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AGEING AND GROWTH OF EEL POPULATION, *Anguilla anguilla*, IN THE LAGOONS OF ARCACHON BAY (FRANCE)

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ABSTRACT

Specimens of eels, collected in the lagoons of Arcachon Bay from April 1977 to October 1978, were analysed for age and growth. The structure of the otolith was described based on examination of the decalcified surface using an scanning electron microscope, and was compared with observations made under an optical microscope. The otolith of Arcachon eels show a narrow summer growth stop in addition to a growth stop formed in winter. The narrow summer growth stop seems to be related to the bad ecological condition of the lagoons in summer. The growth in length of sedentary eels was well represented by the Von Bertalanffy curve, when the exceptionally large eels were not accounted. The successive removal of the large members by the migration to the sea decreases the growth ratio of the sedentary eels as the fish grows older. This size selective migration in part contributes to satisfy Von Bertalanffy's assumption. Length distribution of the exceptionally large eels in relation to age was analysed by comparing them with "normal" sedentary eels and with silver migrating eels, and it is suggested that the exceptionally large eels consist of the animals which probably had the capacity for fast growth when already young.

INTRODUCTION

The exact determination of the age of fish is one of the basic problems in studying fish populations. The age of fishes can be principally estimated by counting the discontinuity marks of their skeletal structures. They are influenced either directly or indirectly by the variations of the environmental conditions where the fish grown. In the case where all members of a population have grown under the same conditions, it is relatively easy to extract a growth pattern of the skeletons. But, when individuals grown in different conditions are mixed, a general pattern of the population can not be easily obtained.

The migratory behavior of eels leads to finding individuals of different origins in a given body of water, and a considerable area must be covered in order to collect specimens in different stages of the life cycle. This is thought to be one of the reasons why one can not extract a general pattern for the ageing and growth curve of the eels, although many attempts have been made to do so.

The lagoons of Arcachon Bay (Fig. 1) have the several merits for the study of eel population. They are ancient salt ponds which are accessible from the sea through the water gates only during the high spring tides because of dikes. Control of the water gates allows the fish alevins to penetrate into the lagoons, but renders their emigration nearly impossible (Labourg, 1976). In consequence, the fish which enters the lagoons are imprisoned for their entire life. This fact causes them to grow under similiar environmental condition.

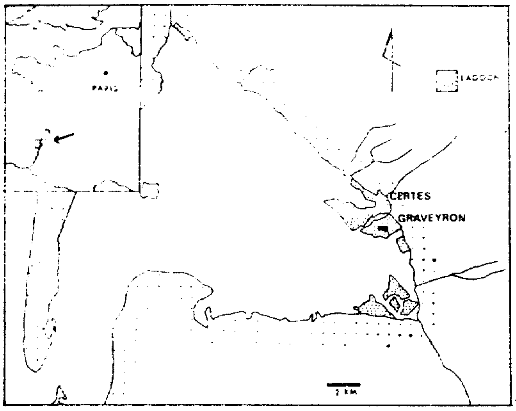

Fig. 1. Lagoons of Arcachon Bay

It is expected that the seasonal growth of the hard parts of fishes is not very different between individuals, showing only systematic variations. In addition, one can collect eels at the different stages of their continental life in the lagoons. Consequently, sampling can be done with relative ease for the population studies.

MATERIALS AND METHODS

COLLECTION OF SAMPLES

Sedentary yellow eels were sampled every three months between April 1977 and October 1978 by means of the eel traps, called "capétchades" on the Mediterranean coast of France. Elvers, penetrating the lagoons from the sea, were caught with a scoop net in the tidal canals in front of the water gates.

LENGTH COMPOSITION

To obtain reliable length composition, intensive fishing was conducted using the eel traps and electric fishing apparatus in April 1978. The former, because of its mesh size, is selective for small animals. The latter was originally thought to show no apparent selectivity with respect to length, but the length classes with low frequencies appeared to be biased because the sampling was done in a limited area of approximately 0.1 hectare. To combine the length frequency distributions obtained by two apparatus, standardization was realized in the length class 39～41cm. This length class was chosen because the traps do not show any apparent selectivity and the frequencies obtained by the electricity is considered to be sufficient to represent the population. A detailed description of the method and the results were given by Lee (1980).

DETERMINATION OF SEX AND AGE

Subsampling was realized by the stratified random sampling method for the determination of sex and age. The determination of the sex of the Arcachon eels was generally achieved by macroscopic examination of the gonads for the animals longer than 30cm in length.

The age of eels can be determined from the otolith by different methods of preparation and observation (Frost, 1945; Christensen, 1964; Smith, 1968; Albrechtsen, 1968; Fawell, 1974), but the grinding and etching method (Frost, 1945) was developed and applied in this study. Some of the otolithes were verified by the examination of the decalcified surface under the scanning electron microscope.

The otolith was placed on the fine carborundum stone and ground on each side with finger or cork. The ground surfaces were washed carefully with a brush and dried in the air. They were finally put in holes previously prepared in a 2mm thick sheet of paraffin on glass slides. Mounting was made with Canada balsam diluted with xylene. This preparation facilitated not only the preservation of a large number of samples but also comparative examination.When needed, a drop of xylen improoves visibility.

To prepare the sagittae for the scanning electron microscope, the sagittae was cut in two through the nucleus or ground on the convex side with a carborundum stone to the plane of the nucleus. They were etched with a 1% HCl aqueous solution for 2~5 minutes. They were then mounted on specimen stubs with conductive paint and vacuums shadowed with gold-paradium for 4 minutes. The prepared specimens were examined under the scanning electron microscope (JSM-35).

ESTIMATION OF GROWTH

For the growth in length of the population, the weighted average lengthes were adjusted to Von Bertalanffy's equation using the program BGCl (Abramson, 1971).

For the individual growth, the fish length corresponding to any growth stop radius of otolith was calculated by Lea's formula(Lea, 1910 in Bagenal & Tesch, 1978):

$$L_n=\frac{S_n}{S}L$$

where L_n=length of fish when growth stop 'n' was formed,

L=length of fish when otolith sample was obtained,

S_n=radius of growth stop 'n',

S=total otolith radius.

RESULTS AND DISCUSSION

STRUCTURE OF THE OTOLITH AND AGE DETERMINATION

Elver otolith and continental age

The elvers collected in April were transparent, pigmented only in the anal and celebral regions. Following the classification of Bertin (1951), they can be classified as being at stage V-B. On reflected light against a dark background, the elver otoliths showed a hyaline center, surrounded by two opaque zones. Concentric growth marks were also observed under the scanning electron microscope, and they were compared to the zones observed on the reflected light under the optical microscope (Pl. I-A):

—the first zone opaque observed on the reflected light under the optical microscope corresponds to the zone between w_1 and w_2 observed under the scanning electron microscope,

—The first hyaline zone to w_2,

—the second opaque zone to the zone between w_2 and w_3,

—the second hyaline zone to w_3.

These three annuli w_1, w_2, w_3 indicate that the elvers probably spent three years in the sea (Schmidt, 1922). Ehrenbaum and Marukawa (1914) called this part of the otolith the sea annuli or elver annuli. The last hyaline zone, formed during the transformation of elver into sedentary yellow eel, is fine and clear compared to the hyaline zones formed later in the continental waters.

The years spent in continental waters are usually recorded in term of age groups; 0 for the the first year, 1 for the second year,... This classification was adopted by Ehrenbaum and Marukawa(1914), with continental age beginning in April-May. Frost (1945) proposed May 1 as the beginning of continental age. This has been generally accepted for the eel population studies. In Arcachon Bay, the elvers penetrate a month earlier than the northern Europe(D'Ancona, 1958). Moreover, the mean water temperature exceeds 12°C during April, from which time the eels begin to feed and grow. Therefore, the beginning of continental life is fixed at mid April for Arcachon eels.

Adult otolith

On the reflected light against a dark background, the otolith showed alternating opaque and hyaline zones. The zone formation varies according to the external and internal conditions of the fish. Little is known, however, of the physiology of otolith formation (Simkiss, 1974). But, it is generally agreed that the opaque zones are formed during the period of the year when fish growth is rapid, while the hyaline zones are formed at the time when there is little or no growth.

An earlier study (Lee, 1977) showed that the different zones of the otolith of Arcachon eels is relatively easy to identify, but that the hyaline or opaque zones consist of several sub-hyaline and sub-opaque zones. These supernumerary zones often complicate age determination.

To identify the supernumerary zones, otolithes collected in different seasons were examined, comparing the observations obtained on the optical microscope with those obtained by the scanning electron microscope.

Otoliths collected in December had thin hyaline zone at the edge(cf. Pl. I-B1). In April of the next year, a thin opaque zone was observed exterior to the hyaline zone (cf. Pl. I-B2). The latter was relatively wide compared to that observed in December. It appears that the hyaline zone is formed during winter. The hyaline zone formed in winter was composed of several thin opaque and hyaline sub-zones. Under the scanning electron microscope, several growth stops alternated (Pl. I). As Lieu (1974) proposed, the fish probably did not stop growth completely during the winter period. The low temperature of early winter or late autumn might effect the physiology. Fish growth stops but regains again in small amounts as result of the relative variation of the ecological conditions.

At the end of July, the formation of a thin hyaline zone was observed exterior to thin opaque zone. The latter is supposed to be formed during spring-early summer, This hyaline zone is not evident in all individuals, but it can be observed clearly in the specimens collected later, when this hyaline zone was surrounded by an apparent opaque zone. Water between the sea and the lagoons is exchanged only during the high spring tides. Red tides were frequently observed in summer, because of a mass mortality of the benthic plants in these stagnant water. It seems that the formation of the thin hyaline zone is related to bad ecological condition during the summer. Under the electron microscope, well defined aragonite crystals were observed at the edge of the otolith (Pl. I-B3). It is thought that the thin marginal hyaline zone is not sufficient to remain during decalcification.

At the end of October, the summer opaque zone becomes enlarged (cf. Pl. I-B4). At this time, the summer growth stop is clearly seen in the inner part of the opaque margin. Comparing this with observations made in December of the previous year, it is felt that the opaque zone is formed from spring to autumn, and it shows a thin hyaline zone at the middle part.

Most of the otoliths collected in April shows that a new opaque zone was formed, though narrow, in all but a few individuals. A number of authors have stated that otolith is much later than body growth regard to opaque zone formation (Frost, 1945; Sinha & Jones, 1975). No large difference between them was observed in Arcachon eels.

The supernumerary zone, or false winter zone, often complicates age determination by the otolith. The summer growth stop described above is thought to be a good example of that. The summer hyaline zone was generally narrower than winter hyaline zone. They were easily identified except in a few old fish.

GROWTH IN LENGTH

Sedentary eel population

The length composition obtained in April 1978 is given in column TOTAL of Tab. 1. The subsample used to determine the age and sex is given in column. n_i. Using the age-sex key of the subsample, the catches (column TOTAL) are redistributed according to the corresponding age and sex (Tab. 1).

The average lengths of each sex of the different age groups were calculated as follows:

—For the elvers(age group 0), it was obtained from 68 individuals collected in April 1977 and in April 1978, which shows;

average length, $l_0=6.76$cm

with standard deviation, s.d. (l_0), $=0.50$cm

—The undifferenciated animals of an age group were distributed half for males and

Table 1. Length frequency distribution for age and sex from a sample collected in April 1978 (M: male, F: female, MF: undifferenciated, n_i: subsample size, N_α and $s(N_\alpha)$: frequency total and its standard deviation for age α, l_α and $s(l_\alpha)$: mean length and its standard deviation for age α. In calculating the frequencies, fractions were rounded off to the nearest unit. See the text for more detailes.

AGE	I	II	III			IV			V		VI		VII	VIII	IX	X+	TOTAL			n_i
SEX / LENGTH	MF	MF	M	MF	F	M	MF	F	M	F	M	F	F	F	F	F	M	MF	F	
11~13	1																	1		1
13~15	9																	9		5
15~17	4	5																9		2
17~19		8					2											10		6
19~21		20																20		6
21~23		8		5			2											15		9
23~25		14		13			3											30		11
25~27		2		11			2											15		13
27~29		2		16			14											32		16
29~31				30			15											45		9
31~33			6		4	22		12	2								30		16	23
33~35			6			34		22	3		9						53		22	24
35~37						30		4	13	9	8						51		13	15
37~39						3		9	3	21		9					6		39	15
39~41									3	22	3	3	7				6		32	12
41~43												31	9						40	9
43~45												27	11						38	7
45~47												13	12						25	2
47~49												2		3	2	2			10	4
49~51													8						8	1
51~																17			17	8
TOTAL N_α	14	59	12	75	4	89	38	47	24	52	20	86	47	3	2	19	146	186	260	198
$s(N_\alpha)$	4.5	20.1	25.9	32.0	13.0	55.4	29.0	46.4	34.7	36.5	34.7	34.5	30.6							
l_α	14.5	21.1	28.8		27.8	33.2		32.5	36.2	38.5	35.7	42.9	44.7	44.8	44.8					
$s(l_\alpha)$	1.1	2.9	3.4		2.9	3.2		3.9	2.1	1.5	2.0	2.4	3.2	0.0	0.0					

half for females for each length class in order to calculate the average length of the sex. The results are given in last two row of Tab. 1 with their standard deviations.

Finally, the weighted mean lengths were adjusted to Von Bertalanffy equation using the program BGC1 given by Abramson.

—Males(n=274) including undifferenciated eels of ages 0-III:

$$L_t=44.8\{1-e^{-0.29(t+0.53)}\}$$

—Females (n=368) including undifferenciated eels of 0-III and excluding exceptionally large eels:

$$L_t=68.8\{1-e^{-0.14(t+0.69)}\}.$$

The Von Bertalanffy equation was relatively satisfactory in describing the growth of sedentary eel population (Fig. 2), when exceptionally large eels were not accounted.

Eels grow principally from spring to autumn,

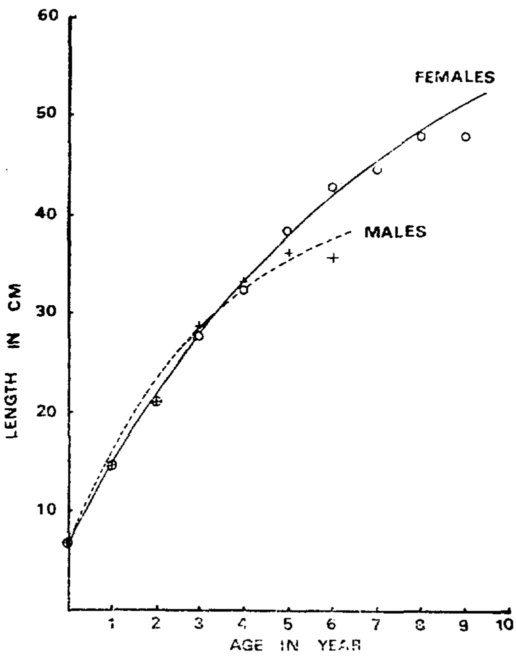

Fig. 2. Growth in length fitted to Von Bertalanffy curve. Crosses and circles represent the average lengths of the males and the females respectively.

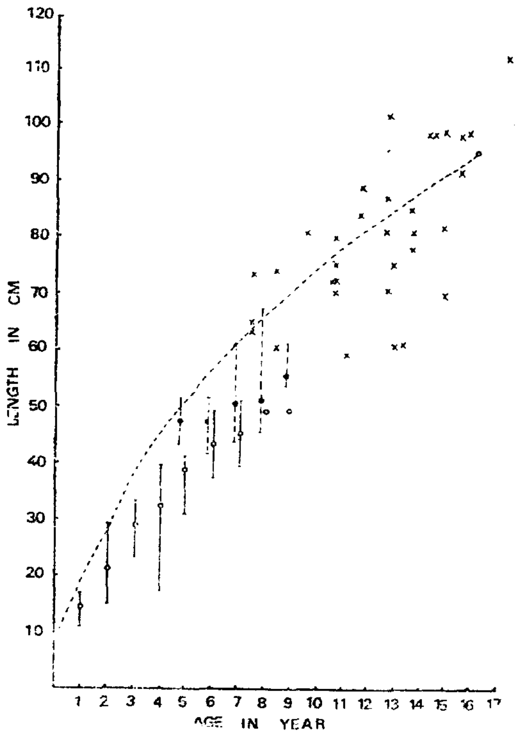

Fig. 3. Ranges and means of the lengthes of the sedentary eels (○), and the migrating eels (●). The crosses indicate the observed lengths of the exceptionally large eels, and the pointed curve represents the back calculated growth from an individual of 95.5cm.

and the migrating eels consist of large members in a given age(Fig.3). In April, when sampling was done for the estimation of the average length, the migration to the sea had finished. The average lengths obtained will have the minimum values of the year for the age groups corresponding to the migrating ages; III to VII for males and V to IX for females. Consequently, the curves obtained theoretically pass through the lower parts of annual ranges of the lengths.

Exceptionally large eels

The sample of this group of fish was few in number. 35 eels were caught during the sampling period. They were all females, easy to seperate by their exceptionally large size and broad heads. They ranged from 58.5cm to 113.5dm in size, from 330g to 3380g in weight, and from VII to XVII in age (Fig.3). The figure 3 shows the ranges and the mean of length for the sedentary eel, the migrating eel, and the exceptionally large eel. Data were collected in April 1978 for the sedentary eel, and between December 1977 and January 1978 for the migrating eel. The latter was taken from Lee(1978). It is noteworthy that the migrating silver eels consisted of large members of an age group. It shows that the simple extension of the ranges of the length of the sedentary eel to age ax's will pass through the lower limit of the scattered points of the exceptionally large eels. In the case of the migrating eel, it will also pass the lower limit of the large eel group. Consequently, it is suggested that only a few individuals, larger than the others of an age group, survive to attain a large size.

To verify the proceeding statement, individual growth was estimated based on the growth marks of the otolith from an exceptionally large eel of 95.5cm(Pl.II). The curve approximately represents observed lengths against age for exceptionally large eels(Fig.3). For their young ages, it passes the upper limits of the continental eel population. This supported the suggestion that exceptionally large eels experienced fast growth when young, and that they were principally large members of the younger ages. Little is known about the origin of the exceptionally large eels, but they probably had the capacity for fast growing when young. That is, some of the large eels in an age group, perhaps with broad heads, could continue continental life for a longer period of time, thereby attaining large size.

D'Ancona(1960) proposed that "silvering" of eels is actual metamorphosis of the fish, and that it is not transient but permanent. In the other hand, Bezdenezhnykh (1973 in Moriaty & Hackett, 1976) described the resorption of the oocytes of the migrating silver eel, when preventing the migration. The latter phenomenon explains partly the presence of the exceptionally large eels in the continental water, as migrating silver eels return to the state of sedentary eels. Some of the large eels of Arcachon lagoons shows the interruptions of growth marks of otolith for the ages corresponding to the migrating time, while others show the regular growth marks (cf. Moriaty & Hackett, 1976). Only based on the observation of otolith, Bezdenezhnykh's description could be applicable for some of the large eels of Arcachon lagoons.

Growth curve in length

The migration of eel to the sea is related to length, and migrating eels are composed of the larger members of a given age. As fish grows older, this size selective migration will lead to the diminution of the growth ratio of the population in the continental waters. According to Von Bertalanffy's assumption, the absorption surface to volume diminishes as the animal grows older, resulting in the diminution of growth ratio. On the other hand, succesive removal of larger members of a population also leads to the same result.

Different authors have demonstrated that broad-headed eels grow more rapidly than those with narrow head, and that, although the ratio between them is not known, it seems to be few in number. Supposing that the migrating mortality is low for the larger members in a given age group comparing to "normal" eels, their relative percentage increases as the fish grows older. As a result, their contribution to average length is small for the young ages, and the growth ratio will diminish. But, as the fish continues the migration to the sea, the contribution of large eels to the average length will increase, resulting in a relative increase in the growth ratio. It has apparently been observed that the growth ratio diminishes for young ages, and increases for old ages(cf. Sinha & Jones, 1967; Frost, 1945). This partly explains why the exponential curve could be fitted to the eel population (Hohendorf, 1966; Bernstsson et al., 1975).

Considering above description, it is hard to apply a simple equation to eel population, particularly for the females, because it is expected that a convex curvature will occur for young ages, and that it will be succeeded by a concave curvature. As exceptionally large eels are few in number, it is desirable to treat them seperatly, if possible, in the study of eel populations. When it is done, the length growth of the female population, as well as the male, can be well represented by Von Bertalanffy's equation, at least, for Arcachon eels.

CONCLUSION

The hyaline zone is formed during the winter, and the opaque zone is formed between spring to autumn in the otolith of Arcachon eels. But, in summer, a thin hyaline zone was observed in the middle part of the summer opaque zone. It seems to be related to the catastrophic aestival conditions of the lagoons.

The succesive removal of the larger members by migration to the sea decreases the growth ratio of the sedentary eels as the fish grows older. This size selective migration partly contributes to satisfaction of Von Bertalanffy's assumption. Consequently, the growth in length of the sedentary eel population is relatively well represented by the V.B. curve. However, some individuals continue continental life attaining an exceptionally large size, which makes it difficult to apply a simple equation for the length growth. It is suggested that the exceptionally large eels consist of the animals which have the capacity for fast growth when already young. When the large eels were treated seperatly, the growth of Arcachon eels was well represented by V.B. curve.

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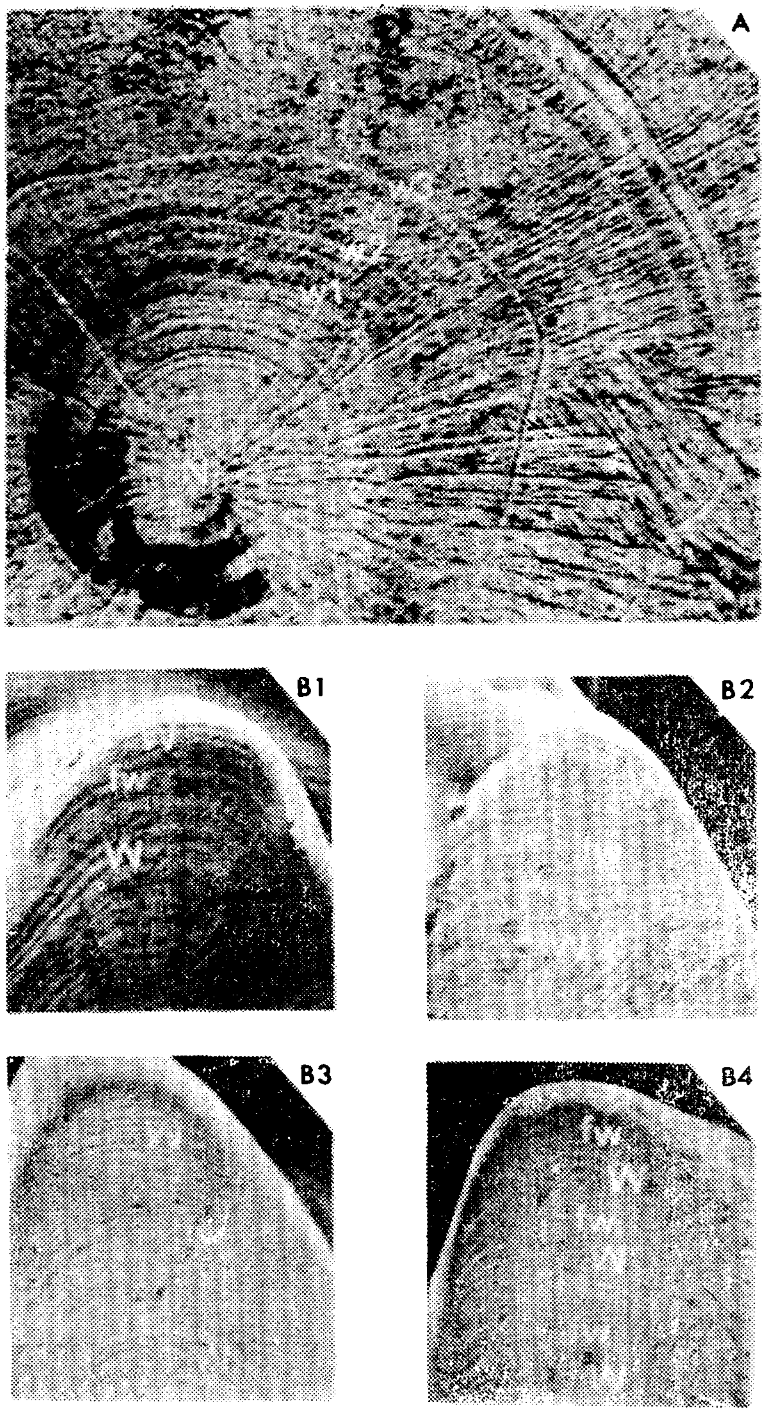
N.B.: This paper is based on the thesis of "Doctorat de Troisième Cycle", presented to University of Sciences and Techniques of Languedoc, France, in July 1979, and titled "Dynamique des populations d'anguilles, *Anguilla anguilla*(L.) des lagunes du Bassin d'Arcachon."

PLATE I



A. Nucleus part of the otolith of the eel. The growth stops w_1 and w_2 were formed in the sea, and w_3 when entering the continental water. The growth stop fw was formed in mid-summer during the first year of continental life. ×240.

B. Decalcified grinding surface of the otolithes collected in December(B1), April (B2), July (B3) and October (B4). ×150. W and fW represent the growth stops formed in winter and mid-summer respectively.

PLATE II

Decalcified grinding surface of the otolith of an exceptionally large eel of 95.5cm in size. 16 growth stops were observed. ×86.

Arcachon灣(佛) 汽水域 뱀장어群(*Anguilla anguilla*)의 年齡과 成長

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要約 : 1977年부터 1978年 10月 사이 Arcachon灣 汔水域에서 採集된 資料를 分析하여 年齡을 査定하고 成長을 推定하였다. 耳石 단면의 構造는 전자 현미경 하에서 觀察하였고, 해부 현미경 하에서 관찰된 결과와 비교하였다. 年輪은 冬期 뿐아니라 夏期에도 幅이 相對的으로 좁은"年輪"이 形成됨이 觀察되었으며, 後者는 夏季에 발생하는 赤潮現象과 관련되어진 것으로 思料된다. 成長은 例外的으로 큰 個體를 除外시켰을 때, Von Bertalanffy式을 적용할 수 있었다. 產卵回遊에 依한 한 年齡群中 큰 個體의 除去는 汔水에 남은 魚群의 成長率을 減少시키고, 이러한 선택적인 큰 個體의 回遊가 Von Bertalanffy의 假定을 만족시키는데 一部 기여하는 것 같다. 例外的으로 큰 個體의 年齡別 體長分布를 "정상적"인 個體들 및 回遊魚群과 비교分析하여, 이들은 어릴때부터 成長이 빠른 個體들中 一部로 構成되어 있음을 제시하였다.