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AGE, SIZE AND VERTEBRAL CALCIFICATION IN THE BASKING SHARK, CETORHINUS MAXIMUS (GUNNERUS)

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With three text-figures and one plate

Abstract

The inshore shoals of basking sharks that appear in spring off the western seabord of Europe have been variously claimed to be part of a seasonal south to north migration, or local, perhaps nuptial, aggregations. The decline in the catches of the Achill Island Fishery in the last decade suggests that the size of the shoals has diminished there. Size/frequency analysis of available records shows a midsummer peak of specimens with a mean length of 3.09 m and a mid-winter peak at 3.52 m; the difference is significant and is ascribed to growth. From this value, coupled with the recorded maximum and minimum sizes, a hypothetical asymptotic growth-curve is calculated. Comparison of this age/length relationship with the observed relationship between length and the number of calcareous "rings" in the vertebral centra suggests that at birth there are seven rings in a precaudal vertebra and that two rings are added annually thereafter. This suggests a possible gestation period of 3.5 years. This in turn, leads to the expectation that, since pregnant (or gravid) females are almost or quite unknown, they must live a hidden, perhaps demersal, life for three consecutive years after their first mating. The size/frequency analysis shows that only three specimens, none of them females, have been recorded between 5.8 and 7.4 metres in length, which on the tentative growth curve, corresponds with fish of average size in their sixth, seventh and eighth years. The fishery catches, though probably insignificant in relation to the total population of the north-eastern Atlantic, would have a devastating effect on a local population of a fish with such a low reproductive rate.

Thompson (1856) states that the western coasts of Ireland are much frequented by the sunfish (basking shark) which appears in March or April and stays until November. The Parliamentary Gazetteer of Ireland (Anon., 1846) refers to their sporadic appearance off the north-west coast but says that they can always be found in the season on a bank located some twelve miles north-west by west off Innisboffin and fifteen and a half miles west south-west of Clare Island. This bank was visited in April, 1964, but not a single basking shark was seen. Wallop Brabazon (1848) gives a detailed account of shark fishing on a bank, probably the same one, although stated to be 100 miles west of Clare Island, and described a method of capture from small boats by the use of harpoons, each attached to some 200 fathoms of line so that wounded fish could be left to tire themselves out and eventually be brought alongside a vessel for killing and removal of their livers, the carcases being left to sink. Brabazon believed that basking sharks migrated during the summer in a northerly direction along the west coast of Ireland. He gave other catching sites as off Achill, Clare Island, Innisboffin, Innishark, Tory Island and the north-west coast of Donegal.

The only commercial fishery for basking sharks in Ireland at the present time is situated at Keem Bay near Achill Head, County Mayo, with an oil extraction plant for dealing with the livers at Purteen Harbour, Keel, some three miles away. Popular illustrated accounts of the fishery have recently been given by S. K. Whitehead (1961), D. F. McCrea (1961), H. MacInnes (1961) and R. P. Gossett (1962). None of these authors refers to the beginning of the present industry by W. J. Sweeney of Achill Sound who has carried out the present fishery at Keel from 1950 up to the present day. Sweeney first experimented with harpoon guns and grenade headed harpoons from catchers at sea before confining the fishing to the western side of Keem Bay. There he first used metal submarine netting before he hit on the present method of employing large sisal nets of one foot mesh for tangling sharks, to be followed by lancing them through the spinal cord just behind the brain with a short steel lance, from a currach. The numbers of sharks landed at Keel between 1950 up to the present (A. E. Went, private communication, 1962), are set out in table 1.

The table shows that over 9,000 sharks were caught in twelve years between 1950 and 1964 at Achill; 1952 proved to be a bumper year with a record catch of 1,808 sharks, but since that time the catch has decreased and, latterly, from 1961 to 1964, there has been a phenomenal decline. Possibly one reason why the fishery has run down is that so many fish have been killed before they have had an opportunity to breed and, though the method of breeding of this fish is not known, it is generally assumed to be viviparous, and a very slow breeder. Whether the loss of fish in the sea area of Keem Bay is compensated for by the immigration of fish from other areas is not known.

On the question of migration, there appear to be two theories. The first is that of a northerly migration in spring and summer. This is favoured by many shark fishermen and is based on the evidence that sharks appear earliest in the south-west and later in the north-west regions of the British Isles. There are fishermen's accounts of sharks swimming in a northerly direction, often in tandem, in large shoals. Since the plankton outburst occurs earlier in more southerly latitudes, it may also be concluded that sharks appear first wherever the plankton is first plentiful. No observers have ever reported a southerly migration of sharks in autumn or winter so that this theory carries no conviction. The second theory is that sharks migrate shorewards from deeper waters in spring and summer to feed on the abundant plankton in the warm bays and shallow waters, and to mate, with the reverse movement in autumn. This theory has the advantage that it will account for the great diminution of sharks at Keem. The numbers caught there (table 1) would be unlikely to have any significant effect on the population of the whole north-eastern Atlantic but might be damaging to a local population of a very slow-breeding fish. The reduced number of fish coming to Keem Bay may also be accounted for to some extent by the effects of the dumping and accumulation of carcases on the bottom of this bay over the years. This might have a polluting effect so that sharks, which have a well-developed sense of smell, might now keep away. However, the winter storms on this part of the coast are of tremendous force and they would scour the bay and rid it of pollution. It would appear that the best explanation of the reduced catches would be that of the overfishing of a local population.

TABLE 1

Numbers of Basking Shark caught at Achill

Year	Number of Sharks
1950	905
1951	1,630
1952	1,808
1953	1,068
1954	1,162
1955	708
1956	977
1957	468
1961	150*
1962	100*
1963	75*
1964	47*
Total:	9,098

* Estimated F. C. Stott

One of the essential items of information required in considering the potentialities of any fishery, is a knowledge of the age-composition of the stocks on which the fishery is based. There is not a single record of the age of even a single basking shark and no completely convincing circumstantial evidence has yet been produced. Matthews (1950: 305) offered a tentative growth-curve showing a maximum size of twenty-nine feet (8.84 m) being reached in five or six years. This curve was based on thirteen measured fish only, and the author was at pains to point out that the curve represented the "least possible time for the attainment of maturity". A few years later Parker & Boeseman (1954: 190) offered a similar but more refined curve based on sixty measured fish. Their purely empirical mean curve is, though the fact was not realised at the time, an exceedingly close approximation to an asymptotic curve that, like the growth-curves of many teleosts, as well as some other poikilothermic vertebrates, fits an equation of the type $Ln = A\ [1\text{-}e^{-(a + bn)}]$ where n is the age, A the asymptotic limit and a and b two constants; for Parker & Boeseman's curve, A is 13.75 metres, a and b are 0.122 and 0.22 respectively, with n the age in years.

The time factor in this curve is essentially the same as in Matthews' earlier attempt and doubts have been expressed about the possibility of such very rapid growth. Watkins (1958: 249), for example, on the basis of the average number of pregnancies that would be required to maintain population numbers at a constant level, has suggested an average life-span of between ten and twenty years. In addition, the asymptotic mean of 13.75 metres appears unlikely since, allowing for the variation that must exist, this value

TABLE 2

March	3.27 m, Fedala; 2.75, 3.50 and 4.0 m, Casablanca (Furnestin, 1958).
April	7.61, 7.63, 7.93, 8.11, 8.12, 8.17, 8.25, 8.47, 8.47, 8.59, 8.60, 8.61 and 8.77 m, Achill Island.
May	1.80, 3.40 m, Casablanca (Furnestin, 1958); 8.55 m, Achill Island.
June	2.90 m, Dunbar; 3.39 m, Achill Island.
July	4.75 m, Achill Island.
September	8.63 m, Iceland (Ehrenbaum, 1925).
October	8.90 m, Iceland (Ehrenbaum, 1928); 4.60 m, Texel (Boeseman, in litt.).
November	3.40 m, Sylter Rif (Ehrenbaum, 1926); 2.85, 3.70, 3.90 m, English Channel (Schnakenbeck, 1955, in litt.); 8.0 m, Viking Bank (Ehrenbaum, 1922).
December	3.40, 4.60 m, English Channel (Schnakenbeck, 1955, in litt.).

leads to the expectation that about two per cent of the individuals of the appropriate age would be nearly sixteen metres in length; there is no credible evidence that such a size is ever reached.

In addition to the sixty dated records of measured fish listed by Parker & Boeseman (1954), we now have a further thirty-three, as shown in table 2.

The histogram of these ninety-three specimens (fig. 1A) indicates that the sample is far from uniformly distributed over the whole size-range. There are two obvious peaks, one in the 2.5-4.0 m zone and the other between 7.5 and 8.9 metres. The latter is very clearly the outcome of biased sampling, nearly all the records having originated in the catches of the commercial fisheries in Irish and Scottish waters. But there is no such obvious explanation of the lower peak. These records are, for the most part, based on chance strandings or on specimens accidentally enmeshed in trawls or drift nets, and it seems possible that the large number of small fish falling victims to these hazards reflects their youth and inexperience; there is a heavy infant mortality.

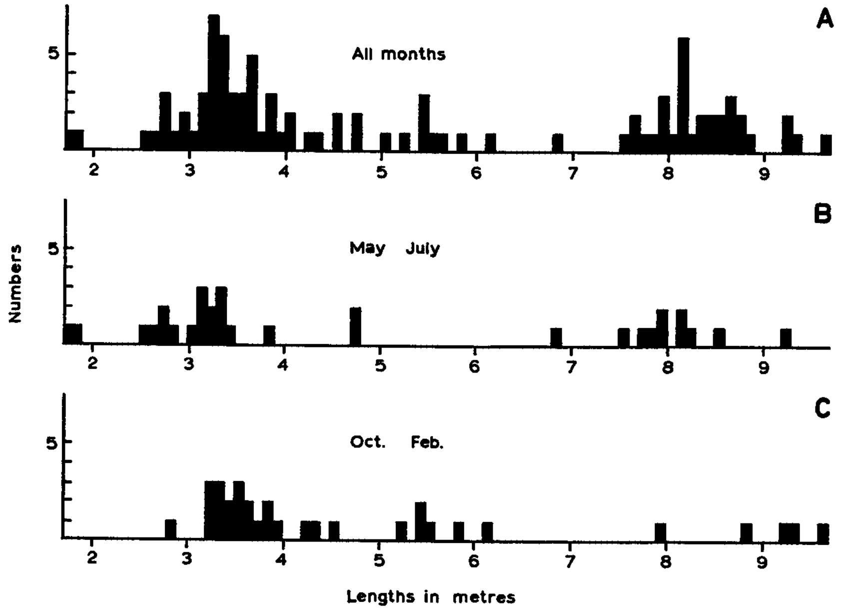

Fig. 1. *Cetorhinus maximus* (Gunnerus). Histograms showing the size-distribution of (A) a sample of ninety-three sharks taken in north-eastern Atlantic waters; (B) midsummer catches (May to June); (C) winter-caught specimens (October to February).

If the 2.5 to 4.0 metre group is analysed into mid-summer and mid-winter samples (fig. 1B, C), there are indications of a shift of the mean value. In the mid-summer sample there are fifteen specimens ranging in size from 2.54 to 3.44 metres with a mean value of 3.09 and a standard deviation of 0.281. In the mid-winter sample of seventeen specimens, the comparable figures are: range 2.85 to 4.0 metres, mean 3.52 m, standard deviation 0.279. The difference of the means in statistically significant and the inferences are (a) that if the two are pure samples of single age-groups (and their coefficients of variability are not markedly dissimilar) there is an increase in length of the order of 0.43 m in the autumn growing season of fish of that particular age, or, (b) that one or other or both of the samples are heterogeneous as regards age, being polluted by a proportion of older or younger individuals. There is nothing to suggest that the latter alternative is the more probable.

The time of year when parturition takes place is unknown, but it is a reasonable assumption that the two smallest specimens ever recorded, one of 1.68 m (Lough Swilly, July 1849, Thompson, 1856) and the other of 1.80 m (Casablanca, May 1955, Furnestin, 1958) were fish of the year. And it seems unlikely that these two are of the same age-group as the summer-caught fish of between 2.54 and 3.44 metres, for that would imply a size-range of 1.76 m (1.68 to 3.44 metres) and a coefficient of variability of seventeen in the first summer compared with a total range of only 1.15 m and a c.v. of 7.9 in a sample of the same size from the next succeeding winter. These considerations suggest that (1) a size of less than two metres is typical of the first summer, (2) a mean size of 3.09 metres is attained in the next summer and (3) that the mean size in the next winter is 3.52 m.

The maximum size that the species attains is a controversial matter. As Matthews & Parker (1950) pointed out, there has been a great deal of exaggeration and the literature abounds in unsubstantiated statements. Lengths of up to fifteen metres have been mentioned but the longest fish that seem actually to have been measured are still De Blainville's specimen of 9.70 m taken in the English Channel and the specimen of thirty-two feet two inches from the western North Atlantic mentioned by Bigelow & Schroeder (1948). Nevertheless, it is possible that larger specimens may exist from time to time and an asymptotic mean of eleven metres, with a c.v. of about eight (as in the samples measured), admits the possibility of individuals of 12.26 m on rare occasions. Such an asymptotic value, coupled with the second year mean values mentioned in the preceding paragraph, fit the equation $Ln = A [1\text{-}e^{-(a+bn)}]$ if a and b are 0.15 and 0.12 respectively and n is the age in years. The mean curve of this equation is shown in fig. 2 with the probable limits within which ninety-five per cent of the population of any given age will lie (i.e. $+-$ 2 S.D.). With such a high degree of variability there is no complete size-range discontinuity even between fish of the first and second years; fish in their first winter can be expected to exceed 3.00 metres in a small proportion of cases (less than 2.14 per cent) whilst a similar proportion of second year fish will be less than 3.02 metres. The amount of overlap in the size range from year to year increases with age so that length becomes progressively less and less reliable as an index of age. Yet the curve suggests that (a) the fish occurring most often in the commercial catches are more than eight and less than twelve years of age and (b) the size at birth is approximately 1.53 metres.

The curve, however, makes two assumptions; that growth is asymptotic and that growth during the spring half-year is at the same rate as in the autumn. Circumstantial evidence from other sources, in default of direct evidence, is clearly needed. The only other criterion that has been proposed for age estimation in this species is the number of calcified "rings" in the vertebral centra. These rings, in reality incomplete coaxial tubes that appear as interrupted rings in cross-sections of the centra, have been claimed to be "annual" rings, but without any evidence to support the claim. Jägerskiöld (1915), for example, says "I am convinced that these rings of growth represent each one year of life..." and Ehrenbaum (1926) on the same basis assigned ages of "at least thirty-two years" and nine years to specimens measuring 8.63 and 3.40 metres respectively. Kyle (1927) who examined the same two fish repeats these figures and adds "The light rings represent perhaps the summer season and the dark the winter" (translation). Other authors have made similar claims about the rings in the centra of other elasmobranchs, e.g. *Raja* (Tretjakov, 1927: 297), *Squatina* (Kyle, 1927: 332) and *Galeus* (Wurmbach, 1932: 60) and *Lamna* (Aasen, 1963: 33).

In his comprehensive review of the calcifications in elasmobranch centra Ridewood (1921) demonstrated that the growing zone of the centrum is peripheral and that, as growth takes place, additional rings are added in that region. But he was of the opinion that the calcifications "developed... in response to the physiological demands for a strengthening of the cartilage for resisting stresses in certain directions...". In vertebrae subject to similar stresses the number of rings would, therefore, be related to age, but only indirectly so and not as a result of seasonal change in, or caused by, the external environment. And this agrees with others of Ridewood's observations that are not compatible with the "annual" ring hypothesis; for instance, in both *Cetorhinus* and *Squatina* there are differences in the number of rings in vertebrae from different parts of the vertebral column, the caudals especially having less than the precaudals and their number diminishing caudad.

If, however, comparisons are made only between vertebrae from the same part of the body, it seems possible that there may be a more or less constant relationship between age and the number of rings. We have accordingly investigated the numbers and arrangement of the rings in a few precaudal vertebrae from fish of known size, as follows.

	Sex	Length	Radius centrum	Rings	Capture date
(a)	♂	4.75 m	46 mm	16	7/63
(b)	♀	7.63 m	61 mm	21 + 6	4/63
(c)	♀	8.77 m	68 mm	21 + 6	4/63
(d)	♀	7.93 m	63 mm	21 + 5	4/64
(e)	♀	8.55 m	72.5 mm	22 + 4	5/64

Previous accounts of the arrangement of the calcifications in the basking shark are almost unanimous in stating that in juveniles they are uniformly arranged to form a series of coaxial tubes, but that in older individuals this, cyclospondylous, arrangement is restricted to the middle of the centra whilst peripherally a series of radially arranged lamellae takes its place. Owen (1866: 33), for example, said that the radial lamellae "extend about one third of the way towards the centre..." and Kyle (1927: 322) reported that in his "thirty-two year old" specimen rings were formed for about the first twenty years (i.e., there were about twenty complete rings in the middle of the vertebrae) but that external to this they "only appear piecemeal and so form only a ridge or crest" on the outer surface. These and similar descriptions have led to the conclusion that "in *Cetorhinus* calcification passes with age from the cyclospondylous to the asterospondylous" and that these conditions are, therefore, of negligible value in the classification of the elasmobranchs (Devillers, 1954: 615).

These accounts seem to have resulted from the examination of dry or macerated material in which the cartilage has shrunk or degenerated. Pl. 1 shows clearly the calcareous rings continuous across the intermedialia in the middle of the centra but becoming discontinuous towards the periphery. It is, however, equally clear, especially from the enlarged segment, that there are continuous rings in the cartilage all the way through to the periphery although in this area the calcification is less extensive. The cartilaginous rings are alternately broad and dark and light and narrow. It is within the narrow rings that calcification takes place and in the youngest (i.e., outermost) rings calcification commences at a number of almost equidistant points.

With the passage of time, as more cartilage is formed externally on the intermedialia, each of the calcified spots spreads laterally from its point of origin but remains confined to the cartilage ring in which it originated.

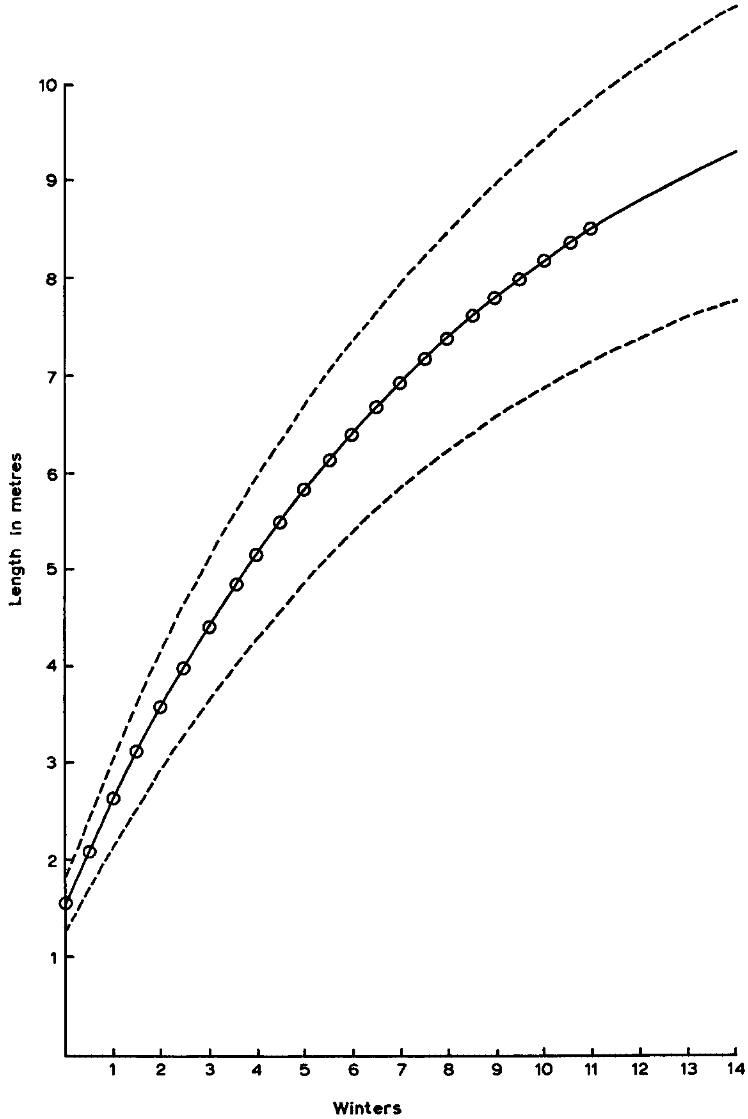

Fig. 2. *Cetorhinus maximus* (Gunnerus). Hypothetical asymptotic growth-curve calculated from the observed increase in mean length from 3.09 m to 3.52 m in a period from mid-summer to the following mid-winter, and an estimated maximum of eleven metres. Broken lines indicate the limits of random variation at two standard deviations from the mean.

Eventually the sheets so formed meet edge to edge to form complete rings (tubes); there is little if any thickening of these calcified sheets with age but the darker zones between them do increase in thickness for a time so that the calcareous rings become more widely separated.

In the list of vertebrae given above, the rings are segregated into two groups, complete (first number) and incomplete. The line of distinction is not always obvious and other potential sources of discrepancies lie in the difficulty of obtaining an exact count in the actively growing peripheral zone and the fact that the rings often divide (or two fuse?) near the line of contact between the intermedialia and the basidorsals or basiventrals. Our counts have been made in the lateral intermedialia along the nine o'clock —three o'clock axis and the radius measurements were made at mid-vertebra along the same line.

Analysis of the spacing of the rings shows that there is a common pattern. The curve in fig. 3 is derived from the averages of the five vertebrate listed above. It is a typical exponential growth curve (Needham, 1964) with inflexion at about the seventh ring from the centre. There was a regular increase in the thickness of the cartilage added between successive rings in the early history of this average vertebra and this continued until the seventh had been formed; after that there was a steady diminution. No matter whether, as the vertebrae increase in diameter, rings are added at regular intervals of time or irregularly in response to mechanical requirements, it seems probable that vertebrae from the same part of the column will achieve, and pass through, the same ring condition at the same size and/or age. And if that be so the curve of ring spacing (fig. 3) in an average precaudal vertebra, extrapolated if need be, will indicate approximately the number of rings and their spacing that may be expected in any size of precaudal vertebra. For instance, in a vertebra with fifteen rings the outermost and innermost may be expected to be separated by about 40 mm, a dimension that is related to the size of the vertebra. Conversely, a vertebra in which the outermost and innermost rings are separated by 50 mm would have twenty rings; and so on.

There is a simple direct relationship between the sum of the distances separating the rings and the radius of the vertebra, and another between the radius and the length of the fish. In the precaudal vertebrae that we have seen the sum of the inter-ring distances averages six millimetres less than the radius; and the radius, in millimeters, is 0.006 times the length of the fish, plus seventeen. So, the sum of the inter-ring distances, on average, is equal to 0.006 times the length of the fish plus eleven, and an average length scale can be substituted in fig. 3 for the inter-ring distance scale. The curve then becomes in effect a graphic representation of the average relationship between the number of rings and the overall length.

A high degree of accuracy is not to be expected since no allowance has been made for individual variation which, to judge from Ridewood's finding (1921: 361) that vertebrae from the branchial region may be twenty-four per cent smaller than those from the precloacal region, must be considerable. Nevertheless, eight individual fish of known size and ring numbers fit reasonably close to the average curve (fig. 3), much closer than could be expected from chance.

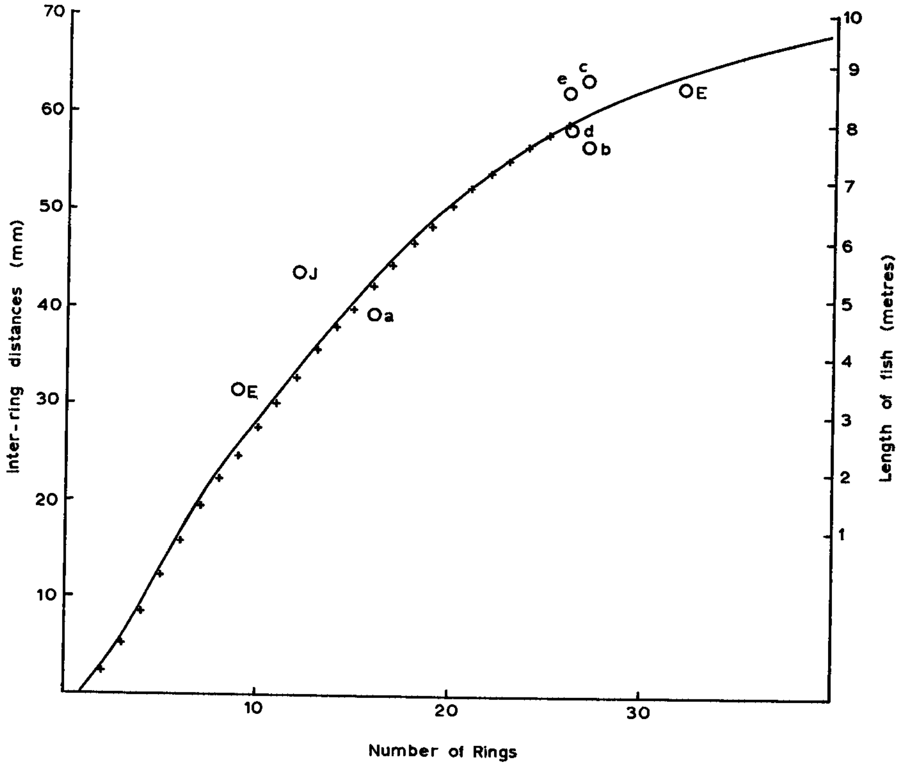

Fig. 3. *Cetorhinus maximus* (Gunnerus). Distances apart of rings in an average precaudal vertebra plotted against the number of rings (crosses). Superimposed as circles are lengths plotted against rings in five fishes (a to e) and three records from the literature; the length scale is based on the average observed relationship between vertebral radius and total length. "E" and "J" are records by Ehrenbaum (1925, 1926) and Jägerskiöld (1915).

When the curve is compared with the hypothetical post-natal growth curve (fig. 2) some correlations emerge. The theoretical average length at age 0 (i.e. at birth) is 1.53 m which corresponds very closely with the inflexion of the "ring" curve immediately above the seventh ring; this indicates a possibility of seven rings at birth. From that point onwards each "annual" increment in length according to fig. 2 corresponds closely with an increase of two rings according to fig. 3. There is still nothing to indicate beyond doubt that the addition of two rings is the direct result of the passage of an annual seasonal cycle though it is tempting to relate it to the dual seasonal plankton maxima. And since the two curves were independently derived from different data the close correspondence between them could be regarded as mutually confirmatory. But the irregularities that occur in a single vertebra, the reduced number of rings in the caudal region and the apparent existence of seven rings at birth are features that do not obviously harmonise with the idea of annual increases of two rings.

There is no apparent reason why there should be a difference in the rate of formation of the calcified rings before or after birth. So, the existence of seven rings at birth suggests a gestation period of three and a half years. Such a lengthy period may appear unlikely since it would mean an extremely slow reproductive rate; but the little that is known on the subject indicates that in other elasmobranchs the gestation period may, indeed, be prolonged. For example, Backus et alia (1956) claim that it is about a year in *Pterolamiops longimanus* (Poey) whilst a similar period has been reported by Iwai (1957) for *Etmopterus lucifer* Jordan & Snyder; Hisaw & Abramowitz (1939) say that it is nearly two years (twenty-two months) in *Squalus acanthias L.* and Gudger (1940) believed that it might exceed two years in *Chlamydoselachus.* A three and a half year period is not, therefore, impossible and there is some slender confirmatory evidence. There have only been two reports, one certainly and the other probably based on hearsay only (Pennant, 1769; Matthews, 1950 : 305), of pregnant females having been observed. It is, therefore, as Matthews (1950) pointed out, probable that the females leave the inshore shoals after mating, before any embryo is macroscopically recognisable, and do not rejoin them whilst still pregnant. It follows that the shoals will only exceptionally contain any females between the ages of x and y, where x is the age at the onset of sexual maturity (when it may be confidently expected that the majority will become pregnant) and y the age in the spring immediately following the termination of this first pregnancy. The sample that we have studied, with ninety-three records, is admittedly small to furnish conclusive evidence, but it seems significant that it contains only three specimens, none of them females, in the size-range 5.8 to 7.4 metres which, according to our tentative growth-curve, corresponds with the size limits (average) of fish in their sixth, seventh and eighth years. As the histogram (fig. 1A) shows, this contrasts strongly with the conditions in other three year age-brackets where both sexes are present and in greater numbers. There are twenty-four fish between 3.55 and 5.8 metres long which is the size range appropriate to individuals in their third, fourth and fifth years and twenty-one between eight and eleven years old (7.4 to 8.47 metres). The length of females at the onset of sexual maturity is not known, but in males it seems to be achieved at an age that bears some relation to the sixth to eighth year bracket. Bigelow & Schroeder (1948), basing their conclusions on changes in the relative size of the claspers with increasing age, have suggested that maturity may be reached at a length of 4.6 to 6.1 metres, i.e. in their fourth or fifth years according to our tentative time scale, whilst Matthews (1950) reports that although spermatophores were absent there was evidence of testicular activity in a specimen of 6.9 metres.

The smaller number of rings in the caudal vertebrae constitutes a less serious objection to the hypothesis of a regular addition of two rings a year. Clearly the caudals cannot be appreciably younger than the precaudals but it is equally clear that, being very much smaller (the terminal centra may have a diameter less than one sixth that of one the larger precaudals), there must be some compensating reduction in the number of their rings. Without this the relative proportions of cartilage and calcareous tissue would inevitably be altered, changing the mechanical properties of the vertebrae. The reduction in the number of rings is not, however, directly proportional to the reduction in centrum diameter. As the plate shows, the rings are more closely spaced in the caudal vertebra; this, though nearly forty per cent less in diameter than the precaudal from the same fish, has only two (7.4 per cent) fewer rings. The extent of the caudal reduction is also very variable, the maximum that has been observed in five fish being in a 7.93 m female where a fifty per cent reduction in diameter is associated with twenty-seven per cent fewer rings.

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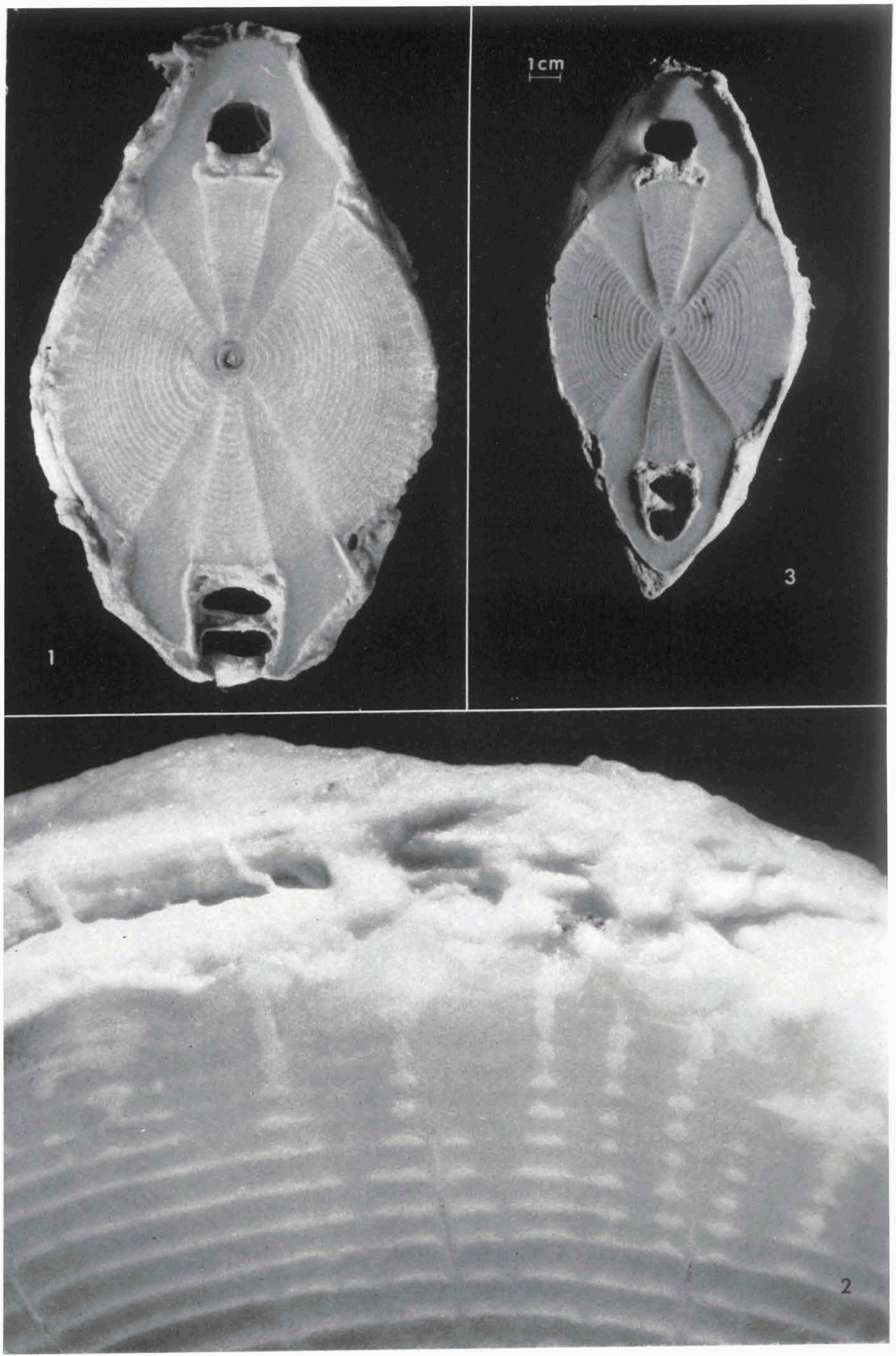

Cetorhinus maximus (Gunnerus). Median transverse sections of vertebrae of an April-caught female of 7.63 metres overall length. 1, a precaudal vertebra; 2, enlarged segment of (1) from the periphery at about nine o'clock showing pre-existing cartilaginous rings in which calcification takes place; 3, a caudal vertebra. The scale (1 cm) refers to fig. 1 and 3.