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Growth and biannual recruitment of *Chlamys varia* (Linne) in Lanveoc area (Bay of Brest).(1)

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RESUME.

La croissance du pétoncle noir *Chlamys varia* L. a été étudiée par marquage, élevage, lecture des anneaux de croissance et analyse des distributions de fréquence de taille. Les paramètres de la courbe de von Bertalanffy ont été ajustés par les moindres carrés, sans transformation de variable, à chaque type de données. Les résultats concordent assez bien entre eux, exception faite de ceux obtenus à partir de l'analyse des distributions de fréquence de taille dont l'interprétation est faussée du fait d'un recrutement bisannuel. La lecture des anneaux de croissance s'est montrée la méthode la plus simple et la plus exacte pour évaluer la croissance. Un intervalle d'une année sépare deux anneaux. La position des anneaux est différente chez les individus nés au printemps et ceux nés en automne ; les courbes de croissance de ces deux catégories d'individus restent différentes durant toute leur vie. Ce type de recrutement bisannuel est dû non seulement à deux périodes distinctes de ponte, mais aussi vraisemblablement à deux périodes de survie préférentielles pour les larves planctoniques : lors des explosions de densité du phytoplancton au printemps et en automne. Un recrutement double pourrait être à l'origine d'une dichotomie du patrimoine génétique de la population par spécialisation de certains individus à se reproduire au printemps d'une part, ou en automne d'autre part ; ce qui pourrait aboutir à un état de spéciation si une des vagues de recrutement tendait, du fait des conditions extérieures, à régulièrement avorter dans un endroit géographiquement isolé. Ceci ne paraît pas être le cas en rade de Brest : par lecture des anneaux il a été possible de retracer l'histoire du succès respectif des 2 vagues de recrutement durant les 5 années antérieures ; les proportions d'individus de printemps et d'automne sont restées remarquablement homogènes d'une année sur l'autre.

I. INTRODUCTION.

Chlamys varia (Linne) is one of the most common species of bivalves in Bay of Brest (France) and is likely to be an important link in the food chains. The local dredge fishery has been predominantly maintained by this species after progressive decline of the scallop stock (*Pecten maximus* Linne). Secondary production and yield assessments for this species are thus particularly important since both on a food chain and on a fisheries point of vue *Chlamys varia* seem to be replacing *Pecten maximus*. A thorough knowledge of growth and recruitment patterns is a preliminary step for such assessments.

MATERIAL.

C. varia, a Pectinid lamellibranch, is widely distributed along the Atlantic coasts of France, it is less abundant in the English Channel and is known from a few points of the Mediterranean sea (LETACONNOUX and AUDOUIN, 1956). It is usually found in sheltered areas such as Bay of Brest (LUCAS, 1965). Most common sizes range from 35 to 45 mm shell lengths ; however 64 mm and 65 mm individuals have been reported by LUCAS and by DALMON (1935). LUBET (1959) has shown on histological bases that *C. varia* mature at sizes ranging from 18 to 27 mm. They are predominantly males at first maturity (LUBET, 1959, LUCAS) ; sex reversals seem possible during whole life span but mostly occur from a male to a female state (LUCAS). DALMON states that at La Rochelle *Chlamys varia* spawn in April - May and in September - October, while LUBET (1959) indicates May - June and September - October for Arcachon populations. REDDIATH (1962) observed spawning in June and later in September - November at Ile of Man ; LUCAS concludes that in Bay of Brest spawning takes place mainly in May - June and in September while very occasionally in July - August and March - April.

In the area surveyed (fig. 1) water depth ranges from 6 to 9 m at lowest spring tides and maximal tidal amplitude is about 6 m. Seasonal temperatures vary between 9 and 18°C ; while salinities usually range from 33,5 p.p.m. to 35,5 p.p.m., althrough 29 p.p.m. were exceptionally observed in December 1976 after heavy rainfalls. Tidal currents range from .005 m/s to .63 m/s at mean spring tides. The bottom is sandy mud, broken shells and pebbles.

FIELD WORK.

Monthly samples were taken from January 1976 to January 1977. The sampling device used was a standard 3.0 cm wire mesh fishermen's dredge for scallops and queen scallops. The 600 m hauls were directed perpendicularly to shore

in order to minimize possible depth gradients in repartition of age groups. *Chlamys varia* often cling by their byssus threads to small stones or dead shells ; this facilitated collection of young individuals which would have been otherwise lost through dredge meshes. All individuals caught in a dredge haul were counted and measured ; sizes of such samples averaged 350 individuals.

900 *Chlamys varia* were measured and tagged with plastic "Dymo" tape secured to their upper shell valves with araldite epoxy resin (fig. 4) and promptly returned to the sea. Tag returns were obtained either from the local fishermen, either by dredging from R.V. "Sainte Anne" of Centre Océanologique de Bretagne (CNEXO).

Extra growth data were provided by Dr LUCAS (Université de Bretagne Occidentale) from a sea floor cage rearing experiment he conducted in 1961 and 1962 (1).

A sample of 117 individuals was taken on November 24, 1976 for measuring shell lengths at growth rings and yielded sufficient data for growth curves. Shells were prepared for ring reading by soaking the valves in a solution of detergent and scrubing them with a wire brush.

DATA PROCESSING.

The data collected did not include information on very early stages such as recently settled spat ; thus no inflection point was expected to be found in left limb of growth curves in length. Data of size at age or increase in size over observed time intervals were fitted to von Bertalanffy growth curves. Shell length is hereon defined as the greatest straight line distance from umbo to ventral margin. Since sex reversal is frequent in natural populations, we did not assess separately growth of males and females.

Four different types of data were used for fitting the von Bertalanffy equation : 1) progression of modes in size frequency distributions sampled monthly 2) sizes at age read directly from growth rings ; 3) size increments between tagging and recapture ; 4) size increments of individuals reared in cages on the sea floor. In the first two instances observations of size at known age are directly available ; the von Bertalanffy growth in length curve was fitted by least squares using an iterated method programmed by TOMLINSON (in ABRAMSON, 1971) and designed

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(1) We acknowledge Dr LUCAS kind permission for using his data.

for unequally spaced age groups with unequal sample sizes for separate ages. This method is more flexible and statistically less approximate than a straightforward regression on the Walford plot ; it involves no transformation of variates L_t (size) and t (time).

In the two last instances the absolute age of the individuals is not supposed to be known ; data is available only on sizes at the beginning and at the end of the experiments, the duration of which are usually variable. FABENS (1965), TOMLINSON (in ABRAMSON, 1971) described and programmed equivallent methods for fitting Von Bertalanffy curves to such data ; both are iterated least squares processes involving no transformation of variates L_t (original size) and L_{t+1} (final size). Parameters K and L^∞ can be accurately estimated, parameter t_o cannot be estimated from such data since no information is available on size at age. We used TOMLINSON's method.

For separating size frequency distributions into component age groups, a technique described and programmed by HASSELBLAD (1966), later modified by TOMLINSON (in ABRAMSON, 1971) was used. It is based on an iterated maximum likelihood estimate of the mean, the standard deviation of sizes and the number of individuals in each of the component groups which are assumed to pertain to normal distributions.

All programs used for this work were either written or adapted from Fortran to HPL language and run on Hewlett-Packard model 92025A desk. computer of Department Scientifique at Centre Océanologique de Bretagne.

RESULTS.

Normal component groups separated from the monthly size frequency distributions are presented in table 1. Chi squares and corresponding probability levels for goodness of fit of the composite ajusted distributions are indicated. The growth curve fitted to this data is presented in fig. 2.

Data on growth increments between tagging and recapture (table 2) yielded growth curve of fig. 3. A growth curve fitted to LUCAS cage rearing data for size increments is presented for comparison on the same figure. Parameter t_o was arbitrarily set equal to 0 since it could not be estimated from these sets of data.

Growth rings were usually easy to read (fig. 4). The frequency distributions of shell lengths, at each of the successive growth rings which were assumed

to be equivalent for age, appeared to be always bimodal (fig. 5). Separate growth curves were fitted for individuals pertaining to each of these modal components (fig. 6) ; we assumed that a one year time interval separated two successive growth rings.

Estimates of parameters t_o, K and L_∞ obtained from all sets of different methods and data are presented for comparison in table 3. Plots of the corresponding growth curves are available in fig. 7.

SYNTHESIS AND CONCLUSION.

According to DALMON two growth rings may be laid every year, one in summer, the other in winter, however summer ring is week and is usually worn away with time. LETACONNOUX and AUDOUIN consider that, around La Rochelle, only one winter ring is laid ever year while the growth rate is almost null from November to February. Our growth curves based on ring readings were built on this asumption and compare very well with growth curves obtained from tagging and cage experiments (fig. 7) ; we shall thus retain the "one ring a year" hypothesis for Bay of Brest. The growth ring technique seems fairly reliable although a few abnormal individuals are to be disgarded when "shock" or "desease" rings are evident, such rings anyhow are easy to differenciate from natural rings.

Interpretation of bimodalism of size frequencies at growth rings is easily found in the "double spawning a year" pattern shown by LUBET (1959) and LUCAS on histological bases. MASON (1957) came to similar conclusions for *Pecten maximus* in Manx waters. However LUCAS mentionned that two extra spawning periods may occur, one in early spring, the other in mid summer ; these spawnings are likely to be very unsuccessfull since they do not seem to generate any recruitment. Young planktonic larvae of *Chlamys varia* probably need proper food conditions, if they are not produced at the time of spring and autumn algae blooms, they may not survive. Thus biannual recruitment is not only explained by a biannual spawning but also by a secondary seasonal survival screening of the planktonic larvae.

At first we had assumed that the first observable rings marked at modal sizes of 27 and 34 mm (fig. 5) were laid during the first winter after birth. This turned out to be a wrong interpretation. In September 1975 spats of *Chlamys varia* were observed to settle on collectors designed for *Pecten maximus* (BUESTEL et al., 1976) ; when grown in suspended cages they did not mark theis 27 mm rings before the second winter of rearing (unpublished data, personal communication of M. BUESTEL and M. MORIZUR, COB). Thus the first macroscopically observable growth ring is in fact laid during the second year of life.

In fig. 5 we may note that growth estimates based one size frequency distributions analysis are misleading. Individuals born in spring (group II) are readily differentiated from individuals born in autumn (group I) by measuring their lengths at the first ring ; size frequency distributions at ring 1 of spring and autumn groups do not overlap. However individuals born in autumn do not catch up in size with those born in spring, instead, ring 3 of autumn group widely overlaps ring 2 of spring group. When size frequency analyses were made, modal groups C and larger were in fact composite groups containing individuals born on spring and autumn of different years. Therefore our estimates of von Bertalanffy parameters obtained by this method are likely to be inaccurate ; this is readily confirmed in table 3 where estimates obtained from all methods are remarquably homogeneous, but for K and t_o in the size frequency instance.

Growth estimates based on size frequency analysis remain of interest for studying annual periodicity of growth rates. In fig. 2 slowing down of growth in winter is easily noticeable and can be attributed to the months of January, February and March during which water temperatures drop below 10°C (fig. 8). During these months a growth ring is likely to have been laid. Highest rates of growth are reached from June to August. However it may not be worth taking in account these minor seasonal fluctuations when an overall growth curve is needed for yield or secondary production models.

It is worth comparing growth curves of individuals recruited in spring and autumn (fig. 6). These curves appear to remain different during the whole life span and converge only towards L_∞. It is thus advisable to evaluate separately mortality, yield and secondary production of each group. As already mentionned individuals are easily sorted out by measuring size at first ring (fig. 5) ; this size ranges from 25,5 mm to 30,5 mm for spring spawned individuals, while for autumn spawned individuals it ranges from 31,5 mm to 36,5 mm.

It is of interest to consider the double spawning on an evolutionnary basis. LUBET (1953) has shown that spawning can be triggered in natural conditions by thermal and chemical excitations, while LUCAS had experimental results showing that reproduction cycle was phased up by photoperiodism. LUCAS further indicates that gametogenesis starts in March and ends in September when light conditions are 12 hours day, 12 hours night. These physiological observations do not explain however how *Chlamys varia* evolved to develop two distinct periods of spawning each year in Bay of Brest, so as to match phytoplankton spring and autumn blooms. This is not known as a general pattern for reproduction of marine invertebrates in Brittany.

One would be tempted to think that there might be partial reproductive isolation between individuals more specialized for spring and others for autumn spawning. LUCAS notes that females gonads may be internally either white or yellow ; spring spawning females have predominantly yellow gonads, autumn spawning females have white gonads. However he observed changes of colour for some individuals during the summer. There might be some genic differences between a spring and an autumn subpopulation although gene flow would be maintained by individuals still able to spawn at both seasons.

This situation would be favorable for speciation if in a closed bay like Bay of Brest one of the reproductive seasons was repeatedly unfavorable during successive years. We were able to reconstitute the past history of the *Chlamys varia* population for up to 5 years by sampling the relative contribution of spring and autumn spawned individuals to the various age groups present in the population (table 4). The catch of a dredge haul taken on May 12, 1977 was entirely sorted out and measured for this purpose. The proportions of spring spawned and autumn spawned individuals turned out to show remarquably constant from year to year ; they average respectively .44 % and .56 % . When tested by a contingency table, the null hypothesis that these proportions did not vary over 5 years was still not discredited at a probability level of .9998. Such a result is very unlikely to be obtained by sampling a regular binomial probability distribution. Since we are unaware of any artificial cause for this consistency, it is tempting to conclude that some regulatory mechanism might exist for maintaing these proportions constant in time and space.

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TABLE 1.

SAMPLE NUMBER	1			2			3			4			5			6		
DATE	09/01/76			20/02/76			24/03/76			13/04/76			04/05/76			02/06/76		
SAMPLE SIZE	328			617			332			373			562			459		
Nb. of iterations	64			46			37			22			90			47		
Chi square	16.487			14.140			17.739			18.043			17.027			25.379		
Dg. of freedom	12			14.000			15.000			11.000			13.000			18.000		
α	0.17			0.436			0.227			0.081			0.198			0.115		
SUB GROUPS	M	σ	P	M	σ	P	M	σ	P	M	σ	P	M	σ	P	M	σ	P
A1																		
A																		
A2																		
B1	29.1	2.51	0.156	30.2	2.57	0.231	31.7	2.87	0.316	30.7	2.64	0.199	32.3	2.98	0.16			
B																34.9	3.23	0.326
B2	34.1	0.63	0.080	34.7	2.21	0.203	36.2	1.01	0.158	35.1	1.31	0.16	34.0	1.13	0.074			
C	38.6	2.56	0.383	38.5	2.36	0.169	38.96	0.61	0.061	39.5	2.00	0.323	39.1	2.70	0.48	40.5	2.34	0.335
D	42.9	1.41	0.022	43.8	2.58	0.27	43.3	2.53	0.288	44.2	2.12	0.223	45.4	2.11	0.201	44.9	2.56	0.231
E	46.8	2.33	0.31	48.7	0.84	0.063	48.1	3.68	0.177	48.4	1.93	0.035	49.2	1.34	0.037	51.3	2.73	0.11
F	53.5	1.35	0.048	52.3	1.76	0.062	-	-	-	52.2	1.58	0.685	53.2	1.85	0.052	-	-	-

SAMPLE NUMBER	7			8			9			10			11			12		
DATE	25/08/76			17/09/76			01/10/76			22/10/76			24/11/76			15/12/76		
SAMPLE SIZE	491			443			486			345			444			350		
Nb. of iterations	250			100			79			45			80			22		
Chi square	25.698			20.334			22.631			19.508			13.634			16.907		
Dg. of freedom	26.000			24.000			18.000			15.000			11.000			16.000		
α	0.112			0.678			0.205			0.192			0.254			0.392		
SUB GROUPS	M	σ	P	M	σ	P	M	σ	P	M	σ	P	M	σ	P	M	σ	P
A1	16.7	1.63	0.050	19.8	1.51	0.022	27.1	3.28	0.265	29.0	2.85	0.16	-	-	-	29.6	3.56	0.270
A																		
A2	23.6	3.0	0.201	27.4	2.53	0.163	34.0	0.30	0.013	34.5	0.56	0.028	-	-	-	33.6	1.83	0.109
B1																		
B	37.4	0.85	0.075	40.3	2.63	0.434	39.6	2.92	0.134	39.6	1.80	0.081	38.3	0.89	0.097	40.7	1.90	0.150
B2																		
C	41.7	2.46	0.440	44.3	1.12	0.147	43.3	1.81	0.35	44.5	2.02	0.436	43.0	1.71	0.405	43.5	1.35	0.080
D	47.3	3.25	0.230	47.8	1.49	0.114	47.7	1.90	0.214	48.8	1.21	0.145	47.6	2.5	0.373	46.1	1.97	0.266
E	-	-	-	51.0	4.23	0.119	53.5	1.30	0.027	52.2	2.75	0.145	51.5	4.12	0.13	49.1	2.91	0.126
F	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

N°	Date of tagging	Size at tagging (mm)	Date of recapture	Size at recapture (mm)
1	15/09/76	28	24/11/76	33
2	15/09/76	30	26/11/76	33
3	15/09/76	27	20/01/77	31
4	15/09/76	19	20/01/77	23
5	15/09/76	48	20/01/77	49
6	15/09/76	47	25/11/76	47
7	15/09/76	53	26/11/76	53
8	15/09/76	54	26/11/76	54
9	15/09/76	49	20/01/77	49
10	15/09/76	52	22/10/76	52
11	22/10/76	52	27/10/76	52
12	15/09/76	57	07/10/76	57
13	15/09/76	47	02/11/76	48
14	15/09/76	51	26/11/76	51
15	15/09/76	50	26/11/76	50
16	22/10/76	49	26/11/76	49
17	22/10/76	46	26/11/76	46
18	22/10/76	53	26/11/76	53
19	22/10/76	49	03/12/76	49
20	08/12/76	49	16/02/77	49 *
21	22/10/76	52	11/03/77	52
22	22/10/76	51	11/03/77	51
23	22/10/76	44	11/03/77	44
24	22/10/76	46	11/03/77	46
25	22/10/76	48	26/11/76	48
26	22/10/76	50	03/12/76	50
27	22/10/76	46	11/03/77	46
28	22/10/76	45	07/03/77	45
29	22/10/76	42	11/03/77	42
30	22/10/76	44	27/10/76	44
31	22/10/76	44	16/02/77	44
32	22/10/76	44	11/03/77	45
33	22/10/76	46	03/12/76	46 *
34	22/10/76	45	16/02/77	46
35	22/10/76	43	11/03/77	43
36	22/10/76	43	11/03/77	43
37	24/11/76	31	20/01/77	31.5
38	24/11/76	32	15/02/77	32
39	24/11/76	47	24/06/77	47 *
40	24/11/76	55	16/02/77	55
41	24/11/76	49	11/03/77	49
42	24/11/76	43	03/12/76	43
43	24/11/76	44	11/03/77	44
44	25/01/77	37	07/03/77	37
45	25/01/77	34	12/05/77	35
46	25/01/77	31	11/03/77	31

* Found dead.

TABLE 2.

PARAMETERS	METHODS				
	Size frequency	Tagging	Growth Rings		Cage rearing
			Group I (September spawning)	Group II (June spawning)	
L_∞	49.84	49.64	52.30	51.96	53.661
K	0.764	0.440	0.447	0.461	0.430
t_o	0.263	-	0.727	0.419	-

TABLE 3.

Proportion of individuals in :	Number of GROWTH RINGS on shell					
	1	2	3	4	5	more than 5
Group I	.57	.55	.56	.57	.56	.60
Group II	.43	.45	.44	.43	.44	.40
Size of sample	75	33	55	28	9	5
Results of 6 x 2 Contingency table	degrees of freedom : 5		chisquare : .1052		probability level : .9998	

TABLE 4.

LEGEND OF FIGURES

Fig. 1 : Geographic location of area surveyed.

Fig. 2 : Von Bertalanffy growth curve fitted to data of mean sizes at age obtained from analysis of the size frequency distributions (table 1). The different symbols correspond, by increasing size, to subgroups A, B, C, D, E and F.

Fig. 3 : Von Bertalanffy growth curves fitted to data of size increments during variable time intervals, obtained from cage rearing and tagging observations.

Fig. 4 : Top : *Chlamys varia* tagged with "Dymo" plastic tape secured by araldite epoxy resin. Bottom : valves cleaned by soaking in a solution of detergent and scrubing with a wire brush.

Fig. 5 : Frequency distributions of lengths at rings.

Fig. 6 : Von Bertalanffy growth curves fitted to data of individuals sizes at age obtained by measuring lengths at rings. Growth curves of individuals born in spring and in autumn are drawn separately.

Fig. 7 : Overview of von Bertalanffy growth curves fitted by the different techniques to the different types of data.

Fig. 8 : Seasonal fluctuations of sea water temperatures at Lanveoc during sampling operations.

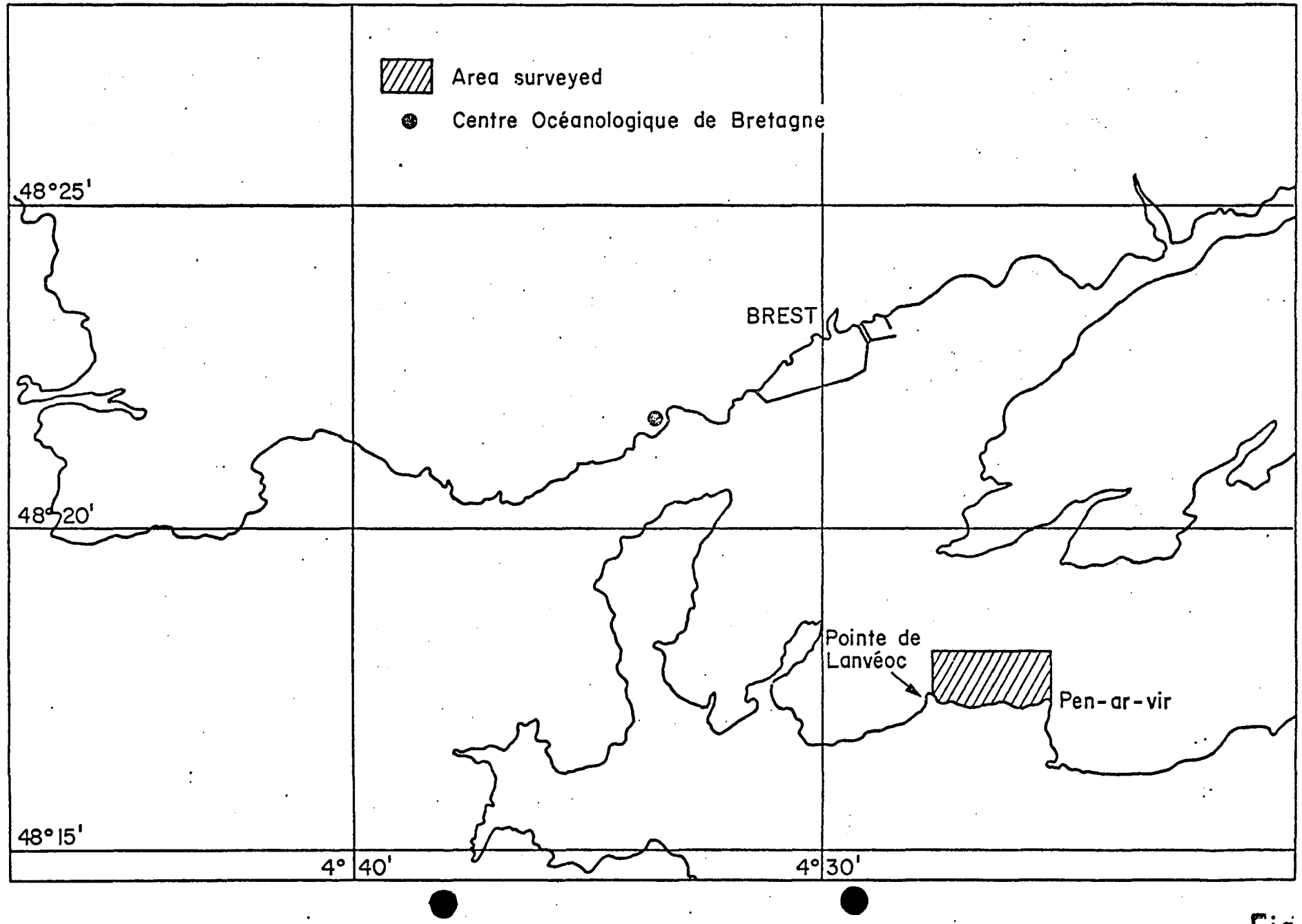

Area surveyed
Centre Océanologique de Bretagne
48°25'
48°20'
48°15'
4° 40'
4° 30'
BREST
Pointe de Lanvéoc
Pen-ar-vir

Fig.1

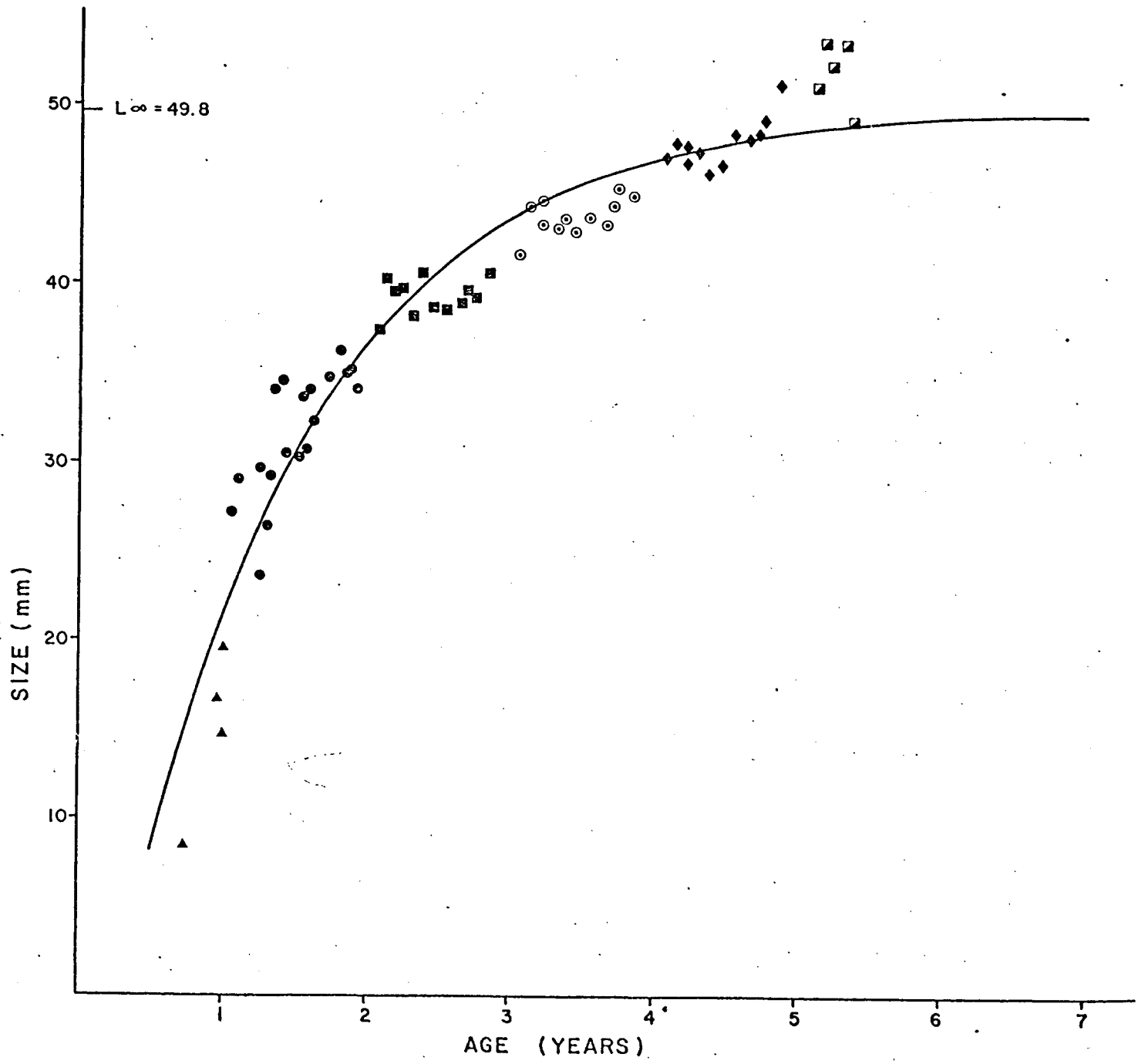


Fig.2

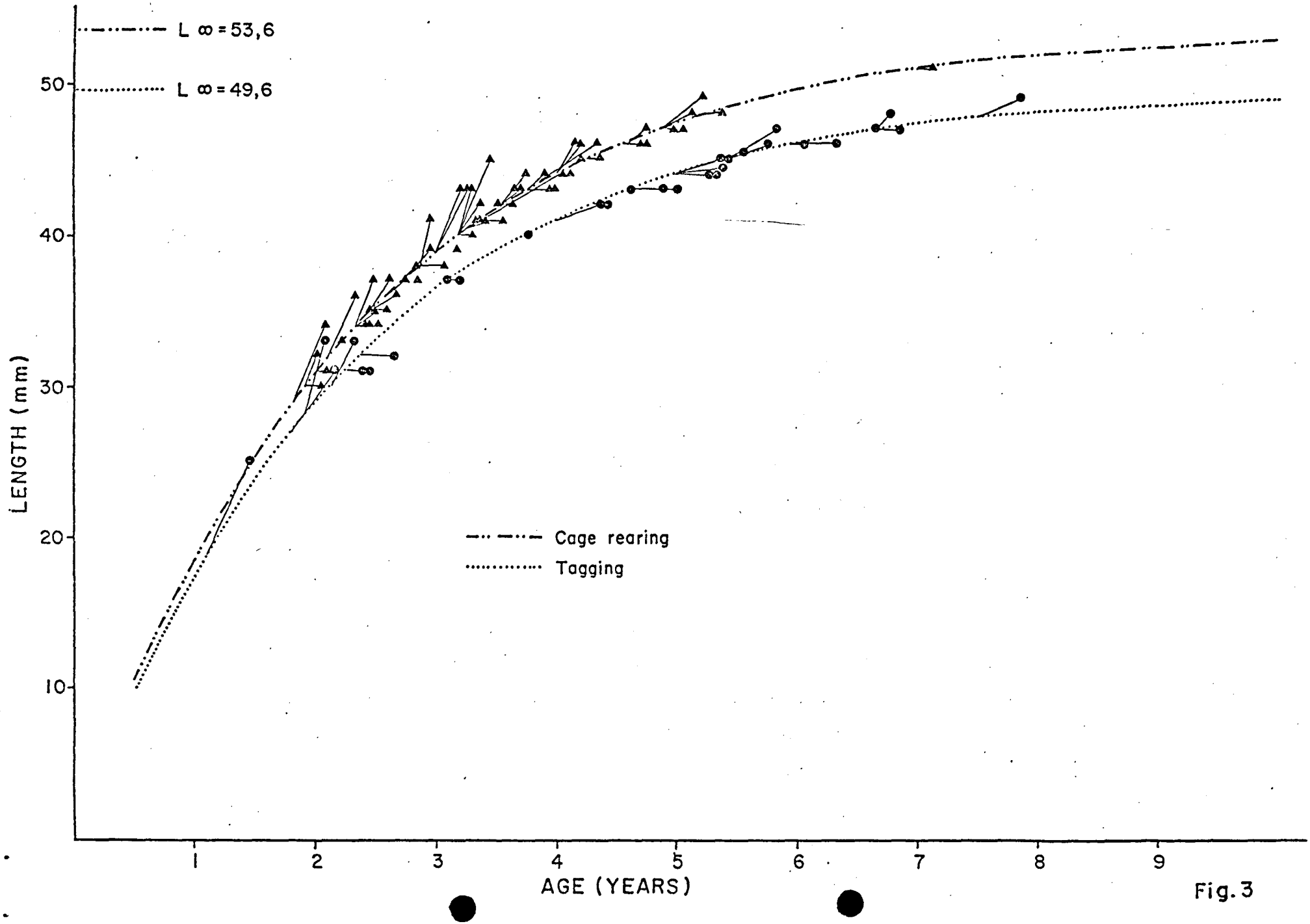
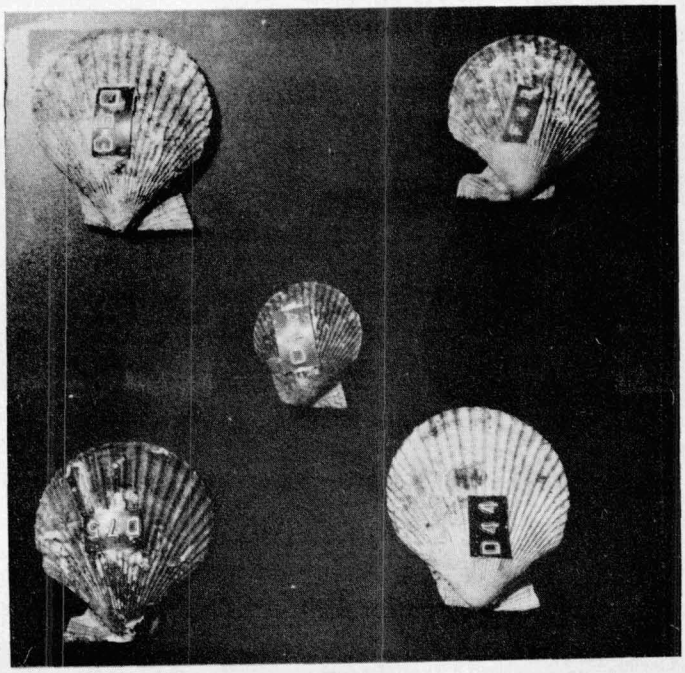

L ∞ = 53,6
L ∞ = 49,6
LENGTH (mm)
50
40
30
20
10
1
2
3
4
5
6
7
8
9
AGE (YEARS)
Cage rearing
Tagging

Fig. 3



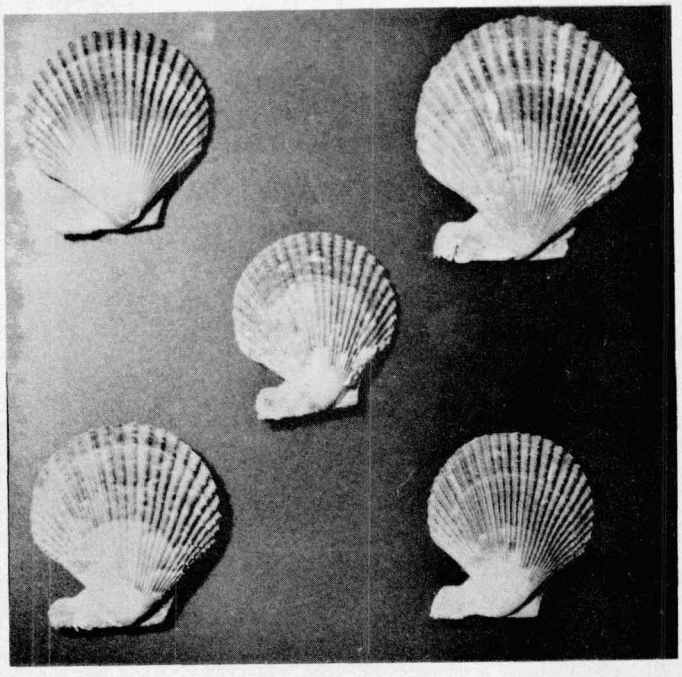


Fig. 4

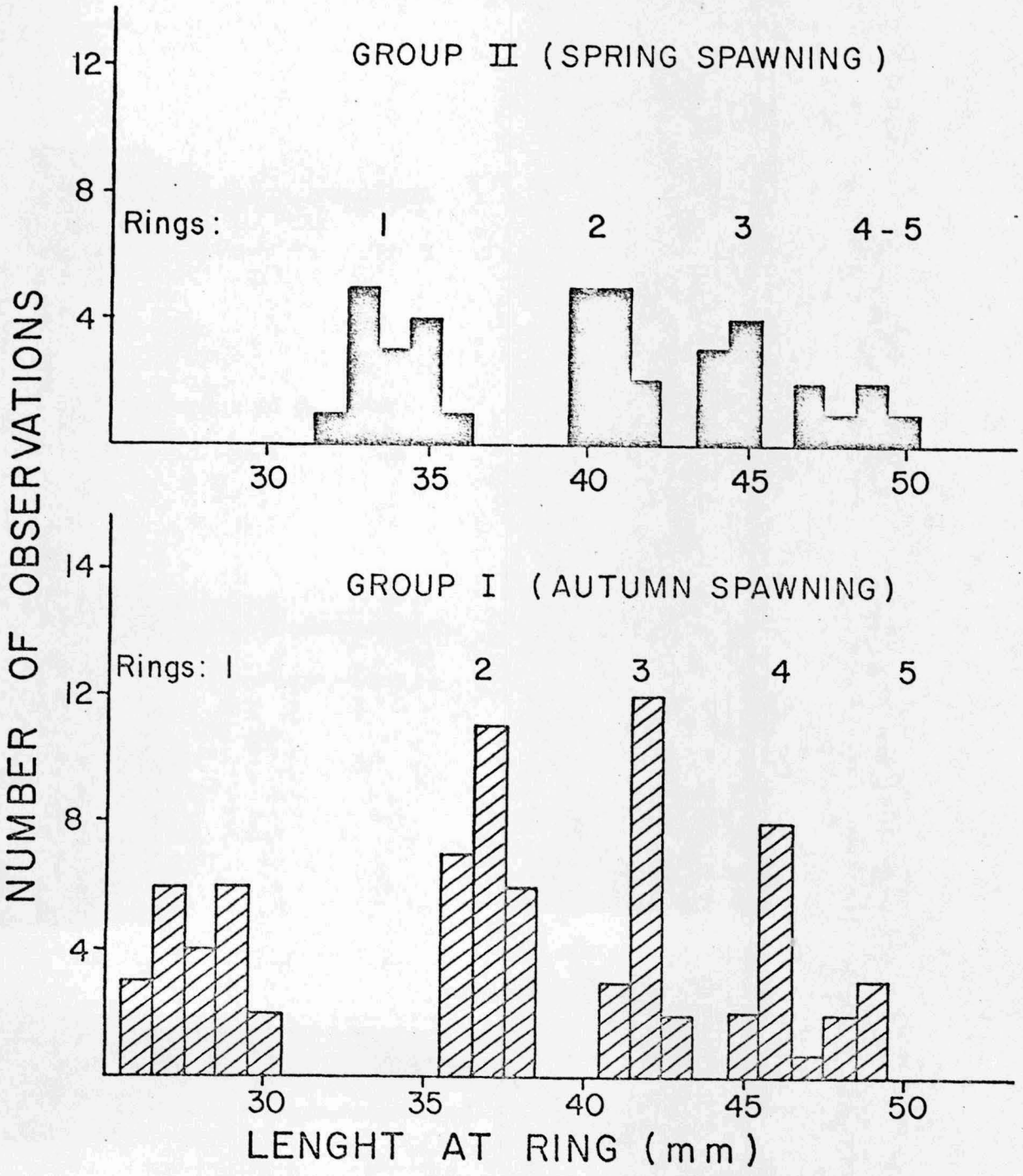

GROUP II (SPRING SPAWNING)
Rings: 1 2 3 4-5
12
8
4
30 35 40 45 50
GROUP I (AUTUMN SPAWNING)
Rings: 1 2 3 4 5
14
12
8
4
30 35 40 45 50
NUMBER OF OBSERVATIONS
LENGHT AT RING (mm)

Fig. 5

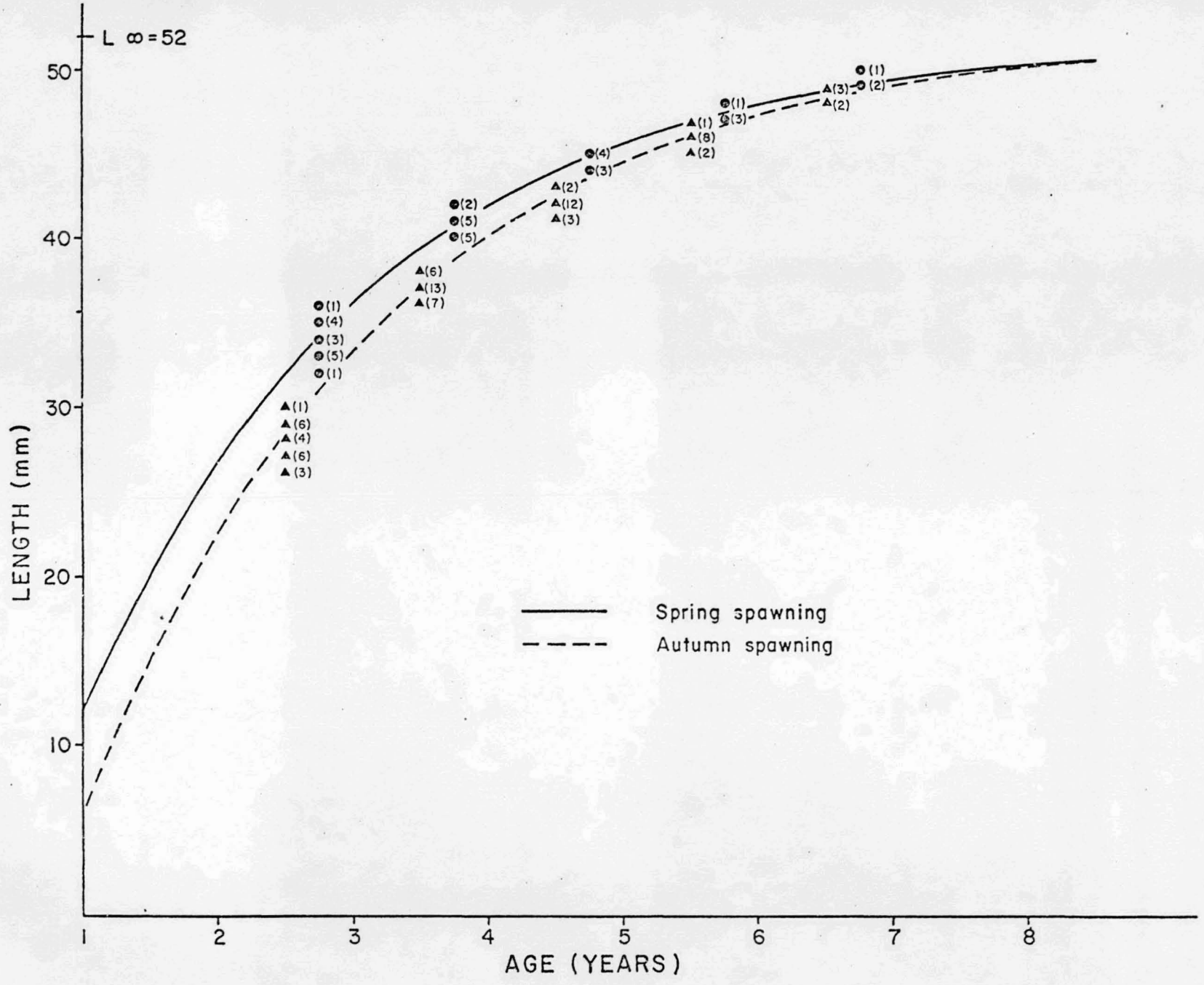


Fig. 6

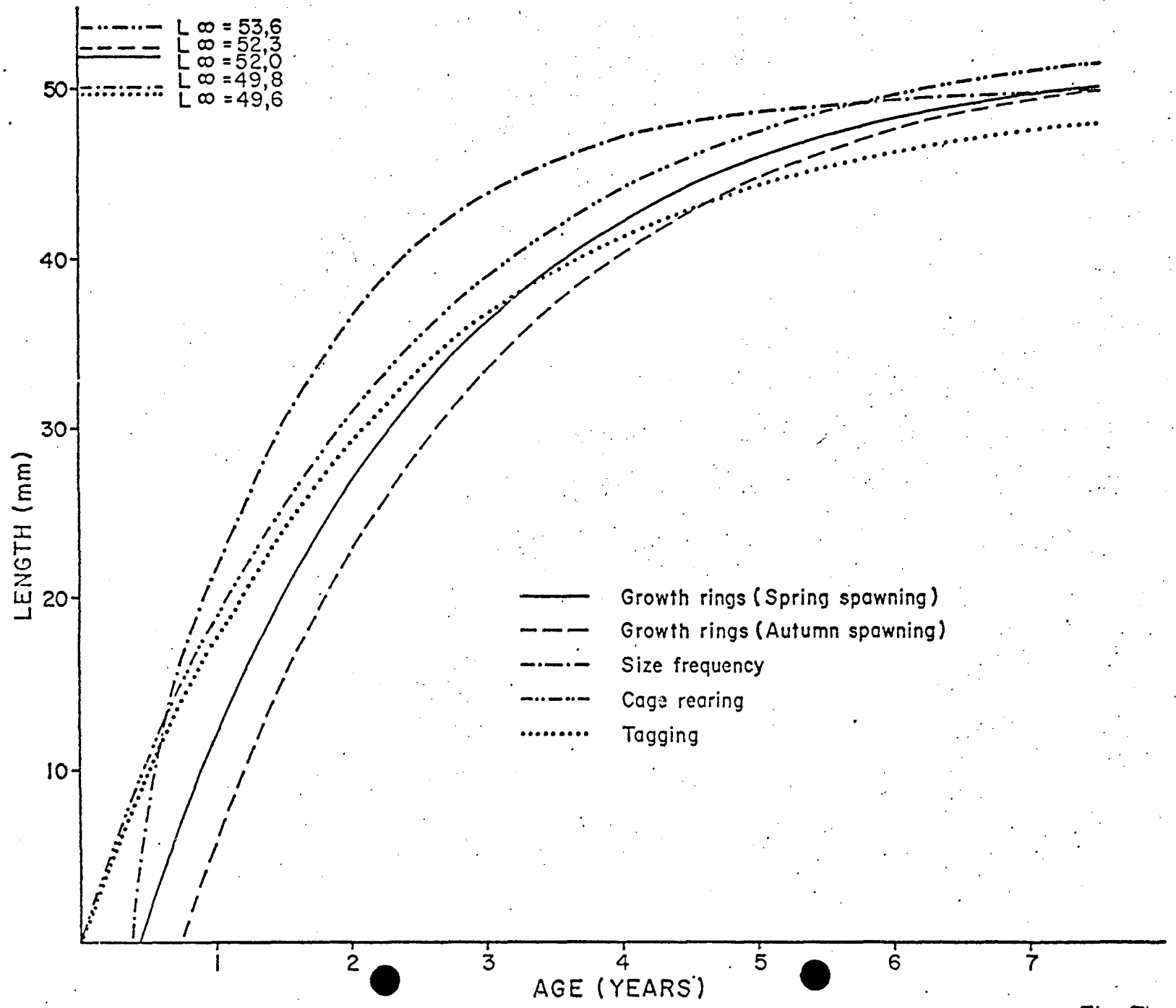

L∞ = 53,6
L∞ = 52,3
L∞ = 52,0
L∞ = 49,8
L∞ = 49,6
LENGTH (mm)
10
20
30
40
50
1
2
3
4
5
6
7
AGE (YEARS)
Growth rings (Spring spawning)
Growth rings (Autumn spawning)
Size frequency
Cage rearing
Tagging

Fig. 7

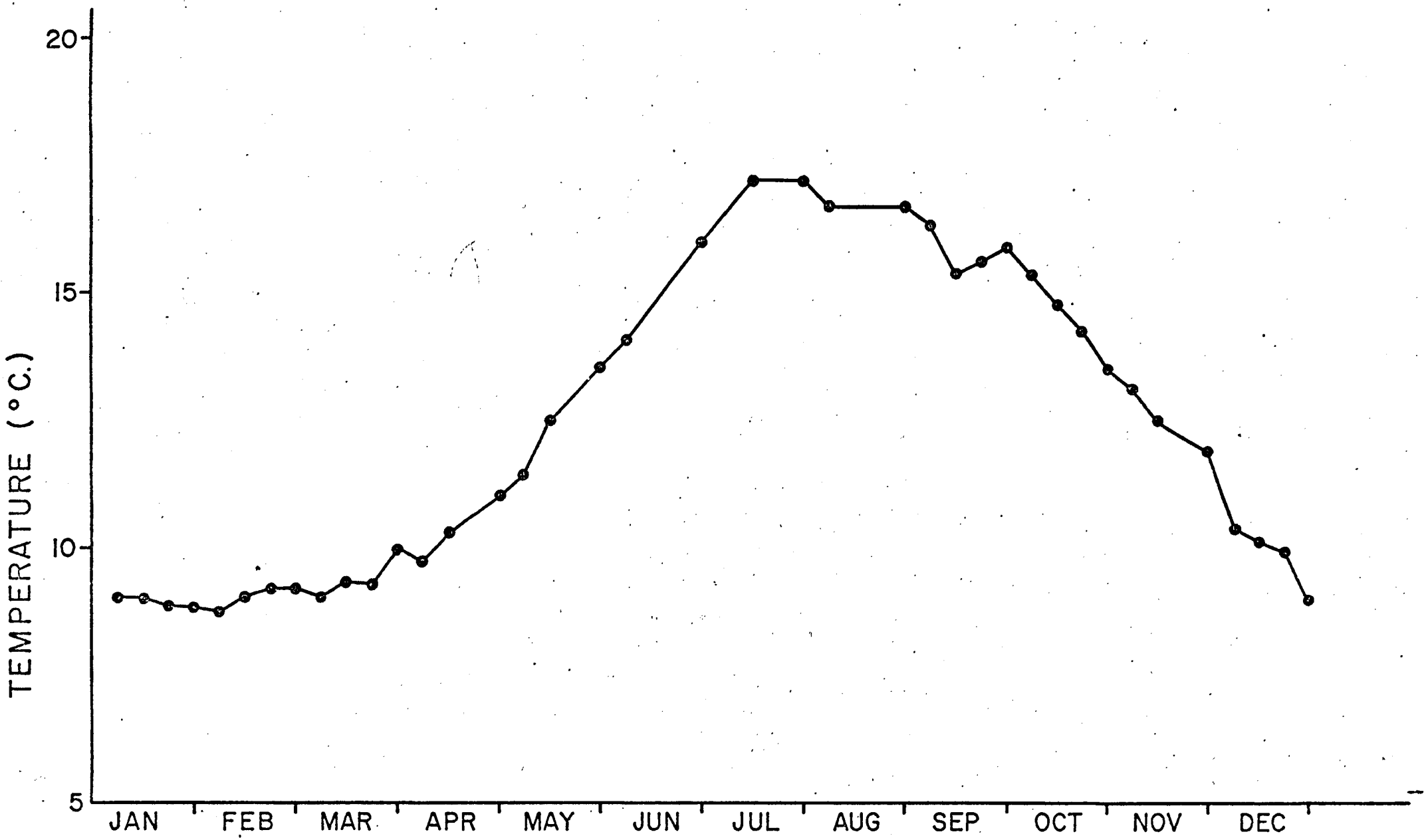

20
15
10
5
TEMPERATURE (°C.)
JAN
FEB
MAR
APR
MAY
JUN
JUL
AUG
SEP
OCT
NOV
DEC

Fig.8