INTERNATIONAL COUNCIL FOR
THE EXPLORATION OF THE SEA

C.M. 1986/G : 52
Demersal Fish Committee

ON THE METHODOLOGY OF LENGTH BACK-CALCULATION FROM OTOLITHS IN FLATFISH WITH PARTICULAR REFERENCE TO BRILL (SCOPHTHALMUS RHOMBUS L.)

by

P. Lucio.
Netherlands Institute for Fishery Investigations
P.O. Box 68, 1970 AB IJmuiden
The Netherlands.

INTERNATIONAL COUNCIL FOR
THE EXPLORATION OF THE SEA

C.M.1986/G:52
Demersal Fish Committee

ON THE METHODOLOGY OF LENGTH BACK-CALCULATION FROM OTOLITHS IN FLATFISH WITH PARTICULAR REFERENCE TO BRILL: SCOPHTHALMUS RHOMBUS, L.

by

P. LUCIO *
Netherlands Institute for
Fishery Investigations
P.O. Box 68, 1970 AB IJmuiden
The Netherlands

ABSTRACT

A description of sagitta otoliths of the flatfish Brill (Scophthalmus rhombus, L) from the North Sea is presented. Special attention is given to the relative symmetry of both sagittae. The nucleus is located in the centre in one otolith (symmetrical otolith) and at about one third of the longitudinal axis in the other (asymmetrical otolith). The asymmetry increases with increasing fish size, in particular in the asymmetrical otolith. Both the symmetrical and asymmetrical otolith grow in direct proportion with body size. From a description of the type of edge of the otolith in the different months of the year it is shown that the rings in the otolith represent true annual rings that are formed between April and June. Results of different procedures for measuring the annual rings are compared and the differences discussed. The back-calculation technique is validated by the correspondance between the mean back-calculated length from 695 brill otoliths sampled in 1984, and the length distribution of brill in demersal young fish surveys. Finally some approaches for the flatfish sagittae selection, preparation and measurement for back-calculation purposes are offered.

* Present adress :
Research Institute for Fish Science and Technology
(A.Z.T.I.,A.B.)
Sukarrieta (Bizkaia). BASQUE COUNTRY - SPAIN.

INTRODUCTION

Brill (Scophthalmus rhombus,L.1758) is a large flatfish that in the North Sea is mainly taken as a by catch in the fishery for sole and plaice. It is relatively important as a food fish, not for the size of its commercial catches, but for its value per unit of weight.

Studies about the age determination and growth of Brill are scarce and are mainly related to the larval and juvenile stadia (CUNNINGHAM 1891a,b, FULTON 1904,1905, JOHANSEN 1915, JONES 1972, REIBISCH 1927, WALLACE 1923). In general these autors have worked with few specimina of Brill scattered over surveys of different years and most of them applying only the length frequency distribution method.

In the present work the sagitta otoliths of Brill are used to determine the age of the fish and study its growth. To validate the age determination it is checked whether the rings in the otolith represent true annual rings. The growth of Brill is studied using the back-calculation method LEA (1910), LEE (1912,1920), FRAZER (1916), BAGENAL and TESCH (1978) and BARLETT et al. (1984). For this approach to the study of growth it is essentiel to know at what time of the year the rings are formed and if both male and female, small and big Brill, form the rings at the same time of the year.

An accurate back-calculation of fish length at succesive ages must be based on an adequate relationship between the growth of an indicator structure (scale, otolith,...) and the body-length throughout its development. Different approaches have been applied : LEA (1910) used a linear relationship, FRASER (1916) and LEE (1920) added different correction factors to the linear relationship, SHERRIFF (1922) and SAETERSDAL (1953) employed a parabolic and a curvilinear relationship respectively. In this paper the relation between the otolith length and body-length is studied in order to choose which backcalculation technique should be adopted.

Brill, as all other flatfish species, has an asymmetrical anatomy due to the particular metamorphosis in the larval stage. The question arises to which extent the sagitta otoliths are asymmetrical and to which extent this affects the backcalculation of body length from both sagitta otoliths.

MATERIALS AND METHODS

The material for this study consisted of Brill sampled from commercial -mainly beam trawl- landings at Dutch fish market of Urk, IJmuiden, Scheveningen and Stellendam in 1984 and 1985. In addition data were used of Brill caught in the Demersal Young Fish Surveys (DYFS) by R/V "TRIDENS" and "ISIS" and of juvenile fish caught in the very shallow beach zone of the Dutch coast. All Brill here studied proceded from the North Sea, mainly from its southern and central part. In FIGURE 1. the positions of commercial samples and of the DYFS samples of 1984 are show. Each individual fish was measured for total length (from the snout to the distal end of the longest caudal fin-ray) to the millimetre below, weighted, sexed and was given an index of sexual maturity; finally the sagitta otoliths were taken.

PREPARATION AND READING OF SAGITTA OTOLITHS

Untreated otoliths of Brill, especially those of older fish, gave difficulties in age-determination. Therefore the burning technique as developed by CHRISTENSEN (1964) was adopted. This method considerably extends the readability of Brill otoliths and eases the procedures of measuring. The sagittae were placed in a brass plate and held in a quick burning Bunsen flame during 1-2 minutes. The otolith changes gradually in colour from white to brown and finally to ash-grey and black. In the case of Brill the most satisfactory results were obtained when the otolith had acquired an ash-grey colour. Then the pairs of sagittae were arranged in some slides with a plasticine basis and read in reflected ligth, by a binocular microscope (12x). The burnt sagitta surfaces were brushed with inmersion oil to clarify the ring structure. Distinct white and brown rings can be seen. Simmilar procedure has been used satisfactory with otoliths from other flatfish: turbot (van LEEUWEN and RIJNSDORP 1986) and from other very different species: horse mackerel (GELDENHUYS 1973, MARECOS 1974). With the aid of a drawing mirror the nucleus, year rings and edges amplificated positions were registered and their distances measured according to different procedures below consigned. The distances were taken from the perpendicular projections of the extreme points of every year ring related to an ideal longitudinal axis passing through the nucleus. Therefore all otolith are

In the preparation of otoliths great care was taken to make the cut exactly through the nucleus. The exact position of the nucleus was determinated by means of a binocular microscope (12x or 25x) and marked by pencil; with the aid of a blunt pincet it was intented to cut the otoliths along the major (longitudinal) axis. In some subsamples the otoliths were cut along the transversal axis. After cutting the otholith surface was polished by machine when necessary and then burned.

DESCRIPTION OF THE BRILL SAGITTAE

The Brill otolith used in this study has been always the sagitta or saccular otolith (FIGURE 2). During metamorphosis, that in cultivated Brill takes place at an age of about 2 months (JONES,1972), the position of sagitta otoliths changes with the rest of the cranial bones (FIGURES 3-4). The two chambers of sagitta otoliths are not more in the same plane, but one upper the other one. In the upper one, a rather 'asymmetrical' otolith is present, in the lower one, a more 'symmetrical' sagitta. The Brill both sagitta otoliths external appearance is showed in the FIGURE 5.

The sagitta has a moderately rounded posterior part -that in the older ones appears almost bilobular- while the "rostrum" or anterior part is more lightly pointed. Dorsally there is a small and little sharp "antirostrum" and generally a lighly "excisura". The ventral, anterior and posterior rims are more or less serrated and grooves perpendicular to the outer margin of the otolith are found mainly in the ventral lateral area in otoliths of older exemplars. A deep groove, the "sulcus acusticus", is found on the proximal surface and runs anteroposteriorly. The sulcus is not divided into an "ostium" and a "cauda", but appears with a wideness almost constant. The inner (proximal or with-sulcus) surface of the otolith is convex while the outer (distal) side is slightly concave; this concavity in the otoliths from some older fish becomes more marked.

The unburnt sagitta viewed by transmited ligth presents a central opaque core or nucleus followed by alternating hyaline (translucent) and opaque zones, more or less concentric. When viewed under reflected ligth the opaque zones appear white and the hyaline dark. The rings are most clarly defined on the distal (outer) surface. On the proximal (inner) surface of the otolith practically no rings can be observed. It is not always possible to follow easily the same zones along the anterior and posterior side of the otolith, in particular in otoliths of Brill older than four year. In the otoliths of older fish the rings on the edge are narrower and more closely spaced.

SYMMETRY IN BRILL OTOLITHS

Two aspects of the symmetry of the sagitta otoliths were studied: 1) the relation between sagittae sizes and sagittae size and body-length and 2) the position of the nucleus.

The relation between sagittae sizes and between sagittae size and body-length were studied in intact, untreated otoliths. Sizes were measured using a binocular microscope with drawing mirror.

The position of the nucleus in both sagitta otoliths was studied in intact, untreated otoliths. The otoliths were put in a petri dish that was filled with water to a constant level. With a binocular microscope (12 times magnification) and drawing mirror and using reflected light against a dark background the total distance from extreme rostrum (anterior part) to posterior rim and the distance from the posterior rim to the center of the nucleus were measured along its longer axis. With these measurements a new parameter was calculated allowing a comparison between otoliths from different fish-sizes: 'Nucleus Position Ratio' (NPR).

NPR(i,j) = (O - N) / N

where, O = total size of the otolith, in arbitrary optical units (1 a.o.u. = 0.083mm); N = distance from the posterior rim to the nucleus center, in the same units; for i = lower (symmetrical) sagitta and j = upper (asymmetrical) sagitta.

The otoliths used to study the symmetry in both sagitta were selected from the market samples (fish size > 30 cm) and from the 1981-1985 DYFS (fish-size <30 cm). A new otolith sample was build up selecting for each sexe five otoliths per cm-bodylength class, that were encountered firstly when going through the market and DYFS samples. For the biggest and smallest sizes of the body lengths distribution less than 5 individuals were available. Only those otoliths were selected that were not damaged or 'crystalline' and in which both upper and lower (symmetrical and asymmetrical) otolith were available. In total 275 pairs of otoliths -120 from males and 155 from females- have been used. The range of body length was 7-49 cm for males and 7-60 cm for females.

ZONATION AND EDGE TYPES IN BRILL SAGITTAE

The seasonal change in the type of edge of the otoliths was studied in otoliths of 1539 fish -529 males and 1010 females- from market samples collected in 1984 and with a length range of 30 to 60 cm. In addition the otoliths of 110 fish from the DYFS, also collected in 1984, were studied (length range: 8 - 52 cm). Indistinctly upper (symmetrical) or lower (assymetrical) otoliths were used. In a subsample of the 1984 market sample otoliths it was observed that edge type in both symmetrical and asymmetrical otoliths were similar.

The type of edge found in each burned otolith was classified according to the following three classes :
1) Opaque (Op), light zone deposited before the formation of the annual ring in the current year,
2) Hyaline (Hy), dark zone corresponding to annual ring of the current year,
3) New Opaque (nOp), light zone formed after the recent deposition of the annual ring.
The discrimination between "Opaque" and "New opaque" categories was made according the wideness of the light edge: for the first half part of the year relatively wide in the former and small in the latter category. In general, this assignment was rather easy, except for some of the older fish from second quarter.

PROCEDURES OF MEASURING

Assuming a direct proportionality between the body length and the sagitta size in the time of formation of every year ring, thirteen different procedures of measuring the distances were planned. The procedures diagrams and formulae used for the back-calculation are presented in the FIGURE 6.

A new index has been stablished for comparing the deviations of the backcalculated results obtained from different procedures with the values achieved from the so considered 'standard procedure' -arbitrary chosen-, that is, the 'Standard Procedure Deviation Index' (SPDI) :

$$SPDI = ((Xij - Xsj) / Xsj) * 100$$

where, Xij = the mean length backcalculated value from the (i) procedure and for the (j) year ring; Xsj = the mean length backcalculated value from the 'standard' (3th. or 'diametrical') chosen procedure and for each year ring.

The comparison of the 13 different backcalculation techniques was carried out using measurements of 53 paired sagittae from fish with a length range of 31-47 cm and divided into five subsamples of 16, 9, 12, 11 and 5 pairs respectively. The 'diametrical' procedure for measuring, that is the 3. (or 8.,11.,12.) was always chosen (FIGURE 6).

Some exact conditions were previously impossed in the selection of sagittae in order to obtain a more accuracy comparison: both otoliths of each pair had to be available, undamaged, the nucleus perfectly evident and the year rings and the edges must appear in the same plane.

BACKCALCULATION OF BODY-LENGTH

The body-length at age was backcalculated from a subsample of 607 otoliths -238 males and 369 females with a length between 30 and 60 cm- collected in the market sampling in 1984. To this sample 88 otoliths -44 males and 44 females with a length between 8 and 51 cm- were added from the DYFS of 1984. Most of the otoliths were symmetrical (87 %) and longitudinally cut (95 %). All the sagittae were at least read twice by the same reader but in different months; when differences in the measurements occured one third measurement was made. Since special difficulty was found in the determination of the first annual ring, which is often not so distinct as the other rings, an extra reading was necessary in many cases.

Two attempts for backcalculation have been made: (1) assuming a direct proportional relationship between the indicator marks (year rings) and the succesive body lengths -LEA's formula (1910)-, and (2) introducing a correction factor in the linear relationship -LEE's formula (1920)-, that is,

$$(1) \qquad Li = (Oi / Ot) * Lt$$

$$(2) \qquad Li = ((Oi / Ot) * (Lt - a)) + a$$

where Lt = fish total body length at the capture (cm); Li = fish body length at the "i" year ring formation time (cm); Ot = sagitta otolith total length (in arbitrary optical units [a.o.u.]); Oi = sagitta diametrical distance for the "i" year ring [a.o.u.]; a = correction factor, corresponding to the 'intercept' value obtained in the predictive linear regression between the Brill bodylengths and the symmetrical sagitta sizes for both sexes combined (TABLE 6 : a = 0.849).

STATISTICAL METHODS

Analysis of variance was carried out used according to (SOKAL and ROHLF 1969). Linear regression models and statistical analysis of slopes and intercepts were studied according to MONTGOMERY and PECK (1982) and RICKER (1973).

RESULTS

SYMMETRY IN SAGITTAE

From the functional linear regressions applied to the scattered data of all symmetrical sagittae against all asymmetrical sagittae data,(FIGURE 7 and TABLE 1) a strict 'symmetrical relation' does not appear. The confidence limits of the slope of the regression lines do not include the slope of the strict symmetrical relation (v=1.00); However the linear regression can be accepted as passing through the origin (u=0). The comparison of mean 'Nucleus Position Ratios' (NPR) for paired -symmetrical (very close to 0.5) and asymetrical (about 0.36)- sagittae clearly indicates that they cannot be accepted to be equal for males, females and sexes combined (TABLE 2). In the symmetrical otolith the NPR value is close to 0.50, whereas in the asymmetrical otolith the NPR=0.36. In both symmetrical and asymmetrical otoliths the NPR value decreases with increasing fish size (FIG 8 and b) This relation is more marked in the asymmetrical otolith and the relation appears to be similar between male and female Brill (TABLE 3).

BODYLENGTH : SAGITTA SIZE RELATIONSHIP

In the FIGURES 9a and 9b the scatter of points of 275 Brill body lengths against (a) upper ('asymmetrical') or (b) lower ('symmetrical') sagittae sizes are presented. It is apparent that the data can be reasonably adjusted to a linear regression model. The expressions of the functional (Y=u+vX) and predictive (Y=a+bX) linear regressions for different groups ('asymmetrical' and 'symmetrical') and sets (males, females, both sexes combined) are presented in the TABLES 4a and 4b. The slopes of the predictive and functional regressions of male Brill fall within the 95% confidence limit of that of female Brill and vice versa, so it can be accepted that both sexes have a common slope and that the regression of the combined data give an adequate describtion of the relation for both male and female.

In the predictive linear regression for the symmetrical otoliths the regression line can be accepted as to pass through the origin, but for the asymmetrical otolith the intercept significantly differs from 0. However, when applying the functional regression it can be accepted that for both symmetrical and asymmetrical otoliths the regression lines pass through the origin.

EDGE TYPES

FIGURE 10a shows the monthly percentages of hyaline edges for males and females in 1984: both distributions are very similar and show only one peak in May. In FIGURE 10b the percentages of occurence of opaque, hyaline and new opaque edges are presented for the sexes combined (see also TABLE 5). The frequencies of edge types from the DYFS otoliths are compared in TABLE 6. From this table it appears that the smaller fish form their annual hyaline ring earlier in the season than the bigger ones. In April-May the proportion of new opaque edges (nOp) appears to be bigger in the smaller fish.

PROCEDURES OF MEASURING

The mean backcalculated lengths at age as obtained by the different procedures are presented in the TABLES 7 and 8. The variances of the different procedures did not differ, except for the 1st and 2nd year ring in the comparison of procedures 1-10 (results not shown). A t-test of the means of the different procedures showed that mainly procedure 9 and 10 gave significantly different results for especially the first two year rings. In general the differences between the procedures are relatively small. Only for the 1st and 2nd year ring differences up to 9% occur (TABLE 9). The differences between the procedures decline for older year rings. The 'standard' procedure for the symmetrical otolith (procedure 3) always gave higher values than that for the asymmetrical otolith (procedure 8).

Back-calculating in the anterior direction (procedure 1 and 4) in symmetrical and in the posterior direction (procedure 7 and 10) in the asymmetrical otoliths gave higher values than the opposite directions. The 'standard' procedure tends to obtain rather average values within the group of symmetrical otoliths. In any case it appears that at more advanced age the difference becomes proportionallysmaller. No significant differences are shown in the mean back-calculated length using transversally cut saggitae (procedure 11 or 12). The back-calculation procedure using otoliths in which the year rings are deposited in a rather iregular (procedure 13), give on average lower body lengths although the difference is not significant.

GROWTH OF BRILL

In TABLES 10a and 10b the mean back-calculated body lengths from commercial and research vessel samples are presented. The length frequency distribution for the first five age groups as obtained by back-calculation of otoliths from commercial samples are shown in FIGURE 11 for the sexes separately. Mean length at age in female is greater than in males for all age groups but especially from age 3 onwards. A statistical test of the mean back-calculated lengths of male and female is presented in TABLE 11.

In FIGURE 12 the back-calculated lengths of yearclasses 1978 to 1982 is compared at an age of 1, 2 and 3 year. From this figure it appears that the mean length by yearclass gradually increases from the 1978 yearclass up to the 1982 yearclass. This gradual shift is apparent at all three ages compared. The results of a multiple comparison of mean back-calculated lengths among yearclasses for the first five ages is given in TABLE 12 and shows that the differences are significant.

COMPARISON OF BACK-CALCULATED LENGTH AND THE SURVEY LENGTH

In order to check whether the length distribution as obtained by back-calculation of otoliths is in agreement with the length distribution of Brill in sea, the seasonal length frequency distributions were studied using data from the Demersal Young Fish Survey along the continental coast of the Nertherlands, Germany and Denmark and from the Beach Sampling Program (see van LEEUWEN and RIJNSDORP 1986). The length frequency distributions are plotted in FIGURE 13 for different periods of the year. In July and August small Brill of the year show up in the catches along the beach. In September-October these 0-group fish can still be recognized in the peak at 7 cm in the beach sampling length distribution. In the deeper water sampled in the DYFS no 0-group Brill are caught. During the following winter, spring and summer the 0- and 1-group Brill can not be easily be detected in the length distributions. Not until the September-October DYFS survey the 1-group appears in the length distribution of both beach samplingsurvey and DYFS. In the latter, two clear peaks occur at about 12 and 26 cm, reflecting the presence of the 1- and 2-group Brill. In April-May again two clear peaks occur at about 15 cm and 30 cm body length, reflecting the same cohorts, now as 2- and 3-group.

The frequency distribution of back-calculated lengths as shown in FIGURE 11 reflects the length distribution of Brill in May and June, when the annual ring is deposited, and thus can be compared best with the survey length distributiions from April-May. A comparison shows a nice correspondence for the 2- and 3- group Brill. From the 1-group Brill (<10cm) only very few individuals were caught in the surveys. In 2-group Brill mean back-calculated length is sligthly higher than the length as observed in the young fish surveys: respectively 18 and 16 cm.

DISCUSSION

As could be expected from the particular process of metamorphosis in flatfish, the sagittae of Brill are relatively different in both the absolute size and in the position of the nucleus. In the smaller, lower otolith the nucleus is located in the center of the otolith, half way along the longitudinal axis. In the slightly larger (3%) upper otolith the nucleus is located at one third from the posterior extreme. These differences justify the use of the terms 'symmetrical' and 'asymmetrical' otolith and are a reason for caution when using the otoliths for back-calculation purposes.

Linear regressions of fish body length agains sagittae size showed a good fit. In the symmetrical otolith no significant difference was found between the regreesion lines for male and female. Because the regression line for male and female combined passes through the origin, the assumption of the back-calculation technique of a strict proportinal relationship is corroborated. One objection, however, can be made to this conclusion: for the calculation of the regression line only otoliths of fish bigger than 7 cm length have been used.

The observation that in Brill sagittae only one hyaline ring is formed each year validates the age determination and corroborates the assumption of the back-calculation technique. The annual ring is formed between April and June, which period coincides with the spawning period. Males and females present a similar pattern in the timing of ring formation but in smaller Brill (< 30 cm) there is an indication that the annulus formation occurs slightly earlier in the year. The annulus formation in these smaller Brill is probably not related to the reproductive cycle because the fish were mainly juveniles.

The hyaline edges of burnt otolith always appear to be very narrow in both small and big fish. However, in the smallest fish examined (8-9 cm) the hyaline edge is especially thin, in many cases causing difficulties in its determination. The examination of the type of edge is easiest done in burnt otoliths. The new opaque (nOp) edge, in general not existent or very narrow in May-June, becomes more and more wide in the second part of the year, opening the possibility to study the seasonal growth from the increasing width in the opaque zone.

Of all experimental measuring procedures employed in this study, the diametrical technique applied to the symmetrical otolith, preferentially cut in the longitudinal plane (procedure 3) seems to be the most adequate technique for the back-calculation of the body-length. It gives average values between the results of the other procedures and it is perhaps easier and simpler to carry out in the routinal praxis. The preference for the use of lower otoliths is based on the fact that in these otoliths the 'Nucleus Position Ratio' is almost constant, whereas in the upper asymmetrical sagittae the asymmetry increases at increasing body-length. However, the results obtained in this study indicate that also the assymetrical otolith can be used when the total diameter of the rings are measured (procedure 8) and that transversally cut otoliths can be used without reasonable suspicion. For the sagittae with a rather iregular ring formation procedure 13 can be applied, taking into account that the back-calculated lengths are sligthly lower than from the 'standard' procedure. Absolute equality in the results obtained from the different procedures does not exist, even in the symmetrical otolith. Part odf the differences can be explained by errors in the preparation, reading and measuring. These are probably not very important and can be reduced when the back-calculation is carried out with large samples.

The back-calculated length of the 2- and 3- group Brill were in reasonable agreement with the length frequency distributions from the young fish surveys. The back-calculated lengths are also in agreemnet with the scarce and scattered data presented by several authors in the beginning of this century, although in some cases their interpretation was different (FIGURE 14). The correspondance between the length distributions obtained from the back-calculation of otoliths and from the young fish surveys validates the back-calculation technique, although the accuracy of the length back-calculation acn not be determined without a special study using tagged fish.

By applying LEE's formula higher back-calculated lengths are obtained. The difference was bigger for the first age (about 0.7 cm) but became progressively smaller for the older fish and disappeared after the 4th age. Perhaps the use of this correction is justified when new dat on the relation between sagittae size and body length become available for small fish (<8 cm). For this moment the direct proportionality (LEA's formule) can be used with reasonable confidence.

The difference between the growth between male and female Brill becomes particularly evident at the age of 3 and is probably related to the generally earlier maturation of male flatfish (ROFF 1982).

In the comparison of the back-calculated length of different yearclasses (TABLE 12 and FIGURE 12) significant higher values were obtained for the more recent yearclasses. For the 1982 and 1981 yearclass this could be related to the fact that in 1984 -the year of observation- these yearclasses were not yet fully recruited to the fishery, so the commercial samples are biased towards the fast growing fish (LEE's phenomenon, LEE 1914). This explanation is partly supported by the results of a comparison of the back-calculated length from commercial samples with that from otoliths samples of young fish survey. In the survey samples from 1984, the mean back-calculated length of yearclasses 1981 and 1982 were smaller. However, this can not explain why the decline in back-calculated length still occurs in yearclass 1980 to 1978, because these yearclasses are fully recruited to the fishery. For this trend at the moment no adequate explanation can be given, although it does not seem to be due to an artefact in the back-calculation or inaccuracies in the otolith measuring.

Finally, it seems very convenient to stress the great care that must be taken in the preparation of otoliths for backcalculation purposes, in particular the process of cuting and polishing. The latter should only be done when strictly necessary, because it is very easy to destroy or diminish the nucleus and first annulus. The sagitta section should pass exactly through the nucleus whose position can be easily checked and marked in the intact otolith external face. The burning of the cut sagittae eases very much the reading and the assignment of yearrings. Only sagittae must be employed accomplishing some conditions : entire and not crystalline otoliths, evident nucleus, complete edges, and nucleus, year rings and edges in the same plane.

ACKNOWLEDGEMENTS

I am greatly indebted to the Netherlands Institute for Fishery Investigations (R.I.V.O.) at IJmuiden for providing so many research facilities and making available all materials. I am also very thankful specially to my supervisor, Mr A.RIJNSDOORP, for all his advices and careful assistance and to Dr. N.DAAN and to P.van LEEUWEN for their help.

The work reported in this paper was performed during a tenure of a 'Research Institute for Fish Science and Technology' (Biscay, Basque Country, Spain) scholarship.

REFERENCES

BAGENAL,T.B. and TESCH,F.W. 1978.- Age and growth. In "Methods for Assessment of Fish Production in Fresh Waters" (T.B.Bagenal, ed.),pp.365. Blackwell,Oxford.

BARTLETT,J.R.et al. 1984.- The use of analysis of covariance in the back-calculation of growth in fish. J.Fish Biol.24,201-213.

CHRISTENSEN,J.M. 1964.- Burning of otoliths, a technique for age determination of soles and other fish. J.Cons.29(1):73-81.

CUNNINGHAM,J.T. 1891.- The rate of Growth of some Sea Fishes and their Distribution at Different Ages. Journ.Mar.Biol.Assoc.2,95-118.

CUNNINGHAM,J.T. 1891.- Report on the Probable Ages of Young Fish collected by Mr.Holt in the North Sea. Journ.Mar.Biol.Assoc.2,344-358.

FRAZER,C.McL. 1916.- Growth of the spring salmon. Trans.Pac.Fish.Soc.Seattle 1915,29-39.

FULTON,T.W. 1904.- The rate of growth of fishes.- 22d.Ann.Rep.Fish.Board for Scotland for 1903.

FULTON,T.W. 1905.- On the distribution and seasonal abundance of flatfishes (Pleuronectidae) in the North Sea. Report on

Fishery and Hidrographical Investigations in the North Sea and adjacent waters for 1902-1903 (Northern Area):471-618.

GELDENHUYS,N.D. 1973.- Growth of the South African maasbanker Trachurus trachurus L. and Age composition of the catches, 1950-1971. Investl Rep.Sea Fish.Brch S.Afr. 101:1-24.

JOHANSEN,A.C. 1915.- Funfter Bericht uber die Pleuronectiden in der Oostsee. Rapp.P.-V. Reun.Cons.Perm.int.Explor.Mer 22:1-104.

JONES,A. 1972.- Studies on egg development and larval rearing of Turbot, Scophthalmus maximus L., and Brill, Scophthalmus rhombus in the laboratory. J.Mar.biol.Ass.U.K.52:965-986.

LEA,E. 1910.- On the methods used in herring investigations. Publs.Circonst.Cons.perm.int.Explor.Mer 53,7-25.

LEE,R.M. 1912.- An investigation into the methods of growth determinations in fishes by means of scales. Publs.Circonst.Cons.perm.int.Explor.Mer 63,3-35.

LEE,R.M. 1920.- A review of the methods of age and growth determination by means of scales. Fishery Invest.,Lond.,Ser.2:4(2),32.

van LEEUWEN,P.I. and A.D.RIJNSDORP 1986.- The analysis of the growth of turbot by back-calculation of otoliths ICES CM. 1986/G:50.

MARECOS,M.L.S., 1974.- Idade e crecemento do carapau do Cunene (Trachurus trachurus trecae Cadenat). Publ.Mimeo.M.E.Bioceanol.Pescas,Angola,17(8):57pp.

MONTGOMERY,D.C. and E.A.PECK, 1982.- Introduction to linear regression analysis.Wiley.New York.

PANNELLA,G. 1980.- Growth patterns in Fish Sagittae, in: "Skeletal Growth of aquatic organisms" (D.C.Rhoads and R.A.Lutz,eds.),pp 519-559,Plenum,New York.

REIBISCH,J. und Mitarbeiter, 1927.- Die Verteilung der jungen Plattfische des ersten Jahrganges an der deutschen Ostseekuste in Jahre 1925.- Wiss.Meeresunters.Abt.Kiel,20.

RICKER,W.E. 1973.- Linear regressions in fishery research. J.Fish.Res.Board Can.30: 409-434.

ROFF,D.A. 1982.- Reproductive strategies in flatfish: a first synthesis. Can.J.Fish.Aquat.Sci. 39:1686-1695.

SAETERSDAL,G.S. 1953.- The haddock in Norwergian waters. II. Methods in age and growth investigations. Repts.Norwergian Fish. and Marine Invest.,10(9):46pp.

SHERRIFF,C.W.M., 1922.- Herring investigations. Report on the mathematical analysis of random samples of herring, with an introductory note by Prof.D'Arcy W.Thompson. Fishery Board for Scotland, Sci.Invest.,1922,No.1,25pp.

SOKAL,R.R. and F.J.ROHLF 1969.- Biometry. Freemen.San Francisco.pp 736.

WALLACE,W. 1923.- Report on experimentals hauls with small trawls in certain inshore waters off the east coast of England. Fishery Invest.,London Ser 2(5)5,30.

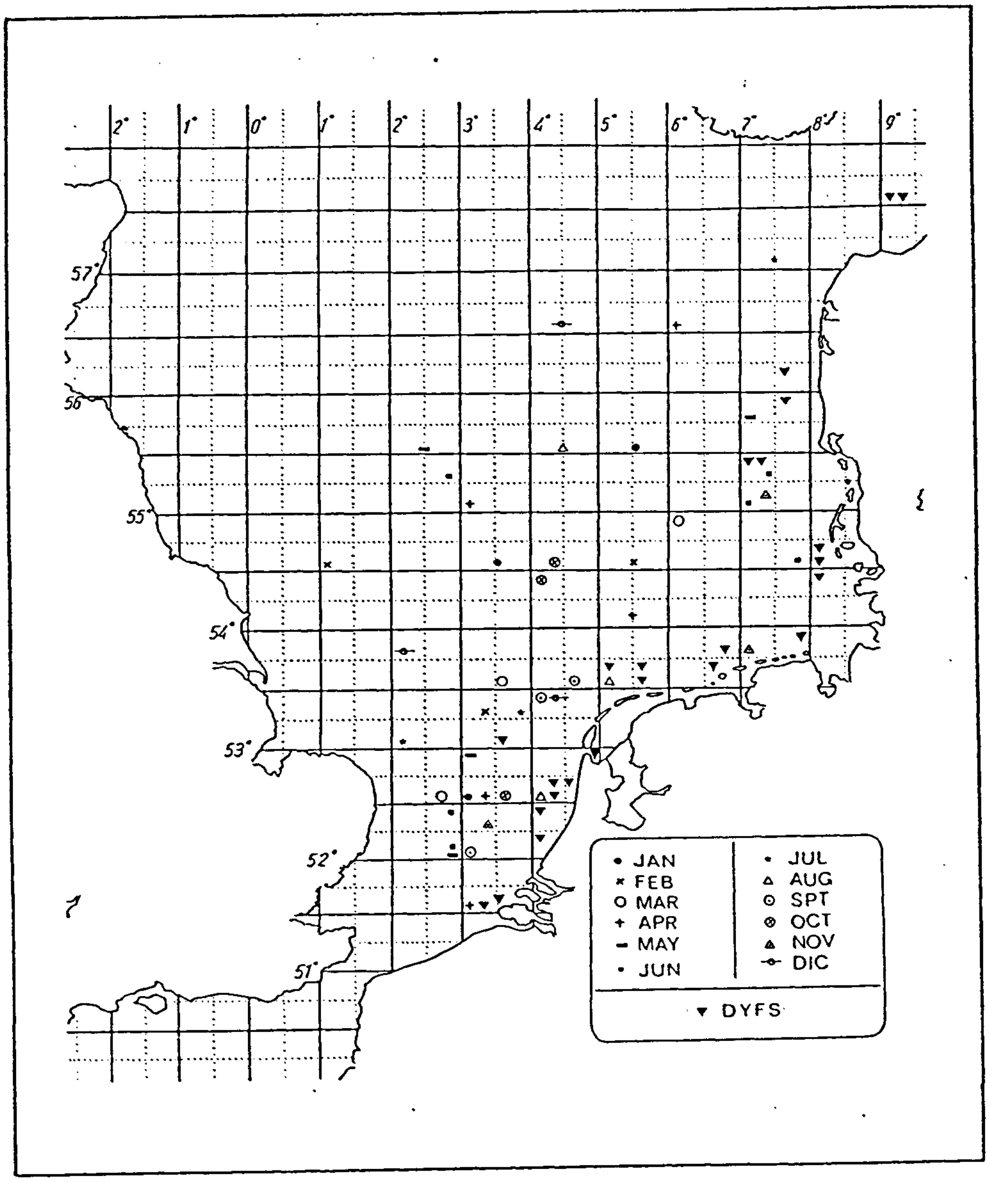


FIGURE 1 : Origin of Brill samples from commercial beam trawl landings in the North Sea from and from Demersal Young Fish Surveys (DYFS) in 1984.

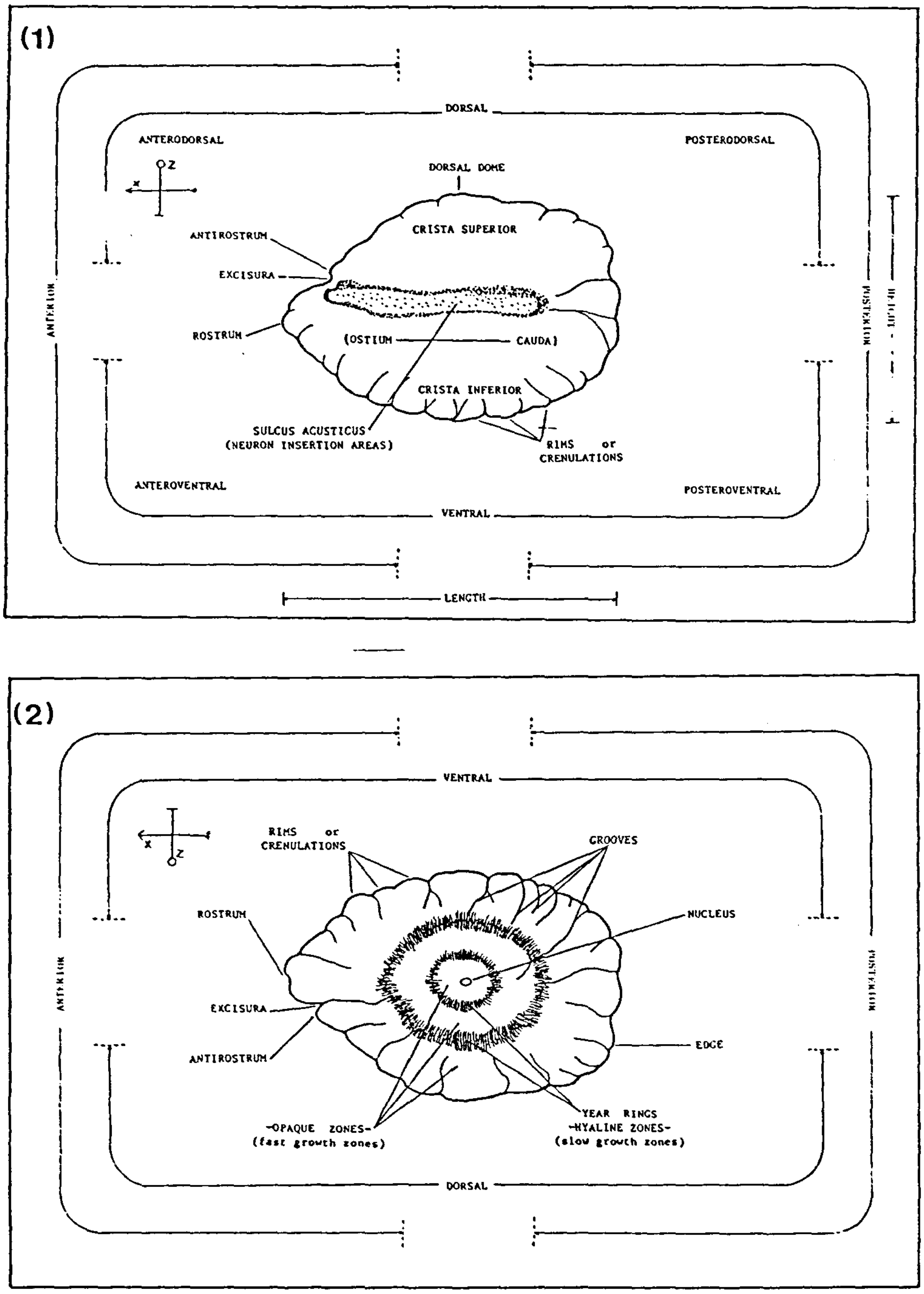


FIGURE 2 : (1) Proximal (or internal) and (2) distal (or external) faces of a Brill lower ('symmetrical') sagitta otolith. Adapted to Brill from FRIZELL and DANTE (1965) and PANELLA (1980) otolith models.

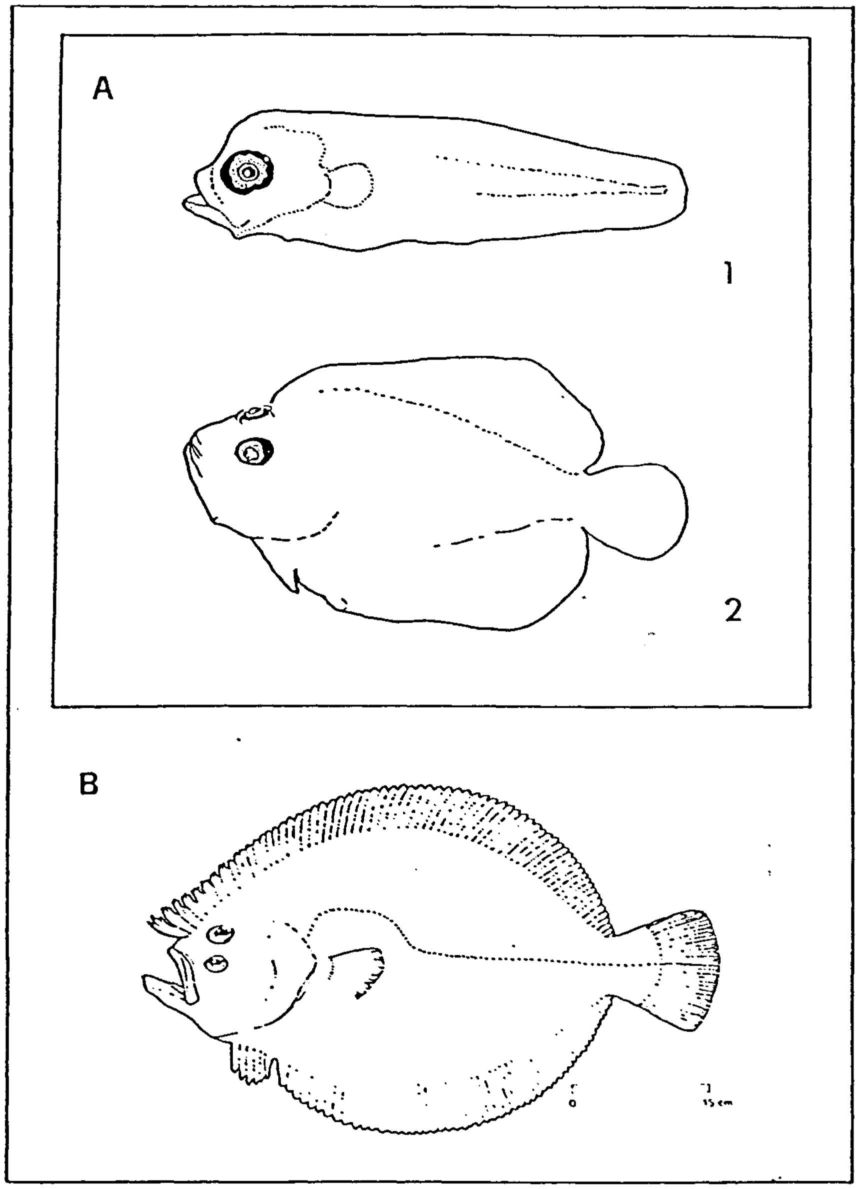


FIGURE 3: A. Stages of larval development of the Brill (at decreasing magnifications). The lengths are: (A/1):5.8 mm; (A/2):17 mm (just metamorphosed; 61 days). Redrawn from JONES (1972).
B. Shape of an adult Brill.

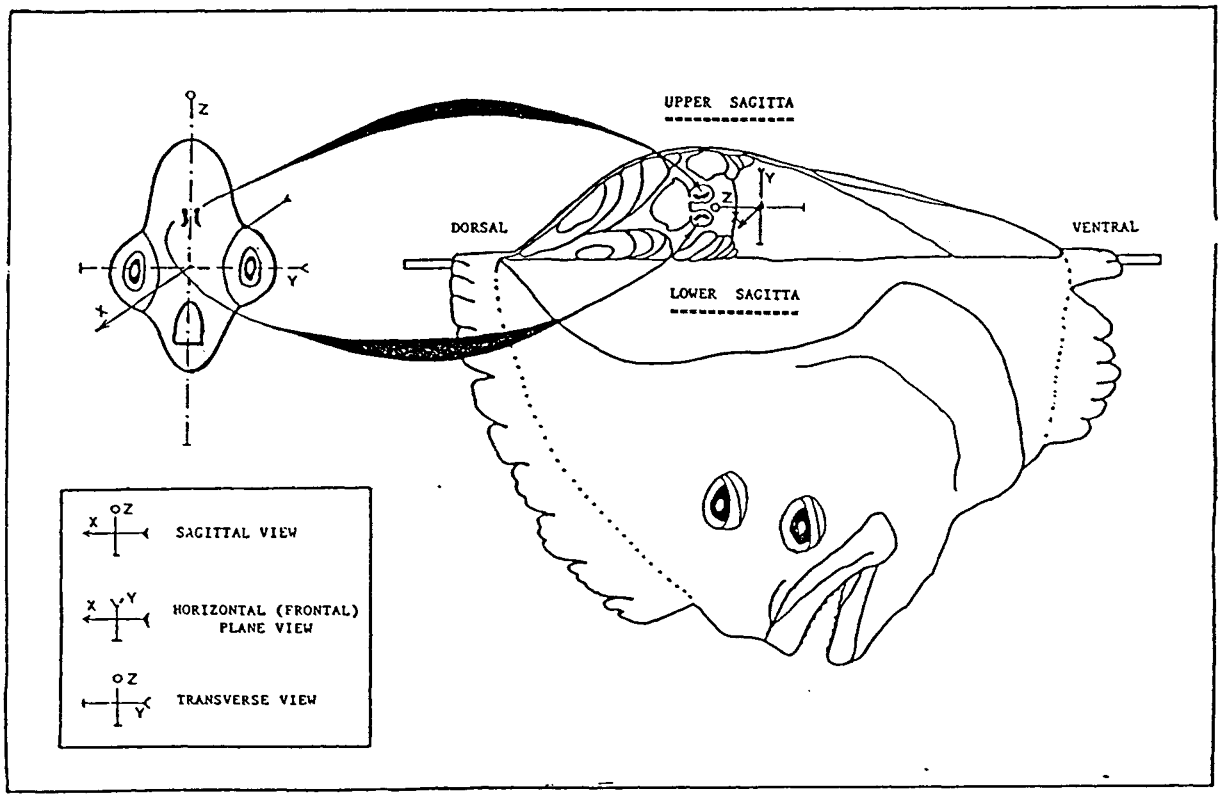


FIGURE 4 : Diagram of sagittae positions in an ideal Brill pre-metamorphosed larva and in an adult exemplar. On the left corner, the axial representations of three different planes (adapted to Brill from the general model of PANELLA (1980).

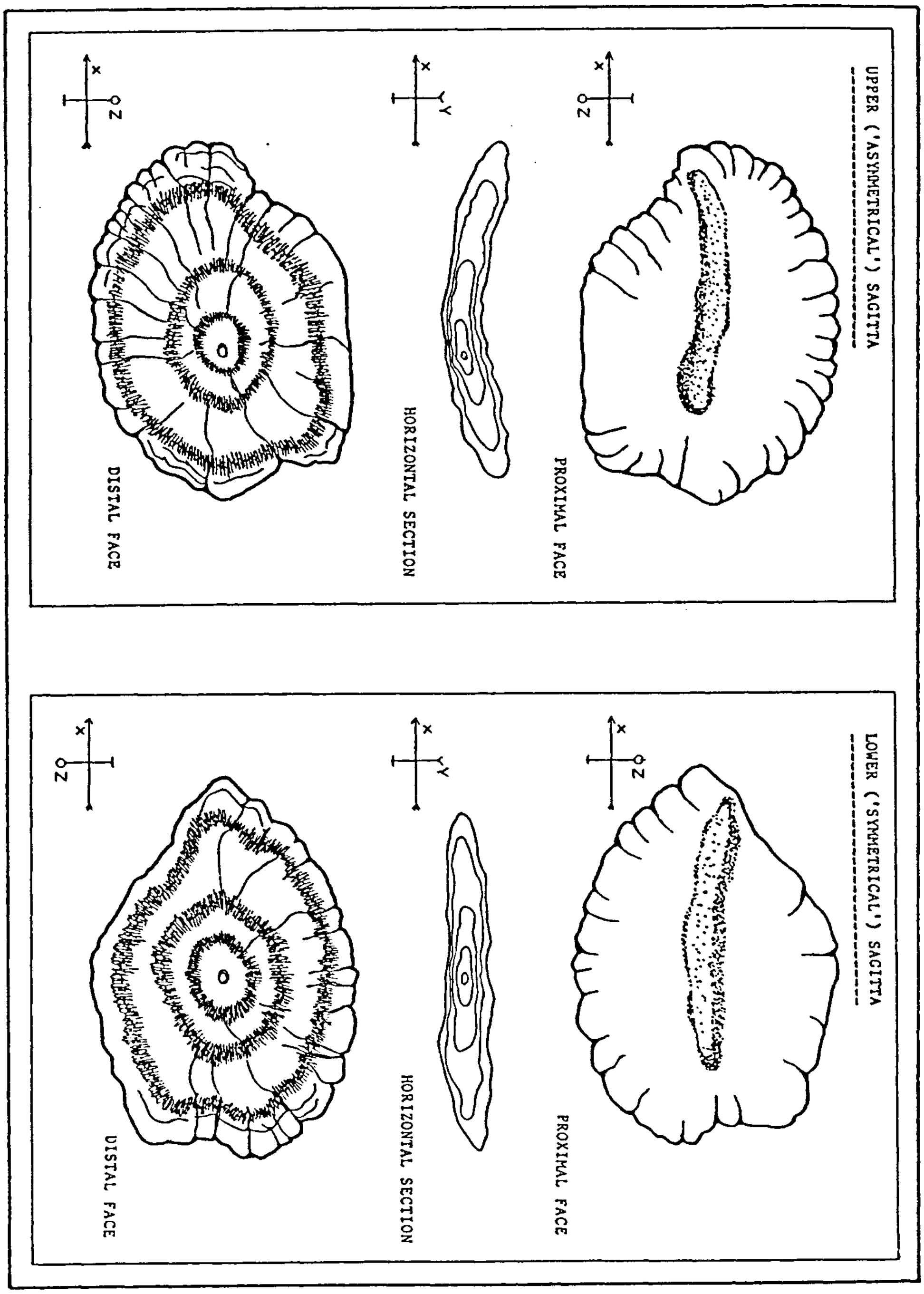


FIGURE 5 : Intact proximal and distal faces and burnt horizontal section of an upper ('asymmetrical') and a lower ('symmetrical') sagitta drawn from a female Brill.

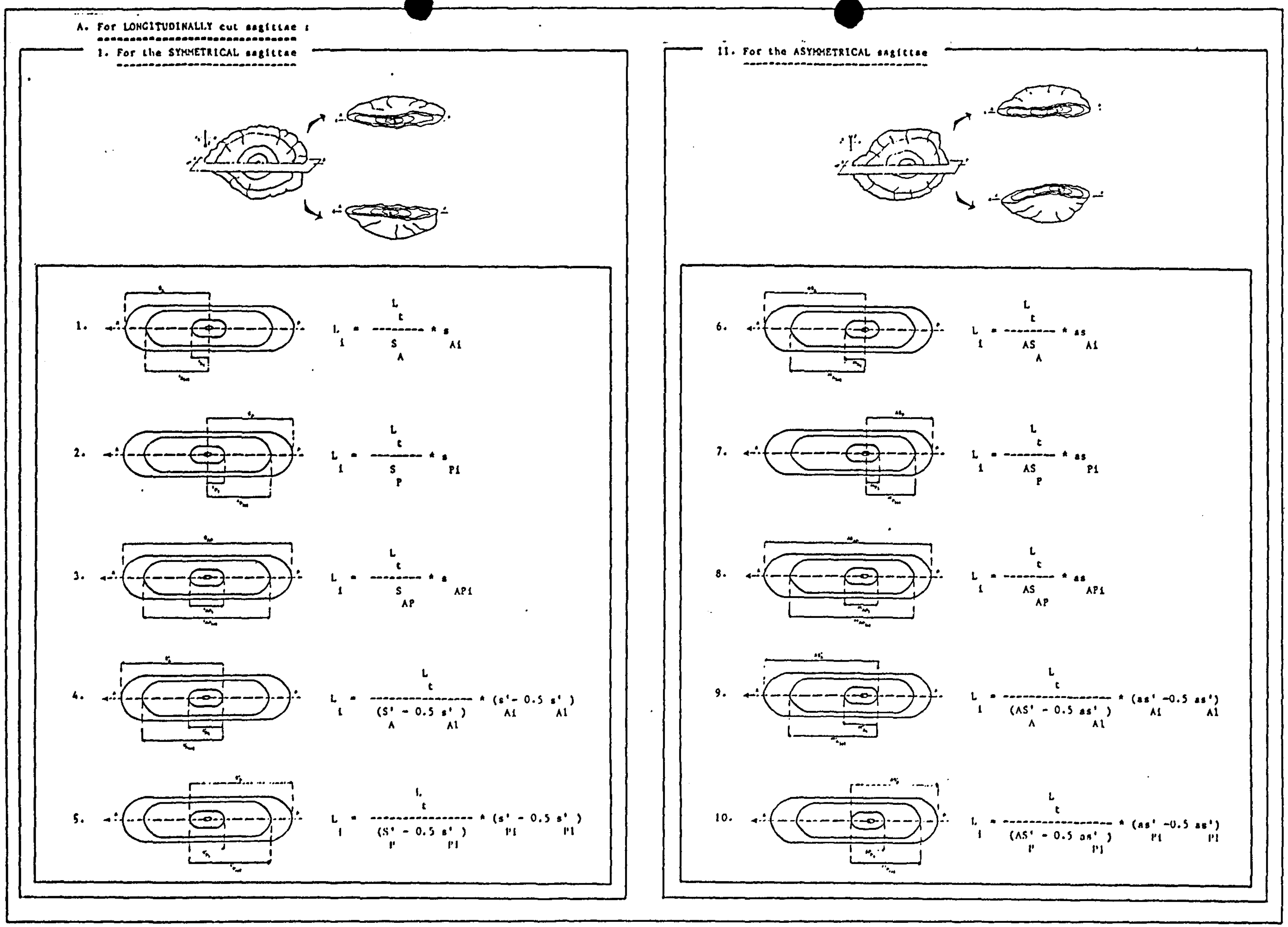
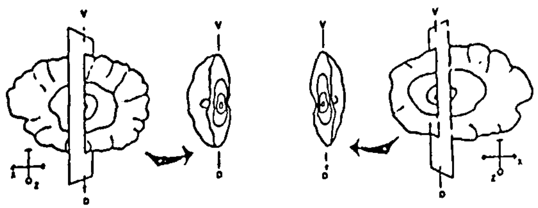
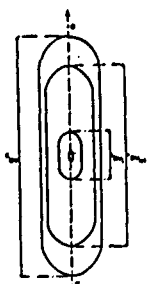


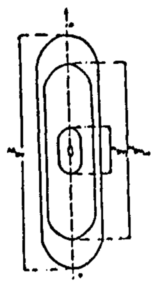
FIGURE 6: Thirteen different procedures diagrams and formulae used for the Brill length back-calculation according to the kind of sagitta and the plane of sectioning employed:
A: LONGITUDINALLY cut for I. SYMMETRICAL otolith and II. ASYMMETRICAL otolith
B: TRANSVERSALLY cut and C: For sagittae with a irregular year ring deposition

B. For TRANSVERSALLY cut sagittae



11. 

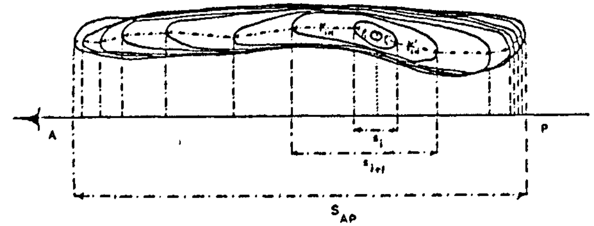
$$L_i = \frac{L_t}{S_{DV}} * s_{DVi}$$

12. 

$$L_i = \frac{L_t}{AS_{DV}} * as_{DVi}$$

C. Otoliths with rather curve year rings disposition

The distances are measured according to hypothetical straight lines that starting from the nucleus center or/and from both more extreme points of each year ring join the next both extreme points of the next year ring and/or the edges.



13. $$L_i = \frac{L_t}{O} * R_i$$

● Notation :

. For 1-12 :

L_t = fish total body length at the capture (in cm)

L_i = fish body length at the 'i' year ring formation time (in cm)

i = 1,2,3,...

S, AS = symmetrical or asymmetrical sagitta otolith total length (in arbitrary optical units : a.o.u.)

s,as = symmetrical or asymmetrical sagitta otolith distance for the 'i' year ring (in a.o.u.)

A,P,AP = anterior, posterior, anterior-posterior sense in the longitudinal axis

DV = dorsal-ventral sense in the transversal axis

. For 13 :

$O = \sum R_i$

$R_i = (r_i + r'_i)$

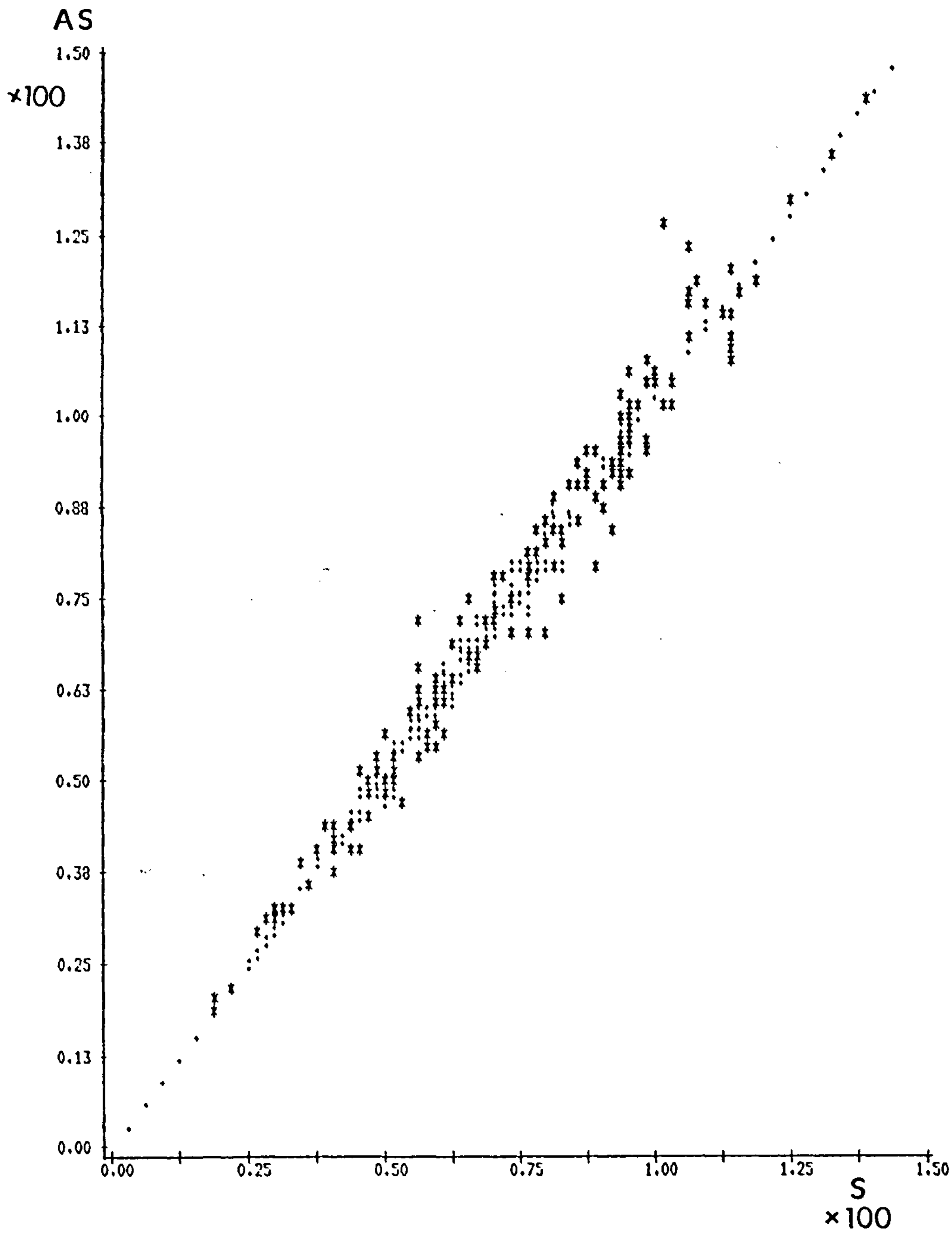


FIGURE 7 : Relationship between upper or 'asymmetrical' (AS) and lower or 'symmetrical' (S) sagittae sizes in arbitrary optical units (a.o.u.) from a sample of 275 Brill paired otoliths. (1 a.o.u. 0.0833 mm).

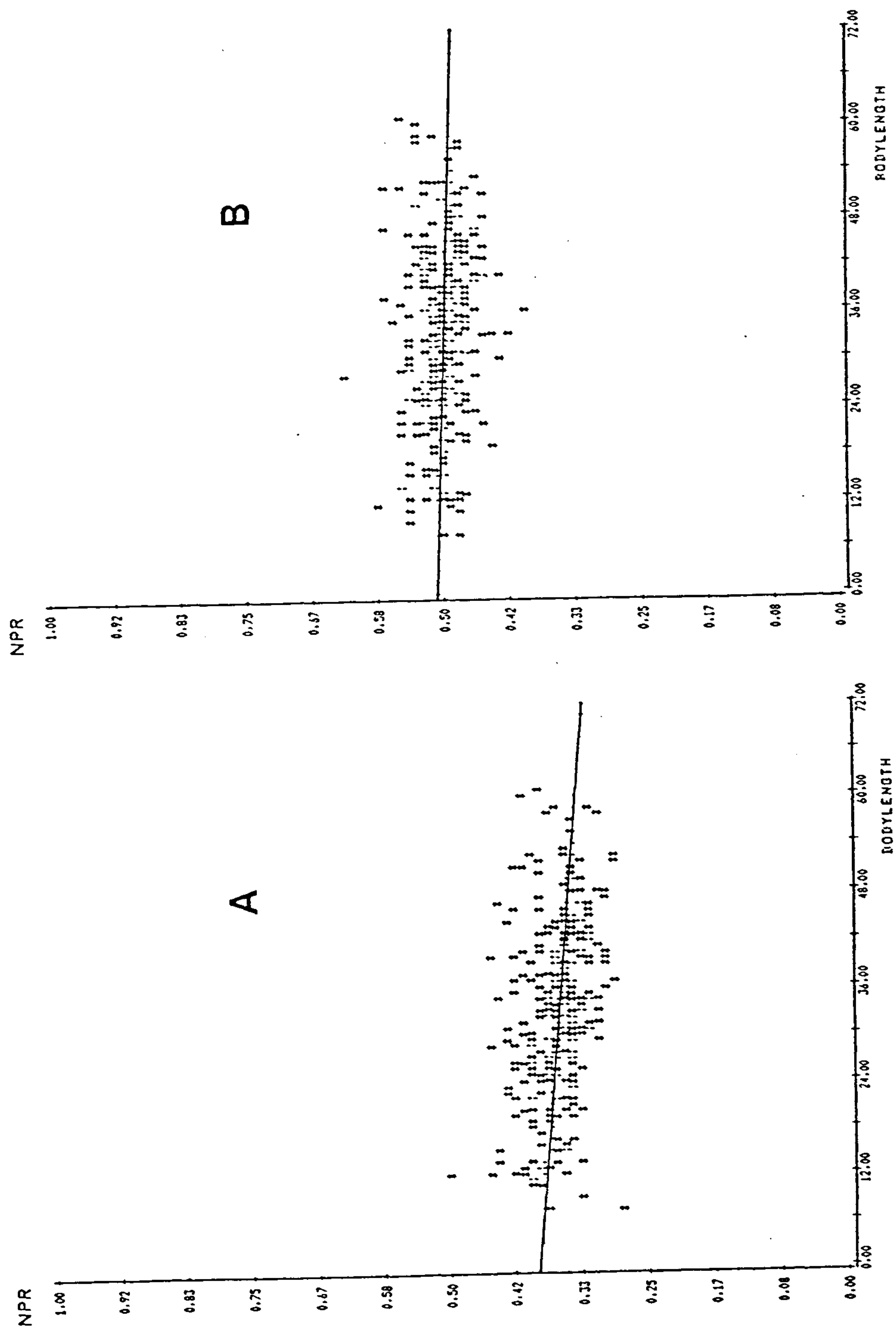


FIGURE 8 : Relationship between 'Nucleus Position Ratio' (NPR) in (A) upper ('asymmetrical' (AS)) or (B) lower ('symmetrical'(S)) sagittae and fish body length (in cm) from a sample of 275 Brill. (For explanation of 'NPR', see the text).

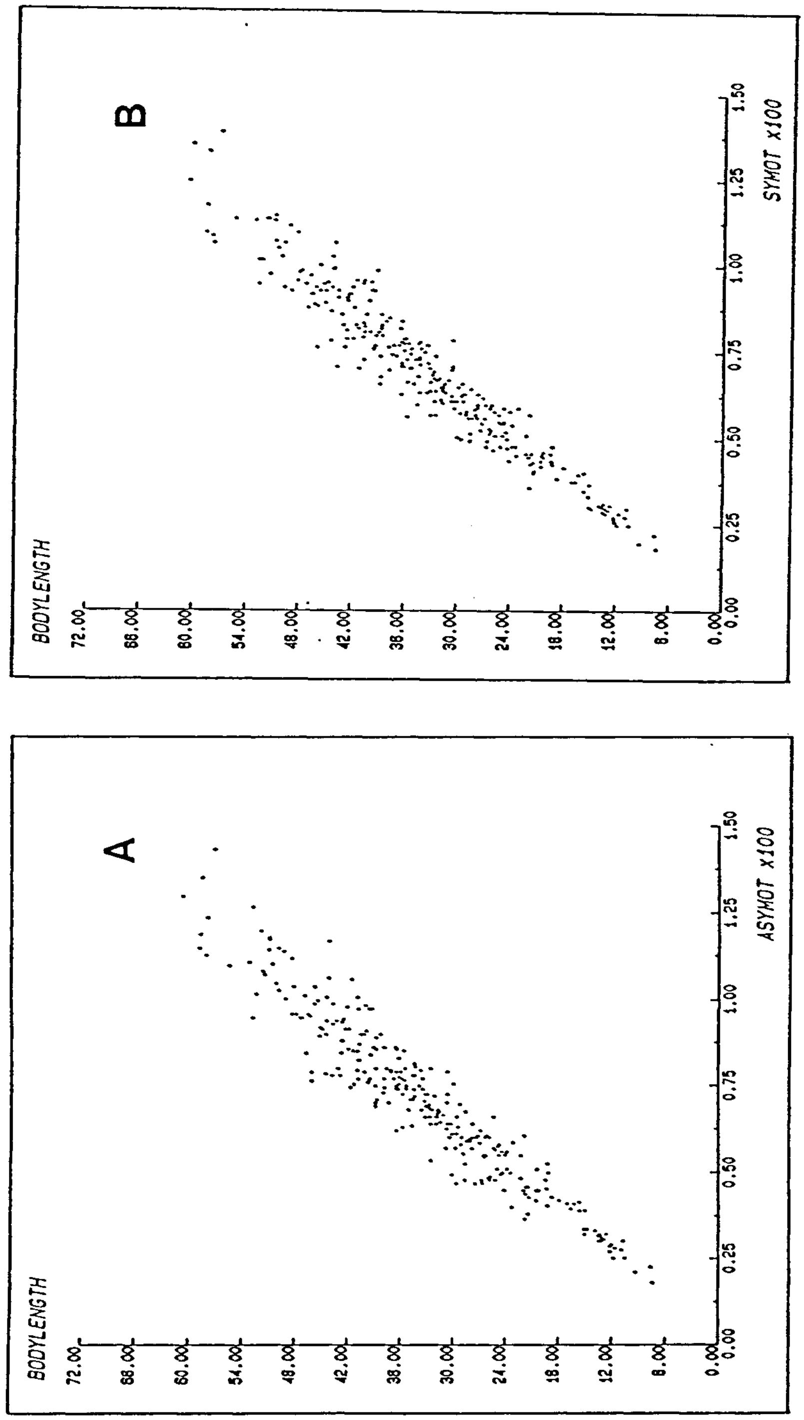


FIGURE 9 : Relationship between Fish Body Length (in cm) and (A) Upper or (B) Lower Sagitta Size (in arbitrary optical units (a.o.u.) of a sample of 275 Brill paired otoliths. (1 a.o.u. = 0.0833 mm).
The functional regression lines are:
A) Y = 0.849383 + 0.469539 X,
B) Y = 1.35830 + 0.449421 X

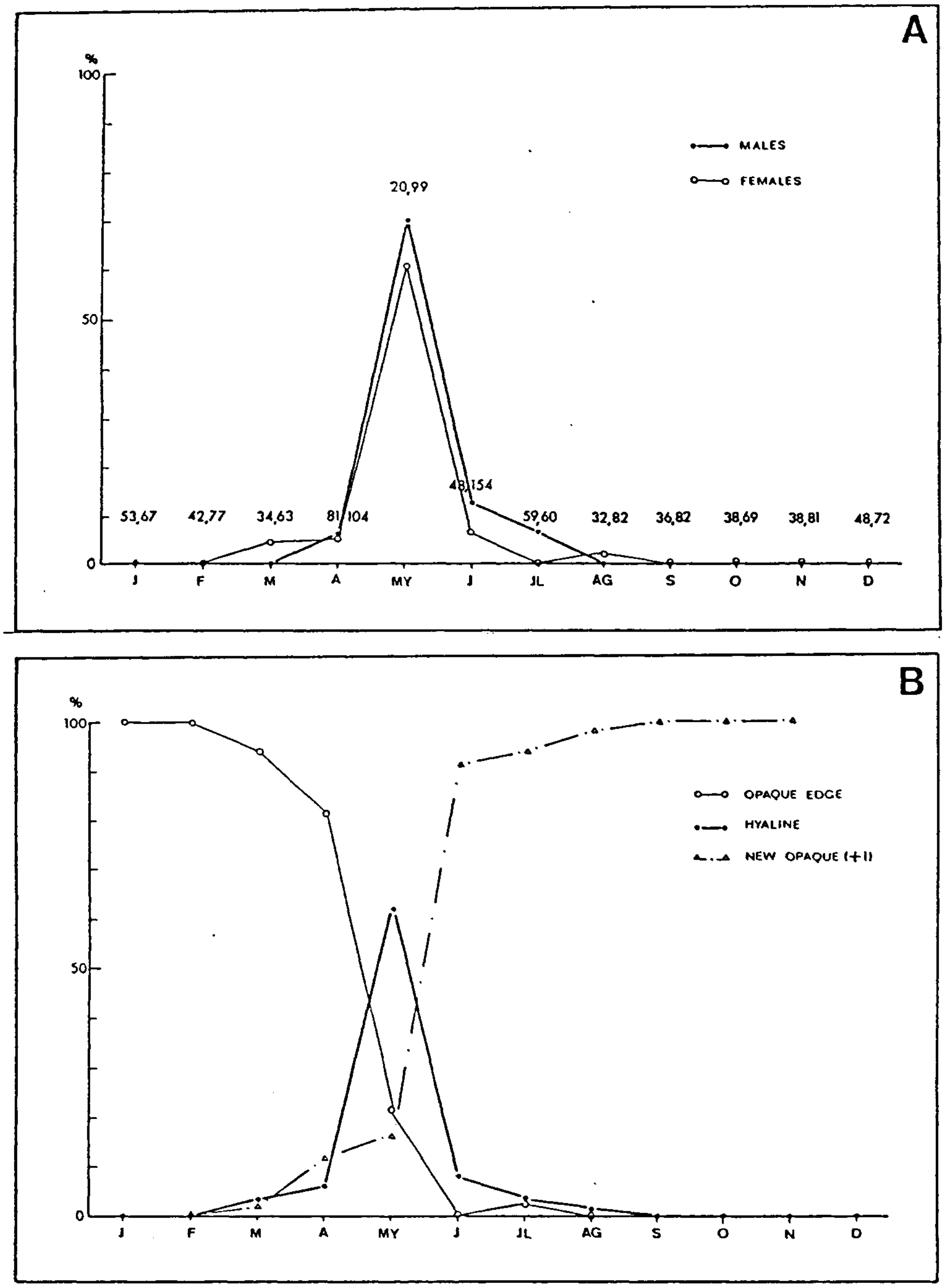


FIGURE 10 : (A) Monthly percentages of hyaline edges in Brill (529 males and 1010 females) sagittae from commercial catches samples in 1984. The numbers corresponds to the number of observations in each month (males, females).
(B) Monthly percentages of opaque, hyaline and new opaques edges in 1539 Brill sagittae in 1984.

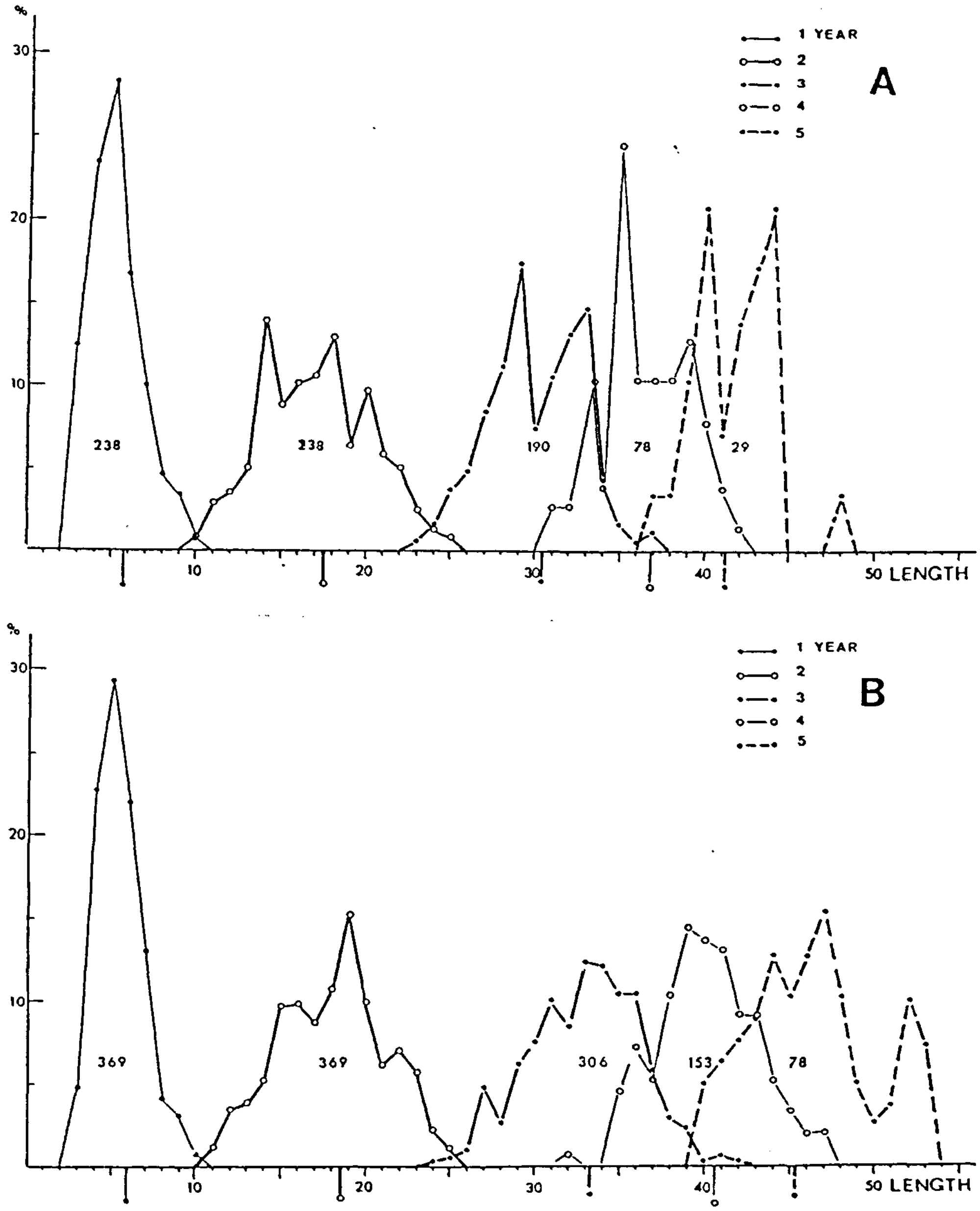


FIGURE 11 : Brill back-calculated lengths frequency distribution,
in percentages, for the 5 first age groups, from
commercial catches samples in 1984 :
(A) for males, (B) for females.

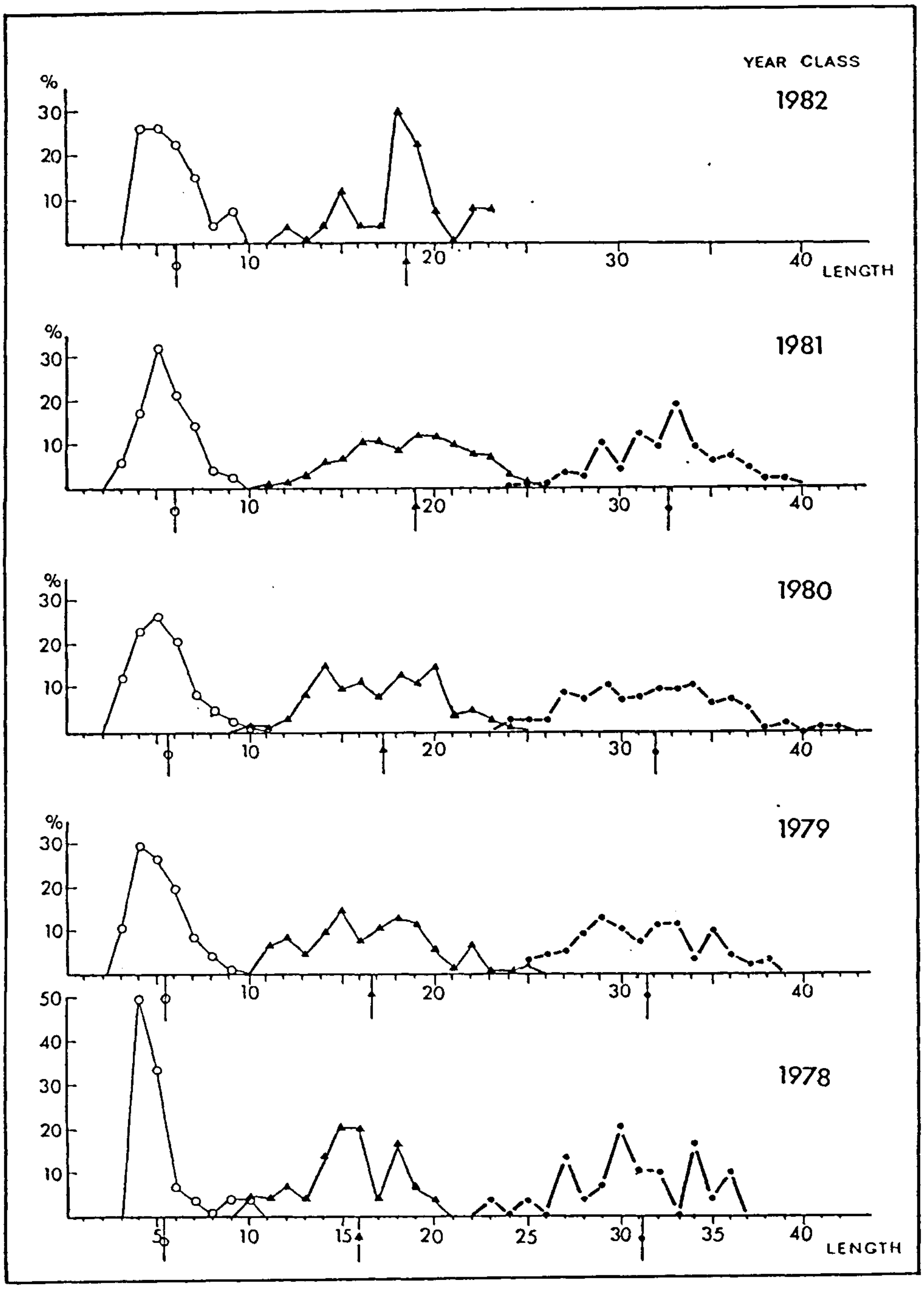


FIGURE 12 : Brill back-calculated lengths distribution, in percentages, for the 3 first age groups according to the 1978-1982 year class.

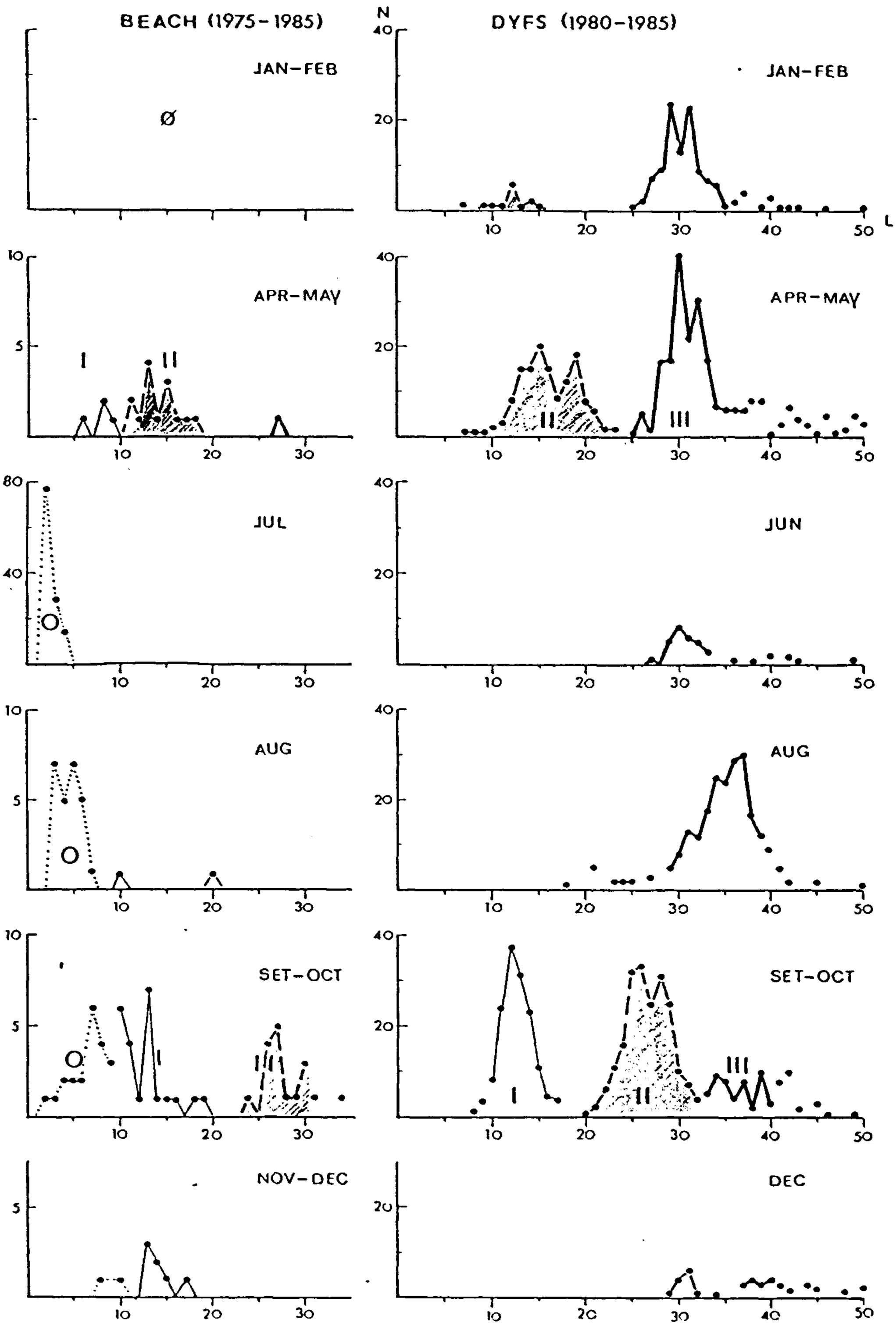


FIGURE 13 : Brill seasonal length frequency distributions, in number of examplars captured in Demersal Young Fish Surveys (DYFS) and beach samples (1975 and 1985).

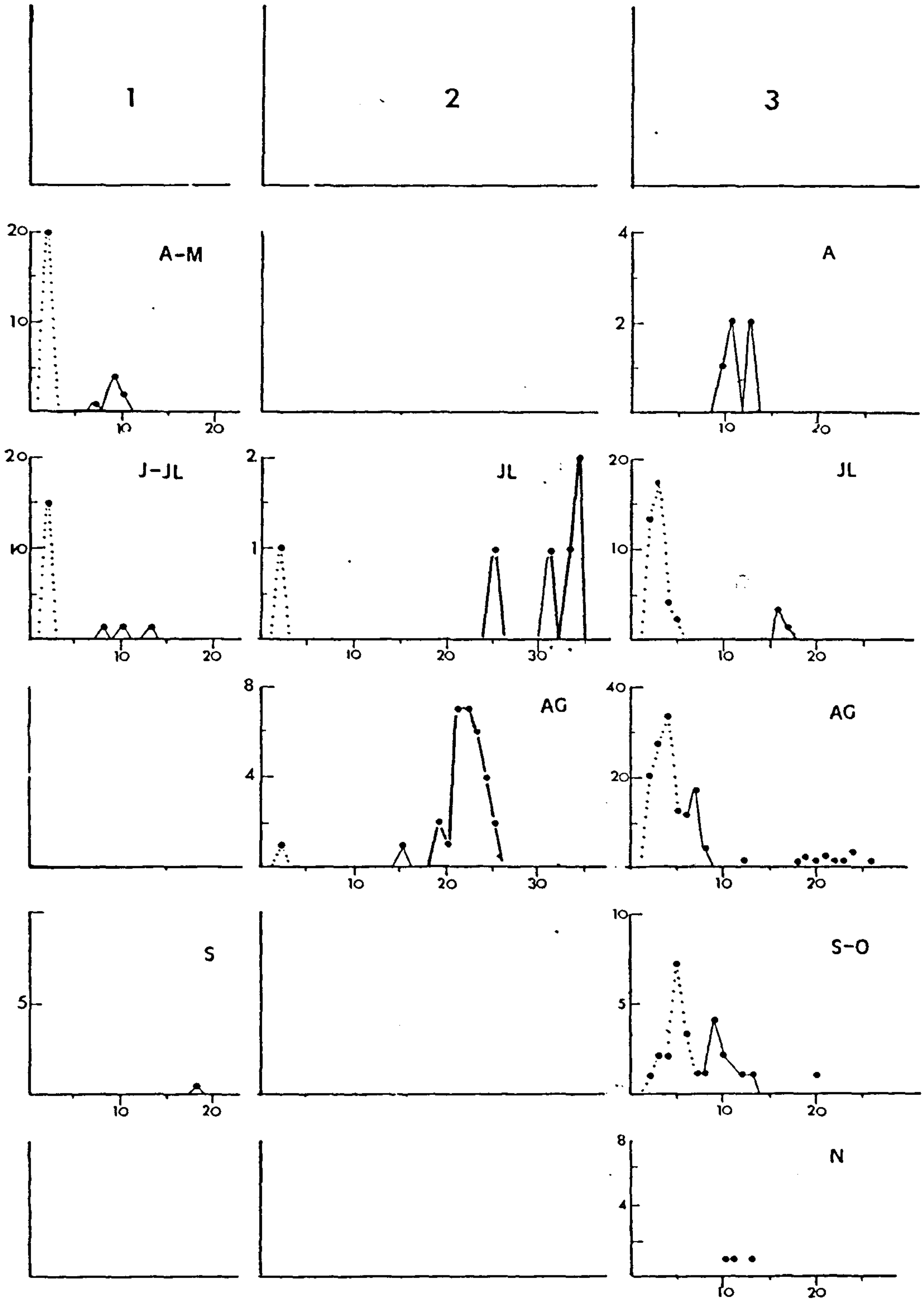


FIGURE 14 : Brill seasonal length frequency distribution in numbers caught in different parts of the North Sea:
(1) CUNNINGHAM (1891, 1892): surveys 1890-91;
(2) WALLACE (1923): surveys 1903-1912;
(3) JOHANSEN (1915): surveys 1905-1913.

TABLE 1 : Results of the functional regression analysis Y= u + vX of upper ('asymmetrical') and lower ('symmetrical') sagittae sizes in arbitrary optical units (a.o.u.) of 120 males, 155 females paired otoliths.

PARAMETER	SET	VALUE OBTAINED	95% C.L.
'u'	MALES	-1.00	-2.89 - 0.88
	FEMALES	-1.16	-3.18 - 0.87
	ALL	-0.91	-2.28 - 0.46
'v'	MALES	1.05	1.01 - 1.06
	FEMALES	1.04	1.00 - 1.06
	ALL	1.04	1.01 - 1.05

95% Confidence Limits calculated as + 1.96 SE .

TABLE 2: Mean 'Nucleus Distance Ratios' (NPR) of paired upper or asymmetrical (AS) and lower or symmetrical (S) sagittae for males, females and sexes combined.

	MALES		FEMALES		COMBINED	
	(AS)	(S)	(AS)	(S)	(AS)	(S)
Number	120	120	155	155	275	275
MEAN	0.365	0.496	0.363	0.501	0.364	0.499
SD	0.034	0.028	0.032	0.031	0.033	0.030
Variance F-ratio:	1.49 S*		1.07 NS		1.23 S*	
Means t-test:	32.78 S**		38.64 S**		50.68 S**	
Means 95% C.L.:	0.358/ /0.371	0.491/ /0.501	0.358/ /0.368	0.496/ /0.506	0.360/ /0.368	0.495 /0.503

Significances : (*) for P< 0.05; (**) for P< 0.01
95% Confidence limits calculated as + 1.96 SE .

TABLE 3: Results of the regression analysis (Y= a + bX) of 'Nucleus Position Ratio' [Y] in upper ('asymmetrical') and lower ('symmetrical') sagittae against body length (cm) [X].

		'a'		'b'		'r'	
GROUP	SET	VALUE	95% C.L.	VALUE	95% C.L.	VALUE	Number
	MALES	0.396	0.377 - 0.415	-0.001	-0.0002 - -0.0004	-0.297	120
AS	FEMALES	0.393	0.378 - 0.408	-0.001	-0.0012 - -0.0004	-0.316	155
	ALL	0.392	0.381 - 0.404	-0.001	-0.0012 - -0.0005	-0.301	275
	MALES	0.509	0.493 - 0.525	-0.0004	-0.0009 - 0.0001	-0.143	120
S	FEMALES	0.517	0.502 - 0.533	-0.0005	-0.0009 - -0.0001	-0.178	155
	ALL	0.511	0.500 - 0.522	-0.0004	-0.0007 - -0.0001	-0.137	275

95% Confidence Limits calculated as : + 1.96 SE .

TABLE 4: Results of the functional (Y=u+vX) and predictive (Y=a+bX) regression analysis of Fish Body Length [Y] (in cm) and upper ('asymmetrical') or lower ('symmetrical') sagittae size [X] (in a.o.u.).

		'u'		'v'		'r'	
GROUP	SET	VALUE	95% C.L.	VALUE	95% C.L.	VALUE	Number
	MALES	0.077	-1.679 - 1.833	0.45	0.43 - 0.48	0.949	120
AS	FEMALES	0.931	-0.675 - 2.537	0.47	0.45 - 0.49	0.961	155
	ALL	0.050	-1.147 - 1.246	0.47	0.45 - 0.49	0.958	275
	MALES	-0.367	-1.981 - 1.247	0.48	0.45 - 0.50	0.959	120
S	FEMALES	0.567	-0.958 - 2.092	0.48	0.46 - 0.50	0.966	155
	ALL	0.353	-1.465 - 0.759	0.49	0.47 - 0.50	0.964	275

		'a'		'b'		'r'	
GROUP	SET	VALUE	95% C.L.	VALUE	95% C.L.	VALUE	Number
	MALES	1.570	-0.187 - 3.326	0.43	0.41 - 0.46	0.949	120
AS	FEMALES	2.234	0.628 - 3.844	0.45	0.43 - 0.47	0.961	155
	ALL	1.368	0.162 - 2.554	0.45	0.43 - 0.47	0.958	275
	MALES	0.871	-0.743 - 2.485	0.46	0.43 - 0.48	0.959	120
S	FEMALES	1.767	0.241 - 3.292	0.47	0.45 - 0.49	0.966	155
	ALL	0.849	-0.676 - 2.375	0.47	0.45 - 0.48	0.964	275

95% Confidence Limits calculated as: + 1.96 SE(b).

TABLE 5: Frequencies of otolith edge types (Op: opaque; Hy: hyaline nOp: recent opaque) in 529 males and 1010 females (>30 cm) from marked samples in 1984.

	MALES			FEMALES			MALES + FEMALES			
EDGE TYPE	(Op)	(Hy)	(nOp)	(Op)	(Hy)	(nOp)	(Op)	(Hy)	(nOp)	Total Number
MONTH										
JAN	53	0	0	67	0	0	120	0	0	120
FEB	42	0	0	77	0	0	119	0	0	119
MAR	33	0	1	59	3	1	92	3	2	97
APR	65	6	10	86	6	12	151	12	22	185
MAY	1	14	5	25	60	14	26	74	19	119
JUN	0	6	42	0	11	143	0	17	185	202
JUL	3	4	52	0	0	60	3	4	112	119
AUG	0	0	32	0	2	80	0	2	112	114
SEP	0	0	36	0	0	82	0	0	118	118
OCT	0	0	38	0	0	69	0	0	107	107
NOV	0	0	38	0	0	81	0	0	119	119
DEC	0	0	48	0	0	72	0	0	120	120
1539										

TABLE 6: Percentages of edge type -(Op),(Hy),(nOp)- in 110 Brill otoliths from D.Y.F.S. (1984) in two seasons (april/may and september/october) and according to fish lengths (less and more than 30 cm).

	For < 30 cm				For >= 30 cm			
EDGE TYPE:	(Op)	(Hy)	(nOp)	Number	(Op)	(Hy)	(nOp)	Number
SEASON								
AP/MY	22.2	36.1	41.7	[36]	33.3	41.7	25.0	[12]
SP/OC	0.0	0.0	100	[52]	0.0	0.0	100	[10]

TABLE 7: Relation of Brill back-calculated mean lengths obtained according to the 13 different procedures od measuring used :
(A) For longitudinally cut sagittae (1-5 :SYM; 6-10 :ASYM)
(B) For transversally cut sagittae (11-12)
(C) For sagittae with rather curve year rings disposition (13)
[N: size sample; M: mean length; SD: standard deviation]

(A)

	PROCEDURE									
	1	2	3	4	5	6	7	8	9	10
1. YEAR RING										
N :	16	16	16	16	16	16	16	16	16	16
M :	6.33	5.91	6.07	6.25	5.98	5.54	6.27	5.77	4.72	7.71
SD:	1.612	1.145	1.149	1.349	1.163	1.081	1.202	1.013	0.940	1.379
2. YEAR RING										
N :	16	16	16	16	16	16	16	16	16	16
M :	18.10	16.64	17.32	18.07	16.81	15.86	18.31	16.66	15.34	18.98
SD:	3.036	2.580	2.507	2.901	2.641	2.357	3.338	2.481	2.254	3.466
3. YEAR RING										
N :	15	15	15	15	15	15	15	15	15	15
M :	32.21	31.07	31.61	32.21	31.07	30.52	31.83	30.91	30.27	32.02
SD:	3.061	3.005	2.949	3.021	3.046	2.107	2.468	1.870	2.010	2.458
4. YEAR RING										
N :	3	3	3	3	3	3	3	3	3	3
M :	41.77	42.43	42.10	41.73	42.47	40.87	41.10	40.93	40.87	41.13
SD:	1.801	2.589	2.193	1.779	2.608	1.026	1.044	0.513	1.026	1.012

(B)

	11	8	11	8	11	8	11	8
	1. YEAR RING		2. YEAR RING		3. YEAR RING		4. YEAR RING	
N :	9	9	9	9	9	9	2	2
M :	5.97	5.24	18.80	18.56	34.20	34.38	39.6	40.2
SD:	1.338	0.917	3.205	3.795	2.798	3.208	0.495	1.414

	3	12	11	8	11	8	11	8		
	1. YEAR RING		2. YEAR RING		3. YEAR RING		4. YEAR RING		5. YEAR RING	
N :	12	12	12	12	11	11	2	2	2	2
M :	6.03	6.42	18.27	18.03	33.05	34.37	39.05	40.6	44.65	44.35
SD:	1.226	1.229	2.846	2.832	2.449	2.150	0.212	2.404	2.333	2.475

	11	12	11	12	11	12
	1. YEAR RING		2. YEAR RING		3. YEAR RING	
N :	11	11	11	11	11	11
M :	6.12	6.24	17.74	17.53	30.59	30.82
SD:	1.367	0.986	2.488	2.417	1.553	1.646

(C)

	3	13	3	13	3	13	3	13	3	13	3	13	3	13
	1. YEAR RING		2. YEAR RING		3. YEAR RING		4. YEAR RING		5. YEAR RING		6. YEAR RING		7. YEAR RING	
N :	5	5	5	5	5	5	5	5	5	5	5	5	3	3
M :	6.66	6.40	17.60	17.22	34.76	33.94	42.50	41.76	47.12	46.48	49.78	49.24	52.17	51.67
SD:	1.711	1.559	2.304	1.946	2.524	2.040	1.815	1.978	3.038	3.479	4.238	4.106	3.121	3.009

TABLE 8 : Results of t-Tests of multiple comparations among means (+) of back-calculated mean lengths obtained from longitudinally cut sagittae (1-10 procedures)

Procedure	Year ring	1	2	3	4	5	6	7	8	9	10
1.	1	----									
	2	0.75	----								
	3	0.47	0.29	----							
	4	0.14	0.61	0.32	----						
	5	0.63	0.13	0.16	0.48	----					
	6	1.42	0.66	0.95	1.28	0.79	----				
	7	0.11	0.65	0.36	0.04	0.52	1.31	----			
	8	1.00	0.25	0.54	0.86	0.38	0.41	0.90	----		
	9	2.89**	2.13**	2.42**	2.75**	2.26**	1.47	2.78**	1.89	----	
	10	2.48*	3.23**	2.95**	2.62**	3.11**	3.90**	2.59**	3.48**	5.37**	----
2.	1	----									
	2	1.52	----								
	3	0.81	1.04	----							
	4	0.03	1.49	0.78	----						
	5	1.35	0.18	0.53	1.32	----					
	6	2.34*	0.81	1.52	2.31*	0.99	----				
	7	0.22	1.74	1.03	0.25	1.04	2.56*	----			
	8	1.50	0.02	0.69	1.47	0.16	0.84	1.72	----		
	9	2.88**	1.36	2.07*	2.85**	1.54	0.54	3.10**	1.38	----	
	10	0.92	2.44*	1.73	0.95	2.27*	3.26**	0.70	2.42*	3.80**	----

(+) t calculated as : (M - M) / V 2/n * MS(within)
t critical values : t(0.05,[150]) = 1.960 ; t(0.01,[150]) = 2.576

TABLE 9: 'Standard Procedure Deviation Index' (SPDI) for the comparison between the 3rd and the other procedures (for explanation of SPDI see the text).

PROCEDURES												
YEAR RING	1	2	3	4	5	6	7	8	9	10	12	13
1.	4.28	-2.64	0	2.97	-1.48	-8.73	3.29	-4.94	-22.24	27.02	6.47	-3.90
2.	4.50	-3.93	0	4.33	-2.94	-8.43	5.72	-3.81	-11.43	9.58	-1.31	-2.16
3.	1.90	-1.71	0	1.90	-1.71	-3.45	0.70	-2.21	-4.24	1.30	0.97	-2.36
4.												-1.70
5.												-1.36
6.												-1.08
7.												-0.96

TABLE 10: Mean back-calculated lengths from sagitta otoliths of
A) 607 exemplars sampled in 1984 from Dutch commercial landings
B) 88 exemplars obtained in DYFS in the same year, and according to the different formulae used:
(1) Strict proportionality ; (2) Lee's formula ('a'= 0.849)
(MEAN length ; SD : standard deviation ; NUM : number of exemplars)

(A) MARKET SAMPLES/1984 (1) LEA's formula

AGE	1	2	3	4	5	6	7	8	9	10	11
MALES:											
MEAN	5.7	17.5	30.5	36.9	41.2	42.9					
SD	1.5	3.2	2.7	2.5	2.4	4.0					
NUM	238	238	190	78	29	7					
FEMALES:											
MEAN	5.9	18.5	33.4	40.6	45.5	49.7	51.6	54.0	56.3	(57.5)	(58.5)
SD	1.4	3.1	3.2	2.9	2.8	2.2	1.8	0.5	0.5		
NUM	369	369	306	153	78	27	10	6	4	1	1
MALES + FEMALES:											
MEAN	5.8	18.1	32.3	39.4	44.3	48.3	51.6	54.0	56.3	(57.5)	(58.5)
SD	1.4	3.1	3.2	2.9	2.8	2.2	1.8	0.5	0.5		
NUM	607	607	496	231	107	34	10	6	4	1	1

(2) LEE' Formula

AGE	1	2	3	4	5	6	7	8	9	10	11
MALES:											
MEAN	6.4	18.0	30.7	37.0	41.2	42.9					
SD	1.5	3.1	2.7	2.5	2.4	4.0					
NUM	238	238	190	78	29	7					
FEMALES:											
MEAN	6.6	19.0	33.6	40.7	45.5	49.7	51.7	54.2	56.3	(57.5)	(58.5)
SD	1.4	3.0	3.1	2.8	2.8	2.2	1.6	0.5	0.5		
NUM	369	369	306	153	78	27	10	6	4	1	1
MALES + FEMALES:											
MEAN	6.5	18.6	32.5	39.5	44.3	48.3	51.7	54.2	56.3	(57.5)	(58.5)
SD	1.4	3.1	3.3	3.3	3.3	3.8	1.6	0.5	0.5		
NUM	607	607	496	231	107	34	10	6	4	1	1

	(1) LEA's Formula					(2) LEE's Formula				
AGE	1	2	3	4	5	1	2	3	4	5
MALES:										
MEAN	5.6	16.6	29.6			6.2	16.9	29.6		
SD	1.3	2.7	2.3			1.2	2.6	2.3		
NUM	44	38	8			44	38	8		
FEMALES:										
MEAN	5.8	17.2	33.5	(45.5)	(49.5)	6.5	17.4	33.6	(45.5)	(49.5)
SD	1.2	2.8	3.3			1.3	2.8	3.2		
NUM	44	41	8	1	1	44	41	8	1	1
MALES + FEMALES:										
MEAN	5.7	16.9	31.5	(45.5)	(49.5)	6.3	17.1	31.6	(45.5)	(49.5)
SD	1.2	2.7	3.4			1.3	2.7	3.4		
NUM	88	79	16	1	1	88	79	16	1	1

II. AGE	1		2		3		4		5	
Variance F-ratio:	1.00	NS	1.03	NS	1.03	NS	1.00	NS	1.15	NS
Means t-test :	8.71	S**	2.76	S**	0.94	NS	0.33	NS	0.00	NS

TABLE 11: Results of the comparison of back-calculated mean length in male and female Brill. The mean length has been back-calculated according two formulae: direct proportionality (LEA) and LEE's formula (between brackets).

AGE	1		2		3		4		5		6	
	M	F	M	F	M	F	M	F	M	F	M	F
NUM	238	369	238	369	190	306	78	153	29	78	7	27
MEAN	5.7	5.9	17.5	18.5	30.5	33.4	36.9	40.6	41.2	45.5	42.9	49.7
SD	1.5	1.4	3.2	3.1	2.7	3.2	2.5	2.9	2.4	2.8	4.0	2.2
Variances F-ratio:	1.15 NS		1.07 NS		1.41 S**		1.35 NS		1.36 NS		3.31 S*	
Mean t-test:	1.67 NS		3.83 S**		10.82 S**		9.60 S**		7.33 S**		4.33 S**	
Means 95% C.L.	5.5/ /5.9	5.8/ /6.0	17.1/ /17.9	18.2/ /18.8	30.1/ /30.9	33.0/ /33.8	36.4/ /37.5	40.1/ /41.1	40.3/ /42.1	44.9/ /46.1	39.9/ /45.9	48.9/ /50.5

S* : Significance for P < 0.05; S** : Significance for P< 0.01

TABLE 12: Comparison of the differences in back-calculated length of different year classes.

(I) ANOVA tables

AGE	1	2	3	4	5
F value:	3.96 S** (3.12 S*)	18.91 S** (17.6 S**)	6.24 S** (4.22 S**)	1.41 NS (1.62 NS)	4.93 S** (4.91 S*)

Comparison among YEAR CLASS	AGE 1	2	3	4	5
82 vs 81	0.51 NS (0.53 NS)	0.45 NS (0.47 NS)			
80	2.91 NS (3.10 NS)	4.32 S* (3.84 NS)			
79	5.30 S* (4.13 S*)	8.57 S** (8.00 S**)			
78	4.69 S* (3.80 S*)	11.72 S** (10.45 S**)			
81 vs 80	4.41 S* (4.62 S*)	31.09 S** (28.65 S**)	6.1 S* (4.48 S*)		
79	9.27 S** (6.25 S*)	43.03 S** (40.95 S**)	12.3 S** (8.37 S**)		
78	5.07 S* (3.70 NS)	29.70 S** (27.04 S**)	7.0 S** (4.44 S*)		
80 vs 79	4.63 S* (0.33 NS)	2.28 NS (2.38 NS)	1.4 NS (0.86 NS)	1.09 NS (1.07 NS)	
78	1.14 NS (0.54 NS)	5.46 S* (4.91 S*)	1.6 NS (0.86 NS)	2.55 NS (3.01 NS)	
79 vs 78	0.12 NS (0.15 NS)	1.65 NS (1.32 NS)	0.2 NS (0.08 NS)	0.76 NS (1.02 NS)	4.93 S* (4.9 S*)

F-values calculated as: MS(two year class compared)/MS(whitin) (SOKAL _ROLFH,1969, pp   )