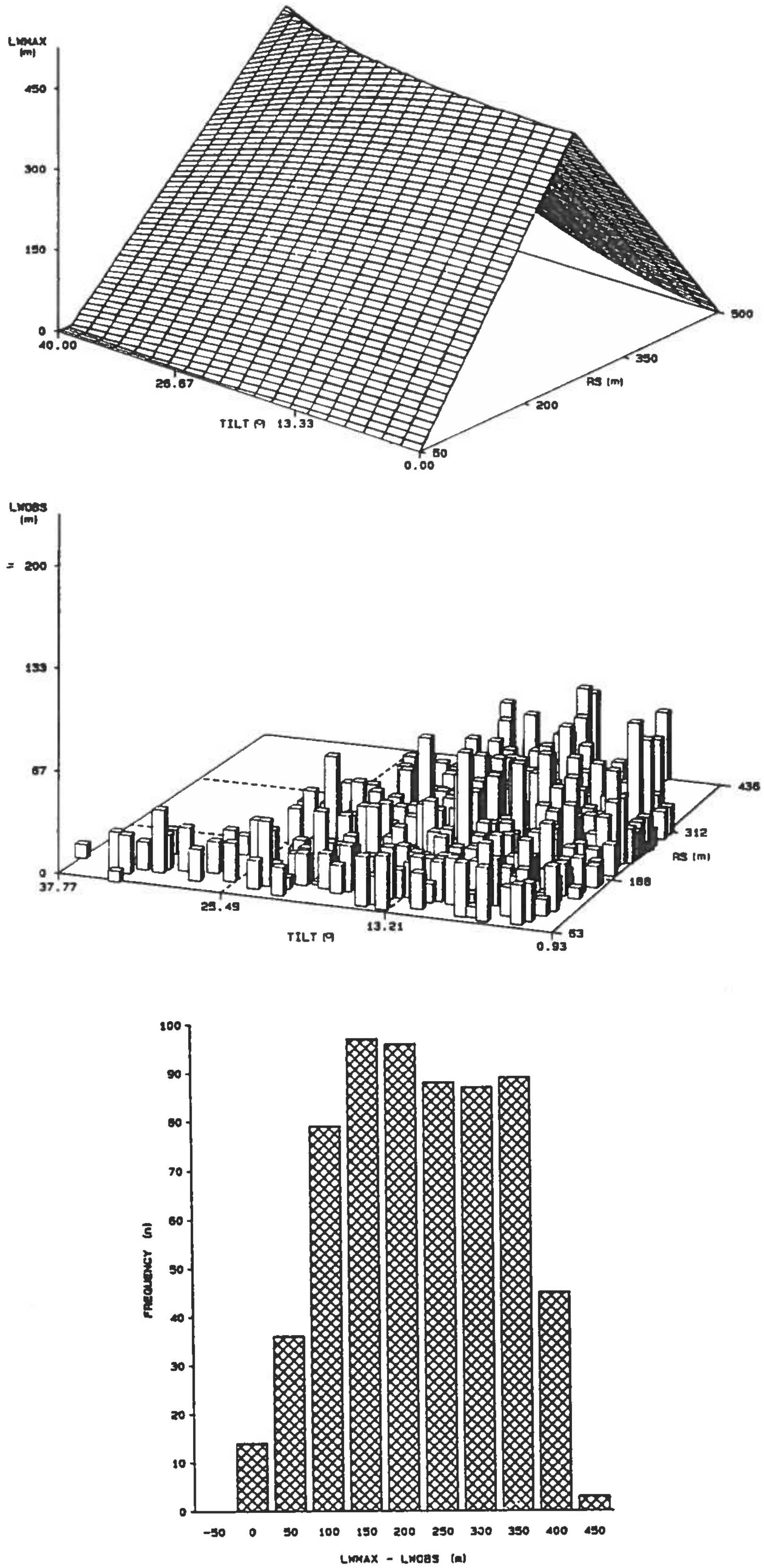

Figure 4. Upper: Maximum projectable extent for lengthwise school dimension as a function of tilt angle and slant distance. Middle: Recorded lengthwise extents of schools in the North Sea 1988-1989. Lower: Difference between maximum projectable and recorded lengthwise extent for schools in the North Sea 1988-1989.

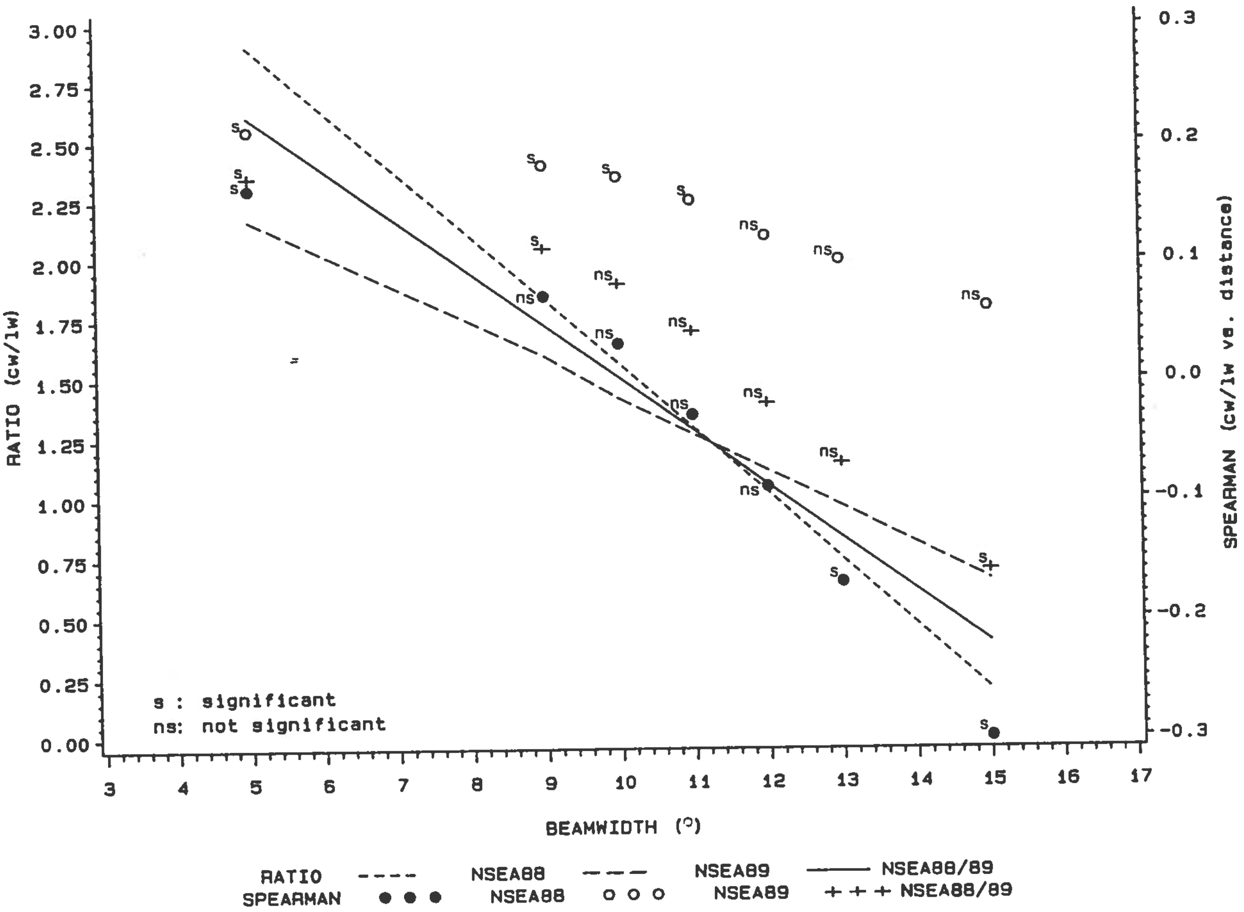

Figure 5. Ratios for crosswise (CW) to lengthwise (LW) extent of the North Sea schools related to horizontal beamwidth, and Spearmans rank correlation for the actual ratio related to horizontal distance vessel-to-school.

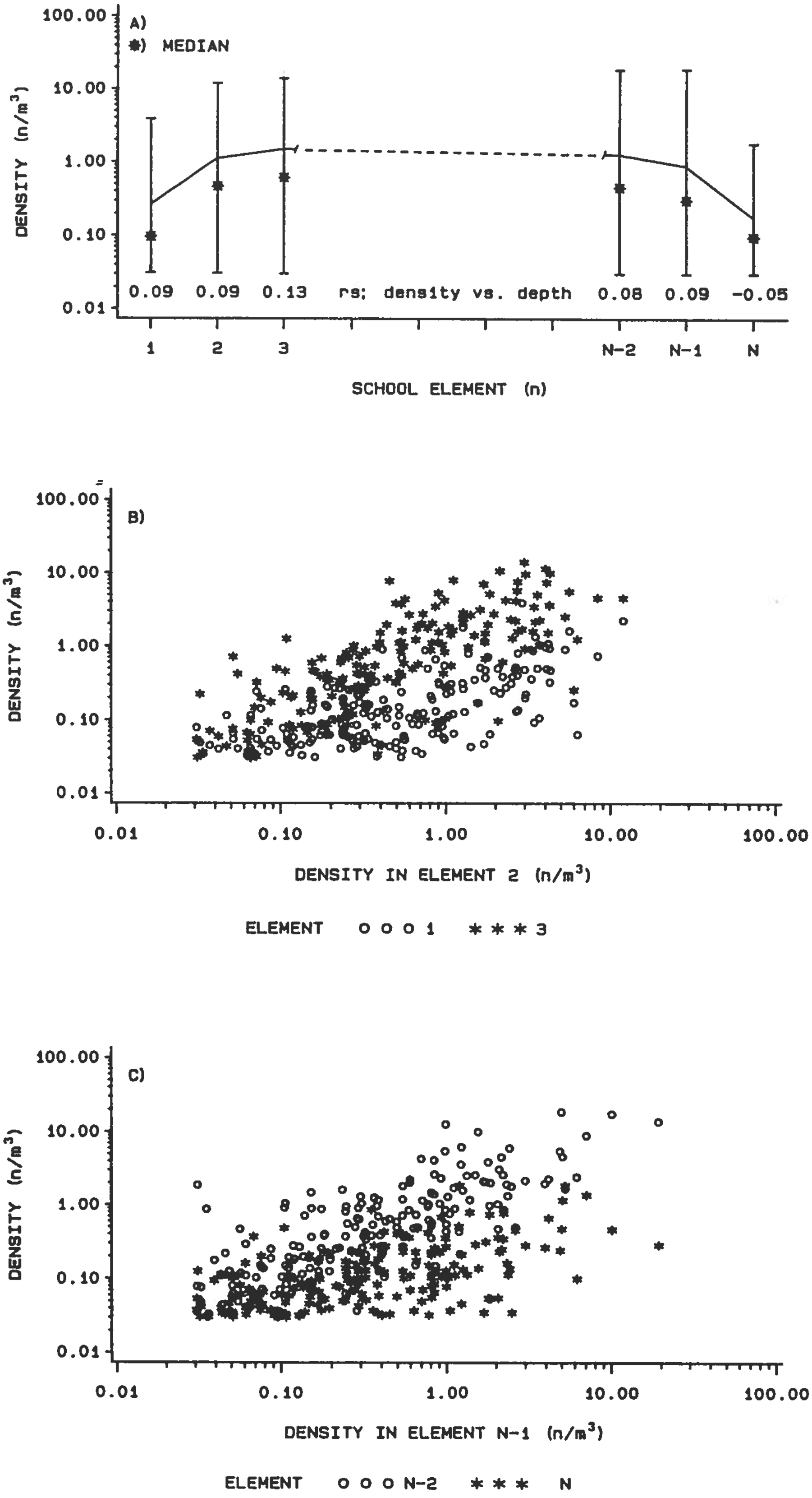

Figure 6. A) Interval of variation (vertical bars), average (line) and median in distributions of fish density for the edge elements of the 'cell'-integrated schools. B), C) Fish density in element 2 and N-1 related to fish density in element 1 and 3 and N-2 and N, respectively.

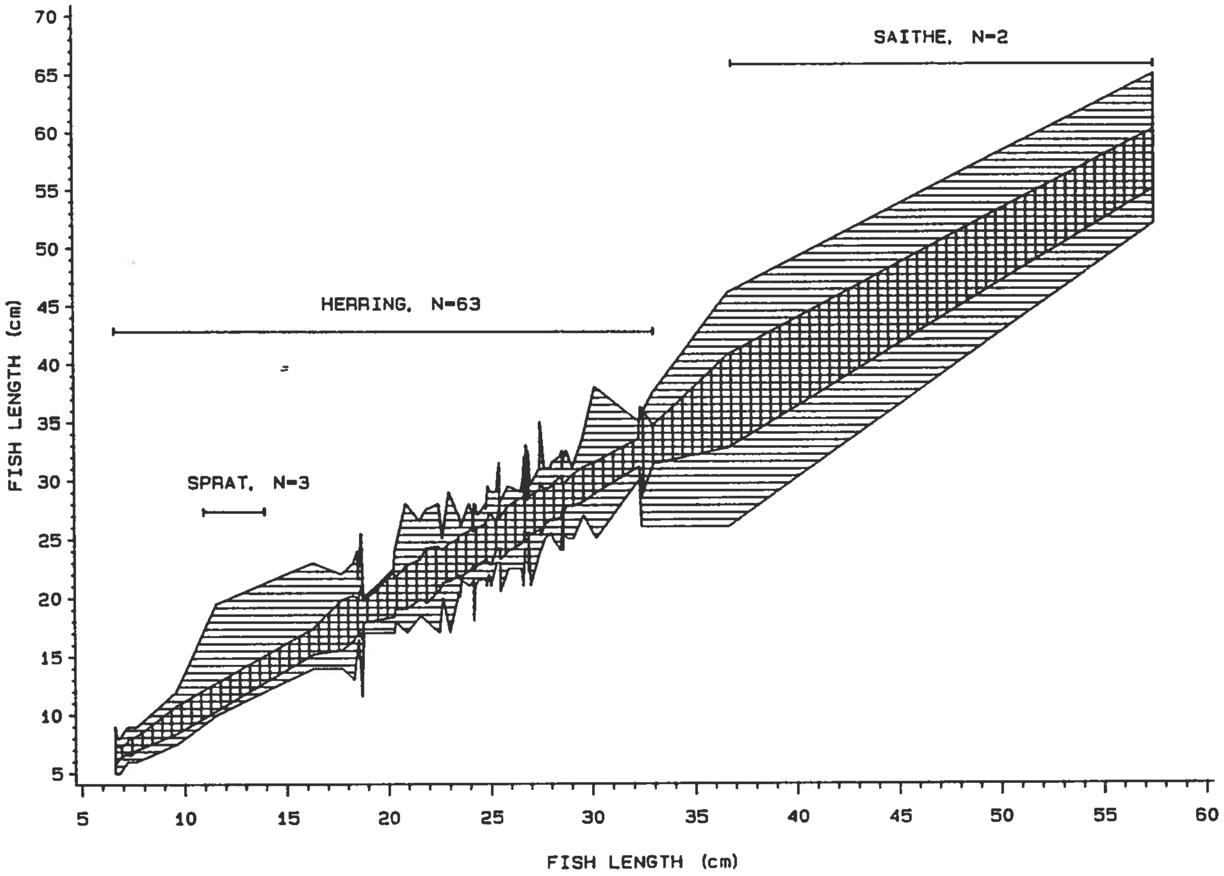

Figure 7. **Interval of variation (hatched) and ± standard deviation (crosshatched) of the length distribution related to corresponding average fish length.**

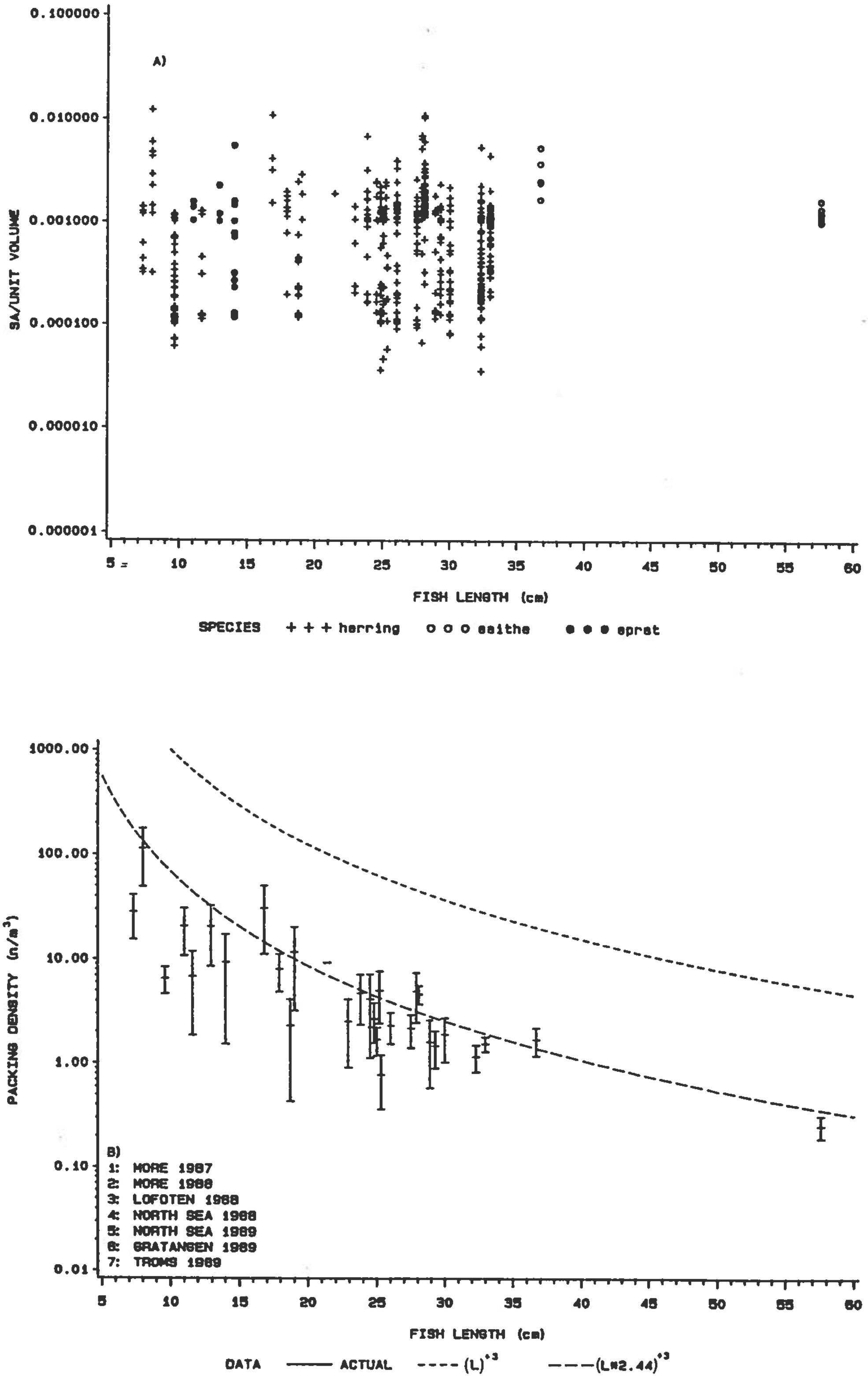

Figure 8. A) Reflected echo energy per unit school volume related to fish length.
B) Average packing density related to fish length (vertical bars: ± standard error)

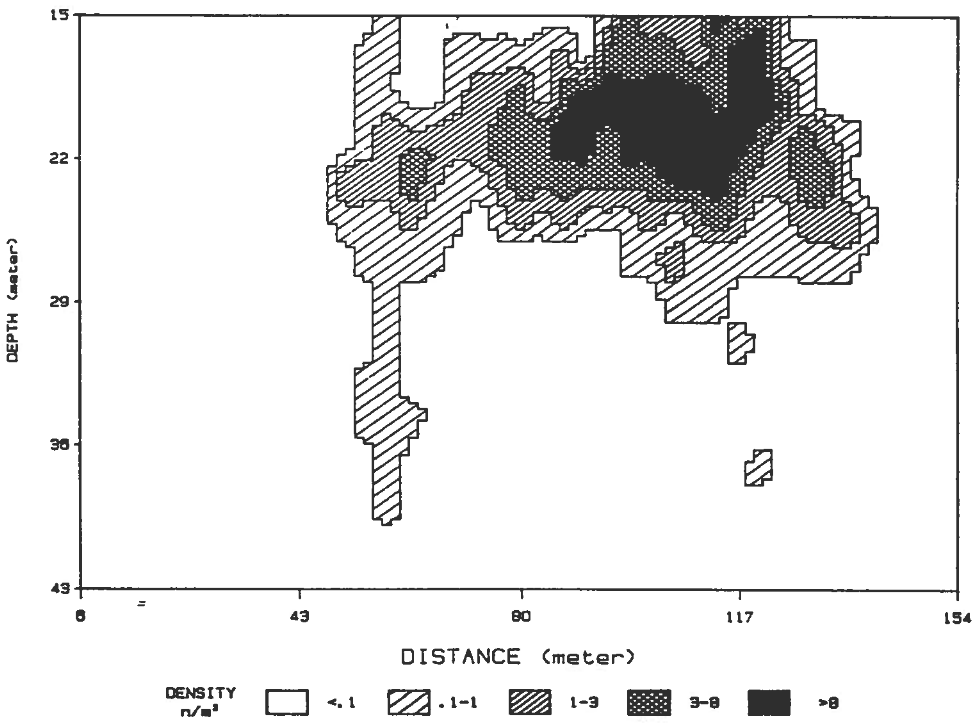

Figure 9. Packing density structure of a herring school.

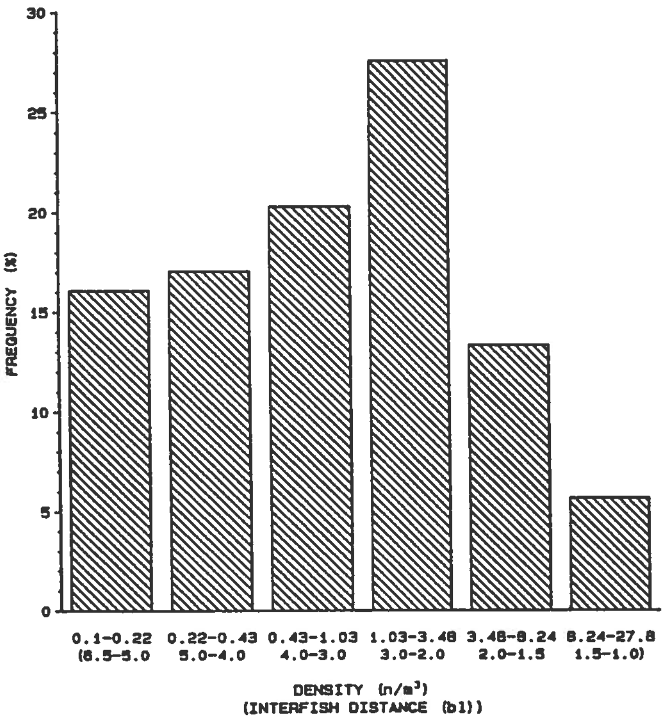

Figure 10. Distribution of packing density of 20 'cell'-integrated herring schools in Gratangen, 1989.

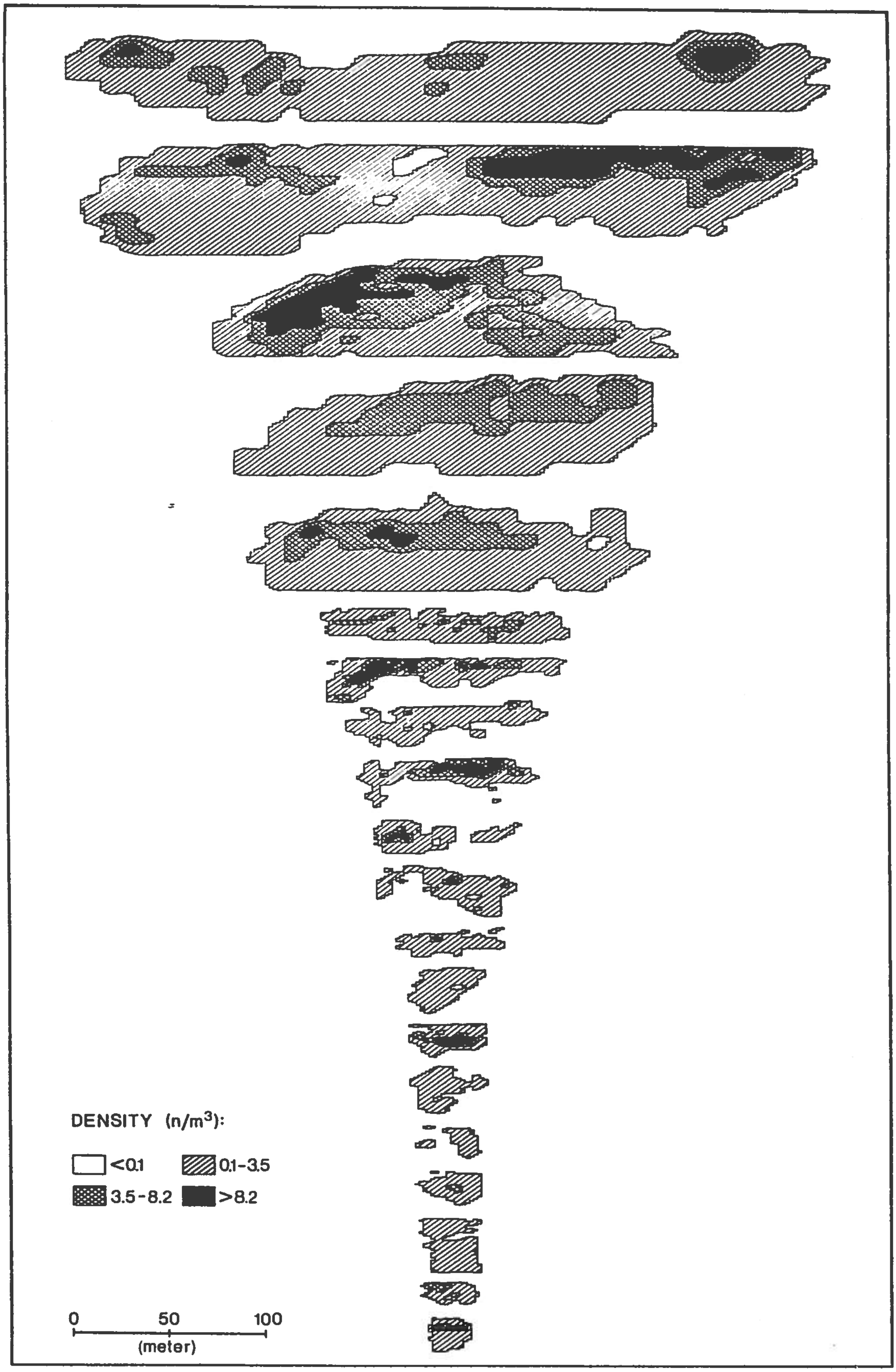

Figure 11. Packing density structure of the Gratangen-schools.

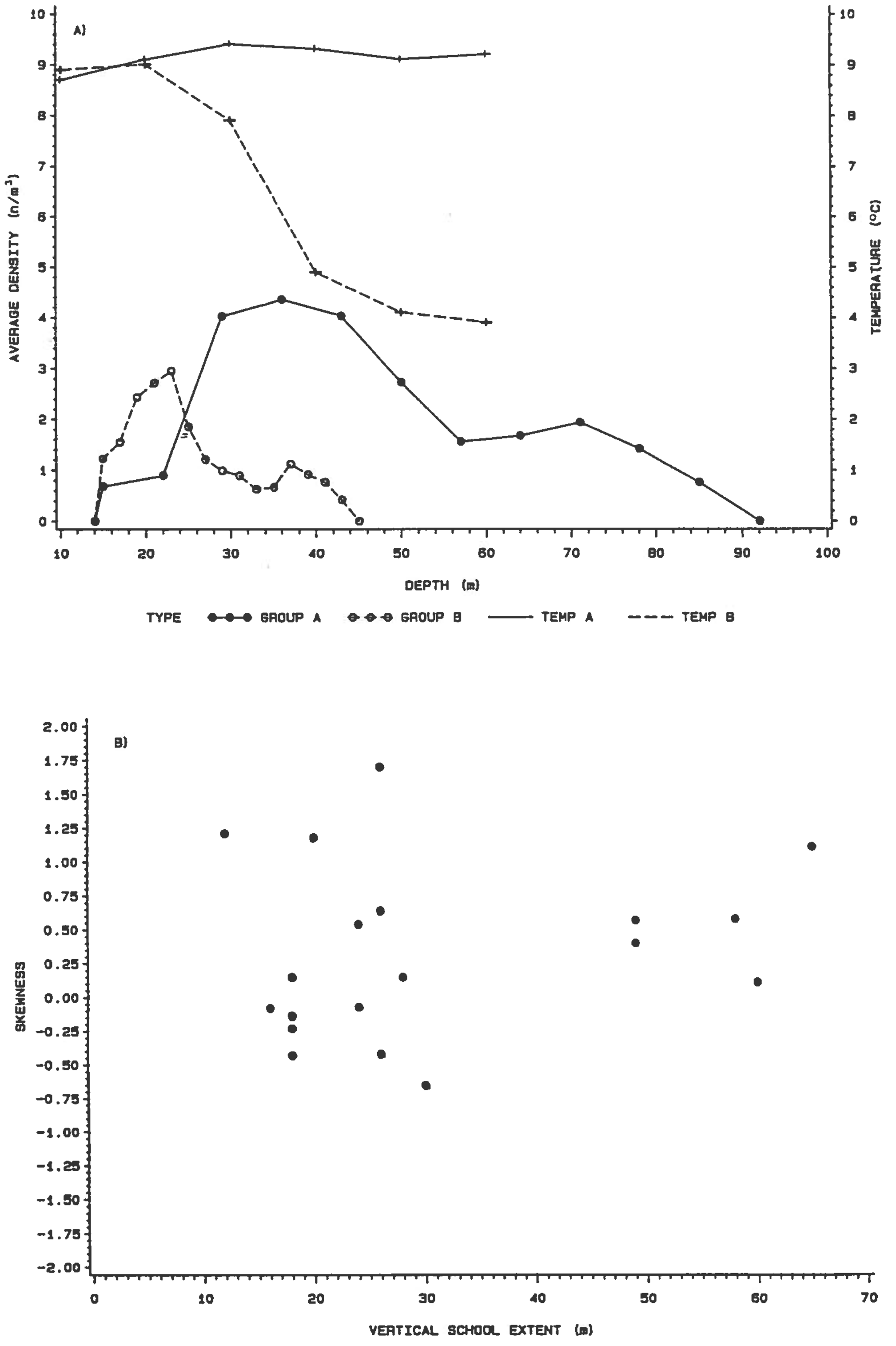

Figure 12. A) Average packing density and sea temperature related to the swimming depth of the 'cell'-integrated Gratangen schools. B) Skewness in the paking density distribution related to vertical extent of the Gratangen schools.

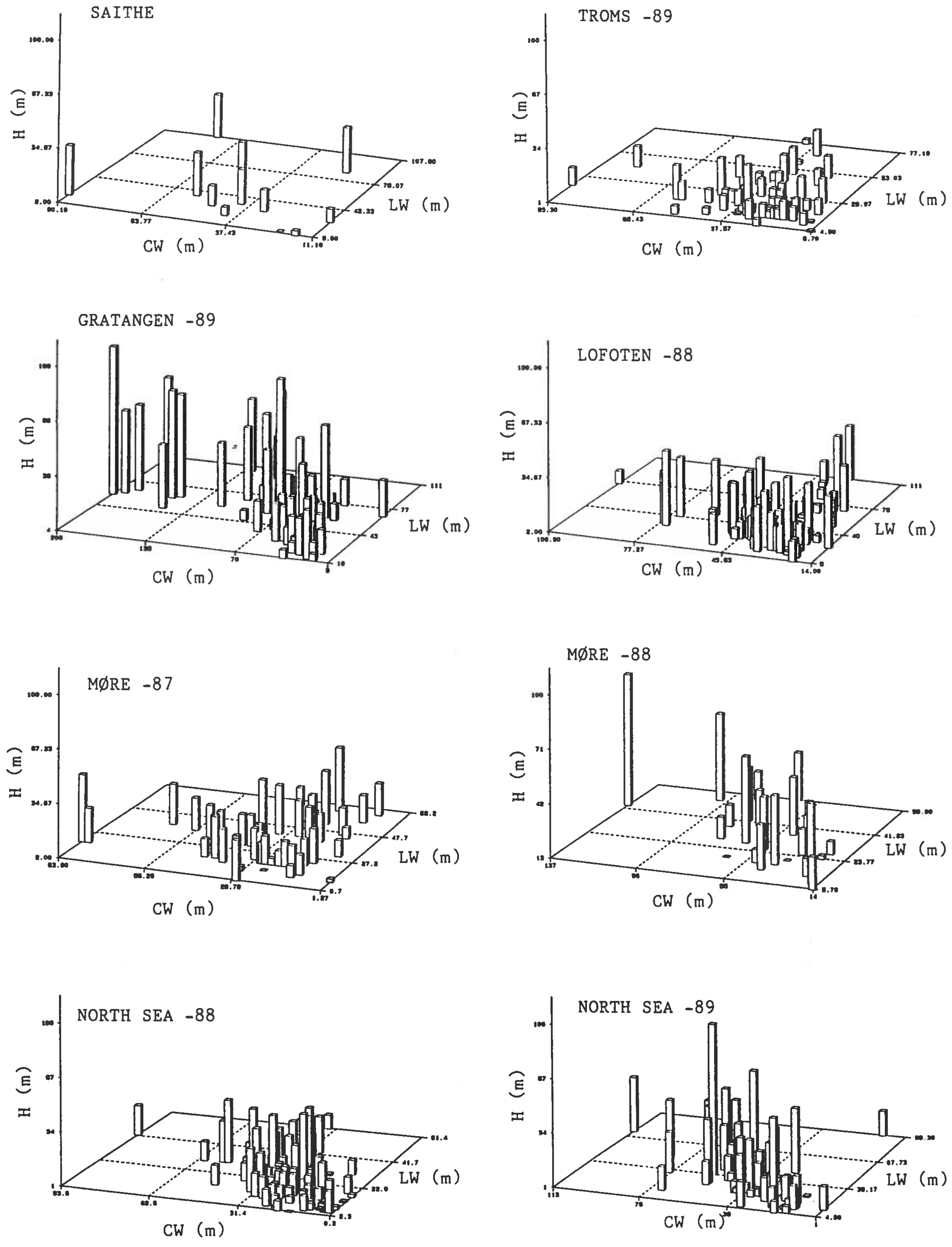

Figure 13. **Horizontal (CW and LW) and vertical (H) dimensions of the saithe schools and the herring and sprat schools in the actual regions and different seasons.**

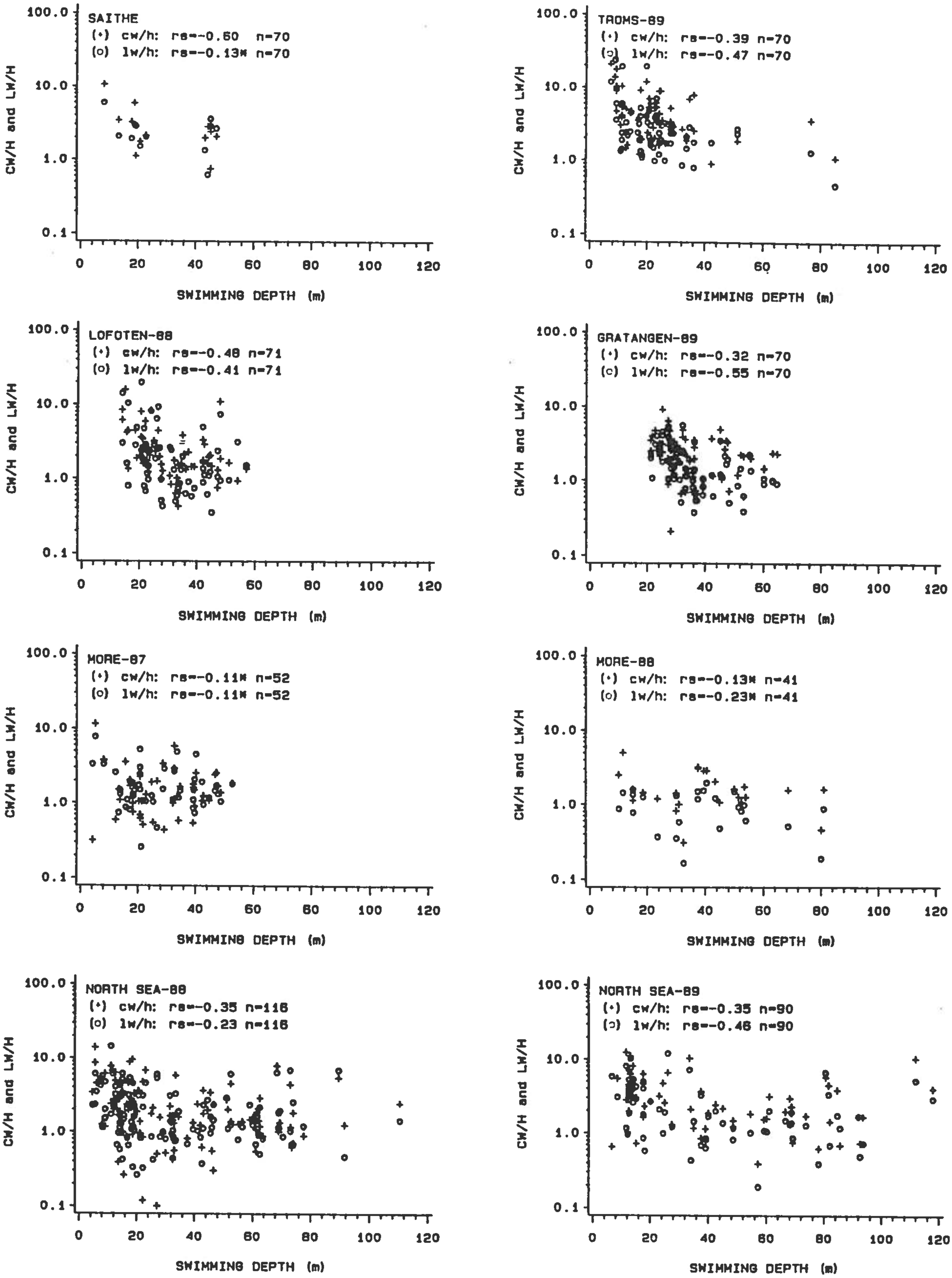

Figure 14. School shape (CW/H and LW/H) related to swimming depth for the saithe schools, and the herring and sprat schools in the actual regions and different season.