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VALIDATION OF AGEING TECHNIQUES ON OTOLITHS OF HORSE MACKEREL (TRACHURUS TRACHURUS L.)

by

A. Eltink and C.J. Kuiter

Netherlands Institute for Fishery Investigations

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Abstract

Except in young fish, age determination in the horse mackerel (Trachurus trachurus L.) presented considerable difficulties. At the Horse Mackerel Age Determination Workshop in Lowestoft (UK) in 1987 participated ten otolith readers. Nine used the same and one used another ageing technique. The ageings of these different methods differed about a factor two. The ageing technique of the minority is likely to be the most accurate one based on the collected evidence. The occurrence of annual year-marks has been tested by following indentifiable year classes through successive years. Only by one of the two existing age interpretation methods this could be done. The ageing technique was finally validated over an age range up to 20 years, because the age range, over which the strong/weak year classes could be followed, overlapped the age range of the validation by the length-frequency method for the youngest age groups. It was concluded that for adult horse mackerel the age interpretation method of only one hyaline ring per annual growth zone should be adopted. If the horse mackerel is a long-lived species (up to approximately 35 years old) as suggested by present age determination, natural mortality will be much lower than assumed before.

To enhance the contrast between hyaline and opaque zones the otoliths should be broken, polished and burnt. It is recommended that the whole otolith as well as the broken, polished and burnt otolith submerged in 70% alcohol are examined under a binocular microscope against a black background with reflected light. Counting hyaline rings as annual rings should not be done on whole otoliths, but in the transverse section on the large ventral lobe, because the growth of the otolith of older fish occurs in the lateromedial axis, resulting in a thickening of the otolith, which makes age reading of whole otoliths of older fish very difficult.

Résumé

A l'exception des juvéniles, la détermination de l'âge du chinchard (Trachurus trachurus L.) présentait des difficultés considérables. L'atelier de Détermination de l'Age de Chinchard qui a eu lieu à Lowestoft (GB) en 1987 a été suivi par 10 lecteurs d'otolithes dont 9 utilisaient la même technique d'âgeage, le dixième utilisant une technique différente avec des attributions d'âge qui différaient par un facteur de 2 environ. La technique de détermination de l'âge de cette minorité est vraisemblablement, en fonction des évidences disponibles, la plus correcte. On peut vérifier l'occurence des marques annuelles en suivant des classes d'âge identifiables à travers des structures démographiques annuelles successives, parce que seule l'une des deux méthodes d'âgeage le permet. La technique d'âgeage a finalement été validée sur une gamme d'âges s'étendant jusqu'à 20 ans parce que la gamme des âges sur laquelle il était possible de suivre les classes annuelles, fortes ou faible, se superposait à la gamme des âges les plus jeunes pour laquelle on disposait, par ailleurs, d'une validation basée sur la distribution des fréquences des tailles. On a pu conclure que chez le chinchard adulte, l'interprétation basée sur l'existence d'un anneau hyalin par zone annuelle de croissance devait être adoptée. Si, comme le suggèrent les recherches actuelles, le chinchard est une espèce à longue durée de vie (35 ans environ), il subit nécessairement une mortalité naturelle inférieure à celle supposée jusqu'alors.

Les otolithes doivent être sectionnés, polis et brûlés pour intensifier le contraste entre zones hyalines et opaques. Que l'otolithe soit entier ou sectionné et brûlé, il est recommandé de l'examiner sous immersion dans l'alcool à 70°, sur fond noir et en lumière réfléchie, à l'aide d'une loupe binoculaire. Le comptage des anneaux hyalins ne doit pas être fait sur l'otolithe entier mais sur une section transversale du grand lobe ventral parce que la croissance des otolithes des chinchards les plus âgés a lieu selon l'axe lateromédian, ce qui a pour conséquence un épaississement des otolithes qui rend leur lecture particulièrement difficile.

Introduction

Age of individual fish is obtained by deciphering the patterns recorded in the calcified tissue, which reflect intrinsic cycles of varying growth rates. Age determination is an essential feature in fish stock assessment for the estimation of mortalities and growth. The use of incorrect growth rates can lead to rather large errors in estimates of stock production. In order to arrive at appropriate management advice ageing procedures must be reliable and provide valid results. New higher estimates of age can greatly reduce the rate of natural mortality and produce a more conservative management strategy.

Except in young fish, age determination in the horse mackerel (Trachurus trachurus L.) presented considerable difficulties. Letaconnoux (1951) and Ramalho & Pinto (1956), for example, were unable to use either scales or otoliths, and they resorted to an analysis of length distributions for data on growth. Barraca (1963) studied different calcified structures for ageing the fish; otoliths were stained with crystal violet to clarify the ring structure. By the length-frequency analysis or Petersen method (Petersen, 1892) she validated the ageings up to age two. Most other authors (Baidalinov and Starosel'skaya, 1964; Polonsky, 1969; Sahrhage, 1970) have attempted to use the unburnt otoliths but have commented on the difficulty of interpreting the ring structure. Macer (1968) started to burn the transverse sections of the otolith, which clarified the ring structure. Sahrhage (1970) stated that further investigations were necessary to solve the question whether or not each hyaline zone should be counted as an annual zone after having tried the burning technique for a limited number of broken otoliths. Migration is mentioned by Sahrhage as a likely factor causing secondary ring structures. Macer (1977) investigated a variety of structures including bones, scales and otoliths to assess their suitability for age determination. Only otoliths showed a consistently clear ring structure, particularly when the ring structure was clarified by a treatment of breaking, polishing and burning. He validated the ageings for the first four years of life by using the length-frequency method

and demonstrated that one hyaline ring occurred per annual growth zone. There was some evidence that later rings after age 4 were also annual, in that it is possible to follow what appear to be strong year classes from year to year. He could not establish for certain whether the large number of rings observed (up to 35) in burnt otoliths of 4 year and older fish were annual: "There is uncertainty as to the interpretation of the rings outside the fourth in otoliths; they could be interpreted as a single zone which has split into several non-annual rings, or as several separate annual rings". The interpretation of one hyaline ring per annual growth zone did conflict at that time with the work of previous authors (Baidalinov & Starosel'skaya 1964, Polonsky 1967), who reported no difficulties in using whole otoliths and a maximum age in their western English Channel samples of 8 and 11 years respectively.

Geldenhuys (1973) demonstrated that horse mackerel will be aged younger when scales are used instead of otoliths. He used the same burning technique as Macer (1968) for otoliths of fish above age 5 and counted all hyaline rings as annual rings. His ageing technique with burnt otoliths was counting year-marks, because he could apparently follow individual year classes from age 4 to 10.

Trouvery (1977) used mainly scales, but she also tried the burning technique on a limited number of transverse sections of otoliths. This caused problems in the interpretation, because there were less rings in the scales compared to the otoliths (e.g. only 8 rings counted on the scales of a 39 cm horse mackerel compared to 26 in the otolith). Therefore, the otoliths were neglected and she only considered the scales.

Marecos et al. (1978) determined the age by counting the hyaline zones of whole otoliths, while differences in the interpretation of true annuli were observed mainly in otoliths over 7 years old (readings were done by two otolith readers). They considered the results as preliminary and referred to the burning technique to be of possible use for horse mackerel otoliths.

Eaton (1983) used both broken/burnt and whole otoliths for age assessment and he stated that it is possible to age horse mackerel without difficulty up to at least 7 years and thereafter it becomes increasingly difficult, but it is apparent that horse mackerel are at least as long-lived as mackerel, 15 years or more.

Fariña (1983) based his theory on the formation of one summer and one winter hyaline growth ring on observations of otoliths of fish of only age 1 and 2, and assumed the same would apply to the adult fish, although he did not state this assumption explicitly in his paper.

The ICSEAF guide for Cape horse mackerel otolith interpretation (ICSEAF, 1986) was prepared by the ICSEAF Working Group on growth and age of Cape horse mackerel with participants from Spain, Japan, Federal Republic of Germany, South Africa, Bulgaria, Portugal and Poland. This Working Group recommended that the age of mature fish should be read on the posterior part on the lateral (external, concave) side of the whole otolith and on the rostrum. Following Wysokiński (1985), cross-sectioning or preparation of slices was considered as time consuming and it was felt not to improve readability to any significant degree. Charring of whole otoliths would give reasonable results. Polishing whole otoliths is recommended for older otoliths. According to this Working Group a spawning ring or zone (secondary structure, false annulus) is laid down, when the spawning season does not coincide with the normal season of hyaline zone formation or when a fish spawns twice in a year. The ICSEAF Working Group did not validate the ageing technique, which they recommended.

The validation of the ageing technique for the ages above 5 was tried by Macer (1977), Kerstan (1985) and Junquera et al. (1988). Macer (1977) did not succeed in following year classes in successive years. Kerstan (1985) stated that scanning electron microscopy and light microscopy proved the relation between otolith surface structures and annual growth zones, but he also stated: "It was confusing, however, that often two protrusions occurred within one annual zone". He concluded that the ageing results from otoliths were consistent and should supply rather constant growth curve parameters

based on radius measurements and length back-calculations. Radius measurements and length back-calculations can probably not be used to validate ageing techniques, which count either one or two hyaline rings in an annual growth zone in otoliths of adult fish, because these will only result in two different growth curves and different growth parameters. Junquera et al. (1988) tried to test whether frequency modes might be identified to discriminate between year-marks and false rings by measuring the distances from the center of the otolith to all hyaline zones. As many radii as hyaline zones have been recorded, but whenever one of them was obviously an annual ring it was recorded separately in order to obtain the frequency distribution of radii belonging to each age. However, these obvious true annual zones are only the only annual zones if the correct ageing technique is used. This method is therefore biassed, being dependent on the input values for the year-marks. This method does not validate the ageing technique, but can only help in deciding to which age the otoliths should be assigned based on the measured radii once one agrees on the ageing technique.

The only strong validation is obtained from the comparison between ageings and the length-frequency distributions (Petersen, 1892), which has confirmed in the first years of life (up to age 4), a single hyaline zone and a single opaque zone are laid down each year (Letaconnoux, 1951; Ramalho & Pinto, 1956; Barraca, 1963; Polonsky, 1969; Sahrhage, 1970; Macer, 1977). However, Fariña (1983) described the formation of one summer and one winter hyaline ring in one annual growth zone in otoliths of fish of only age 1 and 2. These false hyaline summer rings, however, should be recognizable when applying the length-frequency analysis.

Differences in growth parameters and growth curves of horse mackerel, presented by Netherlands, England, Spain and Portugal at the 1983 meeting of the ICES Mackerel Working Group in Copenhagen, could possibly be explained by differences in ageing techniques. It was therefore agreed that those involved should exchange otoliths and compare their ageing results (Anon., 1984). An otolith exchange was then carried out in 1984, which showed that two different ageing techniques were used for adult horse mackerel, of which the ageings differed about a factor two (Eltink, 1985). Otolith readers from England, France, Portugal, Spain, Scotland, Federal Republic of Germany and the Netherlands participated in this otolith exchange. The Netherlands and Scotland counted each ring as an annual ring, while the participants from England, France, Portugal, the Federal Republic of Germany and Spain assumed more than one hyaline ring per annual growth zone. Systematic differences between readers occurred and the ageings of the ageing technique of the latter group were not regarded accurate above age 5. At that time, the Scottish readers had no experience and the Dutch reader had only two years of experience in ageing this particular species.

The age interpretation method, assuming more than one hyaline ring per annual zone in adult fish, was adopted by Marecos et al. (1978), Fariña (1983), Eaton (1983) and Kerstan (1985), who all participated in the 1984 horse mackerel otolith exchange (Eltink, 1985). Both Marecos and Kerstan participated as well in the ICSEAF Working Group on growth and age of Cape horse mackerel (ICSEAF, 1986).

A workshop was proposed for attempting to reach agreement on a standard method of otolith interpretation. However, during the Horse Mackerel Age Determination Workshop in Lowestoft (UK) in April 1987 no progress was made towards agreeing a standard method of otolith interpretation since no method of validation was found to solve the main problem of the interpretation of the outer rings of the larger/older fish (Anon., 1987). In this Workshop participated mainly the same otolith readers from Scotland, England, Ireland, France, Spain, Portugal, Federal Republic of Germany and the Netherlands. All participating otolith readers with the exception of the Dutch assumed, that as soon as horse mackerel start spawning, they produce an extra hyaline ring (secondary ring, spawning ring, false annulus). This problem could obviously not be settled at the workshop meeting without a proper validation of the ageing technique.

Validation means proving a technique is accurate. Accuracy can be proven or estimated. Precision relates to reproducibility and is not a measure of accuracy. The degree of

agreement among readers is a measure of the *precision* of the determinations and not the *accuracy* of the technique (Beamish and McFarlane, 1983).

The aims of this paper are: (i) Validation of the Dutch interpretation technique by means of following year class strength in a series of years. (ii) Provide some idea of the possible level of precision of the ageings by repeated readings by one and the same reader. (iii) Indication of some possible causes of misageing.

Material and Methods

In the fourth quarter of 1981 a few samples of horse mackerel were taken by the Dutch research vessel Tridens. 142 otoliths were collected in a first attempt to read these. Since January 1982 horse mackerel samples were regularly collected by the Dutch freezer trawlers. From each sampled 20 - 25 kg fish a reduced sample of only 25 specimens was taken representative for the length composition and therefore also for the age composition of that particular catch. These fish were measured to the nearest millimeter, weighed to the nearest gram, sex and maturity stage estimated and finally aged. The fish in each representative sample were ordered by length and therefore also aged in a length order. This possibly improved the interpretation of the rings, because the time of deposition hyaline and opaque zones seemed to be dependent on fish length.

Otoliths were washed thoroughly immediately after collection in order to remove the organic material from the surface and subsequently stored dry in envelopes. One out of each pair of dried otoliths was broken transversely across the short axis through the nucleus. The fractured surface of the anterior half of the broken otolith was polished using the apparatus described by Bedford (1964). The rostrum was broken off and the polished part was then put with the convex side of the otolith upward in one of the 50 concave hollows made in the surface of a brass plate (Groot, 1988). Figure 1 shows the two views of the brass plate and the various steps taken before burning the otoliths. The brass plate is heated underneath with a Bunsen flame, which ensures homogenous spreading of the heat over the entire otoliths. To clarify the ring structure these otoliths were carefully charred until darkish brown (Møller Christensen, 1964). The thus treated otolith was mounted in plasticine and submerged in 70% alcohol together with the untreated otolith or, alternatively, the posterior half of the broken otolith. Both were viewed and compared under a binocular microscope using a dark background and reflected light. Shading by means of an object moved between the light and the otolith often improved the readability. Under reflected light, the opaque zones of fast growth appeared white and the hyaline zones of slow growth appear dark. Figure 2A shows the medial view of the left otolith with the internal, convex side up and figure 2B the lateral view of the right otolith with the external, concave side up. The hyaline rings in the burnt otolith were counted in the large ventral lobe near the sulcus acusticus; this is shown on a transverse section of the otolith as indicated in figure 3 from A to B. This area had not made contact with the brass plate during burning and therefore could never be overheated. Each hyaline ring was considered to represent an annual ring.

In order to detect identifiable strong or weak year classes to be followed through successive years, percentage age compositions were obtained by combining by year all representative samples from the spawning area in ICES Division VII j (mainly Great Sole Bank). These combined samples were assumed to represent the age composition of the spawning population. Since juveniles are not represented on the spawning grounds also percentage age compositions were obtained by combining by year all representative samples from the areas where juveniles occur (ICES Divisions VII e, f, g and h (mainly western English Channel)). Age compositions in percentage from 1981 - 1986 from these areas were combined up to age 14, combining the older fish in a 15-year-and-over category (15+). Age compositions in percentage from 1982 - 1987 from the spawning area were extended up to age 29, combining the older fish in a 30-year-and-over category (30+).

In order to get some idea of the potential precision of the age reading proces, 100 otoliths collected in 1986 and covering an age range of 4 - 20 years were selected for rereading after one year by the same reader.

Results

Figure 4 shows the age compositions from 1982 - 1987 of horse mackerel from the spawning area (Division VII j). Figure 4 shows also the age compositions from 1981 - 1986 of horse mackerel from the areas where juveniles occur (Divisions VII e, f, g and h) to show the strength of the year classes as juveniles.

The strong year classes 1979 and 1982 can be followed from age 2 onwards from the juvenile to the spawning area in successive years age compositions. The weak year classes 1981 and 1983 can also be followed from age 2 onwards from the juvenile to the spawning area in age compositions of successive years.

The older strong year classes 1968, 1969 and 1970 can only be followed in the spawning area. Also the weak year classes 1972, 1973 and 1974 can only be followed in the spawning area.

No sampling of horse mackerel caught by commercial trawlers was carried out in 1981. At that time only a few samples were taken in the fourth quarter by a research vessel in a first attempt to read horse mackerel otoliths. This possibly explains this relatively different age composition in 1981. The results were included, because it indicated the strength of the 1979 year class as 2 year olds.

Figure 5 shows deviations between original and repeated age readings one year later by the same reader. The percentage of agreement at the bottom for a particular age group includes also readings of all otoliths of the younger fish; this percentage is about 90% for 4 year olds, and remains at about the 70% level over the whole range up to age 20 despite the relatively high number of otoliths above age 16.

Discussion

The only strong validation is obtained from the comparison between ageings and the length-frequency distributions, which has confirmed in the first years of life (up to age 4), a single hyaline zone and a single opaque zone are laid down each year (Letaconnoux, 1951; Ramalho & Pinto, 1956; Barraca, 1963; Polonsky, 1969; Sahrhage, 1970; Macer, 1977). The ageing technique should therefore be validated for 5 year and older fish. The main question should be solved, whether in adult fish one or two hyaline rings in an annual growth zone are deposited, because the ageings of both ageing techniques differed about a factor two (Eltink, 1985).

Year class extremes can be very important in age and growth studies, when the recruitment in the natural environment is extremely variable. The progression of exceptionally strong and/or weak year classes should then be easily to follow in successive years. Individuals of such year classes persist, despite mortalities, as unusually strong/weak year classes in the population. This provides a method for corroborating the annual occurrence of year-marks or annuli on the calcified structures (Casselman, 1987). The ageing technique is finally fully validated when each annulus or year-mark can be awarded to its specific age.

The evidence provided in figure 4 demonstrates that strong and weak year classes from age 2 onwards can be followed through successive years, when all hyaline rings are counted as annual rings. This demonstrates that only one hyaline ring is laid down annually and that the number of false rings is not significant. But it does not yet validate that a certain annual ring can be awarded to its specific age.

The age validation of the first four years by the length-frequency analysis, for which

also each hyaline ring should be counted as an annual ring, overlaps the above descibed check on the annual occurrence of year-marks from age 2 onwards. Therefore, it validates the assessment of ages up to approximately 20 years of age. The evidence presented supports strongly the age interpretation method, which counts only one hyaline and one opaque growth ring in an annual growth zone in otoliths of horse mackerel. This agrees with the results of Geldenhuys (1973), who counted similarly each hyaline ring as an annual ring. His ageing technique was counting year-marks, because he could apparently follow individual year classes from age 4 to 10.

The following evidence is demonstrating that this validation of ageings really includes the older age groups. The conclusion that year classes 1968, 1969 and 1970 have been very strong is supported by figure 6 (after Macer, 1977), referring to the distribution of rings in otoliths of horse mackerel in January 1973 in the western English Channel. These strong year classes 1970, 1969 and 1968 can be recognized as relatively strong 3, 4 and 5 ringers, although in this area usually only a high percentage of small fish occurs, which Macer assigned to age classes 1 and 2. The year class 1972 as 1-year olds in January 1973 in figure 6 is weak and strong year classes are absent immediately before the 1968 year class, which corresponds to our interpretation.

The agreement in repeated otolith readings by the same otolith reader indicates the potential precision, which might be achieved among different otolith readers, when they would apply the same technique. The percentage of agreement is about 90% for otoliths aged 4 and remains at about the 70% level over the whole range of ages of 6 - 20 (figure 5). This is much higher than achieved in the horse mackerel otolith exchange in 1984 (Eltink, 1985). Moreover, he demonstrated that the standard deviation in age readings was rapidly increasing above age 4 for those readers, who used the ageing technique of two hyaline rings in an annual growth zone. This indicates, that at that time those otolith readers had large differences in opinion concerning the interpretation of which hyaline rings should be considered as year-marks and which ones as false rings.

If the horse mackerel is a long-lived species (up to approximately 35 years old) as suggested by present age reading it would necessarily suffer a much lower natural mortality than assumed before. This species has apparently to sustain long periods of weak recruitment and should live long enough till at least one or more strong year classes are produced. The data presented in figure 4 and 6 indicate that only about seven strong year classes of the horse mackerel in the western areas occurred over a period of about fifty years (1947, 1959, 1968, 1969, 1970, 1979 and 1982). Geldenhuys (1973) also found relatively many weak year classes among the Cape horse mackerel, where only two exceptionally strong year classes (1947 and 1948) formed the bulk of the catches during the period 1950 - 1958.

Possible misinterpretation can be caused by the use of whole in stead of sectioned otoliths and/or by counting the year-marks in different areas of the otolith and/or by a wrong assumption of what causes the hyaline ring formation.

When the first growth zones are laid down, the otolith increases mainly in width and length, but in adult horse mackerel subsequent growth results primarily in increased thickness (Macer, 1968 and 1977; Geldenhuys, 1973; Nazarov, 1978; ICSEAF, 1986). Macer (1968, 1977) concluded that therefore the growth zones are difficult to see in the unsectioned otolith. This thickening of otoliths with age was also observed by Wiedeman Smith (1968), who developed a method of age reading by means of surface-structure examination on transverse sections of otoliths and who found that in turbot the later rings do not reach the flat (lateral) surface of the otoliths and thus escape notice when the annual rings are counted on whole otoliths. Therefore, the use of transverse sections appears to be a prerequisite in this species. Based on the results of the horse mackerel otolith exchange in 1984 thin transverse sections (Bedford, 1983) are probably as good as the broken/polished/burnt otoliths, because the difference of a factor two in ageings was as obvious in the thin sectioned otoliths as well in broken/polished/burnt otoliths (Eltink, 1985).

The sulcus acusticus (figure 2A and 3) partially divides the otolith longitudinally into a larger ventral lobe and a smaller dorsal lobe. The burnt rings are normally clearest in the larger ventral lobe. In some otoliths, different numbers of rings may be observed in different parts, even within the ventral lobe region. In general, the greater number of rings observed closer to the sulcus (Macer, 1977). Sometimes, a hyaline ring appears to bifurcate (Macer, 1977), when one tries to follow a concentric ring within the otolith. This type of rings is called split rings (Wysokiński, 1985; ICSEAF, 1986). Counting the rings on a fixed position such as the large ventral lobe near the sulcus acusticus minimizes the differences in ageings between different readers and therefore enhances precision. However, the proper interpretation of split rings remains to be validated for instance by reading otoliths of tagged fish of known age.

Misinterpretation also might occur by a wrong assumption of what causes the hyaline ring formation. The main difference of a factor two between both examined ageing techniques was caused by the interpretation of the hyaline rings, which were caused either by the winter or spawning season (one hyaline ring in an annual growth zone) or by both the winter season and the spawning season (two hyaline rings in an annual growth zone).

When investigating the possible difference between a hyaline annual winter ring and a hyaline spawning ring, one should try to pinpoint the deposition of the rings to certain external (season) or internal (physiological) conditions by investigating in which months or seasons the hyaline rings are laid down during the prespawning, spawning, feeding and overwintering period for the different horse mackerel populations.

The physiological changes undergone by an individual horse mackerel during the prespawning and spawning periods appear to be associated with the hyaline ring formation in the different horse mackerel populations from different latitudes (Safyanova and Revina, 1967; Geldenhuys, 1973 (figure 6); Overko, 1974; Kompowski and Wysokiński, 1976; Kuderskaya, 1983; Wysokiński, 1985). There is no evidence that in adult horse mackerel the winter season is causing a hyaline ring in addition to the one caused by prespawning/spawning. The prespawning/spawning period seems to cause the hyaline ring formation, being the annulus or year-mark; this year-mark could therefore be better defined as a hyaline spawning ring rather than as a hyaline winter ring.

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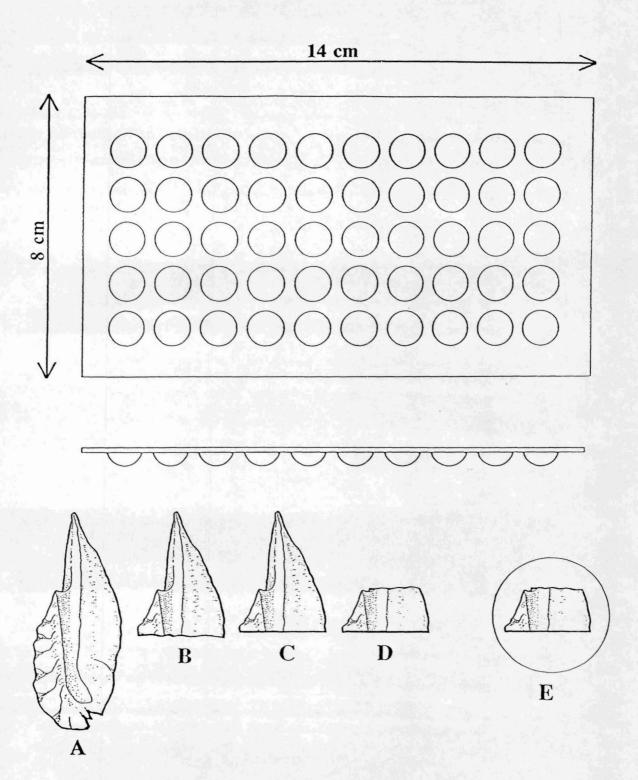


FIGURE 1. Two views of the brass plate, which can be used for burning up to 50 horse mackerel otoliths at the same time. The various steps to be taken for burning the otoliths on this plate are shown below: A. Whole otolith. B. Broken otolith. C. Polished otolith. D. Rostrum broken off. E. Convex side of the otolith upward in one of the 50 concave hollows of the brass plate.

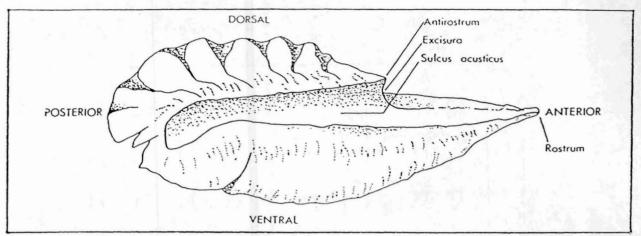


FIGURE 2A. The medial view of the left otolith with the internal, convex side up. (from Geldenhuys, 1973)

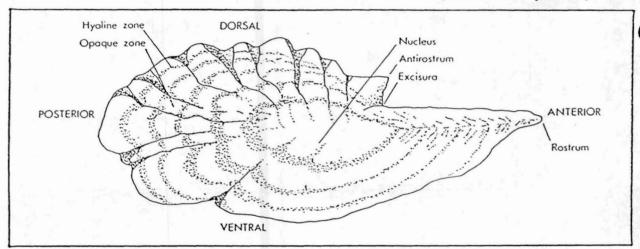


FIGURE 2B. The lateral view of the right otolith with the external, concave side up. (from Geldenhuys, 1973).

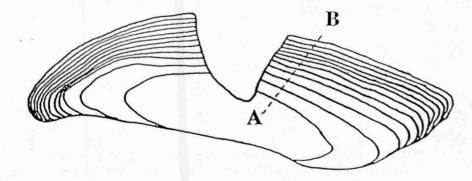


FIGURE 3. A transverse section of the left otolith. The number of hyaline rings were counted in the large ventral lobe near the *sulcus acusticus* from A to B.

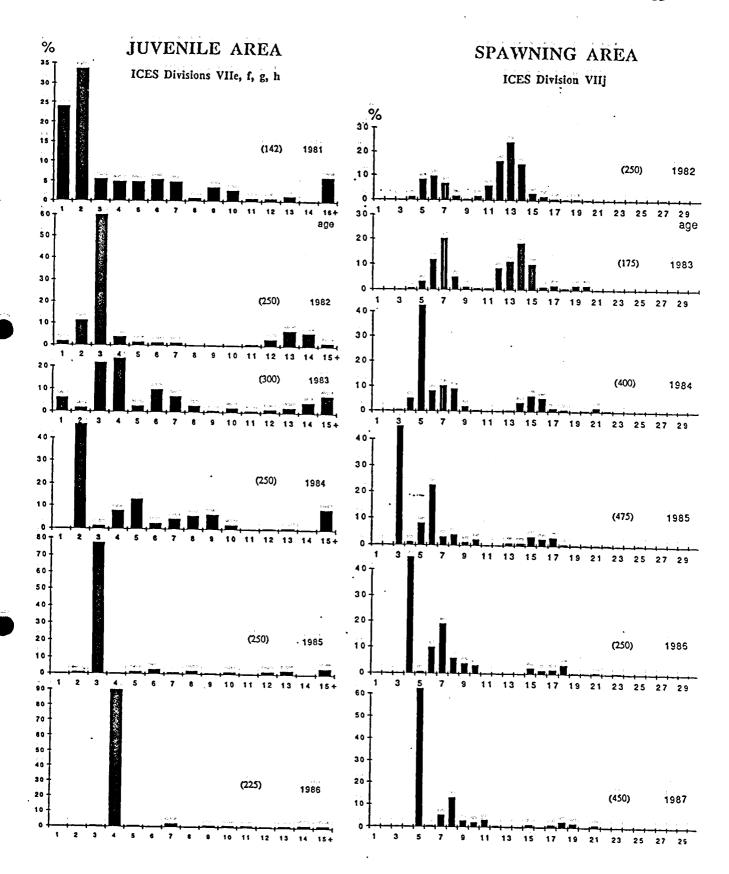


FIGURE 4. Age compositions of horse mackerel from the Dutch commercial fishery from the area where juveniles occur (ICES Divisions VII e, f, g and h) in 1981-1986 and from the spawning area (ICES Division VII j) in 1982 - 1987. The number of otoliths used for age reading is given in parentheses.

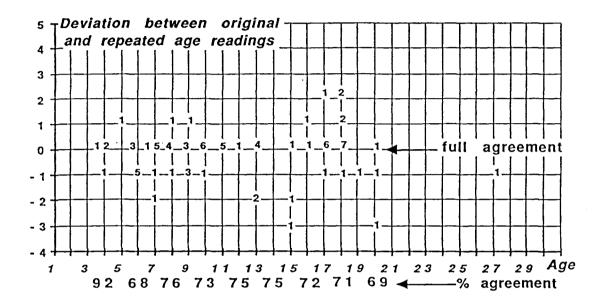


FIGURE 5. The agreement in 100 repeated horse mackerel otolith readings with one year interval by the same otolith reader. The numbers in the figure refer to the number of otoliths, which have a deviation between original and repeated readings as shown on the Y-axis. The number on the X-axis refer to the number of ageings with full agreement. The percentages at the bottom refer to the percentage agreement reached until that particular age and includes therefore all preceding ageings of younger age groups.

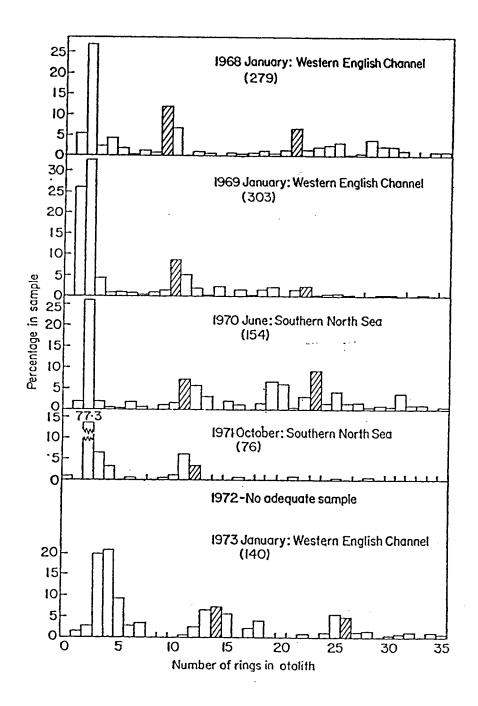


FIGURE 6. The percentage distributions of the number of burnt rings counted in various samples of horse mackerel otoliths, which have been treated using the 'burning technique'. The sample size is given in parentheses (from Macer, 1977).