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A critique of some literature data on the growth, reproduction and mortality of the lamnid shark Cetorhinus maximus (GUNNERUS).

by

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Abstract

Previous literature estimates of growth of the basking shark Cetorhinus maximus (Lamnidae) are revised and the following parameters for the VON BERTALANFFY growth formula are derived from published data:

For the females: $L_{\infty} = 1314$ cm, $W_{\infty} = 17\ 000$ kg, $K = 0.0357$ and $t_0 = - 3.4$ years. For the whole population $L_{\infty} = 1226$ cm, $W_{\infty} = 13\ 820$ kg, $K = 0.045$ and $t_0 = - 2.9$ years.

The exponential coefficient of natural mortality (M) was estimated as $M = 0.103$ for the juveniles (17 years) and $M = 0.048$ for the adults (18 to 31 years).

Introduction

The basking shark Cetorhinus maximus belongs to the largest recent elasmobranchs, ranking second immediately after Rhincodon typus which is reported to reach a length of 20 m (NIKOLSKY, 1957).

HOLDEN (1974) assumed a figure of 1372 cm for L_{\max} to be realistic, PARKER & STOTT (1965) use for their calculations $L_{\max} = 1226$ cm.

Data on the growth rate of such a large fish would be of considerable interest for comparative studies. The present paper is a by-product of such a comparative study (PAULY, 1978 a).

Material

The basis for this study are the data published by PARKER & STOTT (1965). The material consists of the length at age data given in Table I and of the length-frequency data summarized in Table II.

Methods

The methods used here for the estimates of the growth parameter K are the "VON BERTALANFFY Plot" (VON BERTALANFFY 1934) and the "simplified GULLAND and HOLT Plot" (adapted from GULLAND and HOLT, 1959) which are both used with a set value for asymptotic length, here coded " $L_{(\infty)}$ ". The independent value of L_{∞} and the corresponding value of K were determined by non-linear regression. For details on these methods see PAULY (1978 a). PARKER & STOTT (1965) used in their paper an empirical growth formula in which

$$L_t = L_{\infty} (1 - e^{-(a + bt)}) \quad \dots 1)$$

and where their parameters A and n have been here replaced by L_{∞} respectively t for better comparison with the VON BERTALANFFY Growth Formula (VBGF), which has the form:

$$L_t = L_{\infty} (1 - e^{-K(t - t_0)}) \quad \dots 2)$$

It may be mentioned here that equation 1) differs from equation 2) in having an inflexion point.

Results and Discussion

Growth

By grouping their length frequency data into a "mid-summer" and a "mid-winter" sample, PARKER & STOTT (1965) could demonstrate that there is a shift in the length of the smaller fishes which was ascribed to growth. The mean length having increased from 309 cm in mid-summer to 352 cm in mid-winter, PARKER & STOTT (1965) doubled the growth increment of 43 cm in about 6 months to obtain a growth of 86 cm per year of 43 cm at $\bar{L} = 330$ cm. This value, combined with a value of $L_{(\infty)} = 1226$ cm provides an estimate of $K = 0.096$

(Alternatively these values may be used in conjunction with equation 1), where, according to PARKER & STOTT (1965) they produce a value of $a = 0.15$ respectively $b = 0.12$). The value of Table I, used in conjunction with a value of $L_{(\infty)} = 1226$ cm produces an estimate of $K = 0.082$ if it is assumed that two vertebral rings are laid down each year. PARKER & STOTT (1965) made this assumption and found, indeed, that the data of Table I "confirmed" the estimate based on the shift in the length frequencies (indeed $K = 0.096$ 0.082). Equation 1) used in conjunction with values of $L_{(\infty)} = 1226$ cm, $a = 0.15$ and $b = 0.12$ produces an inflexion point at $t_i = 3.5$ years and $L_i = 153$ cm. PARKER & STOTT (1965) interpreted the position of this inflexion point biologically, that is, they equated L_i with the length at birth and t_i with the gestation period. Furthermore, PARKER & STOTT (1965) retained their two-rings-a-year assumption even for the embryos and deduced that the sharks are born with 7 rings (2 x 3.5 years of gestation period). The only evidence advanced by PARKER & STOTT (1965) to back the two-rings-a-year assumption is a citation of RIDWOOD (1921) who was of the opinion that the vertebral rings (calcifications) "developed in response to the physiological demands for strengthening of the cartilage for resisting stress in certain directions." Thus, PARKER & STOTT (1965) continued, "in vertebrae subject to similar stress the number of rings would, therefore, be related to age, but only indirectly so and not as a result of seasonal changes in, or caused by the external environment." It remains unclear then why the physiological demands and the stresses should be the cause for just two rings per year and why should the embryo develop 7 rings? It is quite obvious that a shark's embryo will not be subjected to any structural stress at the rate of the adults.

The concept of growth in C. maximus, as proposed by PARKER & STOTT (1965) thus rests on the following assumptions:

- 1) Growth is more or less uniform during the whole year.
- 2) Two vertebral rings are laid down annually.
- 3) Equation 1) depicts the whole of the shark's growth curve, including its embryonic phase.
- 4) The length at birth and the age since fertilization date are given by the coordinates of the inflexion point of equation 1).

These assumptions do not seem well founded. Equation 1) is an empirical growth curve, and its parameters certainly do not allow for biological interpretations and for extrapolations beyond the range of the values fitted.

It need to be scrutinized in the light of what is known of the biology of C. maximus .

- a) C. maximus is a filter feeder and uses for sieving its planktonic food large gill-rakers, which are resorbed in winter (MUUS - DAHLSTRÖM, 1974). That is, for a period of at least 3 - 4 months, C. maximus cannot feed.
- b) PARKER & STOTT, attempting to elucidate the winter-spring disappearance of C. maximus from the shallow water fishing grounds, reject the hypothesis of a north-south migration (as postulated e. g. by MUUS - DAHLSTRÖM, 1974) and suggest instead an inshore feeding migration. They seem to imply that C. maximus does not feed in winter and spring, that is, for a period of about six months.

So, it can very well be assumed that the growth increment of 43 cm in 6 months at $\bar{L} = 330$ cm corresponds to the whole of the annual growth, as the period covered is when the fish are both in possession of their gill-rakers and feeding inshore.

An annual growth increment of 43 cm at $\bar{L} = 330$ cm and of a value of $L_{(\infty)} = 1226$ cm results in a value of $K = 0.048$. The assumption 2) of the production of two vertebral rings per annum is not backed by evidence. It seems much more likely that the vertebral rings are laid down annually, and are caused by the succession of cold, non-feeding with warm, feeding seasons. The data in Table I and a value of $L_{(\infty)} = 1226$ cm result in a value of $K = 0.041$.

These two new values of K may be averaged to $K = 0.045$. If the assumption is made that the fish grow always according to the VEGF then a value of $t_0 = - 2.90$ years may be derived from the length at birth of 150 cm given by PARKER & STOTT (1965) and MUUS - DAHLSTRÖM (1974).

For comparison, the data of Table I may be used for a direct estimation of L_{∞} and K using a non-linear regression, which yield an estimate of $L_{\infty} = 1314$ cm and $K = 0.0357$. The length at birth, used here as above, produces an estimate of $t_0 = - 3.40$ years.

The closeness of this value with PARKER & STOTT's (1965) assumption of 3.5 years pregnancy is purely fortuitous. From the ungutted weight and length data in EHRENBAUM (1926) a condition factor of 0.75 can be derived, from which an estimate of $W_{\infty} = 17\ 000$ kg can be made.

The growth parameters based on a value of $L_{(\infty)} = 1226$ cm should more or less correspond to the mean growth parameters of the population ($\sigma^{\text{♂}}$ & ♀), while the parameters based exclusively on Table I are biased towards the females.

Reproduction

MUUS - DAHLSTRÖM (1974) write that C. maximus attains sexual maturity at 3 - 4 years of age and at a length of about 7 m. While we doubt the age estimate the mean length at first maturity (L_m), seems to be very realistic, because $\frac{L_m}{L_{(\infty)}} = 0.57$ or $\frac{L_m}{L_{\infty}} = 0.53$ is similar to other very large fishes. Using $L_{\infty} = 1314$ cm, $K = 0.037$ and $t_0 = -3.4$ years, an estimate can be made of a mean age at first maturity (T_m) of about 18 years in females. In males a value of $L_m = 4.6 - 6.7$ m has been determined by BIGELOW & SCHROEDER (1948). This value, incidentally, suggests that the sex specific growth common in fishes ($\sigma^{\text{♂}} < \text{♀}$) also applies to C. maximus.

PARKER & STOTT (1965) do not discuss as to where the females disappear during their assumed gestation period of 3.5 years. HOLDEN (1974), on the other hand, suggested a gestation period of 1 year in C. maximus. This latter value would fit into the offshore-inshore migration pattern proposed by PARKER & STOTT (1965) and explain why no pregnant females are caught in the surface-water fishery investigated by these authors: pregnant females may simply migrate offshore, with the rest of the stock, or perhaps earlier, and give birth to their young in the following spring.

Mortality

PARKER & STOTT (1965) commenting on the relatively large number of small fishes in their length frequency sample write: "... These records are for the most part based on chance stranding or on specimens accidentally enmeshed in trawls or drift nets, and it

seems that the large number of small fish falling victim to these hazards reflect their youth and inexperience; there is a very heavy infant mortality." This statement may be checked by converting the length frequency data available into age frequency data, using our new population growth parameters (Table II).

For further interpretation, these data were pooled into year class triplets, with one mean age and one value for n each (Table III). The data of Table III permit the construction of two "catch curves" (Fig I), if the following assumptions apply:

- a) The age groups 0 to XVII represent a random sample from the juvenile populations of C. maximus.
- b) The age group XXVIII to XXXI represent a random sample from the commercial fisheries, as "nearly all the records have originated in the catch of the commercial fisheries in Irish and Scottish waters" (PARKER & STOTT, 1965).

From the first "catch curve", a value of $Z = 0.102$ may be derived for the juveniles (age gr. 0 - XVII). This value may be assumed to correspond more or less to an estimate of M.

A value of $Z = 0.093$ may be derived from the second "catch curve" (age gr. XVIII - XXXI). Here, we have an exploited stock, and an attempt may be made to split up Z into its constituent parts M and F.

The natural mortality of adult C. maximus may be estimated by means of equation 9) in PAULY (1978 b) namely:

$$\log M = 0.1228 - 0.1912 \log L_{\infty} + 0.7458 \log K + 0.2391 \log T,$$

where L_{∞} is expressed in cm and T is the mean annual water temperature for the stock in question.

The estimate of M for a value of $L_{(00)} = 1226$ cm, $K = 0.045$ and $T = 10^{\circ}\text{C}$ is $M = 0.048$. For the exploited population of Irish and Scottish waters we thus have $Z = 0.093$, $M = 0.048$, hence $F = 0.045$. As no fish nor marine mammal is reported to prey on adults of C. maximus, the estimated value of $M = 0.048$ may correspond to the purely "physiological mortality" discussed in PAULY

(1978 b), and the bodies of dead C. maximus would become a part of the "carcass food chain" (PEARSONS et al., 1972).

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Table I: Length-at-age-data PARKER & STOTT (1965)

Nr.	Sex	Length (cm)	number of vertebral rings	as determined by	Remarks
1	♂	475	16	PARKER & STOTT (1965)	-
2	♀	763	27	-do-	-
3	♀	877	27	-do-	-
4	♀	793	26	-do-	-
5	♀	855	26	-do-	-
6	-	340	9	EHRENBAUM 1925-1928	-
7	-	860	32	-do-	4500-5000 kg
8	-	544	12	JAGERSKJÖLD 1915	as read off Fig. 3 in PARKER & STOTT (1965)

Table II: Length frequency data of PARKER & STOTT (1965) with conversion to age assuming $L_{\infty} = 12.26$ m, $K = 0.045$ and $t_0 = - 2.90$

Length (m)	n	Age (y)	Length (m)	n	Age (y)	Length (m)	n	Age (y)
1.7	1	0.4	4.2	1	6.4	-	-	-
1.8	1	0.6	4.3	1	6.7	7.5	1	18.1
-	-	-	-	-	-	7.6	2	18.6
2.5	1	2.2	4.5	2	7.3	7.7	1	19.1
2.6	1	2.4	-	-	-	7.8	1	19.6
2.7	3	2.6	4.7	2	7.8	7.9	3	20.1
2.8	2	2.9	-	-	-	-	-	-
2.9	2	3.1	5.0	1	8.7	8.1	6	21.1
3.0	1	3.3	-	-	-	8.2	1	21.7
3.1	3	3.6	5.2	1	9.4	8.3	2	22.2
3.2	7	3.8	-	-	-	8.4	2	22.8
3.3	6	4.1	5.4	3	10.0	8.5	2	23.4
3.4	3	4.3	5.5	1	10.3	8.6	3	24.0
3.5	3	4.6	5.6	1	.017	8.7	2	24.6
3.6	5	4.8	-	-	-	8.8	1	25.2
3.7	1	5.1	5.8	1	11.3	-	-	-
3.8	3	5.3	-	-	-	9.2	2	27.9
3.9	1	5.6	6.1	1	12.4	9.3	1	28.7
4.0	2	5.9	-	-	-	-	-	-
-	-	-	6.8	1	15.1	9.6	1	31.1

$\Sigma n = 93$

Table III: Data for the catch curves of Fig.I

Triplets	Age gr.	Mean age (y)	n
1	O, I, II	1	9
2	III, IV, V	4	37
3	VI, VII, VIII	7	7
4	IX, X, XI	10	7
5	XII, XIII, XIV	13	1
6	XV, XVI, XVII	16	1
7	XVIII, XIX, XX	19	8
8	XXI, XXII, XXIII	22	13
9	XXIV, XXV, XXVI	25	6
10	XXVII, XXVIII, XXIX	28	3
11	XXX, XXXI, XXXII	31	1

Fig.I: Catch curves for juveniles and adults of Cetorhinus maximus

